

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3073, 44 pp., 17 figures, 9 tables September 10, 1993

A Revision of the Brazilian Muroid Rodent Genus *Delomys* with Remarks on “Thomasomyine” Characters

ROBERT S. VOSS¹

CONTENTS

Abstract	2
Resumo	2
Introduction	3
Acknowledgments	3
Materials and Methods	4
Gazetteer	5
The Genus	6
<i>Delomys</i> Thomas	7
Comparisons with <i>Thomasomys</i> and <i>Oryzomys</i>	10
Phylogenetic Relationships and “Thomasomyine” Characters	21
The Recent Species	25
<i>Delomys dorsalis</i> (Hensel)	25
<i>Delomys sublineatus</i> (Thomas)	31
The Lagoa Santa Fossils	32
Natural History	34
Habitat Descriptions	35
Discussion	40
References	41
Appendix: Series of <i>Thomasomys cinereus</i> and <i>Oryzomys palustris</i> Examined	44

¹ Associate Curator, Department of Mammalogy, American Museum of Natural History.

ABSTRACT

Species of the Brazilian muroid rodent genus *Delomys* share a unique combination of morphological characters that distinguish them from other Neotropical taxa with pentalophodont molars. A phylogenetic analysis of comparisons among *Delomys*, *Thomasomys*, and *Oryzomys* suggests that "thomasomyine" attributes (shared by *Delomys* and *Thomasomys*) are primitive and therefore provide no evidence for recency of common ancestry. *Delomys*, *Thomasomys*, and other non-oryzomyine pentalophodont genera (e.g., *Abrawayaomys*, *Aepeomys*, *Chilomys*, *Phaenomys*, *Rhagomys*, *Rhipidomys*, and *Wilfredomys*) should be referred to a "plesion" rather than to any formally recognized tribal-level group.

Two valid Recent species of *Delomys* can be unambiguously distinguished based on available material in North American and European museums. *Delomys dorsalis* has distinctively softer fur, longer tail, longer vibrissae, and longer outer digits of the hindfoot than does *D. sublineatus*; several aspects of pelage pigmentation also distinguish these species. Sympatric samples of *dorsalis* and *sublineatus* differ in craniodental measure-

ments adjusted for general size (growth), but no diagnostic qualitative characters of the skull or dentition are known.

The fossils from Lagoa Santa that Winge described as *Calomys plebejus* belong to the genus *Delomys* but are not distinguishable from either of the two Recent species; *plebejus* is therefore a nomen dubium that should not be used except in reference to Winge's hypodigm.

Delomys is restricted to the wet tropical and subtropical forests of southeastern Brazil and northeastern Argentina, wherein its habits have seldom been investigated. Available data from the literature suggest that these rats are nocturnal, predominantly terrestrial, and breed throughout the year, but most remaining aspects of their natural history are obscure. Even less is known about many other nonprimate mammals that occur in the same habitats, a dismal situation given the deteriorating prospects for effective conservation measures. Systematic and natural history studies of mammals endemic to this endangered biome should be given high priority.

RESUMO

Espécies de roedores muroideos brasileiros do gênero *Delomys* possuem uma combinação única de características morfológicas que os distingue dos demais taxa de pentalofodontes neotropicais. A análise filogenética comparando *Delomys*, *Thomasomys*, e *Oryzomys* sugere que as características "tomasominianas" (compartilhadas por *Delomys* e *Thomasomys*) são primitivas e desta maneira não fornecem evidências de origem monofilética. *Delomys*, *Thomasomys*, e outros gêneros pentalofodontes não-orizominianos (p. ex., *Abrawayaomys*, *Aepeomys*, *Phaenomys*, *Rhagomys*, *Rhipidomys*, e *Wilfredomys*) devem ser referidos mais propriamente a um "plesion" do que a qualquer reconhecimento formal ao nível de tribo.

Com base no material disponível nos museus da América do Norte e da Europa, duas espécies válidas de *Delomys* podem ser reconhecidas. *Delomys dorsalis* possui pelagem distintamente mais macia, cauda mais longa, vibrissas mais longas, e os dígitos externos dos membros posteriores mais longos do que os de *D. sublineatus*. Diversos aspectos referentes a coloração da pelagem também diferenciam estas espécies. Amostras simpátricas de *dorsalis* e *sublineatus* diferem em medidas cranio-dentais, devidamente ajustadas para o tamanho

geral (crescimento). No entanto, não são conhecidas características diagnósticas qualitativas baseadas no crânio ou na dentição.

Os fósseis descritos por Winge procedentes de Lagoa Santa como *Calomys plebejus* pertencem ao gênero *Delomys* mas não são distinguíveis de ambas as espécies recentes. Desta maneira *plebejus* é um nomen dubium que não deve ser utilizado exceto em referência ao hipodigma de Winge.

Delomys é restrito à florestas úmidas tropicais e subtropicais do sudeste do Brasil e do nordeste da Argentina, onde os seus hábitos tem sido raramente estudados. Os dados disponíveis na literatura sugerem que estes ratos são noturnos, predominantemente terrestres, e que procriam durante todo o ano. No entanto, os demais aspectos referentes a sua história natural são desconhecidos. Menos ainda é conhecido sobre muitos outros mamíferos não-primatas que ocorrem no mesmo habitat, o que torna a situação desanimadora, levando-se em conta que as perspectivas para medidas efetivas de conservação destas espécies estão bastante deterioradas. Deve ser dada grande prioridade aos estudos sistemáticos e de história natural referentes aos mamíferos endêmicos deste bioma ameaçado.

INTRODUCTION

Species of *Delomys* are muroid rodents of virtually unknown habits that live in wet primary and secondary forests from near sea level to at least 1600 m elevation in southeastern Brazil and northeastern Argentina. Although as many as five names (*collinus*, *dorsalis*, *lechei*, *plebejus*, and *sublineatus*) have sometimes been applied to Recent species (Avila-Pires, 1960a), and despite field observations that two species are sympatric at some localities (Davis, 1945a, 1947), most taxonomic catalogs (e.g., Cabrera, 1961; Corbet and Hill, 1991; Honacki et al., 1982) recognize only *dorsalis* as valid. Because the genus has not been revised, and because type specimens are geographically inaccessible, Brazilian researchers have had to rely on an inadequate primary literature for their taxonomic determinations.

This report evolved from a simple attempt to determine the systematic status of *Calomys plebejus*, a species named by Winge (1887) from fossils collected by the Danish naturalist P. W. Lund in caves near Lagoa Santa, Minas Gerais, Brazil. The species was long presumed to be extinct, but Avila-Pires (1960a) collected apparently similar Recent specimens near Lagoa Santa and referred *plebejus* to *Delomys*. My reexamination of the type series in Copenhagen confirmed Avila-Pires's generic allocation, but the lack of taxonomic consensus at the species level precipitated a broader study.

In the course of comparing *Delomys* with other Neotropical muroids, I realized that the suite of characters traditionally used to divide the pentapodont genera into "thomomyine" and "oryzomyine" groups had never been critically evaluated from a phylogenetic perspective. Indeed, Reig (1980) suggested that these groups are not distinct and included the members of both in a single tribe, the Oryzomyini. Even elementary applications of cladistic principles to analyze the relationships of *Delomys*, however, require much more information about morphological characters than that currently available in the literature. Hence, another motivation for this report.

Herein I provide a diagnosis and description of the genus and compare the two Recent

species that appear to be valid; these descriptive and comparative accounts are hypotheses that should be evaluated by Brazilian researchers with access to more specimens than those currently available in North American and European museums. I compare *Delomys* with *Thomasomys cinereus* and *Oryzomys palustris* (the types of their respective genera), and discuss the phylogenetic implications of observed character similarities and differences; the reevaluation of "thomomyine" characters that emerges from this exercise complements the arguments for oryzomyine monophyly provided in a companion paper (Voss and Carleton, in press). I also review the scant literature on the natural history of *Delomys* and emphasize the urgent necessity for systematic and ecological research on this genus and other mammalian taxa endemic to the rapidly disappearing Atlantic rainforests.

ACKNOWLEDGMENTS

I thank the curators and technical staffs of the museums listed below (in Materials and Methods), my hosts on numerous occasions while I worked in their collections. I am especially grateful to Tove Hatting, Hans Baa-gøe, Frits W. Braestrup, and Mogens Andersen for their kind and thoughtful assistance at the Universitets Zoologisk Museum in Copenhagen.

Recently collected specimens at the Field Museum of Natural History provided crucial data for evaluating species limits in *Delomys*, and the private donations that made this material available deserve acknowledgment: B. D. Patterson's series from Boracéia was obtained with support from the William S. and Janice K. Street Mammal Expeditionary Fund, and P. Hershkovitz's series from Apiaí and Iporanga were obtained with support from the Barbara E. Brown Mammal Research Fund.

This report would have been scientifically and aesthetically impoverished without the graphical accomplishments of Patricia Wynne (figs. 1, 5, 6, 7, 8, 11, 12, 13, 17) and the darkroom skills of Peter Goldberg (figs. 2, 3, 4, 14, 15, 16); my appreciation of their pro-

fessional contributions is, I hope, not the less fresh for frequent repetition! Peling Fong and Bill Barnett provided expert and patient assistance in the production of figures 9 and 10.

Nancy Simmons, Mike Carleton, and Bruce Patterson generously read the manuscript and provided helpful comments for its improvement. Any remaining errors of fact or omission are, of course, my own.

MATERIALS AND METHODS

SPECIMENS: The specimens described in this report are deposited in the collections of the American Museum of Natural History, New York (AMNH); the British Museum of Natural History, London (BMNH); the Field Museum of Natural History, Chicago (FMNH); the Los Angeles County Museum of Natural History, Los Angeles (LACM); the Museum of Comparative Zoology at Harvard University, Cambridge (MCZ); the Museum National d'Histoire Naturelle, Paris (MNHN); the National Museum of Natural History, Washington, D.C. (USNM); the Museu de Zoologia, Universidade de São Paulo, São Paulo (USP); and the Universitets Zoologisk Museum, Copenhagen (UZM).

MEASUREMENTS AND STATISTICAL ANALYSES: I transcribed total length (TL) and length of tail (LT) from specimen tags, and computed length of head-and-body (HBL) by subtracting LT from TL. Alternatively, HBL and LT were sometimes recorded on tags by the collector, and I used these values too. I always measured the length of dry hindfeet (HF) with dial calipers to check the accuracy of values recorded on specimen labels; tabulated values in this report include the claws. All external dimensions are reported to the nearest millimeter.

Cranial and dental dimensions were measured with dial calipers and recorded to the nearest 0.1 or 0.05 mm. The following were measured as described and illustrated by Voss (1991): CIL, condylo-incisive length; LD, length of diastema; LM, occlusal length of maxillary molar series; BM1, breadth of first maxillary molar; LIF, length of one incisive foramen; BR, breadth of rostrum; BPB, breadth of palatal bridge; BZP, breadth of zygomatic plate; LIB, least interorbital breadth; DI, depth of one upper incisor; and

LOF, length of orbital fossa. Zygomatic breadth (ZB) was measured across the squamosal roots as illustrated by Voss (1988).

Descriptive univariate statistics reported herein include the sample standard deviation only if ten or more observations were available for computation; smaller samples are described only by the mean and observed range. I did not tabulate descriptive statistics separately for males and females because size dimorphism is not apparent in the samples at hand.

Multivariate statistics were computed from measurement values transformed to their natural logarithms. General-size coefficients were estimated as the elements of the first eigenvector of the pooled within-group covariance matrix, and the normalized coefficients of general-size-adjusted species differences were computed as described by Voss and Marcus (1992). The interpretation of general-size coefficients in terms of ontogenetic allometry, and the growth-invariance of the residual within- and between-sample variation, is discussed by Voss et al. (1990) and by Voss and Marcus (1992).

ANATOMY: Most of the anatomical terms used in this report are consistent with usages established or referenced by Reig (1977), Carleton (1980), and Voss (1988), but I found it necessary to introduce additional names for structures of the ear region that have hitherto escaped notice in the recent literature of muroid systematics. Those neologisms are explained and illustrated in the context of comparisons with *Thomasomys* and *Oryzomys*.

In evaluating some external characters, either fluid-preserved specimens or well made-up skins (preferably both) should be examined. Thus, in describing length of the vibrissae it is assumed that the pinnae are folded back against the side of the head; if only dried skins are available, it is crucial that the pinnae not have been crumpled or otherwise distorted by careless preparation. Similarly, judging the relative lengths of adjacent digits on dried skins is impossible if the hindfeet were not correctly pinned out by the preparator.

I only recorded mammary counts from females judged to be reproductively mature. Because direct evidence of reproductive activity (observations of pregnancy or lactation

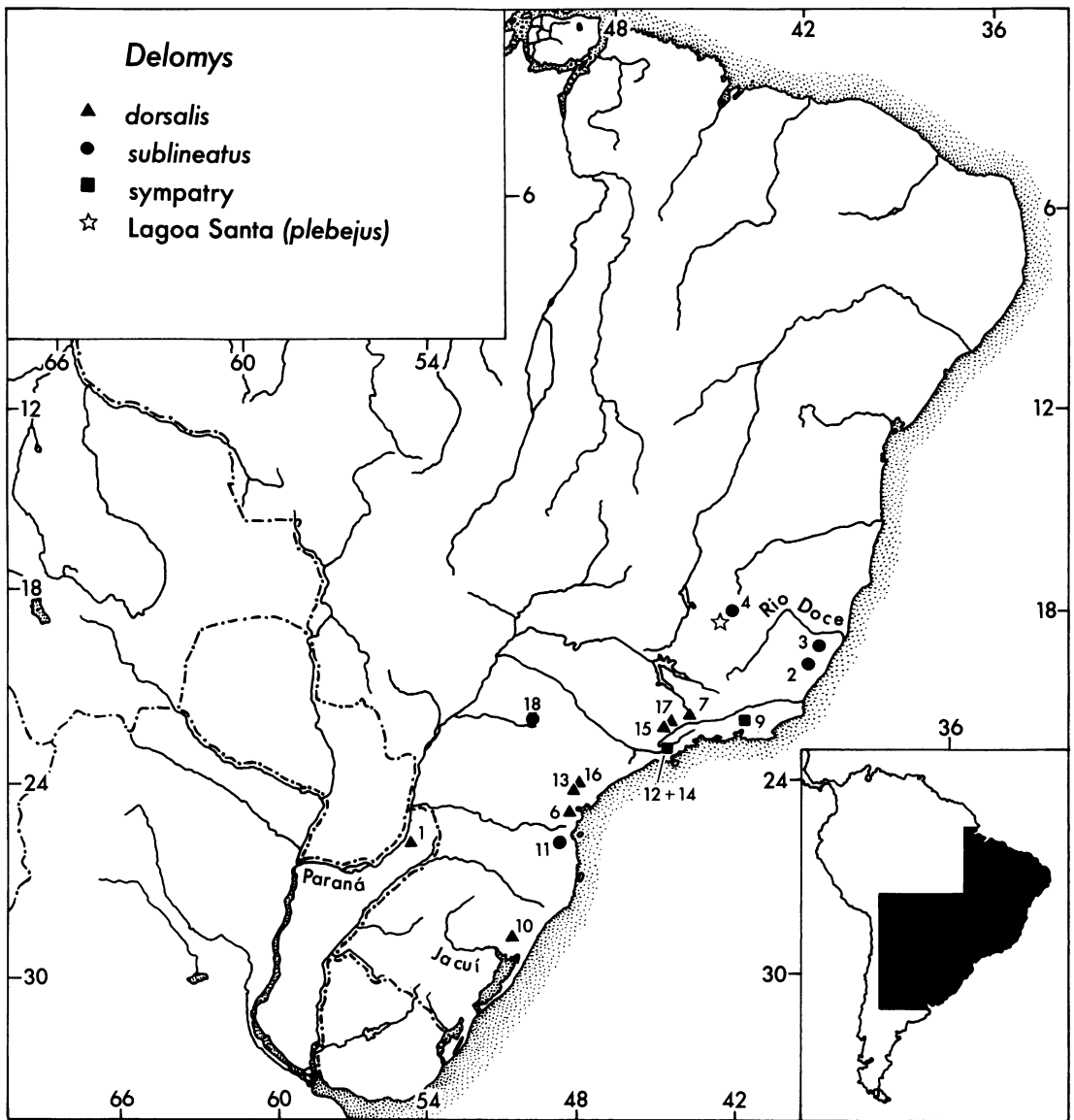


Fig. 1. Collection localities for *Delomys* specimens examined in this report. Other Brazilian localities were mapped by Zanchin et al. (1992), and an additional Argentine locality was mentioned by Massoia (1962). Redford and Eisenberg (1992) mapped three Argentine collection localities but do not cite the source of their geographical data.

recorded on specimen tags) was seldom available, I considered specimens to be reproductively active if teats were large and surrounded by well-defined (hairless or nearly hairless) areolae.

GAZETTEER

Twenty-three place-names are associated with specimens of *Delomys*, but I combined

some adjacent localities for the purposes of mapping (fig. 1) and data analysis. *Italic type* in the list below identifies the largest administrative units within each country (province in Argentina, states in Brazil); **boldface** identifies locality names as cited in the text of this report. Geographic coordinates (degrees and minutes S latitude/degrees and minutes W longitude) are unpunctuated; Brazilian co-

ordinates follow Paynter and Traylor (1991) except as noted. Elevations are provided verbatim (in feet or meters) from specimen tags or cited secondary sources.

ARGENTINA

1. *Misiones, Caraguatay* (2637/5446); elevation ca. 100 m (Paynter, 1985).
2. *Espírito Santo, Engenheiro Reeve* (= Rive at 2046/4128); elevation 400–600 m.
3. *Espírito Santo, Nova Lombardia* (Reserva Biologica de, ca. 1950/4032) and *Santa Teresa* (1955/4036); elevation 500–1200 m in the Nova Lombardia biological reserve, and 659 m at Santa Teresa (Paynter and Traylor, 1991).
4. *Minas Gerais, Conceição do Mato Dentro* (1901/4325), in the Cordilheira do Espinhaço; elevation 771 m (Avila-Pires, 1960a).
5. *Minas Gerais, Lagoa Santa* (1938/4353); elevation ca. 760 m (Paynter and Traylor, 1991).
6. *Paraná, Roça Nova*, in the Serra do Mar, on the railroad from Paranaguá (2531/4830) to Curitiba (2525/4915) according to Thomas (1902); elevation 930–1150 m.
7. *Rio de Janeiro, Itatiaya* (2223/4438), in the Serra da Mantiqueira; elevation 4800 ft (Thomas, 1917).
8. *Rio de Janeiro, Maceiro* (not located).
9. *Rio de Janeiro, Teresópolis* (= “Therezopolis” and “Terezopolis”; 2226/4259), including 5 mi N and nearby localities Fazenda Boa Fé and “Fazenda C. Guinle” (= Fazenda Comari), in the Serra dos Orgãos; elevations all over 800 m (Davis, 1945a).
10. *Rio Grande do Sul, Taquara* (2939/5047), including “Taquara do Mundo Novo” (probably the same locality, but Mundo Novo is at 2932/5048); elevation 29 m at Taquara and ca. 100 m at Mundo Novo (Paynter and Traylor, 1991).
11. *Santa Catarina, Hansa* (= Corupá at 2626/4914); elevation 62 m (Paynter and Traylor, 1991).
12. *São Paulo, Alto da Serra* (= Paranapiacaba at 2347/4619), in the Serra do Mar; elevation ca. 800 m (Paynter and Traylor, 1991).
13. *São Paulo, Apiaí* (vicinity, 2431/4850) and *Iporanga* (vicinity, 2435/4835); elevation ca. 200 m (P. Hershkovitz, personal commun.).
14. *São Paulo, Boracéia* (Estação Biologica de, ca. 2338/4552 according to Heyer et al., 1990) and *Casa Grande* (ca. 2337/4557), both in the Serra do Mar; elevation 800–900 m at Boracéia (specimen tags) and ca. 1000 m at Casa Grande (Paynter and Traylor, 1991).
15. *São Paulo, Campos do Jordão* (2244/4535), in the Serra da Mantiqueira; elevation 1585 m (Paynter and Traylor, 1991).
 - . *São Paulo, Cotia* (not located).
16. *São Paulo, Fazenda Intervalles* (2411/4832), in the Serra de Paranapiacaba; elevation 850 m (Olmos, 1991).
17. *São Paulo, Piquete* (2236/4511), in the Serra da Mantiqueira; elevation 600–900 m.
18. *São Paulo, Salto Grande* (2254/4959), on right bank of upper Rio Paranapiacaba; elevation ca. 368 m (Paynter and Traylor, 1991).
 - . *São Paulo, Taquaral* (several places with this name in state of São Paulo; not located).

THE GENUS

Species of *Delomys* have at one time or another been referred to *Hesperomys*, *Calomys*, *Akodon*, *Oryzomys*, and *Thomasomys*, a nomenclatural odyssey that reflects both the historical development of New World glirology and the ambiguities of traditional generic diagnoses based on only a few “key” characters. Thomas (1917) named *Delomys* to contain species previously classified as *Thomasomys*, but his brief list of distinguishing attributes was not convincing to Osgood (1933b) or Ellerman (1941), and the name has subsequently fallen into general disuse except among South American mammalogists (e.g., Avila-Pires, 1960a, 1960b; Cerqueira, 1982; Reig, 1984, 1986).

An unambiguous diagnosis of *Delomys* and an evaluation of its relationships within the Neotropical muroid fauna are impossible

goals without much more character information than that currently available in the literature. Below, I summarize morphological data from available skins, skulls, dentitions, postcranial skeletons, and fluid-preserved material; I report morphological comparisons among *Delomys*, *Thomasomys*, and *Oryzomys*; and I discuss the phylogenetic implications of observed patterns of character similarities and differences. These accounts, especially the last, are preliminary efforts that should be reevaluated when future systematic studies of the New World muroid fauna permit more sophisticated analyses.

Delomys Thomas

Delomys Thomas, 1917: 196.

TYPE SPECIES: *Hesperomys dorsalis* Hensel (1872), based on a skull, one skeleton, and five fluid-preserved specimens (presumably in Berlin; Gyldenstolpe, 1932) from the Brazilian state of Rio Grande do Sul. Hensel provided no further information about the geographic origin of the type series, and the type locality has not been subsequently restricted. I have not examined the type series, but the original description, measurements, and illustrations (fig. 2) are sufficient to establish *dorsalis* as the name that applies to allopatric populations of *Delomys* from southern Brazil (see the account for this species, below).

DISTRIBUTION: *Delomys* is endemic to the wet tropical and subtropical Atlantic forests of southeastern Brazil and Misiones (Argentina), from about 19 to 30° S latitude (fig. 1). Specimens are apparently unknown from the littoral plain and coastal cordilleras north of the Rio Doce (in the Brazilian state of Espírito Santo) or south of the Rio Jacuí (in Rio Grande do Sul). Dry cerrado habitats probably delimit the western distribution of the genus in Brazil. No *Delomys* have been collected west of the Río Paraná despite intensive faunal inventory efforts in the forests of eastern Paraguay by Philip Myers and his colleagues from the University of Michigan Museum of Zoology.

EMENDED DIAGNOSIS: Members of the muroid rodent subfamily Sigmodontinae (sensu Carleton and Musser, 1984) with six or eight

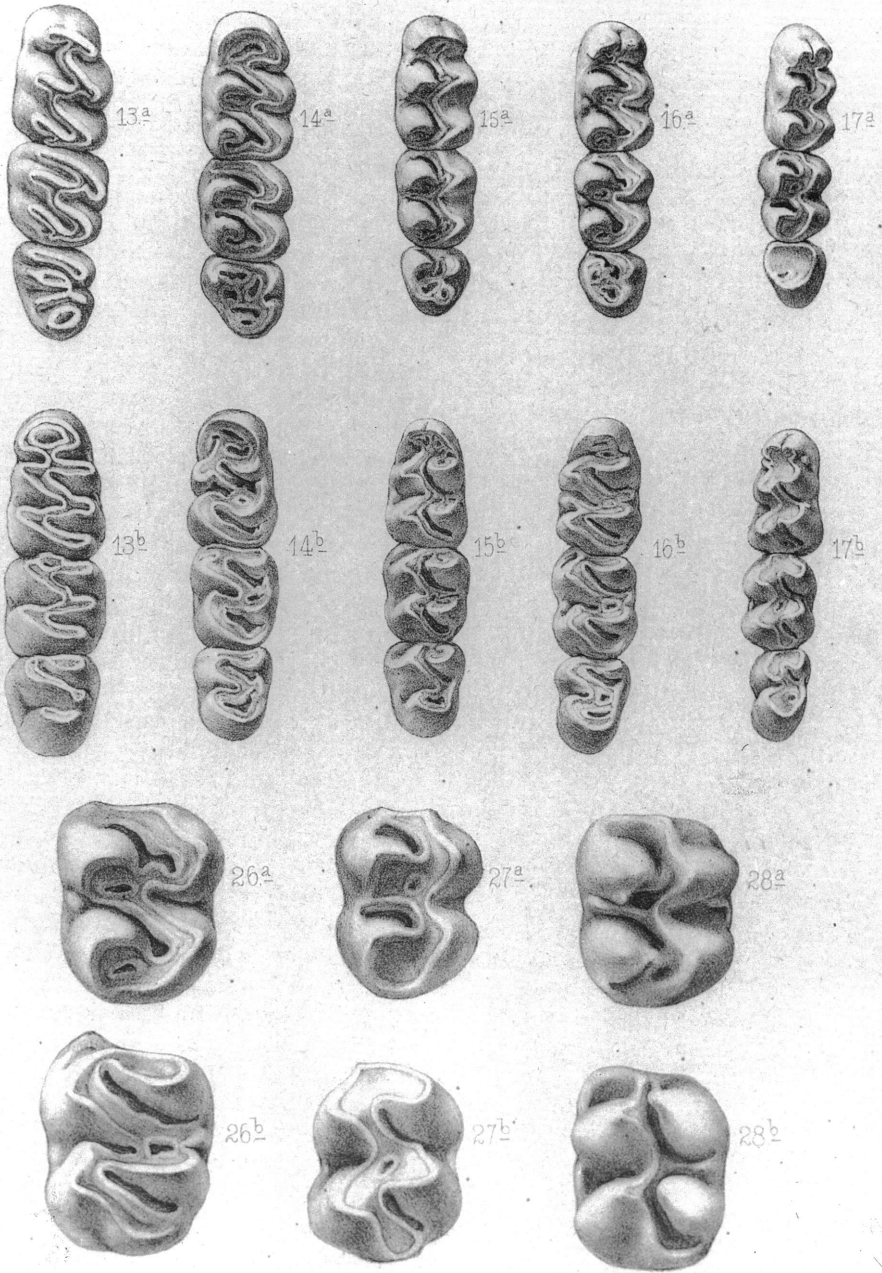
mammæ; long rostrum flanked by small but well-defined zygomatic notches; supraorbital margins rounded, without beads or shelves; interparietal very large; premaxillae and nasals produced as a short tube above incisors; palate short and wide, without posterolateral pits; alisphenoid strut absent; carotid circulation primitive (with complete stapedial supply); tegmen tympani overlaps posterior suspensory process of squamosal; mandible without capsular process of lower incisor alveolus; basihyal without entoglossal process; upper incisors small, narrow, and strongly opisthodont; molar occlusal design incipiently lophodont; M1 with deeply divided anterocone; upper and lower molars with well-developed mesoloph(id)s; m1 with ectolophid; tuberculum of first rib articulates with transverse processes of seventh cervical and first thoracic vertebrae; entepicondylar foramen of humerus absent; 13 ribs.

MORPHOLOGICAL DESCRIPTION: Body pelage short and close (not long and fluffy), but varying in texture (soft or coarse); grizzled yellowish, brownish, or grayish dorsally; with or without a dark middorsal stripe from nape to base of tail; ventral hairs always dark gray basally, but washed with white or light gray tones that contrast with the dorsal coloration. Mystacial, superciliary, genal, submental, interramal, and carpal vibrissae present. Pinnae large, pliant, sparsely covered with short hairs. Manus with five large, fleshy plantar pads (two carpal and three interdigital). Pes narrow (metatarsus longer than digits), with outer digits shorter than middle three (claw of I not extending beyond middle of first phalanx of II, claw of V not extending much beyond second interphalangeal joint of IV); conspicuous tufts of long, silvery hairs present at bases of claws; plantar pads six (two metatarsal and four interdigital), large and fleshy; naked plantar epithelium smooth over heel but indistinctly squamate over distal metatarsus. Tail shorter than, equal to, or longer than combined length of head-and-body; very sparsely haired (epidermal scales conspicuous); without terminal tuft or pencil of long hairs; bicolored (dark above, pale below) or unicolored (all dark). Mammæ eight (in inguinal, abdominal, postaxial, and pectoral pairs) or six (pectoral pair absent).

Skull (in dorsal view) with long rostrum

Zu Hrn Hensel's Abh. Über d. Säugeth. Süd-Brasiliens Phys. Kl. 1872

Taf. II



Druck v. C. Schmidt in Berlin

Druck v. C. Schmidt in Berlin

flanked by small but well-defined zygomatic notches; interorbital region hourglass-shaped, neither conspicuously constricted or greatly inflated, with smoothly rounded supraorbital margins; braincase rounded and smooth, without well-defined ridges or crests. Zygomatic plate neither very broad nor excessively slender; with a distinct, free dorsal edge; anterior margin approximately vertical, not sloping backward from base. Premaxillae produced anteriorly beyond incisors and joined with nasals to form a short, bony tube. Incisive foramina long, but not extending posteriorly between molar rows; widely open, usually with convex (not parallel) lateral margins. Bony palate wide and short (sensu Hershkovitz, 1962), without conspicuous median ridges, deep lateral folds, or complex posterolateral pits. Mesopterygoid fossa wide, with square or (usually) biconcave anterior margin between third molars; bony roof of fossa complete or perforated by very small sphenopalatine vacuities. Alisphenoid strut absent (buccinator-masticatory foramen and foramen ovale confluent or separated by fragile splint of bone that occurs unilaterally in a few specimens). Carotid circulation primitive (orbitofacial circulation supplied by separate branches of large stapedia artery); course of supraorbital stapedia ramus indicated by squamosal-alisphenoid groove and sphenofrontal foramen. Postglenoid foramen separated from large subsquamosal fenestra by slender hamular process of squamosal. Tegmen tympani of periotic overlaps posterior suspensory process of squamosal above anterodorsal lip of bulla. Bullae small; pars flaccida of tympanic membrane present, large; orbicular apophysis of malleus well developed.

Mandible with short, stout, falciform coronoid process; lower incisor alveolus without distinct capsular process. Basihyal without entoglossal process.

Incisors ungrooved, with yellow or yellow-orange enamel bands; upper teeth small, narrow, deeper than wide, and strongly opisthodont.

Maxillary molar rows parallel; principal cusps of upper teeth arranged in opposite labial/lingual pairs; labial and lingual reentrant folds interpenetrating (occlusal design incipiently lophodont); anterocone of M1 divided by deep anteromedian flexus into separate anterolingual and anterolabial conules; distinct anterolophs and mesolophs present on M1 and M2; small posterolophs present in newly erupted dentitions but quickly obliterated with wear. Maxillary molars each with three well-developed roots (anterior, posterior, and lingual; but a small internal-labial root is occasionally present on M1).

Unworn m1 anteroconid usually without distinct anterolabial and anterolingual conulids (anteromedian flexid usually indistinct or absent); anterolophid indistinct or absent on all lower teeth; anterolabial cingulum present on m1 and m2, usually absent from m3; mesolophids and posterolophids well developed on m1 and m2, occasionally distinguishable on unworn m3; ectolophid always present on m1, present or absent on m2, absent from m3. Lower molars each with only two roots.

Tuberculum of first rib articulates with transverse processes of seventh cervical and first thoracic vertebrae; second thoracic vertebra with greatly elongated neural spine; entepicondylar foramen of humerus absent. Thoracicolumbar vertebrae 19; sacrals 4; caudals 29 or more; ribs 13.

Stomach unilocular and hemiglandular, without any extension of glandular epithelium into corpus; bordering fold crosses lesser curvature at incisura angularis (one specimen of *sublineatus*) or between incisura angularis and pylorus (three specimens of *dorsalis*); bordering fold crosses greater curvature opposite incisura angularis. Gall bladder present (at least in *dorsalis*). Phallic and other male reproductive characters undetermined.

CONTENTS: At least two diagnosable species, for which the names *dorsalis* Hensel 1872 and *sublineatus* Thomas 1903 are recommended below.

←

Fig. 2. Plate II from Hensel (1872); figures 16a, 16b, 26a, and 26b illustrate the dental morphology of *Hesperomys dorsalis* Hensel, the type species of *Delomys*.

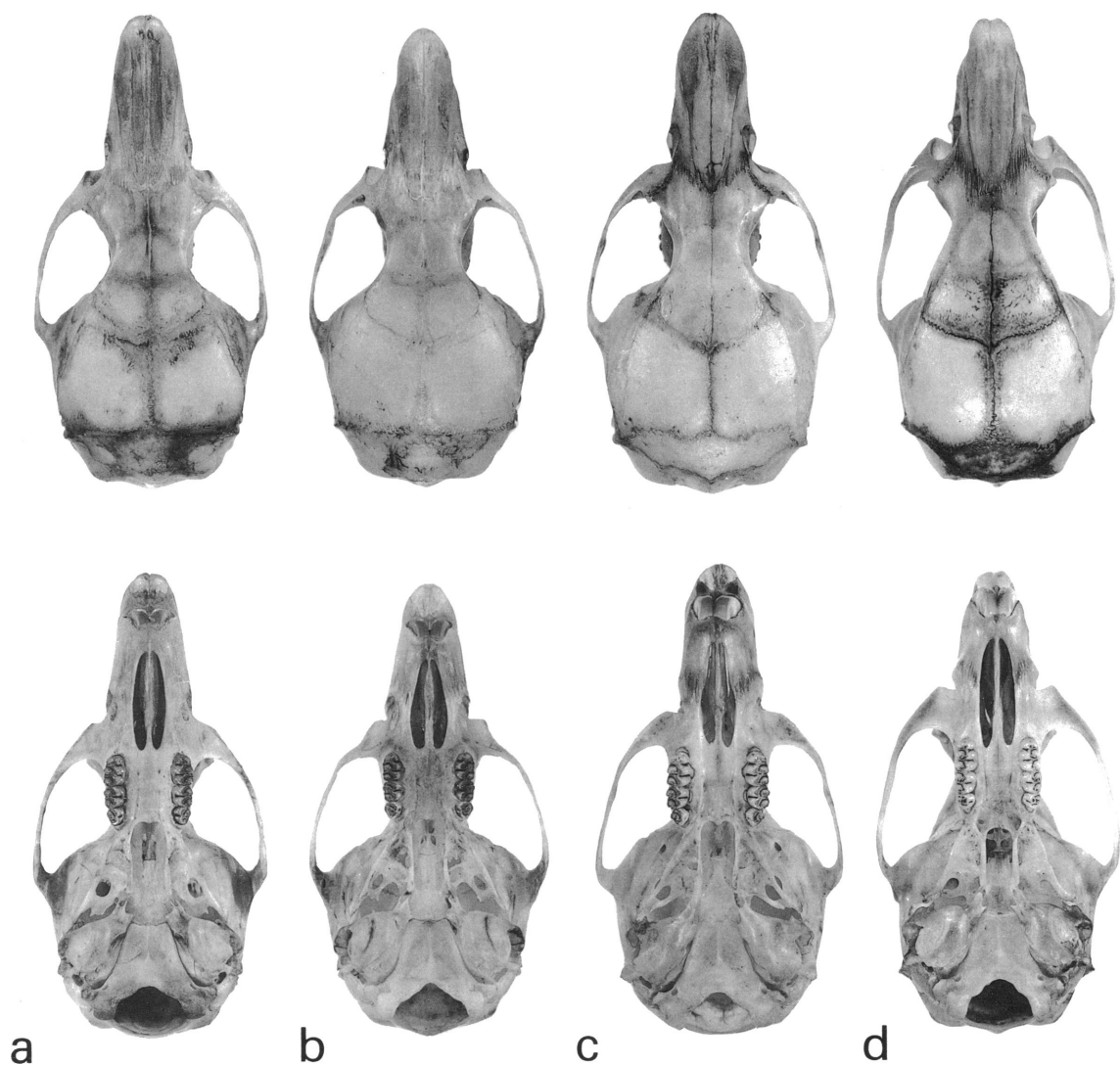


Fig. 3. Dorsal and ventral views ($\times 2$) of skulls. **a**, *Delomys dorsalis* (FMNH 145369); **b**, *Delomys sublineatus* (FMNH 145383); **c**, *Thomasomys cinereus* (LSU 27058); **d**, *Oryzomys palustris* (AMNH 242524).

COMPARISONS WITH *THOMASOMYS* AND *ORYZOMYS*

Species of *Delomys* and numerous other muroid rodents are said to be "pentalophodont" because their molar occlusal pattern includes well-developed mesoloph(id)s in addition to the four transverse crests² that char-

² Anteroloph, paraloph, metaloph, and posteroloph in the maxillary dentition; anterolophid, metalophid, entolophid, and posterolophid in the mandibular molars (see Reig, 1977).

acterize the simpler teeth of "tetralophodont" taxa. The Neotropical pentalophodont genera were divided into "thomasomyine" and "oryzomyine" groups by Hershkovitz (1962, 1966) according to external and craniodental attributes shared with *Thomasomys* or *Oryzomys*, but this dichotomy was rejected by Reig (1980) who referred members of both groups to a single tribe, the Oryzomyini. Although this all-inclusive concept of Oryzomyini has achieved a certain self-referential currency (e.g., Reig, 1984, 1986),

no character data have ever been cited to support it.

Morphological comparisons among *Delomys*, *Thomasomys*, and *Oryzomys* are crucial for evaluating alternative classifications of Neotropical pentalophodonts. Character similarities and differences among these genera have never been adequately described, and the empirical basis for recognizing thomomyines and oryzomyines as natural groups is correspondingly vague. Contradictory perceptions about the relationships of *Delomys* in the older literature also underscore the need for a fresh look at the evidence. Tate (1932: 18) believed that "*Delomys* represents a local . . . radiation in southern Brazil of moderate-sized rats closely allied to *Oryzomys*," whereas Ellerman (1941: 367) remarked that he could not find

. . . any difference of generic value between *Thomasomys* and "*Delomys*" (the *dorsalis* group); as a species group it is clearly distinct but none of its characters are of generic value . . . *T. dorsalis* was referred to *Thomasomys* by Thomas when he indicated what species should be referred to it from *Oryzomys*, and in my opinion should never have been separated from it.

Citing similarities of *Delomys* with both genera, Osgood (1933b: 13) suggested yet another possibility:

By this interpretation *Delomys* would be a form standing directly between *Thomasomys* and *Oryzomys* and it would be quite analogous to *Microryzomys* of the Andean region which stands in the same relative position although with a different combination of characters.

The prephylogenetic vocabulary of this taxonomic dialog does not obscure the essential disagreement, which can be rephrased in more explicit terms: at issue is the relative recency of common ancestry among *Delomys*, *Thomasomys*, and *Oryzomys* and, by extension, the larger implications of their morphological differences for pentalophodont classification.

Descriptions of character variation are phylogenetically ambiguous without information about the polarity of evolutionary transformations. In the comparisons that follow I cite hypotheses of evolutionary direction that have been proposed elsewhere in the literature or provide original observations about the character states of outgroups.

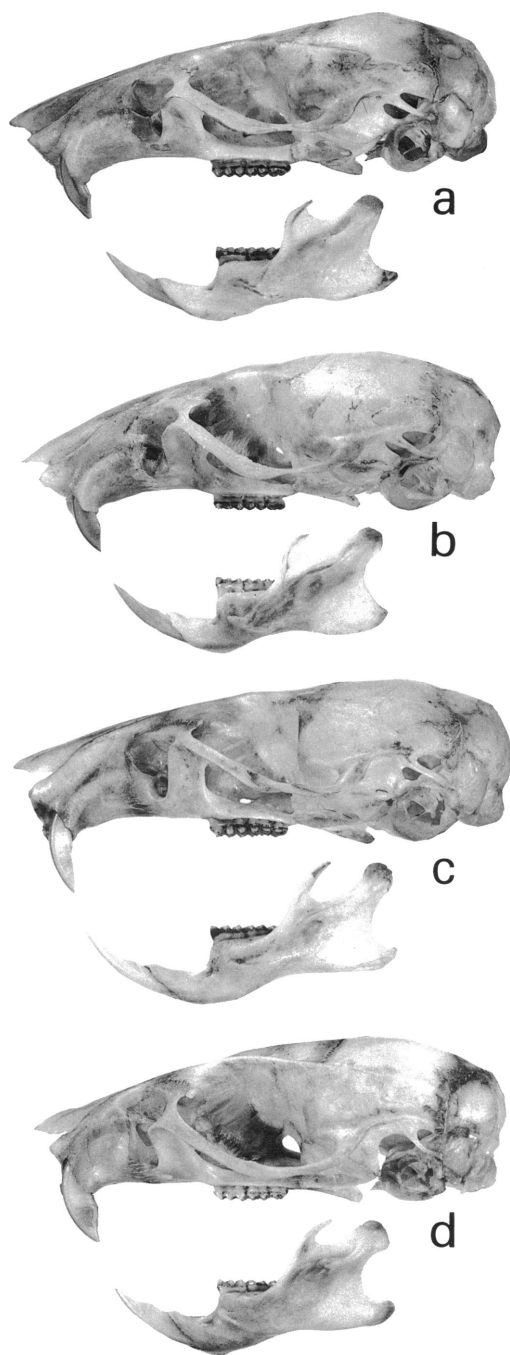


Fig. 4. Lateral views ($\times 2$) of skulls and mandibles. Species and specimens are the same as those in figure 3.

TABLE 1
Outgroup Exemplars Surveyed
 (See accompanying text for explanation)

Tylomyines^a

Nyctomys sumichrasti
Otonyctomys hatti
Ototylomys phyllotis
Tylomys mirae

Neotomines^a

Hodomys alleni
Nelsonia neotomodon
Neotoma (N.) floridana
Neotoma (Teanopus) phenax
Neotoma (Teonoma) cinerea
Xenomys nelsoni

Peromyscines^b

Habromys lepturus
Isthmomyss pirrensis
Megadontomys thomasi
Neotomodon alstoni
Onychomys leucogaster
Osgoodomys banderanus
Peromyscus leucopus
Podomys floridanus

Incertae sedis

Baiomys musculus
Ochrotomys nuttalli
Reithrodontomys (Aporodon) creper
Reithrodontomys (R.) sumichrasti
Scotinomys xerampelinus

^a After Carleton (1980).

^b After Carleton (1989).

In the absence of a well-corroborated cladistic classification of New World muroids, I made the following assumptions: (1) A Neotropical muroid complex united by absence of the entepicondylar foramen of the humerus, a double articulation of the first rib with the transverse processes of the seventh cervical and first thoracic vertebrae, and absence of an entoglossal process of the basihyal, is monophyletic; these character states were identified as derived for muroids by Carleton (1980), and the Neotropical complex that shares them corresponds to Hooper and Musser's (1964) "South American cricetines" minus *Nyctomys* (see also Voss and Linzey, 1981; and Voss, 1988). (2) The sister groups to this predominantly South American muroid fauna are to be found among the tylomyines, neotomines, peromyscines, and

other muroids with simple phalli that inhabit North and Central America; no derived morphological attributes unambiguously support this assumption, which is instead supported only by biochemical comparisons (Sarich, 1985) and geographic proximity. Unattributed statements about outgroup character states in the accounts below are based on my examination of exemplar species (table 1).

Because *Thomasomys* and *Oryzomys*, as currently recognized (e.g., by Musser and Carleton, 1993), each include a heterogeneous collection of unrevised and poorly understood nominal species, the comparisons that follow are restricted to their respective types, *T. cinereus* and *O. palustris*; reference series of both are listed in the Appendix. These accounts do not exhaust the inventory of subtle differences that could be described among *Delomys* and the typical species of *Thomasomys* and *Oryzomys*, but instead emphasize trenchant contrasts, especially in craniodental characters that have traditionally been cited as evidence for intergeneric relationships.

Ungual tufts: The dorsal surface of the muroid hindfoot is typically covered with a sparse, short pelage, but distinctively longer hairs are rooted at the bases of the claws. In *Delomys* and *Thomasomys cinereus*, these unguinal hairs exceed the claws in length and form dense, silvery tufts. In *Oryzomys palustris*, however, the hairs at the bases of the claws are short and do not form distinct tufts; as a consequence, the claws of this species appear naked and conspicuous.

Tufts of long unguinal hairs are uniformly present in tylomyines, neotomines, peromyscines, and other sigmodontines with simple phalli. The condition shared by *Delomys* and *Thomasomys cinereus* would therefore seem to represent the primitive morphology for Neotropical muroids.

Plantar pads: The plantar surface of the hindfoot of *Delomys* and *Thomasomys cinereus* is provided with two metatarsal pads (thenar and hypothenar) and four interdigital pads; all six are large, fleshy mounds that stand out prominently from the rest of the plantar epithelium (which is smooth over the proximal metatarsus but wrinkled and indistinctly squamate distally). The plantar surface of the hindfoot in *Oryzomys palustris*, however, has only five plantar pads; the lat-

TABLE 2
Mammary Counts from *Delomys* Specimens^a

Museum number	Locality ^b	Mammae ^c
<i>dorsalis</i>		
FMNH 26818	Argentina, Misiones, Caragatay	8
BMNH 84.2.8.38 ^d	Brazil, RS, Taquara	8
UZM 1267	Brazil, PR, Roça Nova	8
USP 26936	Brazil, SP, Apiaí	8
USP 27096	Brazil, SP, Apiaí	8
USP 26954	Brazil, SP, Iporanga	8
USP 26988	Brazil, SP, Iporanga	8
USP 27064	Brazil, SP, Iporanga	8
USP 27101	Brazil, SP, Iporanga	8
FMNH 136935	Brazil, SP, Boracéia	6
FMNH 136939	Brazil, SP, Boracéia	6
FMNH 145368 ^d	Brazil, SP, Boracéia	6
FMNH 145372	Brazil, SP, Boracéia	6
FMNH 145378 ^d	Brazil, SP, Boracéia	6
FMNH 145382	Brazil, SP, Boracéia	6
USNM 461063	Brazil, SP, Casa Grande	6
USNM 461064	Brazil, SP, Casa Grande	6
FMNH 53872	Brazil, RJ, Teresópolis	6
<i>sublineatus</i>		
BMNH 28.10.11.31	Brazil, SC, Hansa	8
USP 27007	Brazil, SP, Iporanga	8
USP 27046	Brazil, SP, Iporanga	8
FMNH 141629	Brazil, SP, Boracéia	8
USNM 460536	Brazil, SP, Casa Grande	8
USNM 484222	Brazil, SP, Casa Grande	8
USNM 484226	Brazil, SP, Casa Grande	8
USNM 485086	Brazil, SP, Casa Grande	8
USNM 485096	Brazil, SP, Casa Grande	8
FMNH 26872	Brazil, RJ, Teresópolis	8
MNHN 1967-1456	Brazil, MG, Conceição do M. D.	8

^a Except as noted, mammary counts were obtained from dried skins of reproductively mature females.

^b Within each species, localities are ordered in south-to-north sequence. Abbreviations for Brazilian states: MG, Minas Gerais; PR, Paraná; RJ, Rio de Janeiro; RS, Rio Grande do Sul; SP, São Paulo.

^c Specimens with six mammae lack the pectoral pair.

^d Fluid-preserved specimen.

eral metatarsal (hypothenar) pad is absent and the interdigital pads are small and inconspicuous against the distinctly squamate plantar epithelium of the distal metatarsus.

All tylomyines, neotomines, and most peromyscines have six plantar pads; among the outgroups surveyed by Carleton (1980), only *Onychomys* and *Podomys* (both peromyscines) lack one or both of the metatarsal pads, but neither has a hindfoot remotely resembling that of *Oryzomys palustris*. The plantar morphology of *Delomys* and *Thomasomys*

thus appears to represent the primitive condition for Neotropical muroids.

Mammae: Species of *Delomys* have either six or eight mammae. In all parous female specimens of *D. sublineatus* that I examined, and in some of *D. dorsalis* (table 2), eight teats are arranged in inguinal, abdominal, postaxial, and pectoral pairs (see Voss and Carleton, in press: fig. 8, for a diagram of mammary loci). Other specimens of *D. dorsalis*, however, lack the pectoral pair of teats (see below under Remarks in the account for

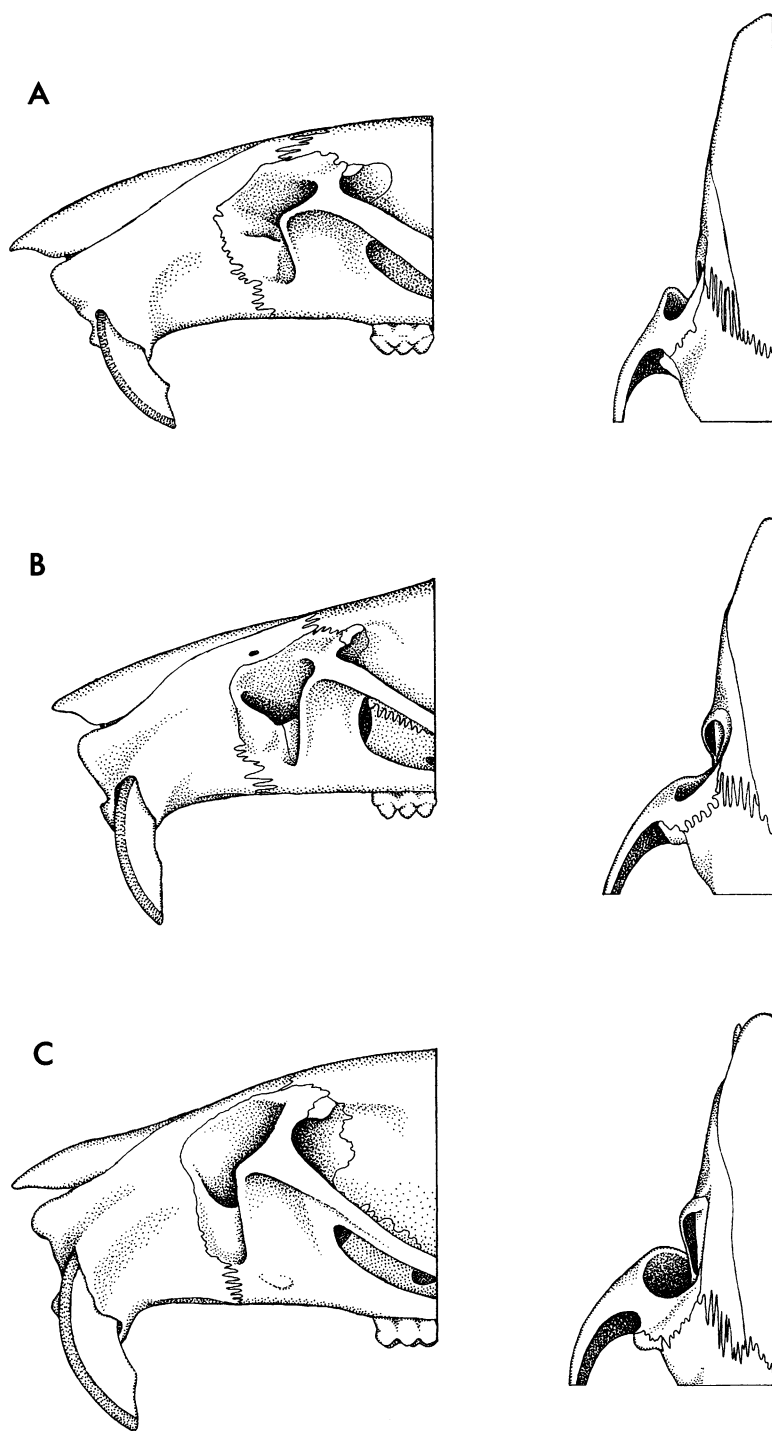


Fig. 5. Lateral and dorsal views of rostra. **A**, *Delomys dorsalis* (USNM 461063); **B**, *Thomasomys cinereus* (LSU 27053); **C**, *Oryzomys palustris* (AMNH 242521).

this species). All female *Thomasomys cinereus* that I examined have only six teats in inguinal, abdominal, and postaxial pairs. Female *Oryzomys palustris* always have paired inguinal, abdominal, postaxial, and pectoral teats, for a total mammary count of eight.

Six mammae (in inguinal, abdominal, and postaxial pairs) or four (inguinal and abdominal pairs only) are present in tylomyines, neotomines, peromyscines, and other North and Central American outgroup taxa (Carleton, 1980; but note that an alternative nomenclature for mammary loci was used therein). The addition of a pectoral pair for a total of eight teats is therefore most parsimoniously interpreted as a derived condition within the Neotropical muroid fauna.

Rostral tube: A distinctive bony tube formed by the premaxillae and nasals is present in *Delomys*. Both pairs of bones are produced considerably beyond the incisors, and their margins are closely approximated to extend the nasal cavity well in advance of the rest of the snout (fig. 5A). This unusual trait, which is somewhat better developed in *D. dorsalis* than in *D. sublineatus*, is responsible for the long rostrum that is noticeable in comparisons of skulls in dorsal view (fig. 3). Skulls of *Thomasomys cinereus* (fig. 5B) and *Oryzomys palustris* (fig. 5C) lack rostral tubes, although the premaxillae are consistently produced further forward in *T. cinereus* than in *O. palustris*.

Most outgroup taxa lack rostral tubes, but several peromyscines (e.g., *Megadontomys thomasi*, *Osgoodomys banderanus*) and one tylomyine (*Ototylomys phyllotis*) have extended and conjoined nasals and premaxillaries resembling those of *Delomys*. I interpret these similarities as convergently derived, but the evidence for polarity of this character is admittedly somewhat ambiguous.

Zygomatic notch and zygomatic plate: A well-formed zygomatic notch of the maxillary bone is present on each side of the rostrum in *Delomys*; the lateral limit of each notch is formed by the free dorsal edge of the zygomatic plate (fig. 5A). Correlated with this morphology is the anterior profile of the zygomatic plate itself, which is approximately vertical and straight or concave in lateral view.

In *Thomasomys cinereus* the zygomatic notches are shallow and indistinct because

the zygomatic plate has no well-defined dorsal edge; instead of standing vertically from its base, the plate has a distinctively sloping anterior profile (fig. 5B). As in *Delomys*, each zygomatic notch of *Oryzomys palustris* (fig. 5C) is well defined by the free dorsal margin of an erect zygomatic plate, the anterior profile of which is straight or concave in lateral view.

Of the outgroup taxa surveyed by Carleton (1980), only *Neotomodon alstoni* and neotomines (except *Nelsonia neotomodon*) have well-developed zygomatic notches, and his analytic results suggest that these evolved convergently. The morphology of the zygomatic plate shared by *Delomys* and *Oryzomys palustris* is therefore most parsimoniously interpreted as derived within the Neotropical muroid fauna.

Interorbital region and temporal crests: The interorbital region of *Delomys* generally conforms to the "hourglass" or "amphoral" morphology in which there is no conspicuous convergence to an anterior point of maximum constriction, and in which the supraorbital margins of the frontals are smoothly rounded (fig. 6A). In a few individuals, the supraorbital margins are gently squared, but sharp edges, beads, or projecting shelves are never developed. The dorsolateral surface of the braincase is smooth, lacking well-developed temporal ridges or crests.

The interorbital region of *Thomasomys cinereus* is essentially similar, without any marked anterior constriction and with gently squared or rounded supraorbital margins (fig. 6B); the dorsolateral surface of the braincase is likewise smooth and unridged. By contrast, the supraorbital margins of *Oryzomys palustris* (fig. 6C) are produced as sharp, dorsally reflected beads that converge to an anterior point of maximum constriction; in older specimens, the supraorbital bead is continuous with a low temporal crest along the dorsolateral contour of the braincase.

HersHKovitz (1962) and Carleton (1980) concluded that a hourglass-shaped interorbital region with rounded margins, which always appears to be correlated with the absence of temporal ridges, is the plesiomorphic condition.

Palate: The bony palate of *Delomys* (fig. 7A) is short because the mesopterygoid fossa

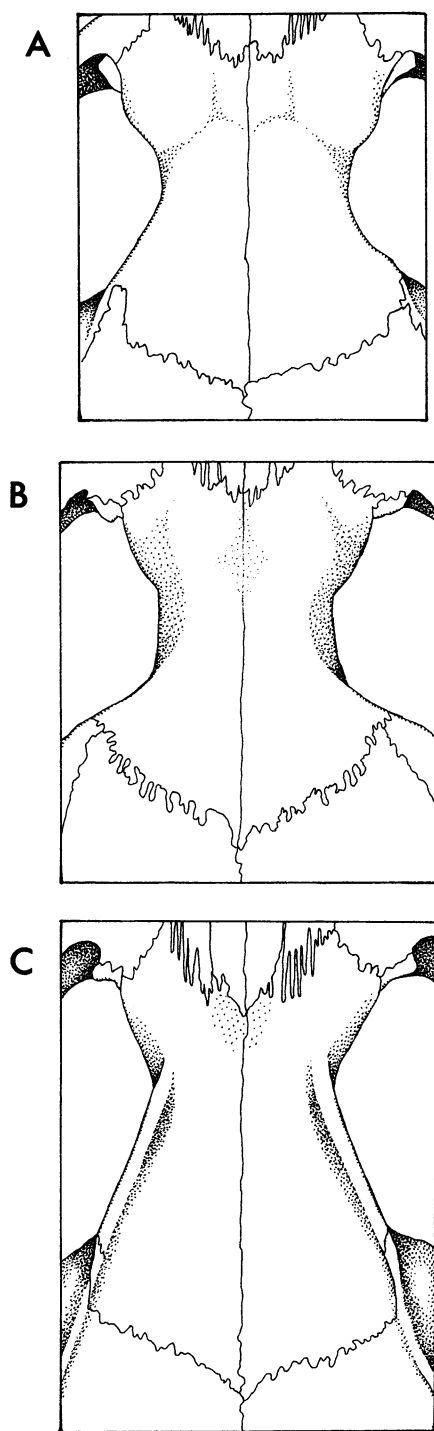


Fig. 6. Dorsal views of interorbital region. A, *Delomys dorsalis* (USNM 461063); B, *Thomasomys cinereus* (LSU 27053); C, *Oryzomys palustris* (AMNH 242521).

extends anteriorly between the third molars (thus, the hard palate is not produced posteriorly behind the molar rows). The posterior margin of the palate is usually biconcave because a small, rounded or pointed process is generally present in the midline. Distinct posterolateral palatal pits are absent although small, simple perforations in the palatines are often present on either side of the mesopterygoid fossa behind the molar rows.

The palatal morphology of *Thomasomys cinereus* (fig. 7B) closely resembles that of *Delomys*, but *Oryzomys palustris* differs conspicuously. The bony palate of *O. palustris* (fig. 7C) is long because the mesopterygoid fossa does not extend anteriorly between the molar rows, and the posterior palatal margin is not biconcave because no median process is developed. Instead, the palatal margins of *O. palustris* form a rounded or pointed arch around the anterior limits of the mesopterygoid fossa. Posterolateral palatal pits are always present and conspicuous in *O. palustris*: one or more are recessed in a shallow fossa between the mesopterygoid fossa and the third molar on each side.

I agree with Hershkovitz (1962) and Carleton (1980) that a short palate without posterolateral pits is probably plesiomorphic.

Sphenopalatine vacuities: The bony roof of the mesopterygoid fossa is substantially complete in most specimens of *Delomys* (fig. 7A) and *Thomasomys cinereus* (fig. 7B), but small sphenopalatine vacuities are sometimes present on either side of the basisphenoid-presphenoid suture. In *Oryzomys palustris* the mesopterygoid fossae is fenestrated by large sphenopalatine vacuities that flank a slender median basicranial bridge (fig. 7C).

The roof of the mesopterygoid fossa is completely ossified or perforated only by minute slits in most tyromyines (e.g., *Nyctomys sumichrasti*, *Ototylomys phyllotis*, *Tylomys mirae*), some neotomines (*Hodomys alleni*), and some peromyscines (*Isthmomys pirrensis*, *Osgoodomys banderanus*). Large sphenopalatine vacuities occur in some neotomines (e.g., *Nelsonia neotomodon*, *Neotoma phenax*), many peromyscines (*Habromys lepturus*, *Neotomodon alstoni*, *Onychomys leucogaster*, *Peromyscus leucopus*), and in other outgroup taxa whose suprageneric relationships are unknown (*Baiomys musculus*,

Reithrodontomys sumichrasti). Given these taxonomic distributions, the polarity of mesopterygoid fenestral transformations within the Neotropical muroid fauna is ambiguous, but Carleton's (1980) conclusion (from a broader survey of muroid taxa) that an unfenestrated fossa is primitive can be noted for the sake of discussion.

Alisphenoid strut: The buccinator-masticatory and accessory oval foramina of the alisphenoid are confluent in *Delomys* because the bony strut that separates these openings in other muroids is absent (see Voss, 1991: fig. 12). Fragile splints of bone are present unilaterally in a few specimens (7 of 99 scored for this trait), but the foramina are apparently never bilaterally separated by alisphenoid ossifications.

In *Thomasomys cinereus* the buccinator-masticatory and accessory oval foramina are almost always separated by robust alisphenoid struts; in a few specimens (4 of 57 scored for this trait) the foramina are unilaterally confluent, but an alisphenoid strut always appears to be present on at least one side. The alisphenoid strut is consistently absent in *Oryzomys palustris*.

The buccinator-masticatory and accessory oval foramina are separated by an alisphenoid strut in tylomyines, neotomines, peromyscines, and other outgroup taxa surveyed by Carleton (1980); the absence of an alisphenoid strut is therefore most parsimoniously interpreted as derived among Neotropical muroids.

Carotid circulation: The carotid arterial circulation of *Delomys* conforms to the taxonomically widespread morphology that Voss (1988: 297–298) designated as pattern 1: a large stapedial artery enters the middle ear through the stapedial foramen, a conspicuous perforation in the petrotympanic fissure on the ventromedial surface of the bulla; the artery passes undivided through the stapes, exits the middle ear through a cleft in the bullar roof, and divides inside the braincase to supply the facial (internal maxillary and ophthalmic) circulation via infraorbital and supraorbital vessels; the supraorbital ramus passes rostrally along the inside wall of the alisphenoid, leaving a translucent groove in that bone, and enters the rear of the orbit

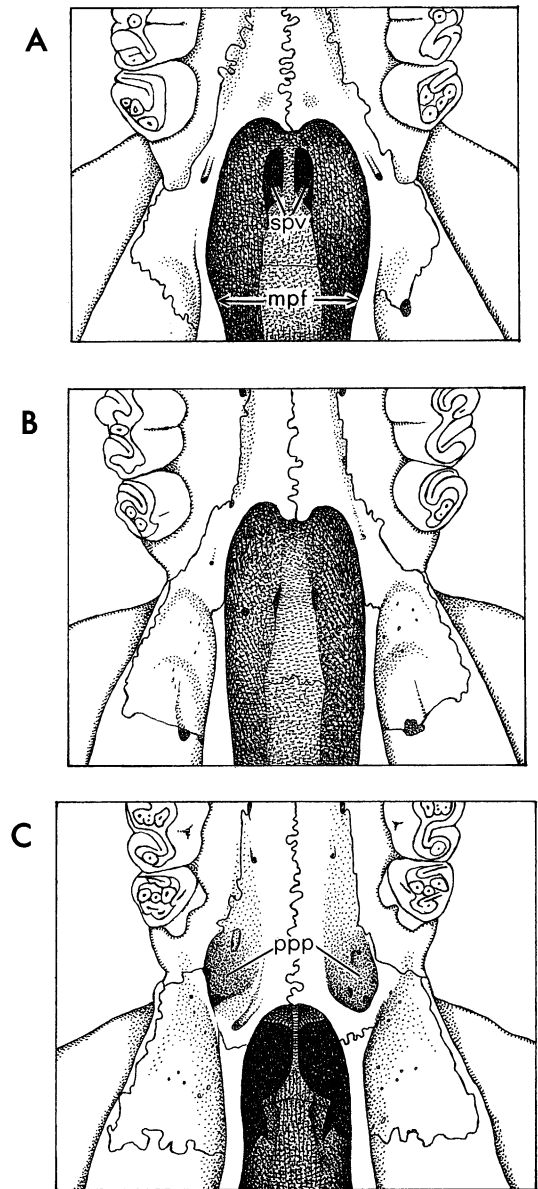


Fig. 7. Posterior palate and mesopterygoid fossa. A, *Delomys dorsalis* (USNM 461063); B, *Thomasomys cinereus* (LSU 27060); C, *Oryzomys palustris* (AMNH 242519). mpf, mesopterygoid fossa; ppp, posterolateral palatal pits; spv, sphenopalatine vacuities.

through the sphenofrontal foramen. The presence of a large stapedial foramen together with an alisphenoid groove and a sphenofrontal foramen are reliable osteological

indicators³ of this type of carotid circulation, as can be verified by tracing fragments of the dried vessels on incompletely cleaned skulls.

The carotid morphology of *Thomasomys cinereus* incorporates the same pattern of stapedia supply as that seen in *Delomys*, but *Oryzomys palustris* lacks a stapedia contribution to the facial circulation. The facial circulation of *O. palustris* is instead supplied by an internal anastomosis from the internal carotid that leaves a translucent groove across the roof of the parapterygoid fossa; the stapedia foramen is minute, and there is no alisphenoid groove or sphenofrontal foramen (Carleton and Musser, 1989: figs. 20, 21). This latter type of carotid circulation is also taxonomically widespread and corresponds to pattern 3 of Voss (1988: 297–298).

I concur with Bugge (1970) and Carleton (1980) that a complete stapedia circulation (pattern 1) is primitive for muroids generally and is likely to be so also within the Neotropical fauna.

Tegmen tympani: The tegmen tympani, an outgrowth of the periotic, forms the roof of the epitympanic recess in therian mammals (van der Klaauw, 1931). In some muroid rodents the tegmen tympani also contributes to the anterior attachment of the auditory complex to the rest of the skull, but this suspensory role is taxonomically variable. To the best of my knowledge, Winge (1887) was the first and only student of muroid systematics to describe species differences in this interesting character.

The rodent ectotympanic bulla adheres tightly to the periotic (or petromastoid) such that the two bones are effectively united to contain and support the auditory apparatus and the semicircular canals. This unit is attached to the squamosal, exoccipital, and basioccipital bones by open sutures filled with connective tissue, an arrangement that presumably cushions the organs of hearing and equilibrium from vibrations caused by gnawing, chewing, and other mechanical activities of the skull. The attachments of the periotic to the occiput are apparently quite conservative among Neotropical muroids, but the

squamosal attachments provide useful character data.

In *Delomys* and *Thomasomys cinereus* (figs. 8A, 8B), the periotic is attached to the squamosal at two points. Posteriorly, the slender hamular process of the squamosal adheres to the dorsal surface of the mastoid tubercle and to the lateral surface of the capsule that contains the semicircular canals. Anteriorly, the periotic is attached to the skull by the tegmen tympani, which overlaps a caudally projecting flange, here named the *posterior suspensory process*, of the squamosal. That this attachment is functionally supportive can be inferred from the concave impression of the tegmen tympani that can be seen on the lateral surface of the posterior suspensory process when the periotic has fallen away from skulls with loosened sutures. Correlated with its supportive role, the tegmen tympani is large in *Delomys* and *Thomasomys*: it fills the floor of the postglenoid foramen and is prominently grooved by the postglenoid vein⁴ that passes over it.

The morphology of the tegmen tympani and its anatomical relations to adjacent structures of the ear region are strikingly different in *Oryzomys palustris* (fig. 8C). The periotic is suspended from the squamosal only posteriorly, via the hamular process. The tegmen tympani does not overlap the squamosal and the latter produces no posterior suspensory process. Of 78 specimens of *O. palustris* that I scored for this trait, edge-to-edge contact (not overlap) between tegmen tympani and squamosal was observed in only two; a perceptible (though often very narrow) gap separated these bones in all others. The tegmen tympani of *Oryzomys palustris* does not fill the floor of the postglenoid foramen and the postglenoid vein exits the braincase in a narrow cleft between tegmen tympani and the swollen dorsal lip of the ectotympanic annulus.

The tegmen tympani broadly overlaps the

³ The passage of the infraorbital ramus is more variable and sometimes leaves no discernible osteological trace.

⁴ I previously (Voss, 1988: 294) referred to this vessel as the transverse sinus following Greene (1935: fig. 223), but that term should be reserved for the intracranial vascular cavity drained by the postglenoid vein of adult eutherians. See Wible (1990) for a lucid explanation of the development and evolution of the mammalian cerebral venous circulation.

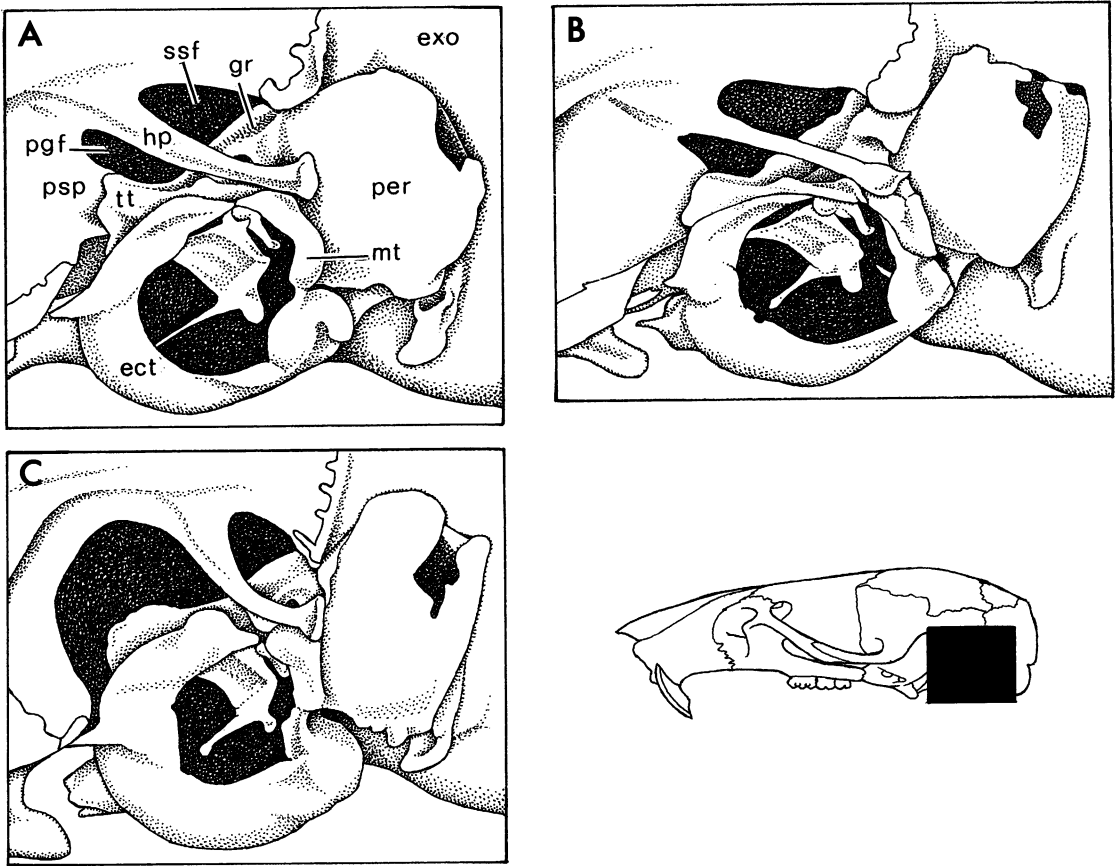


Fig. 8. Left lateral views of auditory region. A, *Delomys dorsalis* (USNM 461063); B, *Thomasomys cinereus* (LSU 27046); C, *Oryzomys palustris* (AMNH 219953). ect, ectotympanic; exo, exoccipital; gr, groove for postglenoid vein; hp, hamular process of squamosal; mt, mastoid tubercle; per, periotic; pgf, postglenoid foramen; psp, posterior suspensory process of squamosal; ssf, subsquamosal foramen; tt, tegmen tympani.

squamosal in all tylomyines, neotomines, peromyscines and other outgroup genera that I examined for this trait; the condition shared by *Delomys* and *Thomasomys cinereus* is therefore likely to be primitive for Neotropical muroids.

Capsular process of lower incisor alveolus: In *Delomys* and *Thomasomys cinereus*, the lower incisor alveolus terminates as an indistinct swelling or a low bony ridge on the lateral surface of the mandible just below the base of the coronoid process. A distinct capsular process contains the posterior terminus of the incisor alveolus in most adult specimens of *Oryzomys palustris*.

A distinct capsular process of the lower incisor alveolus is absent in all outgroup gen-

era except *Onychomys* (Carleton and Eshelman, 1979: fig. 3). The condition shared by *Delomys* and *Thomasomys cinereus* is therefore likely to be primitive.

Incisors: The upper incisors of *Delomys* are small, narrow, and strongly opisthodont (fig. 5A); they seem delicate in situ because they are encased at the anterior extremity of a massive rostrum. By contrast, the larger, broader, and almost orthodont incisors of *Thomasomys cinereus* are set in a relatively smaller rostrum, which makes them look much more prominent in comparison (fig. 5B). The incisors of *Oryzomys palustris* (fig. 5C) are also relatively larger than those of *Delomys* but are similar in shape (degree of opisthodonty).

The range of variation in size and shape of incisors encountered among the outgroups precludes any useful polarization of this character.

Molar occlusal design: The molar dentition of *Delomys* is incipiently lophodont because the lingual and labial folds interpenetrate on the occlusal surface. Interpenetration of the labial and lingual folds effectively increases the occlusal surfaces of enamel lophs and decreases the occlusal prominence of cusps. This characteristic is best appreciated by comparing the principal folds of the upper molars of *Delomys* (figs. 9a, 9b, 11) with their homologs in *Thomasomys cinereus* (figs. 9c, 11) and *Oryzomys palustris* (fig. 9d): the parafllexus and metafllexus of *Delomys* penetrate the toothcrown anterolingually, approximately toward the apices of the protocone and hypocone, respectively; by contrast, the same folds in *T. cinereus* (and *O. palustris*) bend posteriorly around the paracone and metacone. The lingual cusps of *Delomys* are therefore less prominent than those of *Thomasomys* and *Oryzomys*. Because the hypoflexus penetrates between the apices of the parafllexus and metafllexus in *Delomys*, the mesoloph is a robust transverse crest that sweeps across the tooth to join the hypocone; the mesoloph and other transverse crests in the molar dentition of *T. cinereus* (and *O. palustris*) are not as well developed.

Among the outgroups, only species of *Tylomys* have fully pentalophodont molars with interpenetrating labial and lingual folds. *Neotomodon alstoni*, however, has incipiently lophodont molars in which mesoloph(id)s are almost completely suppressed. Neotomine molars have shallowly interpenetrating folds, but these extremely hypsodont teeth are prismatic rather than lophodont. By contrast with these dissimilar morphologies, none of which closely resembles the condition seen in *Delomys*, the arrangement of labial and lingual folds in the pentalophodont dentitions of many peromyscines and some species of *Reithrodontomys* broadly resembles the molar occlusal design of *Thomasomys cinereus* and *Oryzomys palustris*. Although each of the Neotropical taxa compared in these accounts possesses its own unique aspects of molar design, the apparently derived incipient lophodonty of *Delomys* merits emphasis.

Anterocone: The unworn anterocone of *Delomys* (fig. 9a, 9b) is deeply divided by an anteromedian flexus into anterolingual and anterolabial conules, of which the lingual conule is sometimes perceptibly smaller (especially in *D. sublineatus*). The unworn anterocone of *Thomasomys cinereus* (fig. 9c) is likewise deeply divided, but the lingual and labial conules are usually equal in size. The anterocone of *Oryzomys palustris* (fig. 9d) is not divided by a patent anteromedian flexus, but an internal fold partially separates the two conules from behind.

Both divided and "undivided" anterocones occur among the outgroup taxa with no clear pattern to suggest which is primitive for Neotropical muroids. As remarked by Carleton (1980), an undivided anterocone developed from the anterior cingulum after the phylogenetic disappearance of the fourth premolar in pre-Oligocene myomorphs, but the anterocones of such early fossil taxa as *Paracricetodon* and *Eumys* (see Stehlin and Schaub, 1951: figs. 232, 244) are narrow, simple, anterolabial cusps. By contrast, the broad anterocone of *Oryzomys palustris* appears to be a composite structure formed by coalescence of formerly separate labial and lingual conules; I follow Carleton and Musser (1989) by interpreting the internal fold that partially divides the anterocone from behind as the remnant of a formerly patent anteromedian flexus.

Ectolophid: An ectolophid is fused to an ectostylid on the labial cingulum of the first mandibular molar in all specimens of *Delomys* that I examined (fig. 10, arrows); this accessory loph is sometimes developed on the second molar as well. The mandibular molars of *Thomasomys cinereus* and *Oryzomys palustris* consistently lack ectolophids.

Among the outgroup exemplars surveyed, ectolophids are consistently well developed in some peromyscines (*Habromys lepturus*, *Isthmomyris pirrensis*, *Megadontomys thomasi*), in *Ochrotomys nuttalli*, and in *Reithrodontomys creper*. All neotomines consistently lack ectolophids, as may some tylomyines (e.g., *Ototylomys phyllotis*) and species of *Scotinomys*. Polymorphic presence/absence of ectolophids was observed in the other exemplar taxa. Given these observations, it seems prudent to reserve judgment

about the polarity of this character in Neotropical muroids.

Number of ribs: Available postcranial skeletons of *Delomys* (two of *D. dorsalis* and two of *D. sublineatus*) all have 13 ribs. In a much larger skeletal sample of *Thomasomys cinereus*, 30 specimens have 13 ribs, but two specimens (each with a supernumerary thoracicolumbar vertebra) have 14 ribs. In one sample of *Oryzomys palustris*, 15 specimens have 12 ribs, but two specimens (one with a supernumerary vertebra) have 13 ribs.

Thirteen or more ribs are present in all of the tylomyine, neotomine, peromyscine, and other outgroup taxa surveyed by Carleton (1980); fewer than 13 ribs is therefore likely to be a derived condition within the Neotropical muroid fauna.

Gall bladder: A small saccular gall bladder is concealed in the deep fold that divides the median (or cystic) lobe of the liver in *Delomys dorsalis* (seven specimens dissected), but I was unable to find a gall bladder in the distorted and poorly fixed liver of the only available fluid example of *D. sublineatus* (FMNH 145383). The gall bladder is present and well developed in the only two specimens of *Thomasomys cinereus* currently available for dissection (LSU 27145, 27146). *Oryzomys palustris* lacks a gall bladder (Voss, 1991: table 4).

The gall bladder is absent in tylomyines and *Ochrotomys nuttalli*, but is present in all of the other outgroup taxa surveyed by Carleton (1980); I agree with his conclusion that absence is the derived morphology.

PHYLOGENETIC RELATIONSHIPS AND "THOMASOMYINE" CHARACTERS

The division of Neotropical pentaplophodonta into thomasomyine and oryzomyine groups was initiated by Thomas's (1906) discovery that characters of the posterior palate could be used to distinguish *Thomasomys* and *Rhipidomys* on the one hand from *Oryzomys* and *Oecomys* on the other. In the same report, Thomas remarked that most species with short, unpitted palates (in *Thomasomys* and *Rhipidomys*) have six mammae, whereas those with long, pitted palates (in *Oryzomys* and *Oecomys*) have eight. The only cited exceptions to this pattern of character correla-

tion were two Brazilian species of *Thomasomys* (*ferrugineus* and *dorsalis*) with short, unpitted palates but eight mammae; all of the other species of *Thomasomys* then known were from high elevations in the tropical Andes.

The already imperfect correlation between palatal morphology and mammary formula among Neotropical pentaplophodonta was further compromised when Thomas (1917: 193) reported that *Rhagomys rufescens* (from Rio de Janeiro) has six mammae but a posterior palate "... of the general structure of *Oryzomys* and *Oecomys*, not as in *Rhipidomys* and *Thomasomys*." After hypothesizing that *Rhagomys* might be most closely related to *Oecomys*, Thomas remarked that,

... the second group, those with the mesopterygoid fossa continued forward between the posterior molars (*Rhipidomys*, *Thomasomys*, &c) ... needs revision, owing to the diverse characters of some of the forms included in it. In this revision, by removing some of the most diverse into special genera, the groups that remain are rendered more clear-cut and definable, to the great advantage of students of the subject [op. cit.: 193-194].

Phaenomys (containing only *ferrugineus*) was diagnosed from *Thomasomys* by its beaded interorbital margins, reduced anterolingual conule on M1, and eight mammae. *Delomys* (containing *dorsalis*, *collinus*, and *sublineatus*) was diagnosed from *Thomasomys* by the free dorsal margin of its zygomatic plate and by its (usual) mammary count of eight; contrasts in rostral length and braincase proportions were also noted. *Inomys* (containing only *incanus*, from Peru) was distinguished from *Thomasomys* by aspects of cranial shape in which the new genus was said to resemble *Oxymycterus*.

By naming *Phaenomys* and *Delomys*, Thomas (1917: 194) simplified the morphological definition of *Thomasomys* and effectively restricted the geographic range of the latter to "... the northern part of the Andean area, with extension eastwards to British Guiana" (op. cit.: 194). With the discovery of *Thomasomys oenax* from Rio Grande do Sul (Thomas, 1928), however, the range of the genus was again expanded to include the Brazilian shield. This last development pro-

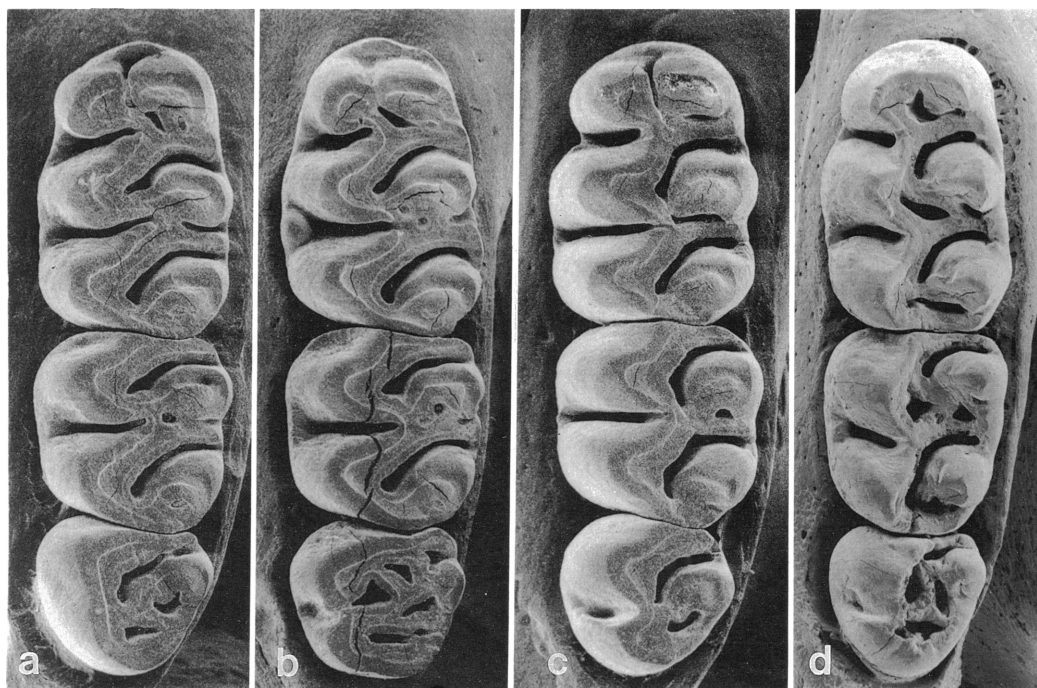


Fig. 9. Left upper molar rows. a, *Delomys dorsalis* (FMNH 145370); b, *Delomys sublineatus* (FMNH 141628); c, *Thomasomys cinereus* (LSU 27056); d, *Oryzomys palustris* (AMNH 234936).

voked an indignant response from W. H. Os-
good (1933b: 13) in his description of
Thomasomys pictipes from northeastern Ar-
gentina:

When the name *Delomys* was proposed, it was argued in its favor that the species included was [sic] geographically removed and isolated from other members of *Thomasomys*. Later, in describing *T. oenax* from the same region, however, Thomas ignores *Delomys*, and calmly states that *oenax* "is a *Thomasomys*, and represents a new species from an area where members of the latter genus had never previously been known . . . A medium-sized species of the most typical *cinereus* section of the genus." By connecting *oenax* directly with *cinereus* in this way, the position of *Delomys* was greatly weakened not only on geographical but on morphological grounds, for *cinereus* (although the type of the genus) is a species in which the zygomatic plate is more projecting than usual in *Thomasomys*. The principal and practically the only cranial distinction of *Delomys* is its projecting infra-orbital [sic] plate, so with two species like *oenax* and *pictipes* in proximity to it, there is little left to separate it except its mammary formula . . .

For the present, therefore, I should prefer to regard *Delomys* (probably with only one species) as a subgenus of *Thomasomys*.

Citing Osgood's (1933a, 1933b) expansive views about generic limits, Ellerman (1941) synonymized not only *Delomys*, but also *Inomys* and *Aepeomys* (another group of Andean species named by Thomas) with *Thomasomys*. For Ellerman, *Thomasomys* was chiefly distinguished by molars "of *Oryzomys* type" (i.e., brachydont and pentalophodont), "narrow" zygomatic plates, unridged interorbital regions, short palates, and six mammae (except in the "*dorsalis* group"). This all-inclusive concept was endorsed by Cabrera (1961) and has not subsequently been critically evaluated by analyses of morphological character data.

The list of "thomasomyine" genera provided by Hershkovitz (1962) included *Nyctomys* and *Otonyctomys*, two Central American tylomysines (Carleton, 1980), as well as the South American genera previously mentioned: *Rhipidomys*, *Phaenomys*, and *Tho-*

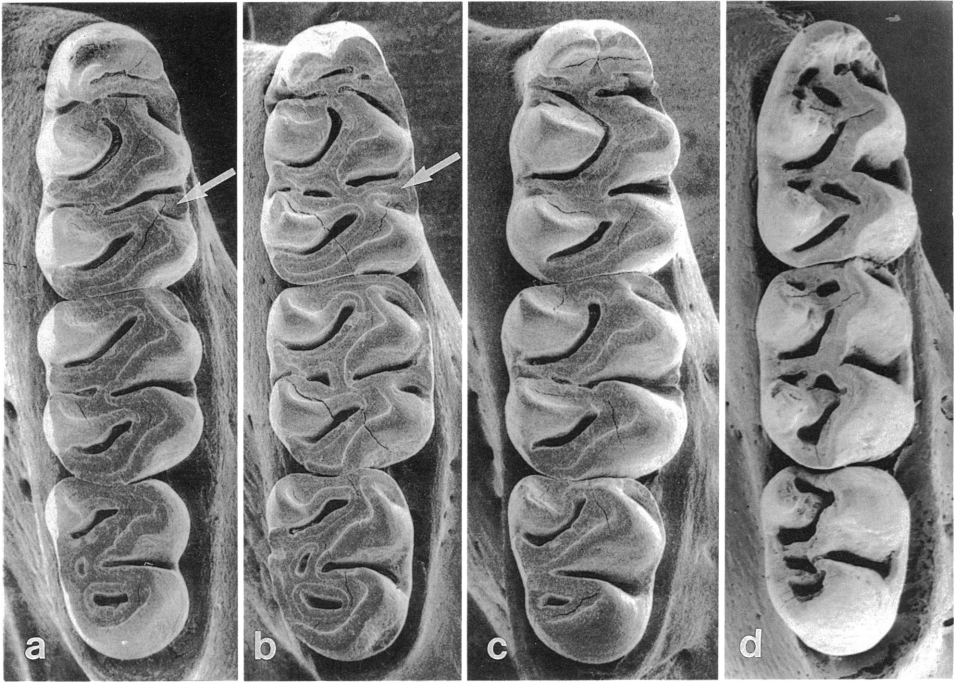


Fig. 10. Right lower molar rows. Species and specimens are the same as those in figure 9. Arrows point to the ectolophid on m1, one of the characters that distinguishes *Delomys* from *Thomasomys cinereus* and *Oryzomys palustris*.

masomys (sensu Osgood-Ellerman-Cabrera). According to this authority,

Thomasomyines include the most primitive of cricetines. They are forest dwelling, broad footed, long tailed, 6-mammate, brachydont-pentalophodont mice with wide-short palate and weakly projecting zygomatic plate. They compose one of the more coherent of the multigeneric groups of South American rodents. Some of the characters shared by the members of the group may be phenetic rather than phyletic but this has yet to be determined [Hershkovitz, 1966: 125].

Because some species of *Thomasomys* have neither longer tails nor broader hindfeet than some oryzomyines, the valid characters in this diagnosis are essentially the same as those emphasized in the earlier literature. Only the inclusion of two Central American genera significantly distinguishes the scope of Hershkovitz's "thomasomyine" group from the core of species originally referred to *Rhipidomys* and *Thomasomys* by Thomas (1917).

A salient aspect of all the published literature on the relationships of *Thomasomys* to other pentalophodont genera is the paucity of characters mentioned: mammary counts, zygomatic plate development, interorbital shape, and palatal morphology virtually exhaust the list of cited attributes. Yet many

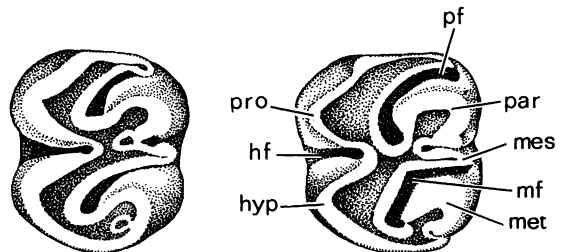


Fig. 11. Occlusal views of second left upper molars. **Left**, *Delomys dorsalis* (FMNH 145369); **right**, *Thomasomys cinereus* (LSU 27058). **hf**, hypofoxus; **hyp**, hypocone; **met**, metacone; **mf**, metaflexus; **mes**, mesoloph; **par**, paracone; **pf**, parafoxus.

TABLE 3
Morphological Comparisons Among *Delomys* and Other Pentalophodont Neotropical Muroids

Characters ^a	<i>Delomys</i>	<i>Thomasomys</i> ^b	<i>Oryzomys</i> ^c
Ungual tufts:	present	present	<i>absent</i>
Plantar pads:	six	six	<i>five</i>
Mammae:	six or <i>eight</i>	six	<i>eight</i>
Rostral tube:	<i>present</i>	absent	absent
Zygomatic notch:	<i>well defined</i>	indistinct	<i>well defined</i>
Interorbit:	"hourglass," with rounded margins	"hourglass," with rounded margins	<i>convergent, with beaded margins</i>
Palate:	short, w/o posterolateral pits	short, w/o posterolateral pits	<i>long, with complex postero-lateral pits</i>
Mesopterygoid fossa:	not fenestrated	not fenestrated	<i>fenestrated</i>
Alisphenoid strut:	<i>absent</i>	present	<i>absent</i>
Carotid circulation:	pattern 1	pattern 1	<i>pattern 3</i>
Tegmen tympani:	overlaps squamosal	overlaps squamosal	<i>no squamosal overlap</i>
Capsular process:	absent	absent	<i>present</i>
Incisors:	small and strongly opisthodont	large and weakly opisthodont	<i>large and strongly opisthodont</i>
Molar design:	<i>incipiently lophodont</i>	not lophodont	<i>not lophodont</i>
Anteromedian flexus:	patent	patent	<i>not patent</i>
Ectolophid:	present	absent	<i>absent</i>
Number of ribs:	thirteen	thirteen	<i>twelve</i>
Gall bladder:	present	present	<i>absent</i>

^a Italicized character states are those believed to be derived among Neotropical muroids. See text for character state definitions and polarities.

^b Character states are those of *T. cinereus*; other species currently classified as *Thomasomys* may possess different attributes.

^c Character states are those of *O. palustris*; other species currently classified as *Oryzomys* may possess different attributes.

more morphological traits distinguish the type species of *Thomasomys* and *Oryzomys* (table 3) and these, together with hypotheses of polarity, provide a more secure basis for systematic inference. One striking result of the character analyses provided in this report is that typical *Thomasomys* exhibits the primitive state for every character whose polarity can plausibly be inferred. This result, of course, depends on the stated assumptions concerning ingroup monophyly and outgroup relationships, and some hypotheses of polarity cannot be defended with much confidence even if those assumptions are granted. Nevertheless, it is certainly fair to say that none of the characters surveyed provides evidence for monophyly either of *Thomasomys* (however construed) or of the "thomasomyine" group of genera.

By contrast, *Oryzomys palustris* exhibits

the hypothetically derived state for 14 of the 18 characters surveyed. Some of these are perhaps autapomorphies or are shared with only a few congeneric species, but others are apparently synapomorphies of a monophyletic group that includes all the oryzomyines of Hershkovitz (1944, 1960) plus several genera that are fully tetralophodont or that have vestigial mesoloph(id)s. This group, which Voss and Carleton (in press) diagnose as the tribe Oryzomyini, obviously cannot include "thomasomyines" (contra Reig, 1980).

Although *Delomys* is not known to share any derived morphological attribute with *Thomasomys*, neither is there any compelling character data to suggest a closer relationship with *Oryzomys*. The two derived conditions unambiguously shared by *Delomys* and *Oryzomys palustris* (a well-defined zygomatic notch and absence of an alisphenoid strut)

are widespread among other Neotropical genera and have probably evolved numerous times in muroid phylogeny. There is currently no morphological evidence that *Delomys* is closely related to any other Neotropical muroid genus, although such evidence might eventually be found in the male reproductive tract and in other unsurveyed organ systems. Zanchin et al. (1992) noted that the diploid numbers of *Delomys* species more closely resemble those of some oryzomyines than those of *Thomasomys*, but karyotypic comparisons are phylogenetically ambiguous in the absence of information about chromosome arm homologies and the polarity of chromosomal rearrangements.

Delomys is one of many pentalophodont genera that cannot be assigned to any demonstrably monophyletic taxon less inclusive than the Neotropical muroid ingroup identified earlier for the purpose of character analysis. Placing these taxa in a formally named tribe, such as the Thomasomyini of Cerqueira (1982) and Redford and Eisenberg (1992), would be a mistake because, inevitably, all coordinate taxa are treated equivalently by nonsystematists. Equally useless is the option of erecting a monotypic tribe for each genus judged to have achieved some arbitrary degree of difference. It is better to emphasize that these taxa share primitive attributes by referring them to a "plesion" in formal classifications (cf. Wiley, 1981); in common parlance they could simply be called "plesiomorphic Neotropical muroids." In addition to *Delomys*, genera that might provisionally be assigned to this category include: *Abrawayaomys*, *Aepeomys*, *Chilomys*, *Phaenomys*, *Rhagomys*, *Rhipidomys*, *Thomasomys* (including *Erioryzomys* and *Inomys*), and *Wilfredomys* (including *oenax* and *pictipes* according to Musser and Carleton, 1993). The characters defined and illustrated above will serve adequately to distinguish *Delomys* from other plesiomorphic Neotropical muroids not explicitly compared with it in this report.

THE RECENT SPECIES

Delomys dorsalis (Hensel)

Hesperomys dorsalis Hensel, 1872: 42.

Hesperomys dorsalis obscura Leche, 1886: 696.

Akodon dorsalis: Trouessart, 1898: 537.

Akodon dorsalis obscura: Trouessart, 1898: 537.

Akodon dorsalis lechei: Trouessart, 1904: 434.

Thomasomys dorsalis: Thomas, 1906: 443.

Delomys dorsalis: Thomas, 1917: 196.

Delomys dorsalis collinus Thomas, 1917: 197.

Delomys dorsalis dorsalis: Gyldenstolpe, 1932: 60.

Delomys dorsalis lechei: Gyldenstolpe, 1932: 61.

Thomasomys dorsalis dorsalis: Ellerman, 1941: 368.

Thomasomys dorsalis collinus: Ellerman, 1941: 369.

Thomasomys dorsalis lechei: Ellerman, 1941: 369.

Thomasomys lechei: Moojen, 1952: 59.

Thomasomys collinus: Moojen, 1952: 60.

Delomys collinus: Avila-Pires, 1960a: 32.

TYPE MATERIAL: As described for the genus.

DISTRIBUTION: From Rio Grande do Sul (Brazil) and Misiones (Argentina) to the south, thence northward along the Atlantic coast at least as far as the Brazilian state of Rio de Janeiro (fig. 1). *Delomys dorsalis* is known to occur sympatrically with *D. sublineatus* in the Brazilian states of São Paulo and Rio de Janeiro, and sympatry is also to be expected in the states of Paraná and Santa Catarina. Populations of *D. dorsalis* in the state of Rio Grande do Sul and in the Argentine province of Misiones, however, are apparently allopatric.

EMENDED DIAGNOSIS: A soft-furred, long-tailed species of *Delomys*; pelage with or without a distinct middorsal stripe from nape to base of tail, and without a lateral line of clear yellow or buff between dorsal and ventral color zones; mystacial vibrissae long, extending to or beyond tips of adducted pinnae; hindfoot covered dorsally with dark-banded hairs; claw of dI extends to middle of first phalange of dII; claw of dV extends to or just beyond first interphalangeal joint of dIV.

KARYOTYPE: A diploid count of 82 chromosomes and a fundamental number of 80 was reported from 20 specimens identified by Zanchin et al. (1992) as *Delomys dorsalis*. The uniformly acrocentric autosomes grade evenly from large to small; the X is a large submetacentric and the Y is the smallest acrocentric of the karyotype (op. cit.: fig. 3).

COMPARISONS: *Delomys dorsalis* and *D. sublineatus* can be identified unambiguously by pelage characters and other aspects of external morphology. The pelage of *dorsalis* is

TABLE 4

Sex and Measurements (in millimeters) of Adult *Delomys dorsalis* from Argentina and Southern Brazil

	Argentina, Misiones, Caragatatay ^a	Brazil	
		Rio Grande do Sul, Taquara ^b	Paraná, Roça Nova ^c
Sex	female	3 males, 3 females	10 males, 2 females
HBL	123	—	115 ± 9 (102–130) 12
LT	120	—	130 ± 8 (112–142) 12
HF	28	27 (27) 1	30 ± 1 (28–31) 12
CIL	—	28.5 (27.4–29.6) 5	28.3 ± 1.2 (26.1–30.0) 11
LD	8.3	8.8 (8.5–9.0) 6	8.5 ± 0.5 (7.6–9.2) 12
LM	4.5	4.5 (4.4–4.8) 6	4.7 ± 0.1 (4.4–4.9) 12
BM1	1.3	1.4 (1.3–1.4) 6	1.4 ± 0.1 (1.3–1.5) 12
LIF	6.1	6.2 (6.1–6.3) 6	6.5 ± 0.4 (6.0–7.0) 12
BR	5.2	5.0 (4.6–5.4) 6	5.0 ± 0.2 (4.6–5.5) 12
BPB	3.2	3.2 (3.0–3.5) 5	3.2 ± 0.1 (3.0–3.4) 12
BZP	2.7	2.6 (2.2–3.0) 6	2.7 ± 0.2 (2.2–3.0) 12
LIB	5.5	5.2 (4.9–5.4) 6	5.1 ± 0.2 (4.9–5.6) 12
DI	1.4	1.3 (1.2–1.4) 6	1.4 ± 0.1 (1.3–1.5) 12
LOF	9.9	9.6 (9.2–10.0) 6	9.7 ± 0.4 (9.0–10.1) 12
ZB	—	16.0 (15.8–16.4) 5	15.6 ± 0.5 (14.7–16.2) 12

^a Measurements of FMNH 26818.^b Summary statistics (mean, observed range, and sample size) for measurements of BMNH 84.2.8.37, 84.2.8.38, 86.9.16.3, 86.9.16.4, UZM 7501, 7502.^c Summary statistics (mean plus or minus one standard deviation, observed range, and sample size) for measurements of BMNH 3.7.1.41–3.7.1.50, FMNH 18177, UZM 1267.

soft and dense, and the individual hairs are so fine that the distribution of dark hair tips in the dorsal fur of adults has the effect of stippling. By contrast, the pelage of *sublineatus* is coarser and less dense, and the thicker dark hairs in the dorsal fur produce a streaked or lined effect. The fresh⁵ dorsal pelage of adult *dorsalis* is generally a rich brown with pale highlights near Cinnamon (Smithe, 1975–81: color 123A), but the overall effect is more somber because of the dense crowding of darker hairs; a blackish middorsal stripe from the nape or shoulders to the base of the tail is often present. Pelts of *sublineatus* are usually paler and distinctly yellowish, near Clay Color or Yellow Ochre (Smithe, 1975–1981: colors 123B, 123C); many specimens lack any trace of a middorsal stripe, and even when a concentration of dark hairs is present along the dorsal midline (e.g., FMNH 26597) the streak seldom extends all the way from the nape or shoulders to the base of the tail.

⁵ Most old museum specimens have dull, faded fur that gives a completely misleading impression of these attractive rats.

In adults of both *dorsalis* and *sublineatus*, the colors of the dorsal and ventral fur are sharply demarcated along a lateral line from cheek to rump; in almost all specimens of *sublineatus*, a band of clear yellow or buff runs along this boundary, but *dorsalis* lacks any distinctive lateral marking.

The mystacial vibrissae are longer in *dorsalis* than in *sublineatus*. On properly made-up skins or fluid-preserved examples of the former species, these hairs extend to or just beyond the tips of the pinnae when whiskers and ears are laid back against the head. In *sublineatus*, the mystacial vibrissae do not extend to the tips of the adducted pinnae.

The pale, short pelage that covers the dorsal surface of the hindfoot appears soiled in *dorsalis* because each hair has an indistinct melanic band that is visible only under magnification. By contrast, the dorsal pelage of the hindfoot appears pure white in most specimens of *sublineatus* because the individual hairs usually lack melanic markings. The hindfoot averages slightly longer in *dorsalis* than in sympatric samples of *sublineatus* (compare the Boracéia samples in tables 5

TABLE 5
Sex and Measurements (in millimeters) of Adult *Delomys dorsalis* from São Paulo and Rio de Janeiro (Brazil)

	São Paulo		Rio de Janeiro, Teresópolis ^c
	Apiai ^a	Boracéia ^b	
Sex	7 males, 6 females	14 males, 10 females	2 males, 3 females
HBL	138 ± 15 (101–154) 12	127 ± 6 (117–135) 18	138 (129–148) 4
LT	135 ± 12 (104–150) 12	132 ± 10 (100–145) 18	134 (125–146) 4
HF	30 ± 1 (27–32) 13	30 ± 1 (28–32) 24	31 (30–33) 4
CIL	29.5 ± 1.7 (25.4–31.4) 13	29.2 ± 1.0 (27.5–30.8) 20	30.2 (29.0–30.9) 4
LD	9.0 ± 0.7 (7.2–9.8) 13	8.8 ± 0.4 (8.2–9.3) 22	9.0 (8.0–9.4) 5
LM	4.8 ± 0.1 (4.6–5.0) 13	5.0 ± 0.1 (4.7–5.2) 22	5.0 (4.8–5.0) 5
BM1	1.4 ± 0.1 (1.4–1.5) 13	1.5 ± 0.5 (1.4–1.6) 22	1.5 (1.4–1.5) 5
LIF	6.6 ± 0.5 (5.3–7.3) 13	6.8 ± 0.3 (6.2–7.2) 22	6.9 (6.6–7.4) 5
BR	5.3 ± 0.2 (4.8–5.7) 13	5.3 ± 0.2 (4.9–5.7) 22	5.3 (5.2–5.5) 5
BPB	3.4 ± 0.3 (2.8–3.8) 13	3.1 ± 0.2 (2.9–3.4) 22	3.2 (2.9–3.4) 5
BZP	2.9 ± 0.2 (2.5–3.2) 13	2.9 ± 0.2 (2.6–3.3) 22	3.0 (2.7–3.2) 5
LIB	5.3 ± 0.1 (5.2–5.4) 13	5.5 ± 0.2 (5.2–5.8) 22	5.4 (5.2–5.6) 5
DI	1.4 ± 0.1 (1.2–1.6) 13	1.4 ± 0.1 (1.2–1.6) 22	1.4 (1.2–1.6) 5
LOF	9.9 ± 0.5 (9.0–10.5) 13	10.0 ± 0.3 (9.4–10.5) 22	10.2 (9.7–10.5) 5
ZB	16.4 ± 0.6 (14.8–17.1) 13	16.4 ± 0.4 (15.9–17.3) 19	16.2 (14.8–17.0) 4

^a Including Iporanga; summary statistics (mean plus or minus one standard deviation, observed range, and sample size) for measurements of USP 26936, 26954, 26960, 26988, 27014, 27047, 27048, 27064, 27091, 27095, 27096, 27101, 27381.

^b Including Casa Grande; summary statistics (see footnote *a*) for measurements of FMNH 136932–136939, 145365–145382; and USNM 461062–461064, 484218–484221.

^c Summary statistics (mean, observed range, and sample size) for measurements of FMNH 53871, 53872; MNHN 1967–1450; and USNM 304574, 304575.

and 6) and the species also differ in digital proportions. The outside digits (I and V) of the hindfoot are longer relative to their neighbors (II and IV) in *dorsalis*: on fluid specimens or properly pinned-out skins, the claw of dI extends to about the middle of the first phalange of dII, and the claw of dV extends to or slightly beyond the first interphalangeal joint of dV. In *sublineatus*, the claw of dI barely extends beyond the base of the first phalange of dII, and the claw of dV does not extend to the first interphalangeal joint of dIV.

Tails are usually about equal to or longer than heads-and-bodies in *dorsalis* (tables 4, 5) and shorter than heads-and-bodies in *sublineatus* (table 6), but differences in collectors' measurement methods and some inexplicably divergent specimens (fig. 12) compromise the systematic interpretation of these data. Tails are usually more distinctly bicolored (dark above, pale below) in adult *sublineatus* than in adult *dorsalis*, but the tails of im-

matures of both species are often dark above and below.

Univariate comparisons of sympatric samples suggest that *dorsalis* averages slightly larger than *sublineatus* in most craniodental measurements (e.g., at Boracéia: tables 5 and 6), but multivariate analyses that adjust for general size (growth) are more informative. Within species, age-correlated general size (table 7, first column) is accompanied by allometric changes in cranial proportions like those previously documented for other Neotropical muroids (Voss et al., 1990; Voss and Marcus, 1992). General-size-adjusted species differences (table 7, second column) are largest for measurements of the molar toothrow (LM, longer in *dorsalis*), the palatal bridge (BPB, broader in *sublineatus*), and the interorbit (LIB, broader in *dorsalis*). Specimen scores on these factors (fig. 13) reveal that the sympatric samples from Boracéia are completely differentiated.

No qualitative aspect of craniodental mor-

TABLE 6
Sex and Measurements (in millimeters) of Adult *Delomys sublineatus*

Santa Catarina, Hansa				Rio de Janeiro, Teresópolis			Minas Gerais
BMNH		BMNH	São Paulo, Boracéia ^a	FMNH	FMNH	FMNH	MNHN
28.10.11.29	28.10.11.30			26596	26598	26597	1967-1456
Sex	male	male	15 males, 11 females	male	male	male	female
HBL	130	140	125 ± 7 (110-138) 24	127	124	138	120
LT	101	110	105 ± 7 (90-116) 24	96	112	127	109
HF	27	29	28 ± 1 (25-29) 26	26	29	29	27
CIL	27.5	27.8	28.0 ± 1.2 (26.0-30.2) 24	26.1	27.8	29.7	28.8
LD	7.6	8.3	8.2 ± 0.5 (7.6-9.1) 26	7.6	7.5	8.8	8.1
LM	4.6	4.7	4.6 ± 0.1 (4.4-4.8) 26	4.5	4.8	4.5	4.9
BM1	1.6	1.5	1.4 ± 0.0 (1.4-1.5) 26	1.3	1.5	1.3	1.5
LIF	5.8	5.8	6.2 ± 0.4 (5.6-7.0) 26	6.1	6.0	6.6	6.1
BR	5.0	5.0	5.2 ± 0.2 (5.0-5.6) 26	4.9	5.2	5.2	5.2
BPB	2.8	2.9	3.2 ± 0.2 (2.8-3.5) 26	3.0	3.1	3.5	3.2
BZP	2.6	2.4	2.7 ± 0.2 (2.4-3.0) 25	2.7	2.7	3.2	3.0
LIB	5.0	4.8	5.0 ± 0.2 (4.7-5.4) 26	5.0	5.0	5.1	5.3
DI	1.3	1.4	1.4 ± 0.1 (1.2-1.6) 26	1.4	1.5	1.5	1.4
LOF	9.8	10.0	10.0 ± 0.4 (9.0-10.8) 25	9.0	9.8	10.0	10.2
ZB	15.6	15.8	16.1 ± 0.7 (14.7-17.4) 25	—	—	—	17.0

^a Including Casa Grande; sample statistics (mean plus or minus one standard deviation, observed range, and sample size) for measurements of FMNH 136931, 141628, 141629, 145383; USNM 460534-460537, 462075, 484222-484226, 485086-485096, 485897.

phology appears to unambiguously differentiate *dorsalis* from *sublineatus*, but two subtle contrasts were discovered after specimens were sorted by the external traits mentioned earlier. (1) In most specimens of *dorsalis* the anterolingual conule of M1 is almost the same size as the anterolabial conule and the outline of the tooth is approximately rectangular, but in *sublineatus* the anterolingual conule is usually smaller than the anterolabial cusp and M1 has an oval outline; this character does not provide an acceptable basis for identification, however, because some specimens have intermediate morphologies or resemble the typical condition of the other species. (2) The rostral tube formed by the premaxillae and nasals above the incisors is somewhat better developed in *dorsalis* than in *sublineatus*, but this character appears to exhibit positive allometry with growth, and is likewise unsuitable for identification due to overlapping variation.

In summary, although only external comparisons (and apparently karyotypes; Zanchin et al., 1992) provide unequivocally diagnostic characters, craniodontal measurements from sympatric samples also provide

compelling evidence that *Delomys dorsalis* and *D. sublineatus* are distinct species. Qualitative craniodontal characters, however, are not sufficient to discriminate these taxa.

VARIATION: Within geographically homogeneous samples, specimens of *dorsalis* exhibit ontogenetic and individual variation in several external characters, but secondary sexual dimorphism is not apparent in the samples at hand. Skins of younger animals, including some with completely erupted dentitions (e.g., FMNH 145365, 145370, and 145371 from Boracéia), are distinctly grayer and generally darker than those of adults, and usually have less well-defined middorsal stripes. Young specimens also tend to be less distinctly countershaded than adults, and often have all-dark tails even in samples where in most adults have partially bicolored tails. Adult skins chiefly differ in the variable development of the middorsal stripe and the overall saturation of the dorsal fur with yellowish or reddish tints.

Variation among populations is difficult to evaluate with the few samples at hand, but some characters suggest geographic trends. The possible taxonomic significance of dif-

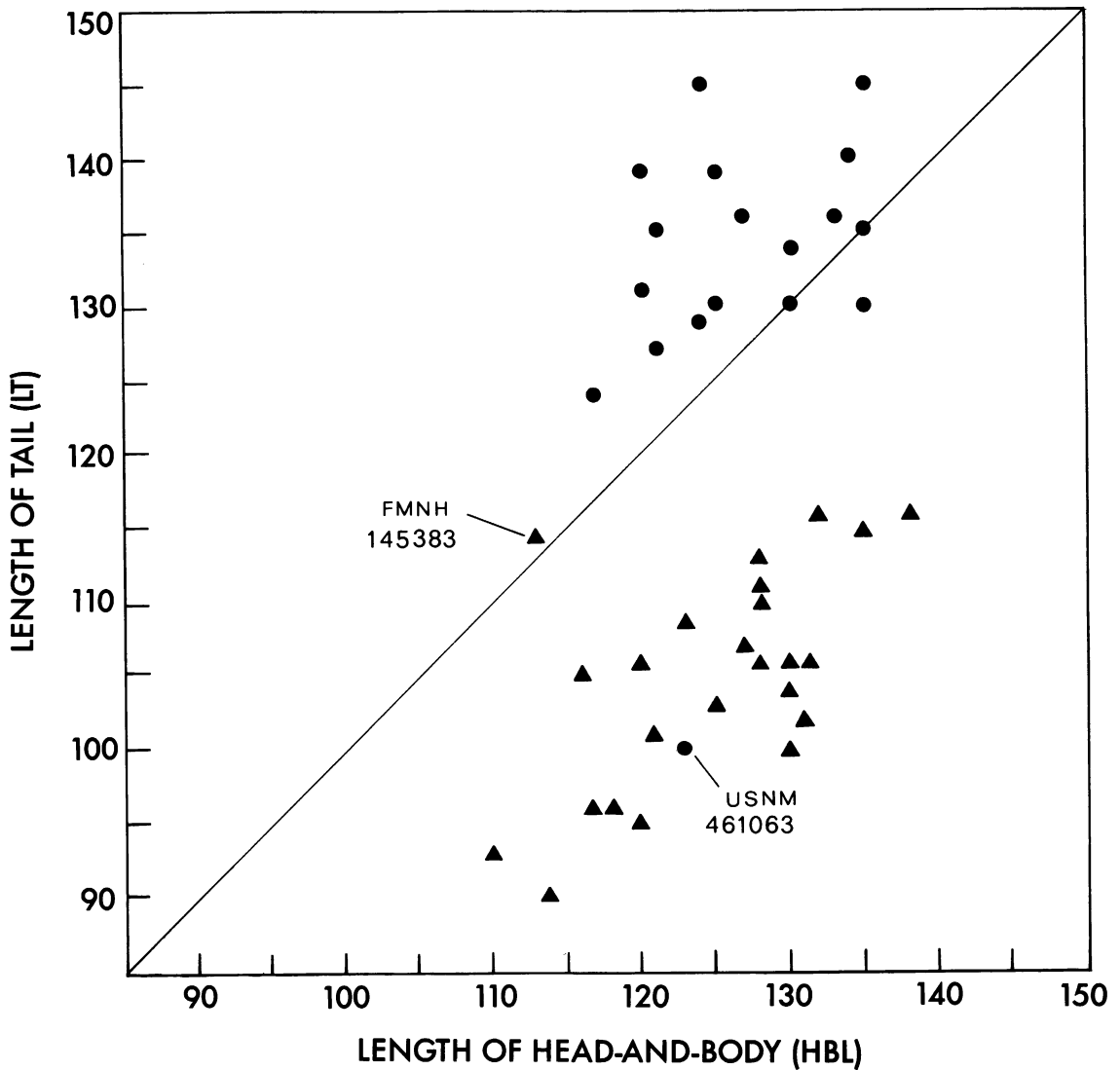


Fig. 12. Joint distribution of tail length (LT) and head-and-body length (HBL) for *Delomys dorsalis* (circles) and *D. sublineatus* (triangles) from locality 14 (Boracéia and Casa Grande). LT = HBL is indicated by the diagonal. I verified the collector's value for LT of FMNH 145383 by remeasuring the tail of the skinned, fluid-preserved carcass, but I was unable to verify HBL because the skull had been detached and cleaned. USNM 461063 is a dried skin from which about half the tail was broken away and lost after preparation; the divergent value of LT for this specimen is therefore impossible to evaluate. Careful attention to consistent external measurement methods in the field might reveal unambiguous species differences, but data distributed like these provide an unsatisfactory basis for systematic inference.

ferences in mammary counts between northern and southern populations, for example, is discussed subsequently (see Remarks). Another trait that may vary significantly among populations is the frequency of white tips on tails, but tail tips on dried skins are fragile

and most series contain only a few intact examples. Tail tips are present on nine skins from Roça Nova (fig. 1: locality 6), however, and none are white; by contrast, most intact tails of specimens from Boracéia and Casa Grande (fig. 1: locality 14) have white tips.

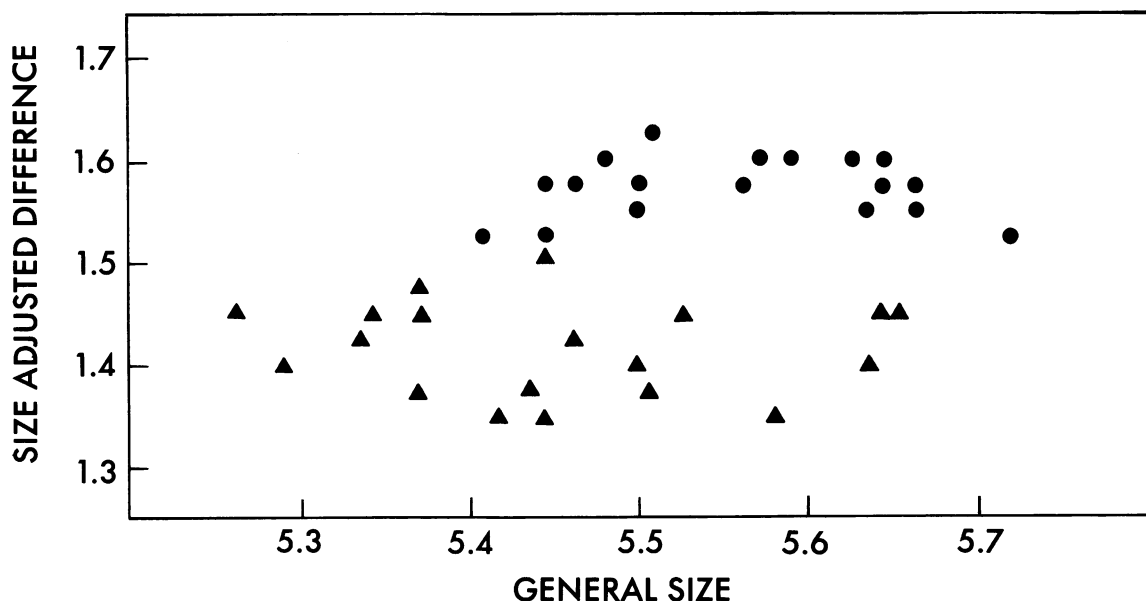


Fig. 13. Scatterplot of specimen scores on factors representing general size and size-adjusted species differences for sympatric samples of *Delomys dorsalis* (dots) and *D. sublineatus* (triangles) from Boracéia (including Casa Grande). Factor coefficients are provided in table 7. Overlapping conspecific observations are not plotted separately.

REMARKS: The type of *Delomys dorsalis collinus* is a specimen in the British Museum of Natural History (BMNH 14.2.23.12) consisting of the skin, skull, and mandibles of an adult male collected 22 August 1913 at 4800 ft (1477 m) on Itatiaya, a mountain in the Brazilian state of Rio de Janeiro (fig. 1: locality 7). The skin (prepared from a fluid-preserved specimen in 1914) lacks the tail tip but is otherwise intact. The cranium is in perfect condition, but the left mandible is broken in two behind the toothrow, and the right mandible lacks the angular process.

Thomas (1917) distinguished *D. d. collinus* from *D. d. dorsalis* on the basis of molar size: length of the upper molar row among his northern specimens (from Rio de Janeiro and São Paulo) measured 5.0 mm, whereas this measurement ranged from 4.5 to 4.7 mm among his southern specimens (from Rio Grande do Sul and Paraná). Thomas remarked that "No doubt the two forms will be found to intergrade, but the difference is so constant locally that it should be recognized by name" (op. cit.: 197). My measurements of molar rows (tables 4, 5) indicate greater variation within both southern and

northern samples than that recognized by Thomas (e.g., 4.4–4.9 mm at Roça Nova; 4.7–5.2 mm at Boracéia), and new material from geographically intermediate localities (e.g., Apiaí in table 5) provides evidence of the intergradation that Thomas predicted.

Thomas (1917) observed that his single female specimen of *D. d. collinus* (probably BMNH 14.2.23.13, a topotype) had only six mammae in contrast to the eight teats of southern specimens and remarked that "... this may possibly be an individual aberration" (op. cit.: 198). It is not. All available female specimens of *D. dorsalis* from Rio de Janeiro and northern São Paulo lack the pectoral pair of teats that is consistently present in southern specimens (and in *D. sublineatus*; table 2). This mammary variation, however, is unaccompanied by other evidence of significant morphological divergence: the eight-mammate mice from Apiaí and Iporanga (fig. 1: locality 13) are indistinguishable in other qualitative characters and in measurements (table 5) from the six-mammate animals collected at Boracéia and Casa Grande (fig. 1: locality 14). The names *collinus* and *dorsalis* could be retained for subspecies distin-

guished by mammary counts alone, an option that should be evaluated by future researchers with larger samples and material from additional localities in São Paulo state.

I concur with Thomas (1902), Gyldenstolpe (1932), and Massoia (1962) that *lechei*, a replacement name proposed by Trouessart (1904) for Leche's (1886) preoccupied *obscura*, should be treated as a subjective junior synonym of *dorsalis*.

SPECIMENS EXAMINED: **Argentina** — *Misiones*, Caraguatay (FMNH 26818). **Brazil** — *Paraná*, Roça Nova (BMNH 3.7.1.41–3.7.1.50; FMNH 18177; UZM 1276); *Rio de Janeiro*, Itatiaya (BMNH 14.2.23.12 [the type of *collinus*], 14.2.23.13), Maceiro (BMNH 14.2.23.11), Teresópolis (FMNH 53871, 53872; MNHN 1967-1450; USNM 304574, 304575); *Rio Grande do Sul*, Taquara (BMNH 84.2.8.37, 84.2.8.38, 86.9.16.3, 86.9.16.4; UZM 7501, 7502 [topotypes of *lechei*]); *São Paulo*, Alto da Serra (BMNH 5.5.2.2, 5.5.2.3; MCZ 25800), Apiaí (USP 26936, 26960, 27047, 27048, 27091, 27096, 27103), Boracéia (FMNH 136932–136939, 145365, 145369–145372, 145381, 145382), Campos do Jordão (MCZ 25798, 25799), Casa Grande (FMNH 136940; USNM 461062–461064, 484217–484221), Fazenda Intervalles (FMNH 143286), Iporanga (USP 26954, 26988, 27014, 27064, 27095, 27101, 27381), Piquete (BMNH 1.6.6.43). Total = 72.

Delomys sublineatus (Thomas)

Oryzomys sublineatus Thomas, 1903: 240.

Thomasomys sublineatus: Thomas, 1906: 443.

Delomys sublineatus: Thomas, 1917: 196.

Thomasomys dorsalis sublineatus: Cabrera, 1961: 428.

TYPE MATERIAL: A specimen in the British Museum of Natural History (BMNH 3.9.4.58) consisting of the skin, skull, and mandibles of an old adult male collected by Alphonse Robert (original no. 1224) on 14 February 1903 at Engenheiro Reeve in the Brazilian state of Espírito Santo (fig. 1: locality 2); Thomas (1903) reported the elevation as 500 m, but Robert's specimen label gives the range 400–600 m. The skin is well preserved except for the extreme tip of the tail, which is missing. Unfortunately, the skull consists only of

TABLE 7
Factor Coefficients for General Size and Species Differences (adjusted for general size) Estimated from Log-Transformed Measurements of Sympatric Samples^a of *Delomys*

	Factors ^b	
	General size	Species differences ^c
CIL	0.333	0.028
LD	0.476	0.117
LM	−0.014	0.478
BM1	0.021	0.323
LIF	0.344	0.375
BR	0.205	−0.098
BPB	0.383	−0.405
BZP	0.309	0.130
LIB	0.145	0.488
DI	0.331	−0.179
LOF	0.247	−0.216
ZB	0.258	−0.064

^a Specimens with complete measurement data from Boracéia (including Casa Grande): 18 *D. dorsalis* and 20 *D. sublineatus*.

^b Specimen scores are plotted in figure 13.

^c Signed to represent divergence of *D. dorsalis* from *D. sublineatus*.

the anterior braincase and facial skeleton; the zygomatic arches are intact, but all of the basicranium, both bullae, the occiput, and the interparietal are missing; the angular process of the left mandible and both coronoid processes are also missing. No occlusal details remain on the upper or lower molars, which are worn down to about the widest parts of their crowns.

Despite the wretched condition of the head skeleton, the diagnostic external characters of the species (see below) are all present on the skin or recorded on its tag. Thomas's (1903: 240–241) description is reasonably accurate except that the mesopterygoid fossa penetrates between the third molars and the posterior palatal margin is therefore not “. . . level with the hinder edge of m³.”

DISTRIBUTION: I have examined specimens of *Delomys sublineatus* from the Brazilian states of Santa Catarina, São Paulo, Rio de Janeiro, Espírito Santo, and Minas Gerais (fig. 1); Zanchin et al. (1992) also reported specimens from Paraná. Except in Espírito Santo and Minas Gerais where it is the only species

of *Delomys* known to be present, *sublineatus* may usually occur sympatrically with *dorsalis*.

EMENDED DIAGNOSIS: A coarse-furred, short-tailed species of *Delomys*; pelage usually without a distinct middorsal stripe, and almost always with a lateral line of clear yellow or buff separating dorsal and ventral color zones; mystacial vibrissae short, not extending to tips of adducted pinnae; hindfoot covered dorsally with (usually) pure white hairs; dI short, claw not extending to middle of first phalange of dII; dV also short, claw not extending to second interphalangeal joint of dIV.

KARYOTYPE: A diploid count of 72 chromosomes and a fundamental number of 90 was reported from 19 specimens identified by Zanchin et al. (1992) as *Delomys sublineatus*. The autosomes consist of three pairs of large submetacentrics, seven pairs of biarmed elements that decrease evenly in size from medium to small, and 25 pairs of large-to-small acrocentrics; the X is a large submetacentric and the Y is a small acrocentric (op. cit.: fig. 2).

COMPARISONS: See the preceding account for *Delomys dorsalis*.

VARIATION: Within geographically homogeneous samples, skins of *Delomys sublineatus* vary chiefly in saturation of the dorsal fur with yellow tints; the duller, grayish skins are usually younger animals and the brightest, adults. The development of middorsal concentrations of darker hairs is also variable within samples, as is the rare occurrence of white-tipped tails. Almost all specimens have a line of clear yellow or yellow-orange (buff) along the cheek and flanks, separating the dorsal and ventral pelage, but a few skins lack this distinctive attribute. No secondary sexual dimorphism or geographic variation in external characters is apparent.

Measurement data (table 6) reveal essential uniformity across the geographic range of this species.

REMARKS: The specimens that Avila-Pires (1960a) reported from Conceição do Mato Dentro as *Delomys plebejus* are here referred to *D. sublineatus*. I have not examined the entire series, but one skin-and-skull preparation received in exchange by the Paris museum (MNHN 1967-1456, formerly MN

13446) conforms in all respects with the diagnosis for *sublineatus* given above. The name *plebejus* should be restricted to the Lagoa Santa fossils on which it is based (see below).

Two skulls unaccompanied by skins (LACM 62910, 62911), both from the Brazilian state of Espírito Santo, are provisionally referred to *sublineatus* in my list of specimens examined, and are plotted as such on the map (fig. 1: locality 3). Their rostral shape, tooththrow measurements (4.8 and 4.7 mm, respectively), and somewhat ovoid first molars better fit the gestalt of *sublineatus* than that of *dorsalis*, but in the absence of truly diagnostic craniodental characters this identification is tentative.

SPECIMENS EXAMINED: **Brazil**—*Espírito Santo*, Engenheiro Reeve (BMNH 3.9.4.58 [the type]), Nova Lombardia (LACM 62910), Santa Teresa (LACM 62911); *Minas Gerais*, Conceição do Mato Dentro (MNHN 1967-1456); *Rio de Janeiro*, Teresópolis (FMNH 26596–26598, 26872, 53873; MNHN 1967-1451); *Santa Catarina*, Hansa (28.10.11.29–28.10.11.31); *São Paulo*, Boracéia (FMNH 136931, 141628, 141629, 145383); *Casa Grande* (USNM 460534–460537, 462075, 484222–484226, 485086–485097), *Cotia* (FMNH 143287), *Iporanga* (FMNH 26952, 26961, 27007, 27046), *Salto Grande* (USNM 141451, 141452). Total = 46.

THE LAGOA SANTA FOSSILS

Of the 25 species that Herluf Winge identified among the Recent and fossil muroids collected by Lund near Lagoa Santa (Voss and Myers, 1991: table 4), only *Calomys plebejus*⁶ possesses the diagnostic characters of *Delomys*. Winge (1887: 47) based his description of *C. plebejus* on “a few pieces . . . of the anterior part of the skull” (“nogle faa Stykker . . . af den forreste Del af Hovedskallen”) excavated from a cave that Lund called Lapa da Serra das Abelhas. Apparently, neither Lund nor other Danish biologists

⁶ Whereas *Calomys* (with type species *C. bimaculatus*) is nowadays understood to contain only tetralophodont phyllotines, Winge (1887) used the name for pentalophodont species currently referred to *Delomys*, *Oligoryzomys*, and *Oryzomys* (see Winge, 1941: 145–146; Hershkovitz, 1962: 129–130; and Voss and Myers, 1991: table 4).

who worked at Lagoa Santa in the mid-19th century (notably J. Reinhardt and E. Warming) collected any Recent specimens, because Winge remarked that,

Of the eleven species of hesperomyines found only in caves [i.e., in cave sediments]: *Hesperomys molitor*, *Habrothrix clivigensis*, *H. angustidens*, *Oxymycterus breviceps*, *O. talpinus*, *O. cosmodus*, *Scapteromys fronto*, *Calomys anoblepas*, *C. plebejus*, *C. rex*, [and] *C. coronatus*, possibly none are now living at Lagoa Santa; no trace of them has yet been found in the masses of bones from Recent owl pellets; but whether they are found [alive] in other parts of South America, there is yet nothing [to be said] (1887: 10, loosely translated).

Subsequently, Winge did receive Recent specimens, from elsewhere in South America, that he recognized to be similar to (or even conspecific with) some of these “extinct” muroids. Two such specimens are *Delomys dorsalis* (UZM 7501, 7502) collected at Taquara do Mundo Novo (fig. 1: locality 10) in or about 1890 by H. von Ihering; they are labeled in Winge’s distinctive hand, and each inscription includes the curt notation “Cf. *Calomys plebejus*.” In his three-volume monograph on mammalian phylogeny (posthumously translated into English), Winge (1941: 150) remarked that *Delomys dorsalis* “. . . is a close relative of *Calomys plebejus*,” but he did not explicitly equate these taxa as synonyms.

Avila-Pires (1960a) was apparently the first to suggest that Recent populations of *Delomys* might be conspecific with the Lagoa Santa fossils, identifying as *D. plebejus* a small series of specimens collected in the Cordilheira do Espinhaço (fig. 1: locality 4) not far from Lagoa Santa. Those specimens, however, exhibit all of the diagnostic attributes of *D. sublineatus* (see under Remarks in the account for that species, above), so the possibility that *plebejus* is a senior synonym requires careful evaluation.

Winge did not designate types in his 1887 monograph, but four partial crania in the paleontological collections of the Universitets Zoologisk Museum are labeled “*Calomys plebejus*/Lapa da Serra das Abelhas” in Winge’s elegant cursive script; the most intact of these is the specimen originally illustrated (fig. 14), and I designate it the lecto-

type. Neither the lectotype nor the three other specimens (here designated paralectotypes) have catalog numbers. The UZM fossil collections contain no mandibles or any fragments of the lower dentition identified as *C. plebejus*, nor did Winge refer to such elements in his original description.

The lectotype consists of the damaged facial skeleton and part of the braincase of a young adult. The anterior parts of the nasals and premaxillae are missing as are most of both zygomatic arches, the left lateral wall of the braincase, the entire basicranium, and the whole occiput; the first left molar and the second right molar are also missing, but the upper dentition is otherwise intact and the occlusal morphology of the remaining molars is well preserved. Because the alveoli of the missing teeth of the lectotype are filled with matrix (an indurated reddish clay mixed with small, clear crystals, probably calcite), the complete dentition illustrated by Winge is obviously a reconstruction. Each paralectotype consists of the rostrum, interorbital region, palatal bridge, and one or both of the maxillary zygomatic roots; both incisors and the entire maxillary dentition are intact in two specimens, but a third lacks its left third molar.

There can be no doubt that *Calomys plebejus* is a member of the genus *Delomys*. All of the intact anatomical structures in these fossils (including the zygomatic notches, interorbital region, zygomatic plate, incisive foramina, palatal bridge, and complete upper dentition) are qualitatively indistinguishable from those of Recent specimens identified as *D. dorsalis* or *D. sublineatus* in this report. In craniodontal dimensions (table 8), the type series of *plebejus* falls almost entirely within the range of variation observed for either of the Recent species (tables 4–6); the single exceptional measurement is the rostral breadth of one paralectotype (BR = 5.8 mm), which exceeds by 0.1 mm any rostral breadth that I measured of *dorsalis*, and by 0.2 mm any of *sublineatus*.

In the absence of any craniodontal characters that unambiguously distinguish *dorsalis* from *sublineatus*, the identification of *plebejus* with either is problematical. The geographical datum, that only *sublineatus* is known from Recent specimens collected in

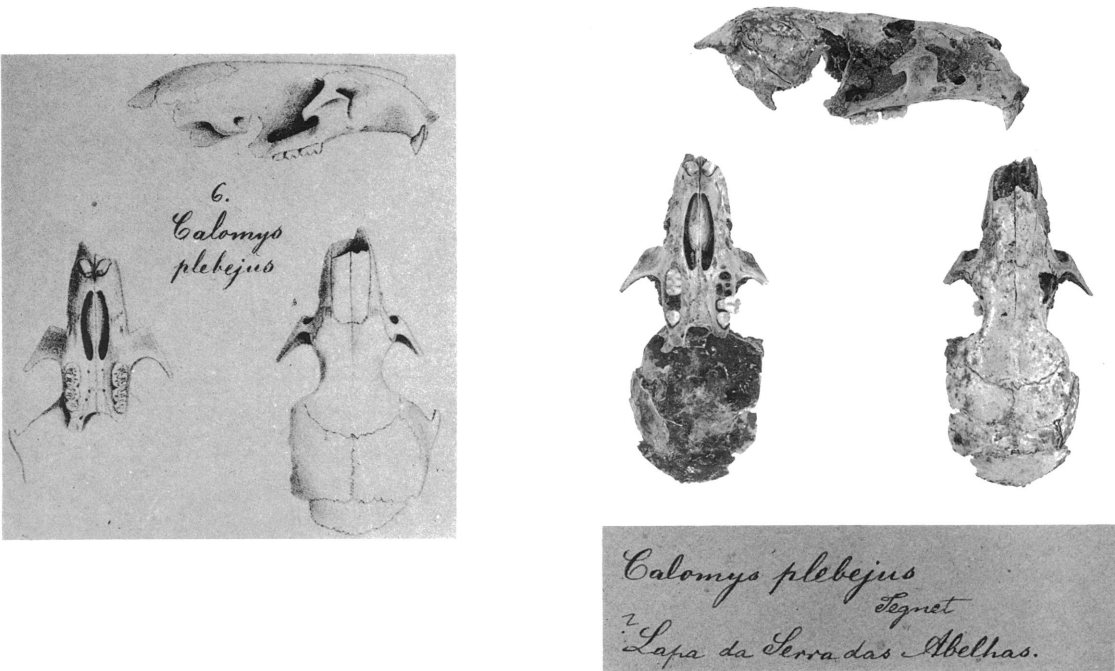


Fig. 14. The lectotype of *Calomys plebejus* with its label (right), and Winge's (1887) illustration (left).

Minas Gerais, is not a compelling reason for synonymy because Minas Gerais remains poorly surveyed for small mammals, and because the Lagoa Santa caves contain fossil specimens of other rodents that are not known to occur anywhere in the state today (Cerqueira, 1982; Voss and Carleton, in press). Furthermore, synonymizing *plebejus* Winge

1887 with *sublineatus* Thomas 1903 would have the highly undesirable consequence of replacing a type specimen with many characters useful for species discrimination by another with none. Thus, although there is no evidence that the taxon represented by the Lagoa Santa fossils is extinct, no biological or nomenclatural purpose is served by synonymizing it with either of the Recent species recognized as valid in this report; *plebejus* is a nomen dubium that should be used only in reference to Winge's hypodigm.

TABLE 8
Craniodental Measurements^a (in millimeters) of the Type Series of *Delomys plebejus*

	The lectotype	A palelectotype	Another	Another
LD	8.2	8.9	9.0	—
LM	4.8	4.9	4.6	4.8
BM1	1.4	1.4	1.4	1.4
LIF	6.6	—	6.8	—
BR	5.1	5.8	—	—
BPB	—	3.4	3.2	—
BZP	2.8	3.1	3.0	2.9
LIB	5.4	5.3	5.4	5.1
DI	1.2	1.6	1.4	1.5

^a None of the skulls is intact and no values are therefore available for CIL, LOF, or ZB.

NATURAL HISTORY

Information about the natural history of *Delomys* is provided by a mere handful of papers, most of which report observations from localities in the Brazilian states of São Paulo and Rio de Janeiro. The following accounts, organized geographically from north to south, summarize essentially everything that has been published on the habits and habitats of *Delomys*. From these a few generalizations are suggested to guide future fieldwork.

HABITAT DESCRIPTIONS

Itatiaya (fig. 1: locality 7) is the principal massif in the Serra da Mantiqueira, reaching a maximum elevation of about 2790 m at Pico das Agulhas Negras. Following Ule's (1896) pioneering botanical explorations, many naturalists have worked on Itatiaya to document the dramatic altitudinal zonation of its flora and fauna. A specimen of *Delomys dorsalis* (the type of *D. d. collinus*) that Thomas (1917) reported from Itatiaya was collected at 4800 ft (1477 m), which is well within the elevational limits of forest growth (Segadas-Vianna, 1968). In his catalog of the vertebrates of Itatiaya, Miranda Ribeiro (1905) observed that *Delomys dorsalis* and *Akodon serrensis* inhabit "galerias subterranas" (probably shallow tunnels under matted roots and moss) and piles of litter in thickets of *Chusquea* (a genus of small bamboos). Presumably, these rodents were encountered in habitats like those described by the ornithologist E. G. Holt two decades later:

This forest . . . [is] indescribable in its profusion of orchids, bromeliads, and other epiphytes, ferns, mossy trunks, and multiplicity of plant forms . . . [but] is not remarkable for the size or height of its trees. The undergrowth is choked with a small species of cane or bamboo, which, being very difficult to cut because of its flinty nature and pliability, makes progress slow and trying (Holt, 1928: 270).

In a later, narrative account for a popular readership, the same author describes an ascent of Itatiaya with vivid impressions of the same forest:

With many a meander, but ever upward, climbed the trail. At 3600 feet it crossed the roaring Campo Bello (here called Rio Maromba) on a rickety old bridge that sooner or later will hurl someone to certain destruction on the rocks below. Bending sharply back upon itself, the trail surmounted, by several switchbacks, another bracken slope, marking the site of an old burn, and then, at about 5000 feet, plunged us into the clouds. We continued through a ghost world of dimly outlined giant trees, hung with sinuous lianas and burdened with giant rosettes of bromeliads, where every leaf was dripping. All about us was only mist, underfoot only mud. As we rode along, we were swept by the long, gracefully

drooping tips of a beautiful species of bamboo, and soaked to the skin (Holt, 1929: 433).

According to Segadas-Vianna's (1968) more explicit but less colorful account of the vegetation, the forest between 1100 and 1700 m elevation on Itatiaya is 20–30 m high with a dense, shrubby undergrowth; mosses, liverworts, vascular epiphytes, and lianas are very abundant. By comparison with the thick-stemmed bamboos that grow along the forest edges at lower elevations, thin-stemmed species (of *Merostachys* and *Chusquea*) predominate in this zone; some of these slender bamboos are climbers that may reach the canopy.

Climatic data are available from two stations on the mountain, one at 816 m elevation (Monte Serrat) and the other at 2199 m (Alto do Itatiaya). Extrapolating from the records provided by Segadas-Vianna and Dau (1968), the mean annual temperature at 1500 m is probably about 16°C and the mean annual rainfall about 2000 mm; in addition to rain, however, the montane vegetation is also drenched by condensation from enveloping clouds (Holt, 1928).

The list of mammals from Parque Nacional do Itatiaia by Avila-Pires and Gouvêa (1977) provides no new ecological information about *Delomys*, and some of the other muroids species reported from the area are obviously misidentified therein (e.g., "*Oecomys simplex*"; see Voss and Myers, 1991: 425). The small mammal faunas of any undisturbed habitats that still remain in the park should be carefully inventoried again and the results documented with fresh voucher material.

Teresópolis, a small political district administered from a town of the same name (fig. 1: locality 9), is situated in the coastal mountains about 100 km north of the city of Rio de Janeiro. The annual cycles of flower and fruit production, and correlated patterns of bird and mammal demography, were studied in the primary and secondary forests of Teresópolis in the early 1940s to investigate the causes of periodic rural outbreaks of yellow fever. The results from this research (Davis, 1945a, 1945b, 1947) provide the best published descriptions to date of mammalian habitats at any Atlantic forest locality; the

following account is abstracted from Davis (1945a) with a few cited exceptions.

Teresópolis comprises generally rolling topography, nowhere less than 800 m elevation, with narrow floodplains along rivers and streams; valley bottoms were intensively cultivated at the time of Davis's investigations, but hillsides were mostly still covered with second-growth forest. Virgin forests persisted only on the slopes of the Serra dos Orgãos that bound the study area to the south. Eleven years of weather records from Várzea de Teresópolis documented a mean annual temperature of 18°C and a mildly seasonal thermal regime that probably applies over the entire region; the average temperature difference between the warmest month (February) and the coldest (July) is only 7.5°C. Rainfall, however, was found to differ dramatically between the two study sites described below.

Ecological investigations were carried out on two estates with different types of forest: on Fazenda Boa Fé all of the forest was second-growth, judged to be about 70 years old, whereas Fazenda Comari was covered with virgin forest that had probably been undisturbed for at least 200 years (maps in Davis, 1945a: figs. 1, 4, 5). Specimens of *Delomys dorsalis* (FMNH 53871, 53872; MNHN 1967-1450; USNM 304574, 304575) from Fazenda Comari (= "Fazenda C. Guinle" on specimen labels) and of *D. sublineatus* (FMNH 53873; MNHN 1967-1451) from Fazenda Boa Fé were collected (perhaps as vouchers) by P. M. Britto and G. Pereira between 14 August 1942 and 14 May 1943; Britto and Pereira were probably two of the "several technicians who faithfully spent many arduous hours in field work and made possible the collection of the great amount of data" (Davis, 1945a: 246). Davis acknowledged the assistance of J. Moojen at the Museu Nacional in identifying mammal specimens (ibid.: 245), but I have not seen determinations initiated by Davis or Moojen on any specimen labels. Nevertheless, as the two species of *Delomys* are easily distinguished by external characters, and as both were obviously present in Teresópolis, there is no reason to question the taxonomic accuracy of Davis's observations:

Thomasomys [= *Delomys*] *sublineatus*. This small rat was found only in second-growth for-

est and is completely terrestrial, even frequenting holes and cavities under tree trunks or roots. When placed on a horizontal limb the rat is able to run along, but it soon loses orientation and falls to the ground. Apparently there is an ill-defined breeding season beginning in July and continuing until February.⁷ Five pregnant females were collected and all had 3 embryos . . . The ratio of males to females collected was 24 to 32. Recaptures of marked individuals indicate that these rats seldom travel far.

Thomasomys collinus [= *Delomys dorsalis*]. This species resembles the previous one except that it was found only in the virgin forest. These 2 species are another example of equivalent species, each filling the same niche in separate types of vegetation. Apparently these rats climb occasionally, for one was captured in a trap on a limb 3 meters from the ground. Thirty-seven males and 29 females were collected. Of 5 pregnant females examined, 1 had 2 embryos, 3 had 3, and 1 had 4 (Davis, 1947: 5-6).

The distinction between virgin and second-growth forest that Davis (1947) emphasized to explain his capture results for *Delomys* and other mammalian species merits further explanation if only because similar distinctions are often cited but seldom well described in the literature. The second-growth forest at Fazenda Boa Fé,

. . . appears [from the exterior] to be uniform in height and composition. Only with considerable practice can any one [tree] species be distinguished from the others; the only trees which stand out are the occasional cecropias and some palms. The color is a uniform green with blotches of flower color in certain seasons and a few leafless trees in the winter. Viewed from the interior the forest is fairly dense, although it is seldom impenetrable. Only in the younger parts where the bamboos are still thick is there much obstruction to vision. In the more mature sections there are many palms of all ages and the trees form 2 distinct layers with a third layer of shrubs near the ground. The height of the forest is about 25 meters in the more mature sections and about 20 meters in the younger parts. Epiphytes and lianas are common (Davis, 1945a: 253).

⁷ The kill-trap results previously reported by Davis (1945a: table 12) as evidence for seasonal breeding by forest mammals in Teresópolis are too sparse to substantiate this inference: reproductive data from only eight adult female *Delomys sublineatus* were apparently recorded in his 12-month study.

By contrast, the virgin forest of Fazenda Comarí was taller with a less cluttered understory:

From the exterior the forest presents a uniform appearance without any outstanding species; only the numerous palms may be distinguished from other trees. From the interior the forest is relatively open and free from vegetation near the ground, and there is a distinct middle layer . . . There are no bamboos except near windfalls . . . Lianas and epiphytes are common. The forest is about 30 meters high (Davis, 1945a: 257).

Davis also documented floristic differences between the two fazendas: only 35 of the 155 tree species identified in his study were common to both sites. This might reflect changes due to succession, but rainfall records suggest an alternative explanation; about 5900 mm was recorded at Fazenda Comarí over a single 12-month period, whereas Fazenda Boa Fé was believed to have received only about 1800 mm in the same year. Therefore, the research areas distinguished as second-growth versus virgin forest also had different climates and may have differed in other unmeasured but ecologically important factors.

Davis (1945a) reported nine species of muroids from Fazenda Boa Fé and Fazenda Comarí (table 9), but I have only examined vouchers of *Delomys* and have simply modernized the nomenclature of the others without confirming the original identifications. Any natural habitats remaining in the vicinity of Teresópolis should be inventoried again for small mammals to complete the faunal survey so ably begun by Davis and his anonymous colleagues.

Boracéia (fig. 1: locality 14) is a biological research station situated at 900 m elevation in the Serra do Mar about 80 km E of the city of São Paulo. A recent monograph on the local frog fauna (Heyer et al., 1990) provides information about the forest habitats (figs. 15, 16) of the 16,450 ha reserve in which the station is located:

The soil is sandy, with a top layer of 10–15 cm of brown soil and on top of that a thin layer of dead leaves scattered with many dead branches and logs. The forest floor surface is usually damp, often soaking wet, and (at least on our visits) even at its driest, it was damp underneath logs.

The area is among the wettest in Brazil. It

TABLE 9
Occurrence of Muroid Species at Two Forested Research Areas in Teresópolis^a

Current taxonomy ^b	Fazenda Boa Fé ^c	Fazenda Comarí ^d
<i>Akodon cursor</i> ^e	71	11
<i>Akodon nigrita</i>	81	12
<i>Blarinomys breviceps</i>	1	
<i>Delomys dorsalis</i> ^f		19
<i>Delomys sublineatus</i> ^g	33	
<i>Nectomys squamipes</i>	1	1
<i>Oligoryzomys elurus</i> ^h	1	
<i>Oryzomys intermedius</i>		3
<i>Rhipidomys mastacalis</i>		10

^a Modified from table 20 of Davis (1945a); table entries are numbers of individuals captured with equivalent trapping effort at both fazendas from September 1942 to May 1943.

^b After Musser and Carleton (1993).

^c Second-growth forest.

^d Virgin forest.

^e *A. arviculoides* of Davis (1945a).

^f *Thomasomys collinus* of Davis (1945a).

^g *Thomasomys sublineatus* of Davis (1945a).

^h *Oryzomys utiaritensis* of Davis (1945a).

gets much rain (the average annual rainfall from 1925–1944 was 3058 mm . . .) and much moisture as fog . . . Temperatures below freezing occur occasionally at Boracéia . . .

The forest around Boracéia is continuous except for the breaks formed by the narrow dirt access road, the aqueduct line, several small rivers and the small manmade clearings around the station itself. . . Though the elevation is low, the topography, wind, high moisture and vegetation have combined to produce a mist forest or cloud forest. The forest has a low, continuous canopy, averaging ca. 5–10 m, highest in the valley bottoms so that the canopy smooths the topography . . . The few emergents are mostly palms. There are some trees with buttresses or stilt roots, but not many. Complexes of horizontal moss-covered roots, a few decimeters above the ground, are more conspicuous and characteristic . . . The undergrowth is relatively open in most of the forest but denser along the streams with herbaceous plants including heliconias . . . Slender climbing bamboos are common, as well as several larger species . . . There are many palms of several species . . . Tree ferns and climbing vines are also common, mostly small with many hanging roots of philodendrons; large lianas are rare. Epiphytic mosses . . . are conspicuous features, growing on branches, roots, twigs and even old leaves as



Fig. 15. Cloud forest habitat of *Delomys* at Boracéia. Cool temperatures, high annual rainfall, and mist produce this luxuriant growth at about 900 m elevation in the Serra do Mar. From a color transparency by W. R. Heyer.

well as on rocks and logs. Only rarely do mosses form a carpet on the ground. Bromeliads . . . grow everywhere—tree, branches and trunks as well as on the ground . . . There are many orchids and epiphytic ferns . . . On many trees the bark is completely covered with epiphytes. Tree trunks tend to be canted from the vertical and are often bent, and usually branch close to the ground; columnar trunks without low branches are not common (Heyer et al., 1990: 238–239).

Both *Delomys dorsalis* and *D. sublineatus* are known from Boracéia. Ten specimens were taken in traps set on the ground by B. D. Patterson (personal commun.) in July 1992: seven of these are *D. dorsalis*, mostly trapped near streams in “riparian” forest (some in traps set for *Akodon nigrata* under and alongside fallen logs); one specimen of *D. sublineatus* was trapped in upland secondary forest, one in “dry” forest near a river, and one within 5 m of a trap that took *D. dorsalis* in wet primary forest. Eight additional specimens of *D. dorsalis* (labeled “ex Inst. A. Lutz”) were collected at Boracéia from

January 1962 to January 1967, but these lack accompanying ecological data.

Delomys has also been taken at the nearby locality of Casa Grande by various collectors from 1962–1972. Casa Grande is located on the edge of the forested reserve about 7 airline km W of Boracéia, but much farther away by road (Heyer et al. 1990). Collectors residing at Casa Grande probably worked in the reserve, but no ecological data are recorded on their specimen tags. However, it is interesting to note that whereas 15 specimens of *dorsalis* and 3 of *sublineatus* are known from Boracéia, the Casa Grande series contains 9 *dorsalis* and 22 *sublineatus*; if these numbers reflect relative abundances at the two localities, habitat differences might be expected. Perhaps significantly, Heyer et al. (1990: caption to fig. 2) observed that Boracéia gets noticeably more rain than Casa Grande.

Carvalho (1965) reported the results of a mark-and-recapture study of small mammals in primary forest at Boracéia. He found *Delomys dorsalis* to be the numerically domi-



Fig. 16. Streamside vegetation at Boracéia. Clear streams with rocky beds are numerous in the forest reserve surrounding Boracéia. The very wet riparian vegetation adjacent to these streams may be a favored microhabitat of *Delomys dorsalis*. From a color transparency by C. W. Myers.

nant species in this habitat and characterized it as terrestrial and nocturnal. Other muroids reported from the same habitat were *Akodon* (*Thaptomys*) *nigrita*, "*Oryzomys subflavus* (?)," and *Oligoryzomys eliurus* ("*Oryzomys nigripes*"). The forest muroid fauna at Boracéia is unlikely to be so depauperate and local inventory efforts should be continued.

Fazenda Intervals (fig. 1: locality 16) is a forested reserve in the Serra de Paranapiacaba in southern São Paulo state. Olmos (1991) reported the results of a mark-and-recapture study near the headquarters of Fazenda Intervals in old second-growth forest at 850 m elevation. Occasional trees at this locality were 20 m high and the habitat was described as a "bamboo forest" in which a giant climbing species as well as smaller bamboos were abundant. The local climate was wet with about 1600 mm of annual rainfall and frequent fog; frost was observed in the winter.

The muroid fauna reported by Olmos from

Fazenda Intervals is the richest yet recorded in the literature from any Atlantic forest locality: *Akodon* "*cursor*" (two karyomorphic forms were found), *Akodon nigrita*, *Akodon serrensis*, *Delomys dorsalis*, *Nectomys squamipes*, *Oligoryzomys eliurus* ("*Oryzomys nigripes*"), *Oryzomys capito*, *Oryzomys ratticeps*, *Oxymycterus hispidus*, and *Oxymycterus* ("*Microxus*") *iheringi*. Of these taxa I have only examined one voucher (of *Delomys dorsalis*, FMNH 143286) from Fazenda Intervals. Olmos found *D. dorsalis* to be the commonest (or at least the most readily trapped) rodent species in his study area, with 94 marked individuals and 331 captures over a 12-month period:

Delomys dorsalis appears to be nocturnal and completely terrestrial.⁸ No individual was cap-

⁸ Because Olmos only set traps on the ground (op. cit.: 556) it is not clear how his data could sustain this interpretation.

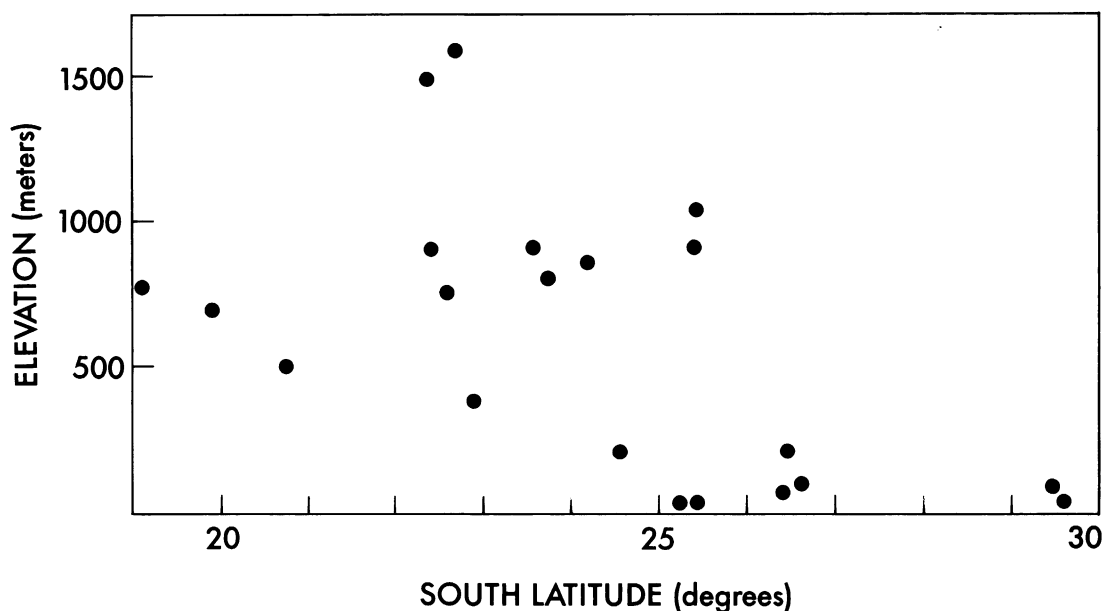


Fig. 17. Joint distribution of latitude and elevation for *Delomys* collection localities. The plotted points include gazetteer entries from this report together with localities reported by Zanchin et al. (1992) and Massoia (1962). The absence of lowland collections from northern (tropical) latitudes is conspicuous and may reflect a preference for cooler habitats like those near sea level in the subtropical south.

tured by day nor escaped by climbing after release. In the laboratory they were relatively slow and unagile. Upon release all individuals moved away, frequently along an exposed root or fallen log and entered a burrow, or hid under litter mounds. Trapped individuals quickly became tame, allowing handling without reaction.

Reproductively active females were captured in every month of the year.

Rio Grande do Sul, the southernmost state in Brazil, was the locus of Hensel's (1872) collecting activities, and I have not been able to fix a more specific geographic source for his observations. According to Hensel (1872: 41–43), *Delomys dorsalis* inhabits the deep virgin forest ("im Innern des Urwaldes") where, like *Akodon azarae* ("*Hesperomys arenicola*") it usually lives beneath the roots of old hollow trees, and does not climb ("Sie scheint sich vorzugsweise unter den Wurzeln alter hohler Bäume aufzuhalten und nicht zu klettern"). Dense, wet forests with abundant epiphytes were once found on the littoral plain at the foot of the coastal escarpment in the northeastern part of the state (Belton, 1984). Taquara (fig. 1: locality 10), the locality where

H. von Ihering collected a series of *D. dorsalis* at 39 m elevation, is in this area and perhaps Hensel made his observations here too.

DISCUSSION

The published and unpublished observations cited above consistently describe *Delomys* species as nocturnal and predominantly terrestrial inhabitants of cool, wet forests. Montane forests are apparently favored at northern (tropical) latitudes, but the southernmost (subtropical) collection localities for the genus are closer to sea level (fig. 17). Several reports (Miranda Ribeiro, 1905; Davis, 1945a, 1947; B. D. Patterson, personal commun.; Olmos, 1991) suggest that these rats move under and among the sheltering clutter of logs, organic debris, mossy roots, and bamboo tangles rather than frequenting open areas on the forest floor. Davis's (1947) record of a specimen of *D. dorsalis* trapped in a tree is unique, but few collectors of small mammals make concerted efforts to sample arboreal microhabitats. Certainly, the longer tail, vibrissae, and outer digits of the hindfoot

in *D. dorsalis* suggest better developed scanorial abilities than does the contrasting morphology of *D. sublineatus*.

Interspecific habitat differences in *Delomys* remain to be convincingly explained. Davis's (1945a, 1947) results from Teresópolis are inconclusive because his two study sites differed in climate as well as vegetational history. The association of *D. dorsalis* with more humid conditions than those apparently favored by *D. sublineatus*, both at Teresópolis and (possibly) at Boracéia, hints that interspecific ecological differences may be determined by moisture gradients rather than forest succession, but more field observations will be needed to test this hypothesis.

Virtually all other aspects of the biology of these rats is obscure. The results from one mark-and-recapture study (Olmos, 1991) suggest that *Delomys dorsalis* breeds throughout the year, but demographic studies supplemented by reproductive autopsies are more informative and should also be undertaken. Sustained programs of kill-trapping on a regular schedule would, in addition to definitive evidence of reproductive condition, also yield stomach contents that could be analyzed for dietary data. Dietary analyses should include microscopic examination for fungal spores and hyphae because fungi are known to be important components in the diets of forest rodents at both temperate and tropical latitudes (Fogel and Trappe, 1978; Emmons, 1982; Meserve et al., 1988). Equipment for

spool-and-line tracking (Miles et al., 1981) could be miniaturized for studies of *Delomys* to obtain information about daytime refugia, and much more could be learned by thoughtful trapping protocols about microhabitat utilization. In fact, with so little known, virtually any well-planned field study is certain to yield novel and interesting results.

The paucity of natural history information about *Delomys* is typical of what is known about the habits and habitats of most mammalian denizens of the wet tropical and subtropical forests that extend from southeastern Brazil to northeastern Argentina and eastern Paraguay. Besides *Delomys*, 13 other genus-group taxa are endemic to this region: *Leontopithecus*, *Brachyteles*, *Abrawayomys*, *Blarinomys*, *Phaenomys*, *Rhagomys*, *Thaptomys*, *Wilfredomys*, *Chaetomys*, *Euryzygomatomys*, *Kannabateomys*, *Nelomys*, and *Trinomys*. Of these, only the primates have received significant attention from field ecologists. Of the muroids, only *Thaptomys*, *Blarinomys*, and *Delomys* are known from more than a few specimens. This deplorable situation is exacerbated by the virtual disappearance of unmodified forest habitats throughout southeastern Brazil where mammalian diversity and endemism is highest (Fonseca, 1985). If much more is to be learned about mammalian evolution, distribution, and ecology in the Atlantic rainforest biome, systematic and field studies of these endemics should be undertaken soon.

REFERENCES

- Avila-Pires, F. D. de
 1960a. Roedores colecionados na região de Lagoa Santa, Minas Gerais, Brasil. *Arq. Mus. Nac.* 50: 25–46.
 1960b. Um novo gênero de roedor Sul-Americano. *Bol. Mus. Nac., nov. ser., Zool.* 220: 6 pp.
- Avila-Pires, F. D. de, and E. Gouvêa
 1977. Mamíferos do Parque Nacional do Itatiaia. *Bol. Mus. Nac., nov. ser., Zool.* 291: 29 pp.
- Belton, W.
 1984. Birds of Rio Grande do Sul, Brazil. Part 1. Rheidae through Furnariidae. *Bull. Am. Mus. Nat. Hist.* 178: 369–636.
- Bugge, J.
 1970. The contribution of the stapedial artery to the cephalic supply in muroid rodents. *Acta Anat.* 76: 313–336.
- Cabrera, A.
 1961. Catálogo de los mamíferos de América del Sur. *Rev. Mus. Argentino Cienc. Nat. "Bernardino Rivadavia"* 4(2): 309–732.
- Carleton, M. D.
 1980. Phylogenetic relationships in neotomine-peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within New World Cricetinae. *Misc. Publ. Mus. Zool. Univ. Michigan* 157: 146 pp.

1989. Advances in the study of *Peromyscus* (Rodentia). In G. L. Kirkland, Jr. and J. N. Layne (eds.), *Advances in the study of Peromyscus*, pp. 7–141. Lubbock: Texas Tech Univ. Press.
- Carleton, M. D., and R. E. Eshelman
1979. A synopsis of fossil grasshopper mice, genus *Onychomys*, and their relationship to Recent species. Univ. Michigan Pap. Paleontol. 21: 63 pp.
- Carleton, M. D., and G. G. Musser
1984. Muroid rodents. In S. Anderson and J. K. Jones, Jr. (eds.), *Orders and families of recent mammals of the world*, pp. 289–379. New York: Wiley.
1989. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): a synopsis of the genus *Microrizomys*. Bull. Am. Mus. Nat. Hist. 191: 83 pp.
- Carvalho, C. T. de
1965. Bionomia de pequenos mamíferos em Boracéia. Rev. Biol. Trop. 13: 239–257.
- Cerqueira, R.
1982. South American landscapes and their mammals. In M. A. Mares and H. H. Genoways (eds.), *Mammalian biology in South America*. Pymatuning Lab. Ecol., Spec. Publ. Ser. 6: 53–75.
- Corbet, G. B., and J. E. Hill
1991. A world list of mammalian species, 3rd ed. London: Oxford Univ. Press.
- Davis, D. E.
1945a. The annual cycle of plants, mosquitoes, birds, and mammals in two Brazilian forests. Ecol. Monogr. 15: 243–295.
- 1945b. The home range of some Brazilian mammals. J. Mammal. 26: 119–127.
1947. Notes on the life histories of some Brazilian mammals. Bol. Mus. Nac. (Rio de Janeiro), Nov. Ser., Zool. 76: 1–8.
- Ellerman, J. R.
1941. The families and genera of living rodents, vol. 2, Family Muridae. London: British Museum (Natural History).
- Emmons, L.
1982. Ecology of *Proechimys* (Rodentia, Echimyidae) in southeastern Peru. Trop. Ecol. 23: 280–290.
- Fogel, R., and J. M. Trappe
1978. Fungus consumption (mycophagy) by small animals. Northwest Sci. 52: 1–31.
- Fonseca, G. A. B. da
1985. The vanishing Brazilian Atlantic forest. Biol. Conserv. 34: 17–34.
- Greene, E. C.
1935. Anatomy of the rat. Trans. Am. Philos. Soc., n. ser. 27: 370 pp.
- Gyldenstolpe, N. C. G.
1932. A manual of Neotropical sigmodont rodents. Kungl. Svenska Ventenskapsakad. Handl. Ser. 3, 11(3): 164 pp. + 18 pls.
- Hensel, R.
1872. Beiträge zur Kenntniss der Säugethiere Süd-Brasilens. Abh. Preuss. Akad. Wiss. (Berlin) 1872: 1–130 + 3 pls.
- Hershkovitz, P.
1944. A systematic review of the Neotropical water rats of the genus *Nectomys* (Cricetinae). Misc. Publ. Mus. Zool. Univ. Michigan 58: 88 pp. + 4 pls. + 2 maps.
1960. Mammals of northern Colombia, preliminary report No. 8: Arboreal rice rats, a systematic revision of the subgenus *Oecomys*, genus *Oryzomys*. Proc. U.S. Natl. Mus. 110: 513–568.
1962. Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Fieldiana Zool. 46: 524 pp.
1966. South American swamp and fossorial rats of the scapteromyine group (Cricetinae, Muridae) with comments on the glans penis in murid taxonomy. Z. Säugetierkd. 31: 81–149.
- Heyer, W. R., A. S. Rand, C. A. G. da Cruz, et al.
1990. Frogs of Boracéia. Arq. Zool., Mus. Zool. Univ. São Paulo 31: 231–410.
- Holt, E. G.
1928. An ornithological survey of the Serra do Itatiaya, Brazil. Bull. Am. Mus. Nat. Hist. 57: 251–326 + 14 pls.
1929. Itatiaya, Brazil's most famous mountain. Nat. Hist. 29: 427–436.
- Honacki, J. H., K. E. Kinman, and J. W. Koeppel
1982. Mammal species of the world. Lawrence, KS: Allen Press.
- Hooper, E. T., and G. G. Musser
1964. The glans penis in Neotropical cricetines (family Muridae) with comments on classification of muroid rodents. Misc. Publ. Mus. Zool. Univ. Michigan 123: 57 pp.
- Klaauw, C. J. van der
1931. The auditory bulla in some fossil mammals with a general introduction to this region of the skull. Bull. Am. Mus. Nat. Hist. 62: 1–352.
- Leche, W.
1886. Ueber einige südbrasilianische *Hesperomys*-Arten. Zool. Jahrb. 1: 687–702 + pl. XVI.
- Massoia, E.
1962. Dos especies de cricétidos nuevas para la Argentina. Physis 23: 27–34.

- Meserve, P. L., B. K. Lang, and B. D. Patterson
1988. Trophic relationships of small mammals in a Chilean temperate rainforest. *J. Mammal.* 69: 721–730.
- Miles, M. A., A. A. de Souza, and M. M. Póvoa
1981. Mammal tracking and nest location in Brazilian forest with an improved spool-and-line device. *J. Zool., London* 195: 331–347.
- Miranda Ribeiro, A. de
1905. Vertebrados do Itatiaia. *Arch. Mus. Nac. Rio de Janeiro* 13: 165–190.
- Moojen, J.
1952. Os roedores do Brasil. Rio de Janeiro: Instituto Nacional do Livro.
- Musser, G. G., and M. D. Carleton
1993. Family Muridae. In D. E. Wilson and D. M. Reeder (eds.), *Mammal species of the World: a taxonomic and geographic reference*, 2nd ed. Washington, D.C.: Smithsonian Institution Press.
- Olmos, F.
1991. Observations on the behavior and population dynamics of some Brazilian Atlantic forest rodents. *Mammalia* 55: 555–565.
- Osgood, W. H.
1933a. The supposed genera *Aepeomys* and *Inomys*. *J. Mammal.* 14: 161.
1933b. Two new rodents from Argentina. *Zool. Ser. Field Mus. Nat. Hist.* 20: 11–14.
- Paynter, R. A., Jr.
1985. *Ornithological gazetteer of Argentina*. Cambridge, MA: Mus. Comp. Zool., Harvard Univ.
- Paynter, R. A., Jr., and M. A. Traylor, Jr.
1991. *Ornithological gazetteer of Brazil*, 2 vols. Cambridge, MA: Mus. Comp. Zool., Harvard Univ.
- Redford, K. H. and J. F. Eisenberg
1992. *Mammals of the Neotropics*, vol. 2. Chicago: Univ. Chicago Press.
- Reig, O. A.
1977. A proposed unified nomenclature for the enamelled components of the molar teeth of the Cricetinae (Rodentia). *J. Zool., London* 181: 227–241.
1980. A new fossil genus of South American cricetid rodents allied to *Weidomys*, with an assessment of the Sigmodontinae. *J. Zool., London* 192: 257–281.
1984. Distribuição geográfica e história evolutiva dos roedores muroideos sul-americanos (Cricetidae: Sigmodontinae). *Rev. Brasil. Genet.* 7: 333–365.
1986. Diversity patterns and differentiation of high Andean rodents. In F. Vuilleumier and M. Monasterio (eds.), *High altitude tropical biogeography*, pp. 404–439. New York: Oxford Univ. Press.
- Sarich, V. M.
1985. Rodent macromolecular systematics. In W. P. Luckett and J.-L. Hartenberger (eds.), *Evolutionary relationships among rodents*. New York: Plenum.
- Segadas-Vianna, F.
1968. Ecology of the Itatiaia Range, south-eastern Brazil. I. Altitudinal zonation of the vegetation. *Arq. Mus. Nac. (Rio de Janeiro)* 53: 7–30.
- Segadas-Vianna, F. and L. Dau
1968. Ecology of the Itatiaia Range, south-eastern Brazil. II. Climates and altitudinal climatic zonation. *Arq. Mus. Nac. (Rio de Janeiro)* 53: 31–53.
- Smithe, F. B.
1975–81. *Naturalist's color guide*. New York: Am. Mus. Nat. Hist.
- Stehlin, H. G., and S. Schaub
1951. Die Trigonodontie der simplicidentaten Nager. *Schweizer. Paleontol. Abh.* 67: 385 pp.
- Tate, G. H. H.
1932. The taxonomic history of the South and Central American oryzomyine genera of rodents (excluding *Oryzomys*): *Nesoryzomys*, *Zygodontomys*, *Chilomys*, *Delomys*, *Phaenomys*, *Rhagomys*, *Rhipidomys*, *Nyctomys*, *Oecomys*, *Thomasomys*, *Inomys*, *Aepeomys*, *Neacomys*, and *Scolomys*. *Am. Mus. Novitates* 581: 28 pp.
- Thomas, O.
1902. On mammals from the Serra do Mar of Paraná, collected by Mr. Alphonse Robert. *Ann. Mag. Nat. Hist.* 7(9): 59–64.
1903. Notes on Neotropical mammals of the genera *Felis*, *Hapale*, *Oryzomys*, *Akodon*, and *Ctenomys*, with descriptions of new species. *Ann. Mag. Nat. Hist.* 7(12): 234–243.
1906. Notes on South American rodents. *Ann. Mag. Nat. Hist.* 7(18): 442–448.
1917. On the arrangement of the South American rats allied to *Oryzomys* and *Rhipidomys*. *Ann. Mag. Nat. Hist.* 8(20): 192–198.
1928. A new *Thomasomys* from Rio Grande do Sul. *Ann. Mag. Nat. Hist.* 10 (1): 154–155.
- Trouessart, E.-L.
1898. *Catalogus mammalium tam viventium quam fossilium*, tomus I. Berlin: R. Friedländer & Sohn.
1904. *Catalogus mammalium tam viventium*

- quam fossilium, quinquennale supplementum. Berlin: R. Friedländer & Sohn.
- Ule, E.
1896. Relatório de uma excursão botânica feita na Serra do Itatiaia. Rev. Mus. Nac. (Rio de Janeiro) 9: 185–223.
- Voss, R. S.
1988. Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. Bull. Am. Mus. Nat. Hist. 188: 259–493.
1991. An introduction to the Neotropical muroid rodent genus *Zygodontomys*. Bull. Am. Mus. Nat. Hist. 210: 113 pp.
- Voss, R. S., and M. D. Carleton
In press. A new genus for *Hesperomys molitor* Winge and *Holochilus magnus* Hershkovitz, with an analysis of its phylogenetic relationships. Am. Mus. Novitates
- Voss, R. S., and A. V. Linzey
1981. Comparative gross morphology of male accessory glands among Neotropical Muridae (Mammalia: Rodentia) with comments on systematic implications. Misc. Pub. Mus. Zool. Univ. Michigan 159: 41 pp.
- Voss, R. S., and L. F. Marcus
1992. Morphological evolution in muroid rodents II. Craniometric factor divergence in seven Neotropical genera, with experimental results from *Zygodontomys*. Evolution 46: 1918–1934.
- Voss, R. S., L. F. Marcus, and P. Escalante P.
1990. Morphological evolution in muroid rodents I. Conservative patterns of craniometric covariance and their ontogenetic basis in the Neotropical genus *Zygodontomys*. Evolution 44: 1568–1587.
- Voss, R. S., and P. Myers
1991. *Pseudoryzomys simplex* (Rodentia: Muridae) and the significance of Lund's collections from the caves of Lagoa Santa, Brazil. Bull. Am. Mus. Nat. Hist. 206: 414–432.
- Wible, J. R.
1990. Petrosals of late Cretaceous marsupials from North America, and a cladistic analysis of the petrosal in therian mammals. J. Vertebr. Paleontol. 10: 183–205.
- Wiley, E. O.
1981. Phylogenetics, the theory and practice of phylogenetic systematics. New York: Wiley.
- Winge, H.
1887. Jordfundne og nulevende Gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien. E Museo Lundii 1(3): 200 pp. + 8 pls.
1941. The interrelationships of the mammalian genera (translated from the Danish by E. Deichmann and G. M. Allen), vol. 2. Copenhagen: C. A. Reitzels Forlag.
- Zanchin, N. I. T., I. J. Sbalqueiro, A. Langguth, R. C. Bossle, E. C. Castro, L. F. B. Oliveira, and M. S. Mattevi
1992. Karyotype and species diversity of the genus *Delomys* (Rodentia, Cricetidae) in Brazil. Acta Theriologica 37: 163–169.

APPENDIX

Series of *Thomasomys cinereus* and *Oryzomys palustris* Examined

The morphological limits of *Thomasomys cinereus* and *Oryzomys palustris* are not adequately documented in the taxonomic literature and future revisionary studies may prove that both species are composite. The following series of specimens were used as the primary source of information about morphological characters discussed in this report:

***Thomasomys cinereus*.**—Skins with skeletons: LSU 27045–27065, 27066–27081, 27130. Fluid-preserved specimens: LSU 27145, 27146. From Peru, Depto. Piura, Cruz Blanca (ca. 33 km by road SW Huancabamba).

***Oryzomys palustris*.**—Skins with skeletons: AMNH 219953, 242517–242521, 242524, 250167, 252716, 252719–252721, 253212, 253215, 253217, 253218, 253220, 254453; from USA, Florida, Highlands Co., 8 mi S Lake Placid. Fluid-preserved specimens: AMNH 239256, 239258–239261, 239263, 239264; from USA, Georgia, St. Catherine's Island.