# SYSTEMATICS AND ECOLOGY OF ICHTHYOMYINE RODENTS (MUROIDEA): PATTERNS OF MORPHOLOGICAL EVOLUTION IN A SMALL ADAPTIVE RADIATION

ROBERT S. VOSS

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 188 : ARTICLE 2 NEW YORK : 1988

Recent issues of the *Bulletin* may be purchased from the Museum. Lists of back issues of the *Bulletin, Novitates,* and *Anthropological Papers* published during the last five years are available free of charge. Address orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, N.Y. 10024.

# SYSTEMATICS AND ECOLOGY OF ICHTHYOMYINE RODENTS (MUROIDEA): PATTERNS OF MORPHOLOGICAL EVOLUTION IN A SMALL ADAPTIVE RADIATION

ROBERT S. VOSS
*Assistant Curator, Department of Mammalogy*
*American Museum of Natural History*

This article completes Volume 188.

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Volume 188, article 2, pages 259–493, figures 1–100, tables 1–59, maps 1–3
Issued November 16, 1988
Price: $19.15 a copy

ISSN 0003-0090

# CONTENTS

## ABSTRACT

Ichthyomyines are ecologically and morphologically distinctive muroid rodents that occur in forested mountains and lowlands from Oaxaca, Mexico, through Central America and northern South America to French Guiana and Peru. This monograph reports museum and field research on ichthyomyine anatomy, taxonomy, morphometrics, functional morphology, ecology, phylogeny, zoogeography, and adaptive radiation.

1. A survey of ichthyomyine anatomy reveals that the genera *Anotomys, Daptomys, Ichthyomys, Neusticomys,* and *Rheomys* share attributes of the integument, dentition, cranium, postcranial skeleton, alimentary canal, and male reproductive tract that distinguish them from all other members of the muroid subfamily Sigmodontinae. Diagnostic ichthyomyine character states include the lack of genal vibrissae, the complete absence of a zygomatic notch, a large bony tubercle for the origin of M. masseter superficialis, an ovoid infraorbital foramen communicating large bundles of trigeminal sensory neurons, absence of a tympanic membrane pars flaccida, attachment of the nuchal ligament to the third thoracic vertebra, a vermiform caecum and spinous lateral crater papillae on the glans penis. Characters that vary among ichthyomyines include pelage color and composition, the presence or absence of a philtrum, the relative size of pinnae, the presence or absence of superciliary vibrissae, the number of separate plantar pads on the manus, the development of fringing hairs on the pes, the number of distinct cusps on m3, the relative length of the nasal bones, the position of supraorbital foramina, patterns of carotid arterial supply, the presence or absence of an orbicular apophysis on the malleus, external and postcranial skeletal proportions, the presence or absence of M. omohyoideus, the distribution of gastric glandular epithelium, the presence or absence of a gall bladder, and the morphology of the penis and bacular cartilage.

2. Based on these and other morphological comparisons, the tribe Ichthyomyini is diagnosed, a new genus is proposed for *Anotomys trichotis,* and the species of *Neusticomys* and *Daptomys* are combined to form one genus for which the former name has priority. Complete descriptions and a critical review of included species are provided for each of the five recognized ichthyomyine genera: *Anotomys* Thomas, 1906; *Chibchanomys,* new genus; *Ichthyomys* Thomas, 1893; *Neusticomys* Anthony, 1921; *Rheomys* Thomas, 1906.

3. Criteria for choosing metric characters that usefully sample variation in size and shape are considered and a measurement protocol for ichthyomyine crania is described. Patterns of metric variation and correlation in a mixed cross-sectional sample of *Rheomys thomasi* are consistent with a hypothesis of postweaning growth in 12 of 17 craniodental measurements analyzed. Relative cranial growth is quantified by the first principal component extracted from each of five sample covariance matrices (of log-transformed measurements) representing five species of ichthyomyines. The resulting estimates of multivariate allometry are compared using vector correlations and appear similar; an average vector is calculated from the pooled (group-centered) data.

Because multivariate relative growth in cranial dimensions appears similar among ichthyomyine species, interspecific variation in cranial size can be quantified from population sample scores on the pooled within-group first principal component. The leading eigenvector extracted from the residual covariance matrix (from regressions of 15 population sample means on their size scores) then describes conspicuous size-independent, interspecific shape variation. Inspection of the residual covariance matrix and of variable loadings on the shape factor extracted from it suggests a pattern of morphological integration among components of the masticatory apparatus and neurocranium; this pattern is heuristically summarized using Wright's formalism of a path diagram.

4. The osseous and muscular elements of the masticatory system are described in detail for *Anotomys leander* and *Ichthyomys tweedii.* Differences in dental morphology and occlusion, and in the orientation of several large mandibular adductors, suggest that the masticatory apparatus of *A. leander* emphasizes effective molar trituration whereas that of *I. tweedii* emphasizes the delivery of a strong incisor bite. These alternative functional arrangements are hypothesized to reflect adaptations to diets of small and large arthropods, respectively. The hypothesis that size-independent variation in craniodental shape among ichthyomyine species (as summarized in 3, above) chiefly reflects adaptive divergence in functionally integrated components of the neurocranium, dentition, and facial skeleton is supported by the consistency of inferred functional relations with observed covariance structures.

5. From analyses of digestive tract contents together with field observations and summaries of published and unpublished information on habitats, ichthyomyines can be characterized as semiaquatic carnivores that derive a substantial fraction of their diets from the benthic arthropod faunas of small forest streams. Despite the ecological uniformity implied by this generalization, however, considerable altitude-correlated variation exists

among the habitats of different ichthyomyine species. Streams inhabited by montane water rats are bordered by cloud forest (or páramo) vegetation and average colder and faster than the warmer, slower streams bordered by lowland rain forests where other ichthyomyine species are encountered in adjacent foothill or piedmont landscapes. In addition, and at least partly in consequence of elevational gradients in water temperature and average current speed, the benthic faunas of high-altitude streams consist predominantly of small arthropods (mostly immature insects), whereas lowland streams may generally support a greater diversity of large arthropods (including abundant decapod crustaceans).

Ichthyomyines are members of diverse rainforest communities of small marsupials, lipotyphlans, and rodents but do not co-occur with any other like-size mammals that regularly forage for arthropod prey in streams. Other aspects of ichthyomyine ecology are obscure.

6. Ichthyomyine monophyly and the relationships of ichthyomyines to other members of the subfamily Sigmodontinae are discussed in terms of the morphological evidence summarized in (1). Ichthyomyines constitute a monophyletic group, perhaps of considerable antiquity, with no clear affinities to members of any other muroid taxon. In addition, the distinctiveness of ichthyomyines together with the lack of diagnostic character states for the Sigmodontinae call into question the phylogenetic status of the subfamily.

Phylogenetic relationships among ichthyomyines are investigated through applications of character compatibility analysis and numerical parsimony methods. Eighteen characters representing a diversity of anatomical systems were chosen for analysis based on the constancy of their expressions within biological populations and on the discreteness of their alternative states. Twelve unique collections (cliques) of mutually compatible characters are present among the data analyzed. A pair of maximal cliques, each containing ten characters, are two orders of magnitude further removed from random expectation than are any other patterns of cladistic character agreement. A resolution of one of these largest cliques is among the most parsimonious trees determined by branch-and-bound algorithms and provides the most biologically compelling estimate of ichthyomyine phylogeny supported by available character data. The monophyly of both *Rheomys* and *Ichthyomys* appears well corroborated and these two genera are hypothesized to be sister-groups more distantly related, successively, with *Anotomys, Chibchanomys,* and *Neusticomys.* The most parsimonious geographic scenario consistent with this phylogeny suggests a South American ancestor for the Ichthyomyini and early cladogenetic events confined to South America. The genus *Rheomys,* containing all and only species endemic to Central America, is conjectured to have evolved from a single northward dispersal across the Río Atrato lowlands.

7. Many mammals prey on freshwater organisms but only a few lipotyphlans and Old World muroid rodents are comparable to ichthyomyines in size and habits. North American water shrews (*Sorex palustris*), three genera of Eurasian water shrews (*Neomys, Chimarrogale* and *Nectogale*), Pyrenean desmans (*Galemys*), small African aquatic tenrecs (*Micropotamogale*), African brook rats (*Colomys goslingi*), Madagascar water tenrecs (*Limnogale*), and three New Guinean aquatic muroids (*Hydromys habbema, H. hussoni,* and *Crossomys moncktoni*) all average about 200 g or less in body weight and prey largely on aquatic arthropods in streams. These mammals resemble one another and differ from closely related, nonaquatic taxa in a number of external and cranial characters; the same characters also distinguish ichthyomyines from nonaquatic New World muroids and apparently represent a consistent pattern of morphological adaptations to semiaquatic carnivory. Such adaptations are readily grouped into functional complexes within which character expressions are correlated, but qualitative comparisons and the few data about habitats and diet available for most semiaquatic lipotyphlans and Old World muroids do not provide a satisfactory basis for more sophisticated analyses of evolutionary patterns.

8. Ichthyomyine adaptive radiation can be described in terms of the interspecific patterns of size-dependent and size-independent cranial variation summarized in (3) together with the results of similar statistical analyses of external and postcranial skeletal dimensions. Cranial and postcranial size factor scores are correlated across ichthyomyine species, as expected, but cranial shape and postcranial proportions are also highly correlated such that species with slender incisors, large molars, and inflated neurocrania also have large hindfeet, short proximal limb bones, and long tails. The correlation between cranial shape and postcranial proportions is not a statistical artifact and does not reflect recency of common ancestry. Instead, ecological covariance resulting from joint elevational gradients in stream flow velocity and in arthropod faunal composition is hypothesized to have imposed stringent adaptive constraints on ichthyomyine skeletal evolution. Correlations of cranial and postcranial shape scores with elevation are significant and consistent in sign with functional interpretation of the factors and knowledge of the ecological gradients. The hypothesis cor-

rectly predicts convergent ecomorphological distributions of hydromyine rodents in New Guinea.

Parsimonious reconstructions of ichthyomyine morphometric evolution together with outgroup comparisons suggest an ancestral morphotype similar to extant species of *Neusticomys* and an ancestral habitat in the tropical South American lowlands or foothills. Ichthyomyine evolution has been characterized largely by morphological divergence of geographically co-occurring lineages; convergence in derived skeletal morphologies between South and Central American lineages is attributed to independent invasions of montane habitats.

9. In their ecological diversity and faunal dominance, South American muroid rodents resemble such other sympatric vertebrate groups as characoid and siluroid fishes, hylid and leptodactylid frogs, tyrannoid birds, and phyllostomid bats. Careful comparisons of these adaptive radiations may discover common causal factors in their evolutionary histories or may reveal differences of significance for theories concerning the origin, distribution, and maintenance of Neotropical diversity. If South American muroids are to be employed in such useful comparisons, however, more basic information about their systematics and natural history must be provided by future research.

## RESUMEN

Los ictiominos son roedores muroides distintivos ecológica- y morfológicamente que se encuentran en las montañas húmedas tropicales y tierras bajas adyacentes desde Oaxaca, México, a través de la América Central y la parte norte de América del Sur hasta la Guayana Francesa y el Perú. Esta monografía señala las investigaciones realizadas en el campo y en el museo sobre la anatomía, taxonomía, morfometría, morfología funcional, ecología, filogenia, zoogeografía, y radiación adaptativa de los ictiominos.

1. El estudio de la anatomía de los ictiominos revela que los géneros *Anotomys, Daptomys, Ichthyomys, Neusticomys* y *Rheomys* comparten atributos del tegumento, dentición, cráneo, esqueleto postcraneal, canal alimentario, y tracto reproductivo del macho que los distinguen de todos los miembros de la subfamilia muroide Sigmodontinae (*sensu* Carleton y Musser, 1984). Los estados de los caracteres diagnósticos de los ictiominos incluyen la carencia de vibrisas genales, la ausencia completa de una escotadura cigomática, un gran tubérculo óseo para el origen del músculo masetero superficial, un foramen infraorbital ovalado que comunica grandes haces de neuronas sensoriales trigéminas, la ausencia de la membrana timpánica *pars flaccida,* la unión del ligamento nucal a la tercera vértebra torácica, un ciego vermiforme y un par de papilas espinosas laterales en el cráter del pene. Los caracteres que varían entre los ictiominos incluyen la composición y coloración del pelaje, la presencia o ausencia de un filtrum (philtrum), el tamaño relativo de las pinnas, la ausencia o presencia de vibrisas superciliares, el número de cojinetes plantares separados en la mano, el desarollo de pelos en los márgenes plantares del pie, el número de cúspides del m3, la longitud relativa de los huesos nasales, la posición de los forámenes supraorbitales, los patrones de circulación carótida, la presencia o ausencia de la apófisis orbicular del malleus, las proporciones externas del cuerpo y del esqueleto postcraneal, la presencia o ausencia del músculo omohyoideus, la distribución del epitelio gástrico glandular, la presencia o ausencia de la vesícula biliar, y la morfología del pene y del cartílago bacular.

2. Basándonos en éstas y otras comparaciones morfológicas, se diagnostica la tribu Ichthyomyini, se propone un nuevo género para *Anotomys trichotis,* y las especies de *Neusticomys* y *Daptomys* son combinadas para formar un género cuyo nombre prioritario es *Neusticomys.* Se proporcionan las descripciones completas y una revisión crítica de las especies incluídas para cada uno de los cinco géneros de ictiominos reconocidos: *Anotomys* Thomas, 1906; *Chibchanomys,* género nuevo; *Ichthyomys* Thomas, 1893; *Neusticomys* Anthony, 1921; y *Rheomys* Thomas, 1906.

3. Se consideran los criterios para seleccionar los caracteres métricos que representen útilmente la variación en tamaño y forma y se describe un protocolo para medir el cráneo ictiomino. Los patrones de variación métrica y de correlación en una muestra poblacional de *Rheomys thomasi* son consistentes con la hipótesis de crecimiento postdestetal en 12 de 17 medidas craneodentales analizadas. El crecimiento craneal relativo en cinco poblaciones de ictiominos es cuantificado por medio del primer componente principal extraído a partir de la matriz de covarianzas de las medidas transformadas logarítmicamente para cada muestra. Las estimaciones resultantes de la alometría multivariada son comparadas utilizando correlaciones vectoriales y parecen similares; se calcula un vector promedio que describe el crecimiento

relativo multivariado en el cráneo a partir de los datos intragrupos combinados (pooled within-group).

Dado que el crecimiento relativo multivariado en las dimensiones craneales se muestra similar entre las especies de ictiominos, la variación interespecífica en el tamaño craneal puede ser cuantificada a partir de los valores (scores) de las muestras poblacionales sobre el primer componente principal intragrupo promediado. El mayor eigenvector extraído a partir de la matriz de covarianzas residual (a partir de regresiones de medias muestrales sobre sus respectivos valores de tamaño) describe entonces la variación en las formas independientemente del tamaño entre las especies de ictiominos. Una examinación de la matriz de covarianzas residual y de los pesos de las variables en el factor de forma extraído a partir de ella sugiere un patrón de integración morfológica entre algunos elementos del aparato masticador y el neurocráneo.

4. Los elementos musculares y óseos del aparato masticador son descritos en detalle para *Anotomys leander* y para *Ichthyomys tweedii.* Las diferencias entre las dos especies en cuanto a la oclusión y morfología dental, y a la orientación de algunos aductores mandibulares grandes sugiere que el aparato masticador de *Anotomys leander* realiza una efectiva trituración molar mientras que el de *Ichthyomys tweedii* realiza una fuerte mordida incisiva. Se propone que estas disposiciones funcionales alternativas representan adaptaciones a las dietas de pequeños y grandes artrópodos respectivamente. La correspondencia entre las relaciones funcionales inferidas y las estructuras de covarianzas anteriormente observadas apoya la hipótesis de que la variación de la forma (separada del tamaño) craneodental entre las especies de ictiominos (como fue resumida en 3) principalmente refleja la divergencia adaptativa en los componentes funcionalmente integrados del neurocraneo, la dentición, y del esqueleto facial.

5. A partir de los análisis de los contenidos del tracto digestivo junto con observaciones de campo y revisiones de información publicada y no publicada sobre los habitats, los ictiominos pueden ser caracterizados como carnívoros semiacuáticos que obtienen una fracción sustancial de sus dietas a partir de faunas de artrópodos bénticos de riachuelos en bosques. A pesar de la uniformidad ecológica implicada en esta generalización, existe considerable variación correlacionada con la altitud entre los habitats de las especies de ictiominos. Los riachuelos habitados por ictiominos en las montañas están bordeados por vegetación de bosque nublado (o páramo) y por lo común son más fríos y rápidos que los riachuelos más cálidos y lentos bordeados por bosque lluvioso tropical donde se encuentran otras especies de ictiominos en las vertientes de piedemonte y las tierras bajas. Además, y al menos parcialmente como consecuencia del efecto de los gradientes altitudinales en la temperatura y en la velocidad de la corriente del agua, la fauna béntica de los riachuelos de las montañas consiste principalmente de pequeños artrópodos (la mayoría estadíos larvales de insectos), mientras que los arroyuelos de tierras bajas generalmente tienen una mayor diversidad de artrópodos grandes (incluyendo abundantes crustáceos decápodos).

Los ictiominos son miembros de diversas comunidades de pequeños mamíferos no voladores (marsupiales, insectívoros y otros roedores) en los bosques nublados y bosques lluviosos neotropicales, pero no co-existen con ningún otro mamífero de tamaño similar que regularmente busque artrópodos en los riachuelos. Otros aspectos sobre la ecología de los ictiominos no se han dilucidado todavía.

6. La monofilia de los ictiominos y sus interrelaciones con otros miembros de la subfamilia Sigmodontinae se discuten en términos de la evidencia morfológica resumida en (1). Se sugiere que los ictiominos comprenden un grupo monofilético, quizás de antigüedad considerable, sin afinidades claras con los miembros de cualquier otro taxón muroide. Por lo demás, la distinción de los ictiominos junto con la carencia de estados diagnósticos para los Sigmodontinae lleva a cuestionar el status filogenético de la subfamilia.

Las relaciones filogenéticas entre los ictiominos se investigan mediante la aplicación de análisis de compatibilidad de caracteres y de métodos de parsimonia numérica. Dieciocho caracteres representantes de varios sistemas anatómicos fueron elegidos para el análisis sobre la base de la constancia de sus expresiones dentro de poblaciones biológicas y sobre lo discreto de sus estados alternativos. Doce colecciones únicas (cliques) de caracteres mutualmente compatibles están presentes entre los datos analizados. Un par de "cliques" máximos, cada uno conteniendo diez caracteres, tienen probabilidades de encuentro al azar que están dos órdenes de magnitud por debajo de la probabilidad de cualquier otro patrón de arreglo cladístico. Una resolución de uno de estos "cliques" máximos es uno de los árboles más parsimónicos determinados por los algorítmos "branch-and-bound" y constituye la estimación filogenética biológicamente más confiable apoyada por los caracteres disponibles. La monofilia tanto de *Rheomys* como de *Ichthyomys* parece estar bien corroborada y se hipotetiza que estos dos géneros son grupos hermanos de relación cada vez más distante con *Anotomys, Chibchanomys,* y *Neusticomys.* El escenario geográfico más parsimónico consistente con esta filogenia sugiere un ancestro suramericano para los Ichthyomyini y eventos cladogenéticos tempranos confinados a América del Sur. El género *Rheomys,* el cual agrupa exclusivamente a todas las especies de ictiominos endémicos de Centro América, se conjectura que procede de una dispersión única hacia el norte a través del valle del Río Atrato.

7. Muchos mamíferos depredan organismos dulceacuícolas, pero tan sólo unos pocos insectívoros y roedores muroides del Viejo Mundo son comparables en tamaño y hábitos a los ictiominos. La musaraña acuática de Norte América (*Sorex palustris*), tres géneros de musarañas acuáticas de Eurasia (*Chimarrogale, Neomys* y *Nectogale*), el desmán pireneo (*Galemys pyrenaicus*), pequeños tenrecs acuáticos africanos (*Micropotamogale*), un ratón acuático africano (*Colomys goslingi*), el tenrec acuático de Madagascar (*Limnogale mergulus*) y tres muroides acuáticos de Nueva Guinea (*Crossomys moncktoni, Hydromys habbema* y *H. hussoni*); todos tienen un peso promedio de aproximadamente 200 gramos o menos y depredan principalmente los artrópodos acuáticos en los riachuelos. Estos mamíferos se asemejan el uno al otro y difieren de los taxa no acuáticos estrechamente relacionados con ellos en muchos caracteres externos y craneales. Dichos caracteres también distinguen a los ictiominos de muroides no acuáticos del Nuevo Mundo y representan un patrón consistente de adaptaciones morfológicas a la carnivoría semiacuática. Tales adaptaciones pueden ser agrupadas en complejos funcionales dentro de los cuales (y quizás entre los que) las expresiones de caracteres aparecen correlacionadas. Pero las comparaciones cualitativas y los pocos datos disponibles sobre los habitats y la dieta para la mayoría de los insectívoros semiacuáticos y muroides semiacuáticos del Viejo Mundo no proporcionan una base satisfactoria para un análisis más sofisticado del patrón evolutivo.

8. La radiación adaptativa de los ictiominos puede ser descrita en términos de los patrones interespecíficos de variación métrica craneal resumidos en (3) junto con los resultados de análisis estadísticos similares de las dimensiones externas y del esqueleto postcraneal. Los valores de los factores de tamaño craneal y postcraneal están correlacionados a través de las especies ictiominas, tal como se esperaría. Pero la forma craneal y las proporciones postcraneales están también altamente correlacionadas de manera tal que las especies con incisivos delgados, molares grandes y neurocráneos globosos también tienen patas traseras grandes, huesos proximales de los miembros cortos y colas largas. La correlación entre la forma craneal y las proporciones postcraneales no es un artefacto estadístico y no refleja la propincuidad al ancestro común. En cambio, se hipotetiza que la covarianza ecológica resultante del efecto de los gradientes altitudinales sobre la velocidad de la corriente y sobre la composición de la fauna de artrópodos en los riachuelos ha impuesto fuertes restricciones adaptativas en la evolución del esqueleto ictiomino. Las correlaciones de los valores de la forma craneal y postcraneal con la altitud son significativas y consistentes en signo con la interpretación funcional de los factores y con el conocimiento de los gradientes ecológicos. La hipótesis predice correctamente distribuciones ecomorfológicas convergentes en los roedores hidróminos de Nueva Guinea.

Las reconstrucciones parsimónicas de la evolución morfométrica ictiomina junto con las comparaciones con los grupos de referencia (outgroups) sugieren un morfotipo ancestral similar a las especies vivientes de *Neusticomys* y un habitat ancestral en las tierras bajas o vertientes de piedemonte en la América del Sur tropical. La evolución de los ictiominos ha sido caracterizada en gran parte por la divergencia morfológica de linajes geográficamente co-existentes. La convergencia en las morfologías derivadas de los esqueletos entre los linajes centro- y sudamericanos se atribuye a invasiones independientes de los habitats de montaña.

9. En su diversidad ecológica y dominancia faunística, los muroides neotropicales se asemejan a otros grupos de vertebrados simpatricos tales como peces caracoides y siluroides, ranas hílidas y leptodactílidas, aves tiranoides, y murciélagos filostomátidos. Comparaciones cuidadosas de estas radiaciones adaptativas pudieran revelar factores comunes causales en sus historias evolutivas o pudieran revelar diferencias de importancia para las teorías respecto al origen, distribución y mantenimiento de la diversidad biológica en los trópicos del Nuevo Mundo. Si se van utilizar los muroides neotropicales en tales comparaciones útiles, todavía falta mucha información básica sobre su sistemática e historia natural que deberá ser proporcionada por futuras investigaciones.

# INTRODUCTION

Ichthyomyines are muroid rodents that prey on aquatic insects, crustaceans, and other small animals in tropical forest streams throughout most of Central America and northern South America. The first ichthyomyine specimens sent to European museums were described by Winge (1891) and Thomas (1893) who identified many of the morphological adaptations to semiaquatic carnivory that characterize these unusual rats and mice. All ichthyomyines have small eyes, small external ears, partially webbed hindfeet fringed with specialized hairs, stiff mystacial vibrissae provided with enlarged sensory nerves, a distinctive dentition, and simple digestive tracts. The current taxonomy (summarized by Honacki et al., 1982) arranges 14 ichthyomyine species in five genera: *Anotomys* Thomas, 1906 (including *A. leander* and *A. trichotis*); *Daptomys* Anthony, 1929 (*D. oyapocki, D. peruviensis, D. venezuelae*); *Ichthyomys* Thomas, 1893 (*I. hydrobates, I. pittieri, I. stolzmanni*); *Neusticomys* Anthony, 1921 (*N. monticolus*); and *Rheomys* Thomas, 1906 (*R. hartmanni, R. mexicanus, R. raptor, R. thomasi, R. underwoodi*).

Ichthyomyines are members of a large Neotropical muroid fauna that is part of the New World subfamily Sigmodontinae (Carleton and Musser, 1984); in South America alone, 52 genera and about 250 muroid species are presently recognized. To Simpson (1950), South American muroids were just "field mice" that exhibit "a low degree of regional differentiation" whose northern ancestors invaded the continent over a Panamanian landbridge in the late Pliocene or early Pleistocene. Other mammalogists, however, have emphasized the wide divergence in habitats, diets, and anatomical characters among extant Neotropical muroids and cite complex patterns of South American endemism as evidence for older episodes of adaptive radiation in situ (Hershkovitz, 1966, 1972; Reig, 1980, 1984).

While the absolute chronology of Neotropical muroid evolution is unlikely to be established in the absence of compelling fossil evidence, the patterns of cladogenesis and adaptation responsible for Neotropical muroid diversity can be inferred from morphological and ecological comparisons among members of the living fauna. Ichthyomyines provide the opportunity to analyze such data within a small group of related species that utilize a narrow range of habitats and food resources and for which the adaptive context of morphological evolution might therefore be demonstrated. To date, however, no comprehensive survey of ichthyomyine anatomy has been attempted, the evolutionary relationships among ichthyomyine lineages have not been analyzed, and only a few notes have been published to substantiate inferences about ichthyomyine ecology.

In May and June of 1978 and from November 1979 to August 1980 I trapped ichthyomyines in Venezuela and Ecuador to obtain complete specimens for dissection and to collect information about their natural environments and diets. Those materials, together with other specimens and fieldnotes in American and European museums, form the basis of this report. Here I describe anatomical characters that vary among ichthyomyines or that distinguish ichthyomyines from other members of the subfamily Sigmodontinae. I define the tribe Ichthyomyini and revise the taxonomy of ichthyomyine species and genera. I analyze skeletal morphometric variation within ichthyomyine populations and suggest functional interpretations for size-independent interspecific patterns. I report analyses of stomach contents, provide ecological descriptions of collection localities, and summarize information from other sources to identify consistent similarities and significant differences among ichthyomyine diets and habitats. I discuss the evidence for ichthyomyine monophyly and evaluate several alternative estimates of ichthyomyine phylogenetic relationships. I document resemblances in habitat, diet, and morphology between ichthyomyines and unrelated small mammals from other zoogeographic regions and consider the evolutionary implications of such ecomorphological correlations. Finally, I examine patterns of skeletal morphometric integration in a cladistic framework and propose a hypothesis of ichthyomyine adaptive radiation that is consistent with available ecological information, functional analyses, and outgroup comparisons. I conclude by reviewing what is presently known about muroid evolution in the New World tropics and suggest how future research on these rodents might usefully contribute to causal hypotheses about Neotropical vertebrate diversity.

## ACKNOWLEDGMENTS

Throughout a year of camping and collecting in South America I was accompanied and assisted by Paul Kaarakka. Together we trapped, described, photographed, and labeled specimens, working by lamplight at our notes and preparations late into the tropical nights. Many of Paul's photographs illustrate this and other publications or manuscripts based on our joint fieldwork in 1979 and 1980.

In Ecuador and Venezuela we enjoyed the friendly assistance and hospitality of Amelia Diaz de Pascual, Pedro Durant, Francisco Fernandez Y., Sergio Figuerroa, Beth Goldstein, Francisco Mago L., Gonzalo Medina P., Edgardo Mondolfi, Miguel Moreno E., Juhani Ojasti, Fernando Ortiz C., Jaime Pefaur, Roger Pérez, and Oswaldo Reig. The Instituto de Zoología Tropical (Universidad Central de Venezuela, Caracas), the Groupo de Ecología Animal (Universidad de los Andes, Mérida), and the Museo Ecuatoriano de Ciencias Naturales (Quito) extended their sponsorship and logistic support during fieldwork from 1978 to 1980. Collecting and export permits were provided by the helpful personnel of the Ministerio del Ambiente y de los Recursos Naturales Renovables (Venezuela) and the Ministerio de Agricultura y Ganadería (Ecuador).

Paul and I were cordially received in many rural settlements throughout Ecuador and Venezuela. *Campesinos* and *indígenas* were everywhere our hosts, and theirs was a simple and spontaneous hospitality; they forgave us our gringo eccentricities and invited us to share their homes, their meals, and the daily rituals of their communal life. *A Ustedes estamos muy agradecidos.*

This research would have been impossible without the financial generosity of many institutions. From 1976 to 1980 I was partially supported by a National Science Foundation Predoctoral Fellowship, and, in 1982, by a Predoctoral Fellowship provided by the Horace H. Rackham School of Graduate Studies at the University of Michigan. In addition, funds to support field and museum research were provided by (in roughly chronological order) the Society of Sigma Xi, the Department of Mammalogy of the American Museum of Natural History, the National Science Foundation (DEB7910189), the Horace H. Rackham School of Graduate Studies of the University of Michigan, the American Society of Mammalogists, the University of Michigan Museum of Zoology, the Explorer's Club of New York, and (inadvertantly) the Department of Naval Research and the North Atlantic Treaty Organization. During the final preparation of this manuscript I was supported by postdoctoral fellowships at the Smithsonian Institution and at the American Museum of Natural History.

Numerous museums in Venezuela, the United States, and Europe (listed with their abbreviations in Materials and Methods) loaned me many valuable specimens and tolerantly extended those loans for several years; the generosity of their curators and the professional competence of their technical personnel are gratefully acknowledged. For their hospitality and assistance when I visited their respective institutions I especially wish to thank Mike Alberico (Universidad del Valle, Cali), Mogen Andersen and Hans Baagøe (UZM), Syd Anderson (AMNH), Ian Bishop (BMNH), Mike Carleton (USNM), Carl Edelstam (NHRS), Charles Handley (USNM), Jean Ingles (BMNH), Guy Musser (AMNH), Francis Petter (MNHN), and Chris Smeenk (NHRS).

Much in these pages is owed to many at (or from) the University of Michigan where this monograph first took shape as my doctoral thesis: to Donald W. Tinkle, whose encouragement and example meant more to me than I knew while he was alive; to Phil Myers, my thesis chairman, who provided unfailing support, advice, and comaraderie throughout the course of my graduate studies; and to Mike Carleton, one of the finest mentors that any young mammalogist could hope to have as a friend. For their dedication to clear thinking and for the imagination that each brings to bear on his own research I am also grateful to other gifted teachers: George Estabrook, Phil Gingerich, Emmet Hooper, Arnold Kluge, Guy Musser, Gerry Smith, and Bob Storer.

This text has benefited from the critical attention of colleagues who read all or parts of it: M. D. Carleton, G. K. Creighton, L. H. Emmons, A. L. Gardner, P. D. Gingerich, L. R. Heaney, D. J. Klingener, L. F. Marcus, G.

G. Musser, P. Myers, J. M. Ryan, G. R. Smith, R. W. Storer, D. O. Straney, and R. E. Strauss. J. Felsenstein and F. L. Bookstein also suggested several improvements. Of course, none of these individuals are responsible for errors in fact or interpretation that may remain. Isa Torrealba and Patricia Escalante translated my difficult abstract into comprehensible Spanish. Lauren Wilson, Muriel Williams, Pat Brunauer, and Christine Iaderosa patiently word-processed many drafts of the final manuscript. Paul Kaarakka photographed all of the habitats illustrated here and Peter Goldberg photographed most of the skulls. Joan Whelan and Andrew Simon produced all of the SEM images except figures 13, and 56–61. Jim Ryan drew figures 5 and 6, Pat Wynne drew figures 11, 14, 15, 18, 19, 21–24, 26, 72, and 94, and Karen Klitz is responsible for figures 8–10.

Lastly, I record a very special acknowledgment to Alison Adams, Sue Campbell, Andrea Pesce, Marcia Robertson, and Ken Creighton; whatever may be of lasting value here owes much to their support and affection.

# MATERIALS AND METHODS

## SPECIMENS

This study is based on skins, skulls, postcranial skeletons, and fluid-preserved specimens that belong to the following institutional collections: the American Museum of Natural History, New York (AMNH); the British Museum (Natural History), London (BMNH); the Colección de Vertebrados, Universidad de Los Andes, Mérida, Venezuela (CVULA); the Field Museum of Natural History, Chicago (FMNH); the Fort Worth Museum of Science and History, Fort Worth (FWMSH); the Departamento de Microbiología, Universidad del Valle, Cali, Colombia (HTC); the Los Angeles County Museum, Los Angeles (LACM); the Museum of Zoology of Louisiana State University, Baton Rouge (LSU); the Museo de Biología, Universidad Central de Venezuela, Caracas (MBUCV); the Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); the Museum National d'Histoire Naturelle, Paris (MNHN); the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); the Museo de Zoología, Universidad Politécnica, Quito (MZUP); the Natural Historie Riksmuseet, Stockholm (NHRS); the Academy of Natural Sciences, Philadelphia (PANS); the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); the Texas Cooperative Wildlife Collection, College Station (TCWC); the University of Michigan Museum of Zoology, Ann Arbor (UMMZ); the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); and the Universitets Zoologiske Museum, Copenhagen (UZM).

## EXTERNAL AND CRANIAL MEASUREMENTS

I measured Total Length (TL), Length of Tail (LT), Length of Hind Foot (HF), and Length of Ear (Ear) on freshly caught specimens following the standard American procedure described by Hall (1981: 1125–1126); values were recorded to the nearest millimeter (mm). External measurements recorded by other collectors were used only if the standard American procedure was known to have been followed by them. Length of Head and Body (HBL) was obtained by subtracting Length of Tail from Total Length. When study skins were unaccompanied by measurements of known derivation, I measured the dried hindfeet with dial calipers. Undistorted dried hindfeet yield measurements that are usually within 1 mm (plus or minus) of values determined from fresh material.

I measured crania with dial calipers and recorded measurement values to the nearest 0.1 mm. The set of cranial measurements that I employ throughout this monograph are illustrated in figures 1 and 2 and defined below following their standard abbreviations.

CIL, Condylo-Incisive Length: Measured from the exposed greater curvature of an upper incisor

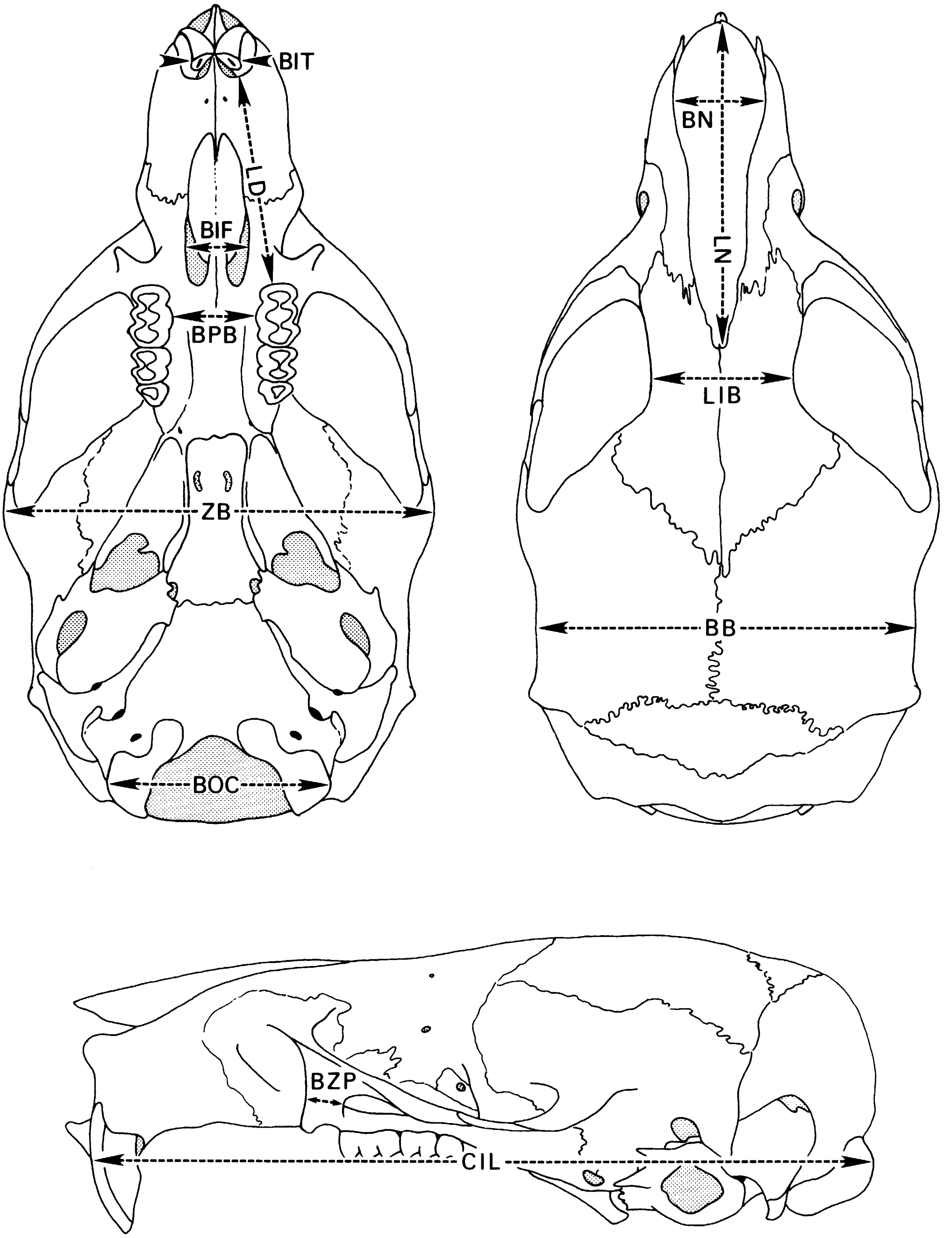


Fig. 1. Limits of 12 cranial and dental dimensions. See text for definitions and explanations of abbreviations.

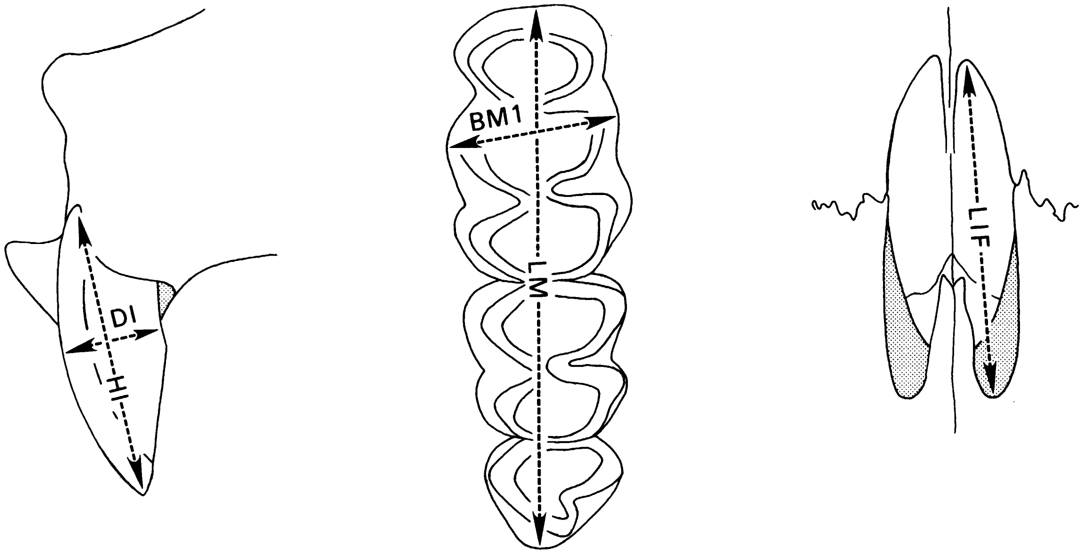


Fig. 2. Limits of five additional cranial and dental dimensions. See text for definitions and explanations of abbreviations.

to the articular surface of the occipital condyle on the same side.

LD, Length of Diastema: Measured from the crown of the first maxillary molar to the exposed lesser curvature of the upper incisor on the same side.

LM, Length of the Maxillary Molars: The occlusal length of the maxillary molar series.

LIF, Length of the Incisive Foramina: The inside length of one incisive foramen.

BIT, Breadth of the Incisor Tips: Measured across the enameled tips of both upper incisors.

BIF, Breadth of the Incisive Foramina: The greatest inside breadth across both incisive foramina.

BPB, Breadth of the Palatal Bridge: Measured between the protocones of left and right first maxillary molars.

LN, Length of Nasals: The greatest length of either nasal bone.

BN, Breadth of Nasals: The greatest breadth across both nasal bones.

LIB, Least Interorbital Breadth: The least distance across the frontal bones between the orbital fossae.

ZB, Zygomatic Breadth: The greatest breadth across the zygomatic processes of the squamosal bones.

BB, Breadth of Braincase: Measured across the smooth lateral surface of the braincase immediately posterodorsal to the squamosal zygomatic processes.

BZP, Breadth of the Zygomatic Plate: The least distance between anterior and posterior edges of the inferior zygomatic root.

BM1, Breadth of M1: Measured across the protocone–paracone cusp pair on the first maxillary molar.

HI, Height of Incisor: The length of the chord that subtends the exposed greater curvature of an upper incisor.

DI, Depth of Incisor: The distance between greater and lesser curvatures of an upper tooth.

BOC, Breadth of the Occipital Condyles: The greatest breadth across the dorsal lobes of both occipital condyles.

## AGE CRITERIA

I used toothwear, dental eruption, basicranial suture closure, and pelage characteristics as criteria by which to judge the relative age of ichthyomyine specimens. Anatomical terms used below to define these criteria are explained elsewhere in appropriate sections of this monograph.

I recognize six stages of dental ontogeny referred to throughout the sequel as Tooth Wear Classes and abbreviated as TWC 1, TWC 2, etc.

TWC 1: M3 unerupted or unworn; successive dentine basins on M1–2 discrete, not connected by median channels of dentine.
TWC 2: M3 fully erupted and slightly worn; some (but not all) of the dentine basins on M1–2 narrowly connected by median channels of dentine.
TWC 3: M3 well worn; all of the dentine basins on M1–2 narrowly connected by median channels of dentine.
TWC 4: Dentine basins on M1–2 broadly connected by median channels of dentine, but the reentrant enamel folds still present.
TWC 5: All maxillary molars without reentrant folds; occlusal surfaces only of dentine contained by a thin enamel rim, but not worn below the widest part of the crown.
TWC 6: All upper molars worn below the widest part of their crowns.

The sphenoccipital suture is an open, transverse seam that separates the basioccipital and basisphenoid bones of young muroid rodents. Among ichthyomyines, this suture fuses completely in older animals; the basicranium between the auditory bullae then appears smooth and undivided. I also recognize an intermediate condition in which the suture is "closed," that is, no longer completely open but with persistent traces of the separation between basioccipital and basisphenoid bones.

Species of *Daptomys, Ichthyomys,* and *Rheomys* undergo at least one maturational molt from a soft, dull, and wooly immature pelage to a harder, glossy adult pelage. In *Anotomys leander, A. trichotis,* and *Neusticomys monticolus,* however, the pelages of young and old animals are alike and no distinctions between immature and adult pelts are apparent.

Ontogenetic information about individual specimens or series of specimens is usually abbreviated throughout the text. Toothwear classes are designated by their assigned numbers (1–6, above), basicranial suture closure by letters (o = open, c = closed, f = fused), and pelage by letters (i = immature, a = adult, n = no distinction). Abbreviated ontogenetic data are provided with toothwear, suture closure, and pelage designations separated in that order by diagonal strokes. Thus, 5/f/a describes a specimen in toothwear class 5 with a fused sphenoccipital suture and in adult pelage.

## COMPUTATIONS

All of the statistical analyses that I report were implemented using the Michigan Interactive Data Analysis System developed by the Statistical Research Laboratory of the University of Michigan, Ann Arbor. Except where otherwise indicated, the statistical procedures used herein are described by Conover (1980), Dixon and Massey (1969), and Morrison (1976).

The computer program that I used for character compatibility analysis was CLINCH (Version 3.1), written by K. L. Fiala and G. F. Estabrook; for probability analysis of compatible characters I used COMPROB, written by C. A. Meacham. All numerical parsimony procedures were executed using PAUP (Version 2.3), written by D. L. Swofford.

## ANATOMICAL METHODS

Most of the dissections reported below are of specimens originally fixed in 10 percent buffered formalin and subsequently transferred to 70 percent ethanol. Osteological materials are mostly dermestid-beetle-prepared skeletons. Phalli were cleared in 2 percent potassium hydroxide, stained with Alizarine Red S, and stored in glycerine following the protocols described by Hooper (1958) and Lidicker (1968).

Anatomical descriptions of masticatory muscles required more involved preparations. Masticatory muscles were usually dissected from whole heads that had been fixed in formalin and stored in ethanol, but specimens of *Rheomys mexicanus* were originally preserved in strong indigenous beverages. Determinations of fiber direction, aponeurotic attachments, and other details were facilitated by frequent use of Weigert's variation of Lugol's Solution (Bock and Shear, 1972). Areas of origin and insertion of muscle fibers and aponeuroses were recorded on camera lucida drawings of beetle-prepared crania and mandibles; little variation was noted between replicated dissections. In all of the heads dissected, care was taken to determine that the jaw had been fixed in its usual resting position, that is, with the mandibular molars displaced anteroventrally about a millimeter or less from centric occlusion.

All of the masticatory muscles from both sides were carefully freed from their bony attachments and stored separately in 70 percent ethanol. Wet weights of the dissected muscles were determined to the nearest 0.001 g using a Mettler P163 precision balance: each muscle was removed from preservative, blotted dry between paper towels, weighed, and returned to the preservative; this procedure was repeated three times for each muscle and the mean value of the three weights recorded. Wet weights reported below are usually averages of left and right side muscles.

After determination of wet weights, all of the masticatory muscles from one side (right or left) of each of the examples of *Anotomys leander* and *Ichthyomys hydrobates tweedii* (a total of six specimens) were immersed separately in 30 percent nitric acid for 48 hours in order to dissolve connective tissues; the acid was removed by pipette and replaced with 50 percent glycerine (10 parts glycerol: 7 parts ethanol: 3 parts distilled water). The internal architecture of the muscles was determined from these softened preparations. Fiber lengths were measured using an ocular micrometer mounted in a Wild M-5 stereomicroscope. Finally, all of the measured fibers were returned to the acid-digested, glycerine-stored preparations. These preparations, composed of just the contractile material of each muscle, were then suspended in absolute ethanol, filtered onto preweighed discs of Milipore filter paper, and washed again with absolute ethanol in a Milipore vacuum filter; the washed fibers were then oven-dried at 95–100°C for 6 hours. Dry weights were determined to the nearest 0.0001 g on a Christian Becker Model EA-1 torsion balance.

## HABITAT DESCRIPTIONS

At each locality where I collected ichthyomyines I recorded information about local topography and phytophysiognomy. Capitalized vegetation formation names (e.g., Lower Montane Rain Forest) are defined by Grubb (1977). I found Holdridge's Life Zone Model (Holdridge, 1967) to be unusable in the field for the same reasons explained by Myers (1969).

Data on the physical characteristics of streams were obtained from standardized 100 m surveys centered at the location where the first ichthyomyine specimen was trapped in each watercourse. At this point and at each of 10 stations (5 upstream and 5 downstream) spaced 10 m apart, stream width and depth at midstream were measured. The frequency of riffles, pools, and cascades (as defined by Bishop, 1973: 19–20) were noted. At each of three points along each 100 m stream survey, water velocity was measured with floats and a stopwatch. While the streams were being trapped, water temperatures were recorded daily (usually between 0600 and 0800 hours) with a pocket mercury-bulb thermometer. Dry-bulb maximum–minimum thermometers installed in shady situations at streamside provided measurements of ambient air temperatures.

Elevations were determined with a Thommen 2000 pocket altimeter; altitudes reported below are mean values of repeated observations and have a standard error of plus or minus 3–4 m.

## DIET ANALYSIS AND STREAM FAUNAL SAMPLING

Complete alimentary tracts were dissected from fluid-preserved ichthyomyines and their contents removed to 70 percent ethanol. Macroscopically distinctive prey fragments (tergites, antennae, mouthparts, legs, gills, etc.) were sorted and identified by matching them with corresponding parts of intact arthropod specimens collected from the same streams in which the rodents had been trapped (stream sampling methods are described below). After removal of these larger fragments, the finely masticated residuum in each gut was cleared in potassium hydroxide and hydrogen peroxide and stained with Alizarine Red S in order to heighten optical contrasts between vertebrate bone fragments (if present) and the nonosseous tissues of invertebrates.

Specimens of the stream benthic invertebrate fauna were collected with kickscreens (Hynes, 1961; Edmunds et al., 1976), by lifting small stones from the water and removing adherent organisms with forceps (Stout and Vandermeer, 1975), or by lifting large stones in the current and collecting the drifting organisms washed from beneath them in handnets held downstream. A consistent effort was made to sample all recognizable stream biotopes (e.g., pool bottoms, riffles, rootmats, leafpacks, cascades). Collecting was generally continued until no new kinds of organisms were encountered in many successive samples.

Taxonomic determinations of the stream arthropods I collected were provided by Richard W. Baumann (Plecoptera), Oliver S. Flint (Megaloptera and Trichoptera), Ralph W. Flowers (Ephemeroptera), Lenora K. Gloyd (Odonata), Richard W. Merrit (Diptera), John T. Polhemus (Hemiptera), and David S. White (Coleoptera).

# COMPARATIVE MORPHOLOGY

Morphological comparisons provide the primary data for taxonomic revision and phylogenetic analysis as well as the phenotypic evidence of ecological adaptations. Muroid systematics has traditionally relied on comparisons of skins, skulls, and dentitions, but the few, indefinite characters that have usually been recorded from such standard preparations of ichthyomyine specimens are an unsatisfactory basis for either classification or evolutionary hypothesis testing.

This section describes morphological characters that vary among ichthyomyine species and genera or that distinguish ichthyomyines from other muroid rodent taxa. Such useful information can be obtained from comparisons of integuments, crania, dentitions, postcranial skeletons, muscles, digestive tracts, and genitalia. Available evidence regarding the functional significance of observed morphological differences is discussed where appropriate here, or is reserved for more detailed analysis in subsequent parts of this monograph.

## EXTERNAL MORPHOLOGY

Size and General Aspect: Ichthyomyines are small to medium-size muroids. The combined length of head and body, determined from adult specimens, ranges from a little more than 100 mm for *Neusticomys monticolus* to almost 200 mm for large examples of *Ichthyomys hydrobates tweedii*; adult weights for these two species, averaging about 40 g and 120 g, respectively, also bracket the range of ichthyomyine variation.

In general appearance (fig. 3), ichthyomyines are brownish or blackish-gray rodents with short, blunt muzzles, small eyes and ears, large hindfeet, and hairy tails. Closer attention to external morphology, however, reveals many other characters that serve to distinguish members of the tribe from other muroids as well as to identify different species and genera.

Body Pelage: Adult ichthyomyines exhibit one or the other of two distinctive pelage types that differ in color, in texture, and in the kinds of hairs that compose them.

1. In species of *Daptomys, Ichthyomys,* and *Rheomys* the dorsal body pelage is brownish and consists of three kinds of hair that comprise two pelage layers: a deep, wooly underfur and a superficial, glossy overfur.

The underfur is soft to touch and appears dull and lusterless. This pelage layer is composed of fine, wavy, and densely spaced wool hairs. Wool hairs are gray for most of the length of each hair, but have brownish tips. The wool hairs of the underfur form a thick, cohesive felt beneath the glossy overfur of highland species of *Rheomys* and *Ichthyomys.* In species of the lowland genus *Daptomys* and in lowland representatives of *Rheomys* and *Ichthyomys,* however, the underfur is shorter and less dense.

The overfur consists dorsally, of two kinds of hairs, buffy-banded awns and dark guard hairs. Awns are longer but fewer than the wool hairs of the underfur. The basal ¾ or more of each awn is fine and straight (not wavy like the wool hairs), but near the surface of the underfur each awn is bent caudally so

Fig. 3. *Ichthyomys stolzmanni.* Reproduced from Thomas's (1893) color plate XXVIII.

that the distal part of the hair comes to lie almost flat over the wool hairs. The slender basal part of each awn is gray, but the exposed distal portion, often flattened, is brownish with a broad band of bright buff across its middle. Guard hairs are longer than awns. Like awns, guard hairs have slender grayish basal portions within the underfur, but the thickened distal part of each guard hair is not flattened and is entirely dark brown or blackish.

The unruffled dorsal surface of ichthyomyine pelages of this type appears grizzled because of the mixture of buffy-banded awns and darker guard hairs in the overfur. Variation in the proportion of awns to guard hairs, in the width of the buffy band on individual awns, and in the darkness of the guard hairs all contribute to the overall hue of the dorsal pelage. Because the emergent distal portions of both awns and guard hairs are highly polished, the unruffled overfur of a fresh pelage appears glossy and glitters in bright light.

The pelage is countershaded (washed ventrally with white or silver-gray) in species of *Ichthyomys* and *Rheomys,* but in *Daptomys* the venter is brownish and scarcely paler than the dorsum.

The immature pelage that precedes the definitive adult type described above is softer and uniformly dark gray-brown. Typically, immature pelts are not glossy because wool hairs predominate in the pelage; guard hairs are sparsely distributed and there is no well-defined overfur. The two specimens of *Daptomys venezuelae* (AMNH 69907, 69908) on which Anthony (1929) based his description of that genus and species are both young animals (TWC 2) in just such a dull, wooly, immature pelage; Anthony was therefore unable to appreciate the similarities among the mature coats of *Daptomys, Ichthyomys,* and *Rheomys* detailed above. Instead, he emphasized resemblances in texture and color between the (immature) coats of his specimens of *D. venezuelae* and adult skins of *Neusticomys monticolus,* a species whose very different mature pelage is described below.

2. *Anotomys leander, A. trichotis,* and *Neusticomys monticolus* exhibit a distinctive adult pelage that is composed only of a thick, velvety pelt of dark wool hairs among which are scattered many long, fine, blackish guard hairs; the pelage does not have the layered aspect described for the preceding type. When fresh, these pelts are dull blackish-gray dorsally, a somber hue that is unrelieved by any tinge of brown. The venter of *N. monticolus*

is gray, only a little paler than the upperparts; *A. leander* and *A. trichotis* have silver-washed venters.

The distinctive blackish-gray dorsal coloration of ichthyomyines with this pelage type is unmistakable in fresh skins, but these coats fade with age to a dull shade of rusty brown. Consequently, literature descriptions of old pelts of *Anotomys leander, A. trichotis,* and *Neusticomys monticolus* often erroneously attribute reddish or brownish tints to the fur of these mice. Anthony (1921), for example, described the color of the type of *N. monticolus* as "uniform clove-brown (Ridgway)," but the specimen, collected in 1916, was five years old at the time that Anthony described it. By contrast, the type specimen of *A. leander* was only a year old when Thomas (1906) described its dorsal coloration as "uniform dark slaty (near 'slate black')." That same specimen was brownish-gray seventy-six years later, however, and contrasted sharply in color with the slaty-black dorsal pelage of recently collected specimens that I brought to the British Museum to compare with it in 1982. Choate (1970) described apparently similar fading effects in dried shrew skins.

The pelage of immature *Neusticomys monticolus, Anotomys leander,* and *A. trichotis* is indistinguishable from the adult condition.

PHILTRUM: In most muroid rodents, and in all sigmodontines with the exception of a few ichthyomyine species, the hairy muzzle is divided by a groove of naked skin, the philtrum, that extends down the midline from the rhinarium to the margin of the upper lip (see Brown, 1971: fig. 1). The presence of a philtrum is readily demonstrated in fresh or fluid-preserved specimens of *Daptomys, Neusticomys, Ichthyomys,* and some species of *Rheomys* by spreading apart the left and right mystacial pads to reveal this median cleft of hairless, elastic epithelium. On dried skins the philtrum can be seen as a hard, brown strip of naked tissue unless the upper lip has been carelessly cut or grossly distorted in preparation. The philtrum is broad and conspicuous in *Daptomys* and *Ichthyomys,* but narrower and less obvious in species of other genera in which it occurs. *Anotomys leander, A. trichotis, Rheomys underwoodi,* and *R. mexicanus* lack a philtrum; in these ichthyomyines the muzzle is entirely hairy and undivided by naked tracts of skin.

PINNAE: Ichthyomyine pinnae are small, rounded, and well-haired—or they are absent. The pinnae are largest (visible above the fur on the side of the head) in *Neusticomys monticolus, Daptomys, Ichthyomys* (see fig. 3), and some species of *Rheomys.* Even among these ichthyomyines, however, the pinnae are diminutive by comparison with the external ears of other sigmodontines. In *Anotomys trichotis, Rheomys mexicanus,* and *R. underwoodi,* smaller pinnae are buried in the fur of the side of the head and are not visible above the unruffled surface of the pelage. Definitive pinnae are absent altogether in *Anotomys leander*; only a low ridge of sparsely haired skin encircles the posterior and dorsal margins of the external auditory canal in this species.

VIBRISSAE: Of the primitive complement of mammalian vibrissae described and illustrated by Beddard (1902), Pocock (1914), Brown (1971), and Brown and Yalden (1973), only the mystacial, submental, interramal, superciliary, and carpal groups are represented among ichthyomyines. Genal, subocular, anconeal, medial antebrachial, and calcaneal vibrissae are uniformly absent.

Superciliary vibrissae, consisting of one or a few long, stiff hairs just above each eye, are always present on specimens of *Anotomys leander,* but are consistently absent in all other ichthyomyine species. Submental vibrissae occur as a tuft of short, stiff hairs on the fleshy apex of the chin anterior to the mandibular symphysis and are present in all ichthyomyines. Interramal vibrissae are represented by one or a few long, stiff hairs arising either from a single tract on the ventral midline between the mandibular rami or from a pair of tracts flanking the midline; *Anotomys leander* alone appears to lack interramal vibrissae. Carpal vibrissae are always present as one or a few stiff hairs rooted medially at or just proximal to the wrist.

The vibrissal groups described above are all better developed in most other sigmodontines, which also possess additional kinds of vibrissae (e.g., prominent genal hairs) not found among ichthyomyines. By contrast, the mystacial vibrissae of ichthyomyines are highly developed, numerous, and morphologically distinctive. Ichthyomyine mystacial vibrissae bear greater resemblance to the stiff mystacial hairs of pinnipeds, otters, and many semiaquatic lipotyphlans (see Ling, 1977; Pocock, 1921; and Kuhn, 1964 for representative illustrations) than to those of terrestrial sigmodontines.

Mammalian mystacial vibrissae are arranged in longitudinal rows that roughly parallel the upper oral margins (Pocock, 1914; Dunn, 1958; Wineski, 1985). Among ichthyomyines these rows are widely spaced dorsally, but are arranged progressively closer ventrally, nearer the mouth. Within rows, vibrissae are more closely spaced anteriorly than behind. Therefore, the mystacial hairs are very numerous and closely spaced anteroventrally, on the upper lip beneath the rhinarium, and are few and widely spaced posterodorsally, between the rhinarium and the eye.

Within rows of mystacial vibrissae, the more posterior hairs are the longest, and the longest hairs of the entire vibrissal array are the most posterior of the middle rows. Laid back alongside the head on fresh or fluid-preserved specimens, these longest hairs extend well behind the ear. Anteriorly, the very short vibrissae of the upper lip form a dense brush of recurved bristles directed ventrally and medially toward the mouth and the upper incisors. It is the density and relative development of these anterior vibrissae of the upper lip that exhibits the greatest variation among ichthyomyine tactile hairs (fig. 4). All of the mystacial vibrissae, but especially those on the upper lip, are best developed in *Anotomys leander, A. trichotis* (fig. 4, left), *Rheomys underwoodi,* and *R. mexicanus*; species of *Ichthyomys* (fig. 4, right) and *Daptomys* have mystacial vibrissae that are sparse by comparison; *Neusticomys monticolus* and the smaller species of *Rheomys* have mystacial arrays of intermediate density.

Muroid mystacial vibrissae are each rooted in a follicle that is surrounded by a large blood sinus, sensory nerve endings, and sebaceous glands; each follicle, together with its vascular supply, mechanoreceptors, and glands, is enclosed in a capsule of collagen and elastin fibers. These vibrissal capsules are embedded in a dermal body of dense connective tissue and voluntary muscles, the mystacial pad, through which the mystacial artery and infraorbital nerve also ramify (Wineski, 1985). It is the thickness and extent of the mystacial pad supporting stiff and numerous vibrissae that is responsible for the blunt aspect of the ichthyomyine muzzle that is evident in figures 3 and 4.

MANUS: The dorsal surface of the ichthyomyine manus is covered with short hairs, but the plantar surface is entirely naked. The pollux is a diminutive digit with a rounded nail, but the remaining fingers are well developed and each bears a strong, sharp claw. Most terrestrial sigmodontines have similar forefeet in these respects, and there is, indeed, no evidence of semiaquatic specialization in the ichthyomyine hand.

Species of *Neusticomys* and *Daptomys* together with *Anotomys trichotis* have five large plantar pads, the usual muroid complement (Romankowowa, 1955; Dukelski, 1927; Tullberg, 1899), on the palm of the manus (fig. 5A). These pads consist of a distal triplet of interdigital tubercles (numbered from medial to lateral) and a proximal pair of carpal tubercles. The medial carpal pad (at the base of the pollux) is called the thenar, and the lateral carpal pad the hypothenar (Brown and Yalden, 1973). These five pads are all separate—in the living animal each has some capacity for independent movement due to the creases of elastic skin between them.

*Anotomys leander* and species of *Rheomys* have fewer separate plantar pads on their forefeet (fig. 5B). A free thenar pad and two free interdigital pads (the medialmost, 1 and 2) are readily identifiable, but a single large lateral pad is in the position usually occupied (among other species) by the hypothenar and interdigital 3. I interpret this single large, lateral pad on the manus of *A. leander* and *Rheomys* to represent a fusion between ancestrally free hypothenar and third interdigital pads. In *Rheomys mexicanus* and *R. underwoodi* the thenar pad and interdigital 1 are partly fused as well.

MAMMAE: All ichthyomyine species for which adult female specimens are known have six mammae in three pairs: one on the ventrolateral surface of the thorax behind the

Fig. 4. Frontal, dorsal, and lateral views of mystacial vibrissae of *Anotomys trichotis* (left, MBUCV I-2795) and *Ichthyomys hydrobates tweedi* (right, UMMZ 155784).

forelimbs (postaxial), one on the abdomen (abdominal), and one in the groin region between the thighs (inguinal). Three ichthyomyine species (*Daptomys oyapocki, D. peruviensis,* and *Ichthyomys pittieri*) are known only from males and their mammary complements are unknown. Six mammae have previously been reported for ichthyomyine species by Winge (1891), de Winton (1896), Hooper (1968), and Musser and Gardner (1974), but the literature also includes two erroneous ichthyomyine mammary counts. Burt and Stirton (1961) and Goodwin (1959) reported four and two mammae from *Rheomys thomasi* and *R. mexicanus,* respectively; I have examined the adult females described

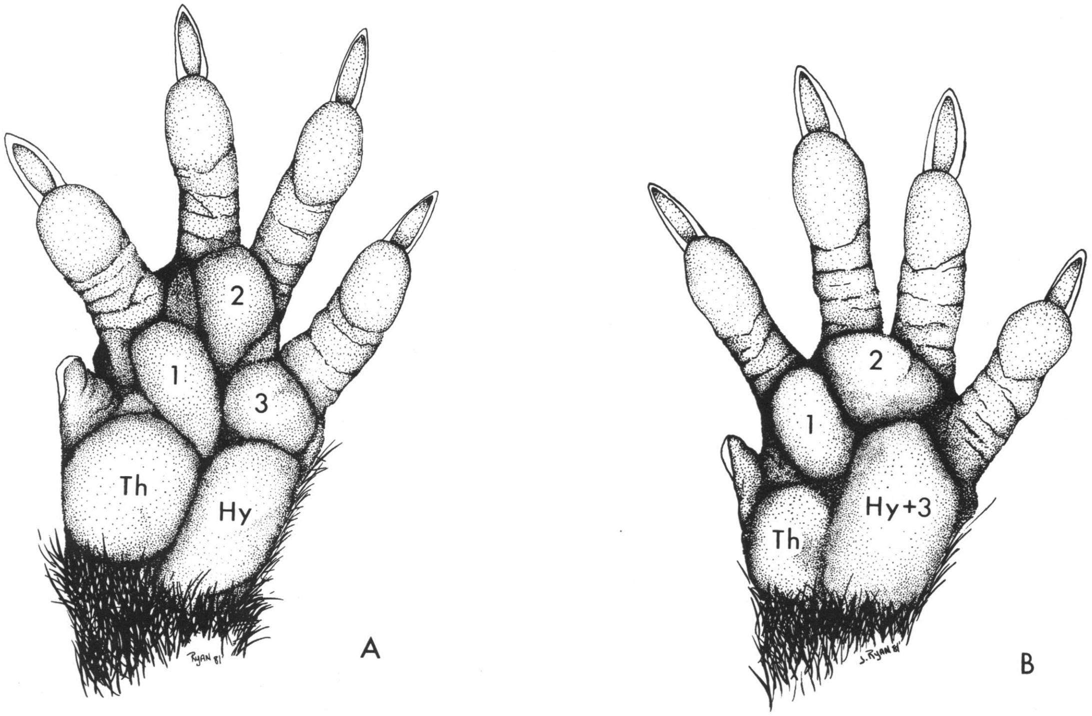


Fig. 5. Plantar view of left manus. **A,** *Anotomys trichotis* (UMMZ 156376); **B,** *Rheomys hartmanni* (UMMZ 111985). **Hy,** hypothenar pad; **Th,** thenar pad; **1,** first interdigital pad; **2,** second interdigital pad; **3,** third interdigital pad.

by these authors, however, and determined that all have six mammae in the anatomical arrangement described above.

Six is not an unusual number of mammae among other muroids although eight (four pairs) is the commoner count (Arvy, 1974). Neotropical muroids with eight mammae (e.g., *Oryzomys* and related genera) have a pectoral pair of teats in addition to the postaxillary, abdominal, and inguinal pairs represented among ichthyomyines.

PES: The ichthyomyine pes has five nonopposable, claw-bearing digits. The dorsal surface is covered with short hairs, but the plantar surface, including the heel, is entirely naked. These characteristics are common to the hindfeet of many other sigmodontines, but ichthyomyines are distinctive in most of the remaining external features of this appendage. The hindfeet of five ichthyomyine species are illustrated in plantar view in figure 6.

Along the metatarsal margins and between the digits, fringing the entire naked plantar surface of the foot, is a continuous comb of stiff hairs. This distinctive feature of ichthyomyine hindfeet is only weakly developed in *Daptomys* and *Neusticomys* (fig. 6A) but it is well developed in all other members of the tribe (e.g., fig. 6B–E). On the large hindfoot of *Rheomys mexicanus* (fig. 7), the fringing hairs may exceed 3 mm in length.

Among terrestrial sigmodontines, the three median digits (II, III, and IV) of the hindfoot are longer than the medialmost (I) and lateralmost (V) digits. Among strictly cursorial species (e.g., *Sigmodon hispidus*) digits I and V are so short that the tips of the claws on those digits do not extend more than halfway along the first phalange of the adjacent digits II and IV, respectively. In all ichthyomyines, however, the tips of the claws of digits I and V extend at least to the first interphalangeal joint of the digit adjacent to each. In *Daptomys* and *Neusticomys* (fig. 6A) the hindfoot is narrow, the outside digits (I and V) extend

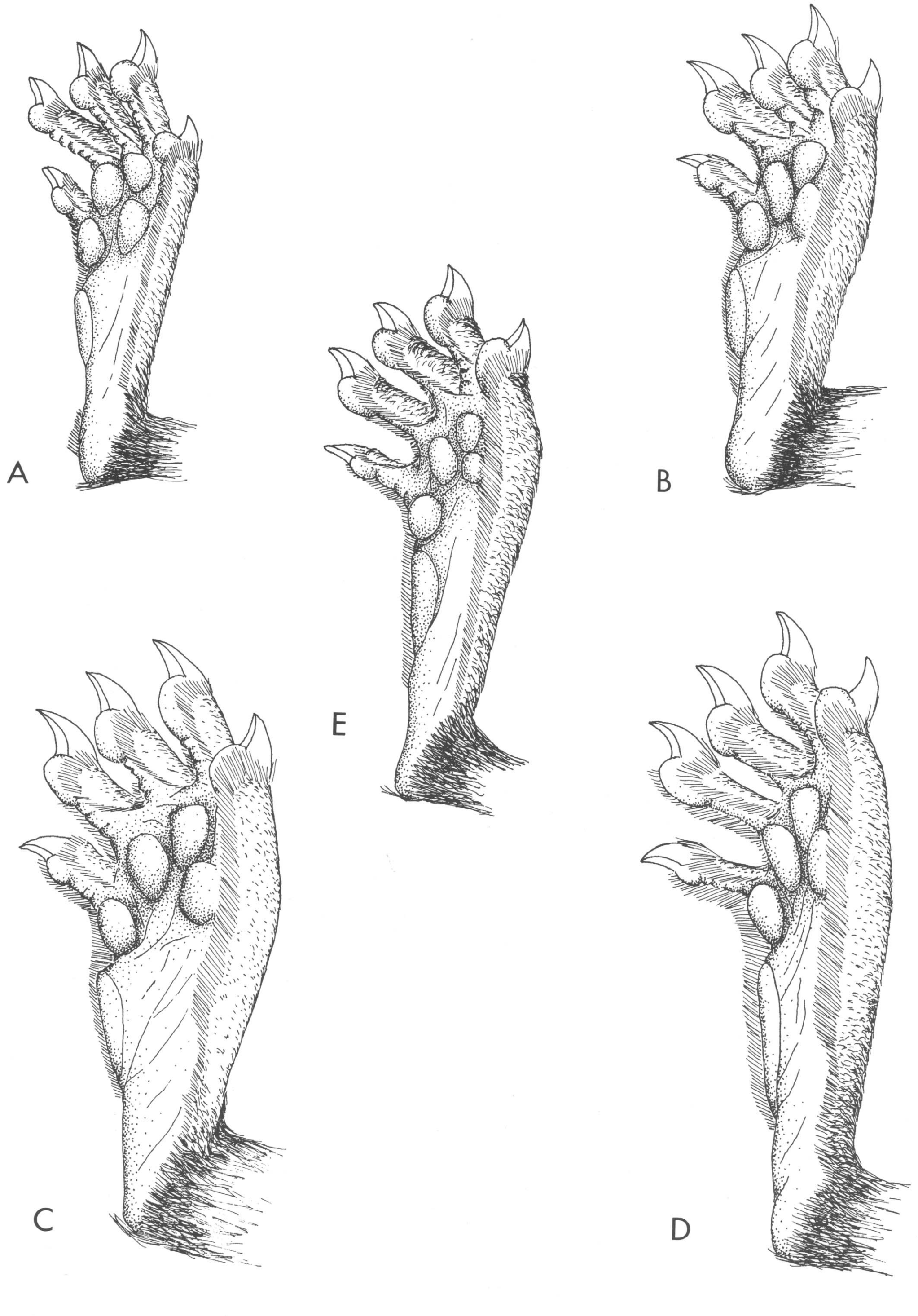


Fig. 6. Plantar view of left pes. **A,** *Neusticomys monticolus* (UMMZ, 155790); **B,** *Rheomys hartmanni* (UMMZ 111985); **C,** *Ichthyomys hydrobates tweedii* (UMMZ 155782); **D,** *Anotomys leander* (UMMZ 126295); **E,** *Anotomys trichotis* (UMMZ 156376).

just to or only a little beyond these limits, and the ancestral disparity in length between the middle three and two outside toes is still obvious. In all other ichthyomyines (fig. 6B–E), however, the hindfoot is broad and the claws of digits I and V extend well beyond the first interphalangeal joints of their neighbors.

Webbing occurs between digits II, III, and IV of the pes in all ichthyomyines. In *Anotomys leander, A. trichotis, Daptomys, Ichthyomys,* and *Neusticomys,* webbing does not extend quite to the first interphalangeal joints of digits II–IV; in these taxa, digits I and V are usually free of conspicuous webs. Webbing is best developed in species of *Rheomys* in which webs between digits II–IV extend fully to or just beyond the first interphalangeal joints; digits I and V are also connected by small webs to neighboring digits II and IV.

In most sigmodontines there are six plantar tubercles on the hindfoot, consisting of two tarsal pads and four interdigital pads. All ichthyomyines lack a definitive hypothenar (lateral tarsal) pad, but some specimens of *Daptomys venezuelae* together with the holotype of *D. oyapocki* exhibit a small, indistinct tubercle lateral to the thenar (medial tarsal) pad that may correspond to the hypothenar of other sigmodontines.

When relaxed, the ichthyomyine pes assumes a characteristically flattened, pronated configuration (fig. 7). From manipulation of the joints of fresh specimens, it is apparent that the lateral margin forms the leading edge as the hindfoot is flexed and drawn forward in the recovery stroke of swimming; the folded digits and hairy fringes contribute to a fusiform cross section in this attitude. When the pes is extended, the digits are unfolded and spread, stretching the webbing between them, and the hairy fringes expand to increase the effective propulsive surface. Photographs of living specimens of other semiaquatic mammals with similar hindfeet (e.g., Niethammer, 1970: Hutterer and Hürter, 1981) illustrate convergent functional modifications in action.

TAIL: Muroid tails are usually covered with conspicuous epidermal scales arranged in encircling rings from base to tip. Such tails appear naked, but three bristlelike hairs emerge from beneath the posterior margin of each scale to provide a sparse caudal pelage that may be largely tactile in function. Ichthyomyine tails, by contrast, are densely covered with longer hairs and do not have a naked appearance; faint scutulation is sometimes visible through the thinner caudal pelage of *Daptomys* and *Neusticomys,* but in the remaining genera definitive epidermal scales are not evident even under high magnification. Caudal hairs are densest ventrally, and the midventral hairs are conspicuously longer than the hairs on the dorsal and lateral surfaces of the tail. In all ichthyomyines the midventral caudal hairs are longest and most densely concentrated distally; in *Anotomys leander, A. trichotis, Rheomys mexicanus,* and *R. underwoodi* these stiff, compacted hairs form a distinct midventral keel along the distal one-half to one-third of the tail.

Fig. 7. Plantar view of left pes of *Rheomys mexicanus* (AMNH 205313).

## DENTITION

INCISORS: Thomas (1919) proposed a terminology for rodent incisor morphology based on the anterior angle that the chord of the exposed greater curvature of the tooth makes with the occlusal plane of the molars. Rodent upper incisors are termed opisthodont when this angle is less than 90°, orthodont when this angle is about equal to 90°, and proodont when the angle exceeds 90°. Ichthyomyine incisors approach the orthodont condition and contrast with the commoner, more strongly opisthodont configuration of upper incisors among other muroid species.

The tips of ichthyomyine upper incisors usually wear to divergent lateral points such that the juxtaposed cutting edges of both teeth form an inverted-V-shaped blade in frontal view (for pertinent illustrations of dental characters see taxonomic accounts and functional morphological discussions in subsequent sections of the text). The expression of this unusual wear pattern is best developed in ichthyomyine species with broad incisors whose anterior, enameled surfaces are inclined medially, toward the midsagittal plane. Species of *Ichthyomys* exhibit this morphology most clearly. Ichthyomyines with narrower incisors sometimes develop sharp lateral points on these teeth but the anterior, enameled surfaces are not inclined medially; species of *Anotomys* and *Rheomys underwoodi* have very slender incisors of this type while other ichthyomyine taxa usually exhibit intermediate morphologies.

The shapes of ichthyomyine lower incisors covary with the upper teeth. In species with broad upper incisors whose stout cutting edges are provided with sharp lateral points, the lower incisors are thick and strongly recurved. By contrast, in species with slender, less robust upper incisors, the lower teeth are procumbent, fine, and delicate.

MOLARS: Most ichthyomyines have three upper and three lower molars, but the unique specimen of *Daptomys oyapocki* lacks upper and lower third molars (Dubost and Petter, 1978). Left and right maxillary molar rows are always parallel.

The first molars are the largest in both upper and lower dentitions, averaging 50–57 and 41–50 percent of the maxillary and mandibular toothrows, respectively. The second molars are appreciably smaller, with maxillary and mandibular teeth averaging 31–34 and 33–36 percent of their respective series. Third upper molars are much the smallest teeth in the maxillary dentition, ranging from 16–21 percent of the toothrow. Lower third molars vary considerably in relative size, from 26–30 percent of the mandibular toothrow in some species of *Rheomys* and *Ichthyomys* to 20–21 percent in the remaining genera. Although the third molars of some ichthyomyines are relatively small by comparison with the size of these teeth in many other sigmodontines, ichthyomyines are not diagnosable on the basis of dental proportions alone.

Table 1 contains summary statistics for the molar dimensions of 21 *Rheomys thomasi* from Mt. Cacaguatique, El Salvador. Dental measurements of males and females overlap completely in this as in all other ichthyomyine samples I have measured, so I pooled the sexes for analysis. Ichthyomyine molars have closed roots and, once formed, do not grow further; measurements of individual teeth are therefore not subject to ontogenetic variation except by abrasion. Coefficients of variation are very small (less than 3.0) for total lengths of the maxillary and mandibular toothrows and for lengths of the first upper and lower molars. Third molars, upper and lower, exhibit the highest relative variability for homologous measurements within their respective toothrows, a common pattern in muroid dentitions (Van Valen, 1962; Bader, 1965; Gould and Garwood, 1969; Carleton and Eshelman, 1979). Second molars usually exhibit intermediate levels of relative variability. Although coefficients of variation for all of the molar dimensions in this sample are small, the absolute range of variation in whole toothrow lengths provided in table 1 suggests cautious evaluation of the slight differences in these measurements that have sometimes been used to diagnose ichthyomyine species.

The occlusal design of ichthyomyine molars is simple but distinctive (see figures accompanying the taxonomic accounts, below). Each tooth consists of one or more pairs of opposite labial and lingual cusps, and each pair of opposing cusps is separated from other such pairs on the same tooth by opposite labial and lingual reentrant enamel folds. Successive cusp pairs on the same tooth are connected by median enamel ridges that are called mures on the upper teeth and murids on the lower teeth (see Reig, 1977, for explanations and illustrations of molar nomenclature). Contained between opposing labial and lingual cusps are broad, concave regions of worn dentine; these intercuspal dentine basins are separate on newly erupted teeth, but the mures (and murids) quickly wear away with age to form interconnecting median channels of dentine.

The principal cusps on ichthyomyine molars consist of protocones, paracones, metacones, and hypocones on the maxillary teeth and protoconids, metaconids, hypoconids, and entoconids on the mandibular teeth. A large anterocone contributes two additional cusps to the first upper molar and a relatively smaller anteroconid one or two small cusps to the lower first molar, but other enameled structures that often complicate the occlusal surfaces of sigmodontine molars (Reig, 1977) are inconspicuous or absent in ichthyomyine dentitions. Small anterolophs(ids), posterolophs(ids), and mesolophs(ids) are often present on newly erupted teeth, but they are usually obliterated with only slight wear; they are never so well developed as they are among pentalophodont sigmodontines.

Variation in molar morphology among ichthyomyines chiefly concerns the heights and shapes of the principal cusps. In *Anotomys leander, A. trichotis, Rheomys mexicanus,* and *R. underwoodi,* the principal molar cusps are tall and sharp when unworn; in occlusal view, the cusps appear anteroposteriorly compressed and the reentrant folds that separate successive cusp pairs are spacious. Also associated with this morphology are high, transverse enamel crests formed by the anterior margins of opposite cusps on the upper molars, and by the posterior margins of opposite cusps on the lower molars. By contrast, molar cusps in species of *Ichthyomys* are low and not very sharp, even when unworn; in occlusal view such cusps do not appear anteroposteriorly compressed, and the reentrant folds that separate successive cusp pairs are narrow. These molars typically develop broad, scooped-out basins of exposed dentine between opposite cusps, and the transverse enamel crests formed by opposing cusp margins are quickly worn away. The smaller species of *Rheomys,* together with *Daptomys* and *Neusticomys monticolus,* exhibit molar morphologies that are intermediate to the two extremes characterized above. The functional significance of these differences in molar morphology is treated elsewhere (see Mastication, Diet, and Craniodental Function).

TABLE 1
**Statistics of Molar Measurements (in millimeters) of 21 Specimens of *Rheomys thomasi thomasi*[a]**

| | Range | Mean | Standard Deviation | Coefficient of Variation |
|---|---|---|---|---|
| Lengths | | | | |
| M1–M3 | 4.15–4.60 | 4.32 | 0.11 | 2.55 |
| M1 | 2.15–2.35 | 2.25 | 0.05 | 2.43 |
| M2 | 1.25–1.50 | 1.36 | 0.06 | 4.17 |
| M3 | 0.80–0.95 | 0.87 | 0.05 | 5.86 |
| m1–m3 | 4.25–4.70 | 4.43 | 0.09 | 2.13 |
| m1 | 1.85–2.00 | 1.92 | 0.04 | 1.93 |
| m2 | 1.35–1.55 | 1.47 | 0.05 | 3.66 |
| m3 | 1.10–1.25 | 1.20 | 0.05 | 4.47 |
| Widths | | | | |
| M1 | 1.35–1.55 | 1.42 | 0.05 | 3.44 |
| M2 | 1.25–1.40 | 1.32 | 0.05 | 3.47 |
| M3 | 0.90–1.15 | 1.00 | 0.06 | 5.65 |
| m1 | 1.20–1.35 | 1.29 | 0.04 | 3.05 |
| m2 | 1.25–1.45 | 1.34 | 0.05 | 4.02 |
| m3 | 0.95–1.10 | 1.01 | 0.04 | 4.39 |

[a] From Cerro Cacaguatique, El Salvador.

The morphology of upper and lower third molars exhibits additional variation among ichthyomyines. The third maxillary molar is always small and consists at most of an anterior portion representing the paired protocone and paracone and a small posterior vestige of a presumably ancestral metacone/hypocone pair. Alternatively, the posterior remnant is absent and M3 is a simple, peglike tooth. Lower third molars are large in *Rheomys* (except *R. mexicanus*) and *Ichthyomys* (except *I. pittieri*), consisting of distinct anterior and posterior moieties representing the protoconid/metaconid and entoconid/hypoconid cusp pairs, respectively. In *R. mexicanus, I. pittieri,* and members of the remaining ichthyomyine genera, however, m3 is a much smaller tooth that consists only of the protoconid/metaconid pair with or without a small, spurlike posterior vestige of the entoconid/hypoconid lobe.

MOLAR ROOTS: The first and second upper molars each have one lingual and two labial roots; the lingual root is never divided. Small, threadlike rootlets that are not constant in occurrence or location are also present on these teeth in most specimens. The first and second lower molars each have two roots, one anterior and one posterior. Third molars, upper and lower, exhibit considerable variation in root number. Primitively, third upper molars may have had three roots and lower third molars two, as do the more anterior teeth in their respective series (Carleton, 1980); some ichthyomyines exhibit this condition, but the number of third-molar roots may vary even within local populations. Thus, upper third molars of *Ichthyomys hydrobates tweedii* from the Río Pachijal drainage of western Ecuador may have either three roots (BMNH 34.9.10.175, AMNH 71385) or two (BMNH 34.9.10.172, AMNH 71384). I have not, therefore, attempted to document possible species differences in root number for these teeth.

## HEAD SKELETON

Ichthyomyine crania exhibit substantial age-correlated variation in size and shape within local populations, and striking contrasts in cranial size and shape are also obvious in comparisons of adults of different species. The quantitative description of such variation in absolute and relative cranial dimensions is presented below in a separate account (see Cranial Morphometrics). The present section details qualitative aspects of ichthyomyine cranial morphology, i.e., those features not conveniently represented by measurements. Descriptions are organized under four headings: (A) Gross Cranial Architecture, (B) Cranial Foramina and Fenestrae, (C) Carotid Arterial Supply, (D) Auditory Bullae and Ossicles, and (E) Mandible and Hyoid.

GROSS CRANIAL ARCHITECTURE (FIGS. 8–10): The most distinctive feature of the anterior part of the ichthyomyine cranium in dorsal view is the absence of zygomatic notches. Present in all other living Sigmodontinae, the zygomatic notch is a semioval recess, open rostrally, in the anterodorsal margin of each maxillary bone (fig. 11A). The lateral border of the zygomatic notch is formed by the free dorsal edge of the zygomatic plate; the depth of the zygomatic notch is therefore greater in muroid species with wider zygomatic plates. Ichthyomyines have slender zygomatic plates that lack a free dorsal edge, and each maxillary zygomatic process therefore curves smoothly onto the dorsolateral surface of the rostrum without emargination (fig. 11B, C).

Other features of the rostral region vary among ichthyomyine species. In all members of *Ichthyomys*, the nasal bones are short and do not extend anteriorly as far as the premaxillae; the nasal orifice is therefore exposed when skulls of these rats are viewed from a dorsal perspective (fig. 11C). In all other ichthyomyines, the nasals are longer and extend anteriorly to conceal the nasal orifice from dorsal view (fig. 11B). Ichthyomyine nasals are widest anteriorly and, in most specimens, taper posteriorly to more-or-less attenuate or rounded tips at midline.

Ichthyomyine rostra vary conspicuously in relative width. Species with large incisors (*Ichthyomys, Daptomys*) have broad rostra—the flaring lateral margins of the incisor alveoli are joined with the incurving anterodorsal edges of the maxillary zygoma, and the nasolacrimal capsules (containing the nasolacrimal foramina) are concealed from dorsal view (fig. 11C). Species with slender incisors (*Anotomys leander, A. trichotis, Rheomys mexicanus,* and *R. underwoodi*) have narrower rostra from which the nasolacrimal capsules project conspicuously on either side (fig. 11B). *Neusticomys monticolus* and the smaller species of *Rheomys* have rostra of intermediate breadth: just the tips of the nasolacrimal capsules are exposed when skulls of these species are observed in dorsal view.

The interorbital region of the ichthyomyine cranium is concave- or parallel-sided, and is narrowest behind the eyes. The supraorbital margins are smoothly rounded, without squared edges or beads. In these respects, ichthyomyines contrast with other muroid species in which the interorbital margins are beaded or sharp-edged and converge anteriorly to a well-defined, genuinely interorbital constriction (see Hershkovitz, 1962: fig. 42). The interorbital region of most ich-

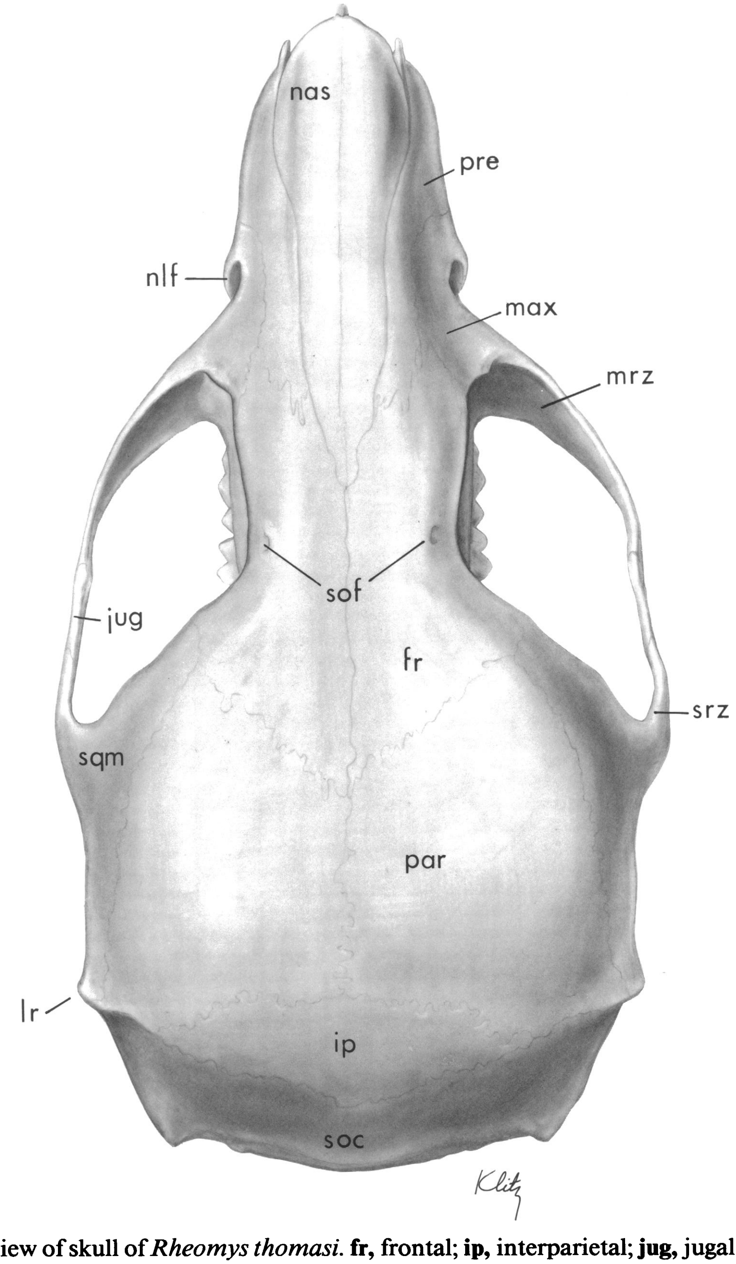


Fig. 8. Dorsal view of skull of *Rheomys thomasi.* **fr,** frontal; **ip,** interparietal; **jug,** jugal; **lr,** lambdoidal ridge; **max,** maxillary; **mrz,** maxillary root of zygomatic arch; **nas,** nasal; **nlf,** nasolacrimal foramen; **par,** parietal; **pre,** premaxillary; **soc,** supraoccipital; **sof,** supraorbital foramina; **sqm,** squamosal; **srz,** squamosal root of zygomatic arch.

thyomyines narrows with age as bone is eroded to accommodate the growing mass of the anterior temporalis muscle; ontogenetic constriction of the interorbital region is most pronounced in large adult specimens of *Ichthyomys.*

The braincase is thin-walled and globose in most young ichthyomyines and in adult *Anotomys leander, A. trichotis,* and *Rheomys underwoodi.* Postweaning growth of the facial skeleton, however, results in a conspicuous ontogenetic decrease in the relative (but not

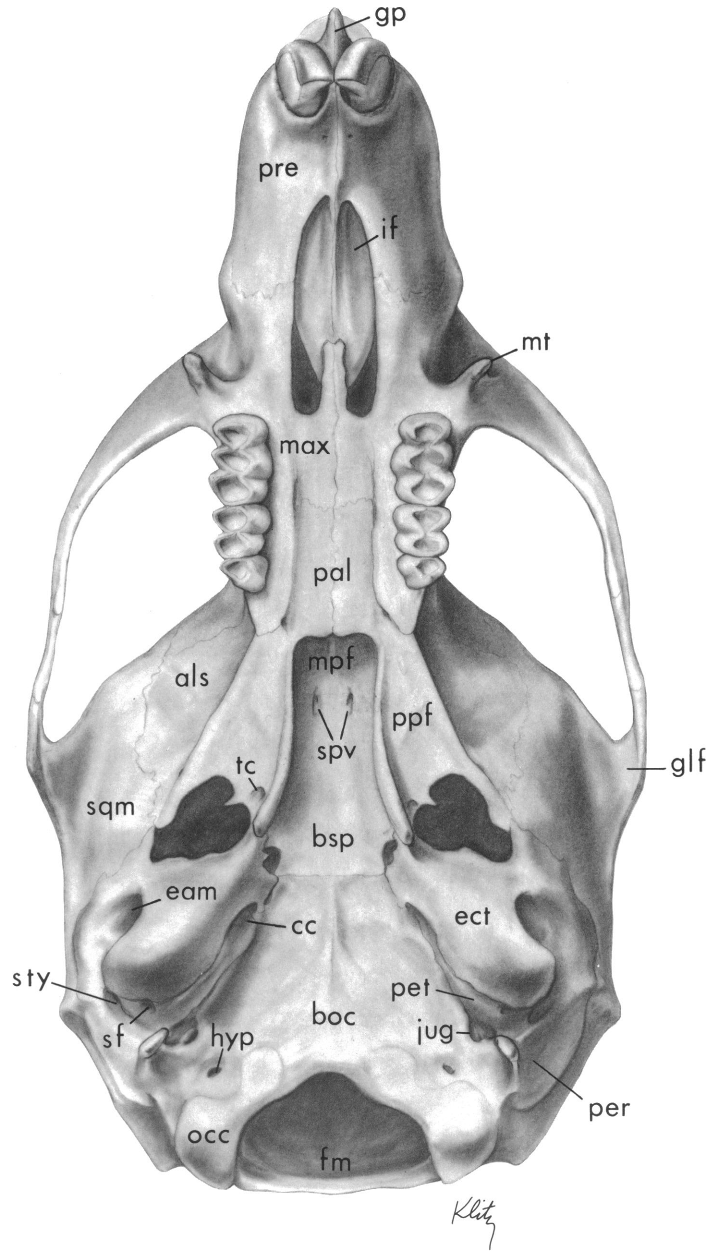


Fig. 9. Ventral view of skull of *Rheomys thomasi.* **als,** alisphenoid; **boc,** basioccipital; **bsp,** basisphenoid; **cc,** carotid canal; **eam,** external auditory meatus; **ect,** ectotympanic part of auditory bulla; **fm,** foramen magnum; **glf,** glenoid fossa; **gp,** gnathic process; **hyp,** hypoglossal foramen; **if,** incisive foramen; **jug,** jugular foramen; **max,** maxillary; **mpf,** mesopterygoid fossa; **mt,** masseteric tubercle; **occ,** occipital condyle; **pal,** palatines; **per,** periotic capsule of mastoid; **pet,** petrosal part of auditory bulla; **ppf,** parapterygoid fossa; **pre,** premaxilla; **sf,** stapedial foramen; **spv,** sphenopalatine vacuities; **sqm,** squamosal; **sty,** stylomastoid foramen; **tc,** transverse canal.

absolute) size of the braincase, and this proportional diminution is greatest in those species with large incisors. The shape of the braincase in some ichthyomyines is also altered in older specimens by the addition of bony sculpture associated with muscle at-

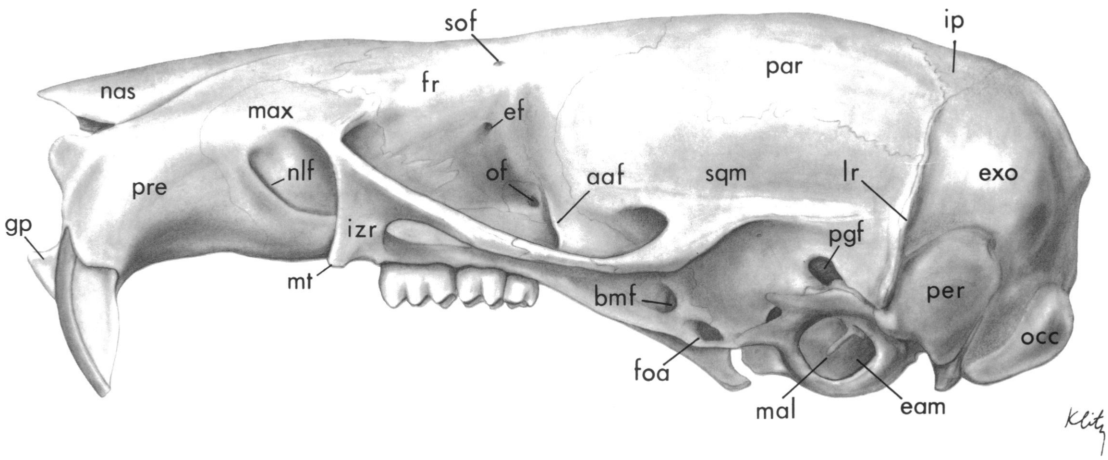


Fig. 10. Lateral view of skull of *Rheomys thomasi*. **aaf,** anterior alar fissure; **bmf,** buccinator-masticatory foramen; **eam,** external auditory meatus; **ef,** ethmoid foramen; **exo,** exoccipital; **foa,** foramen ovale accessorius; **fr,** frontal; **gp,** gnathic process; **ip,** interparietal; **izr,** inferior zygomatic root; **lr,** lambdoidal ridge; **mal,** malleus; **max,** maxillary; **mt,** masseteric tubercle; **nas,** nasal; **nlf,** nasolacrimal foramen; **occ,** occipital condyle; **of,** optic foramen; **par,** parietal; **per,** periotic capsule of mastoid; **pgf,** postglenoid foramen; **pre,** premaxillary; **sof,** supraorbital foramen; **sqm,** squamosal.

tachments and by the remodeling that accompanies basicranial flexion (see below). Ichthyomyines lack the distinct temporal ridges that crease the dorsolateral aspect of the braincase in some other sigmodontines, but in species of *Ichthyomys* the bony scars that mark the attachment of the aponeurosis of origin of the anterior temporalis on each side of the braincase become prominent with age and may join at dorsal midline for several millimeters behind the orbits to form a low midsagittal crest. Lambdoidal ridges are produced along the squamosal-exoccipital sutures in older adults of all ichthyomyines; usually these ridges are small and inconspicuous, but in large adult *Ichthyomys* they may form flaring lateral crests.

The zygomatic arches are drooping and delicate in most ichthyomyines, but in adult *Daptomys* and *Ichthyomys* the zygomatic processes of the maxillae and squamosals flare broadly from the sides of the rostrum and braincase, respectively. In all ichthyomyines the jugal is a slender bone that is often lost when skulls are cleaned; in some species it may not ossify completely (Musser and Gardner, 1974).

The interparietal is a small, triangular or irregularly oblong element. It is smallest (and occasionally absent) in species of *Ichthyomys.*

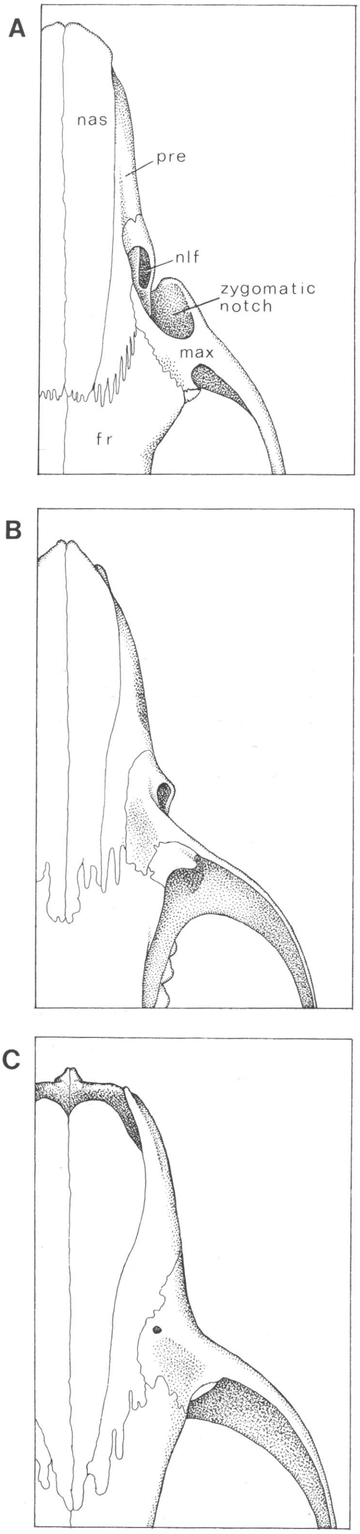
In adult specimens of *Ichthyomys,* and possibly *Daptomys* (few fully adult examples of *Daptomys* are available), the occipital condyles are produced posteriorly beyond the occiput and are fully exposed in dorsal view. In other ichthyomyines, the condyles are concealed from dorsal view beneath the bulging, rounded supra- and exoccipitals, or just the tips of the condyles are visible.

When ichthyomyine skulls are viewed from a lateral perspective the line of the dorsal profile appears characteristically flattened or depressed over the orbits. In most species the dorsal line from the tips of the nasals to the occiput is gently biconvex—the profile rises in the midrostral region above the superior zygomatic root of the maxilla, then sinks over the orbits just behind the posterior tips of the nasals and rises again over the braincase. The curve of the dorsal profile is often subtle and the top of the skull may appear almost flat in some specimens. In *Anotomys leander, A. trichotis,* and *Rheomys underwoodi* the dorsal profile is nearly straight from the nasal tips to just above the orbits, but behind the eyes the frontals bulge upwards, tracing the dome of a greatly inflated braincase.

The gnathic process of the premaxillae (figs. 9, 10, gp) is a rounded or acuminate tab of bone that projects anteriorly between the bases of the upper incisors and extends well beyond the anterior curvature of those teeth in all ichthyomyines. The gnathic process is present, but usually just as an inconspicuous bony ridge, in other sigmodontines. The large gnathic process of ichthyomyines relates to the greater development of their mystacial vibrissae: the gnathic process provides a bony surface for the origin of M. nasolabialis profundis pars media inferior (Rinker, 1954, illustrates this muscle for *Sigmodon hispidus*), the fibers of which insert within the deep connective tissue layers of the mystacial pad (Wineski, 1985).

In all adult ichthyomyines a stout bony spur, the masseteric tubercle (figs. 9, 10, 12A, mt), projects anteroventrally from the base of the inferior zygomatic root and is the site of attachment for the tendon of the superficial masseter. In most muroids the origin of the superficial masseter is marked only by a small, oval patch of rugose bone (fig. 12B, osm). Among other sigmodontines, only species of *Megadontomys* and *Scotinomys* have distinct processes associated with the tendon of the superficial masseter (see Musser, 1964, and Hooper, 1972, for illustrations), but these are not so well developed as ichthyomyine masseteric tubercles. Masseteric tubercles exhibit ontogenetic and interspecific variation among ichthyomyines. In very young animals the tubercle may be absent (as on the subadult holotype and unique specimen of *Daptomys oyapocki*); they are always best developed in adults. The tubercles may or may not project ventrally below the alveolar plane of the maxillary molars; Hooper (1968) pointed out apparently consistent differences between two species of *Rheomys* in this character, but the position of the masseteric tubercle above or below the molar alveoli is subject to individual variation within several populations of *Ichthyomys*.

The inferior zygomatic root (fig. 10, izr) is narrow in all ichthyomyines by comparison



←

Fig. 11. Dorsal view of rostrum. **A,** *Zygodontomys brevicauda* (AMNH 189365); **B,** *Rheomys mexicanus* (AMNH 205320); **C,** *Ichthyomys hydrobates tweedii* (AMNH 71389). **fr,** frontal; **max,** maxillary; **nas,** nasal; **nlf,** nasolacrimal foramen; **pre,** premaxillary.

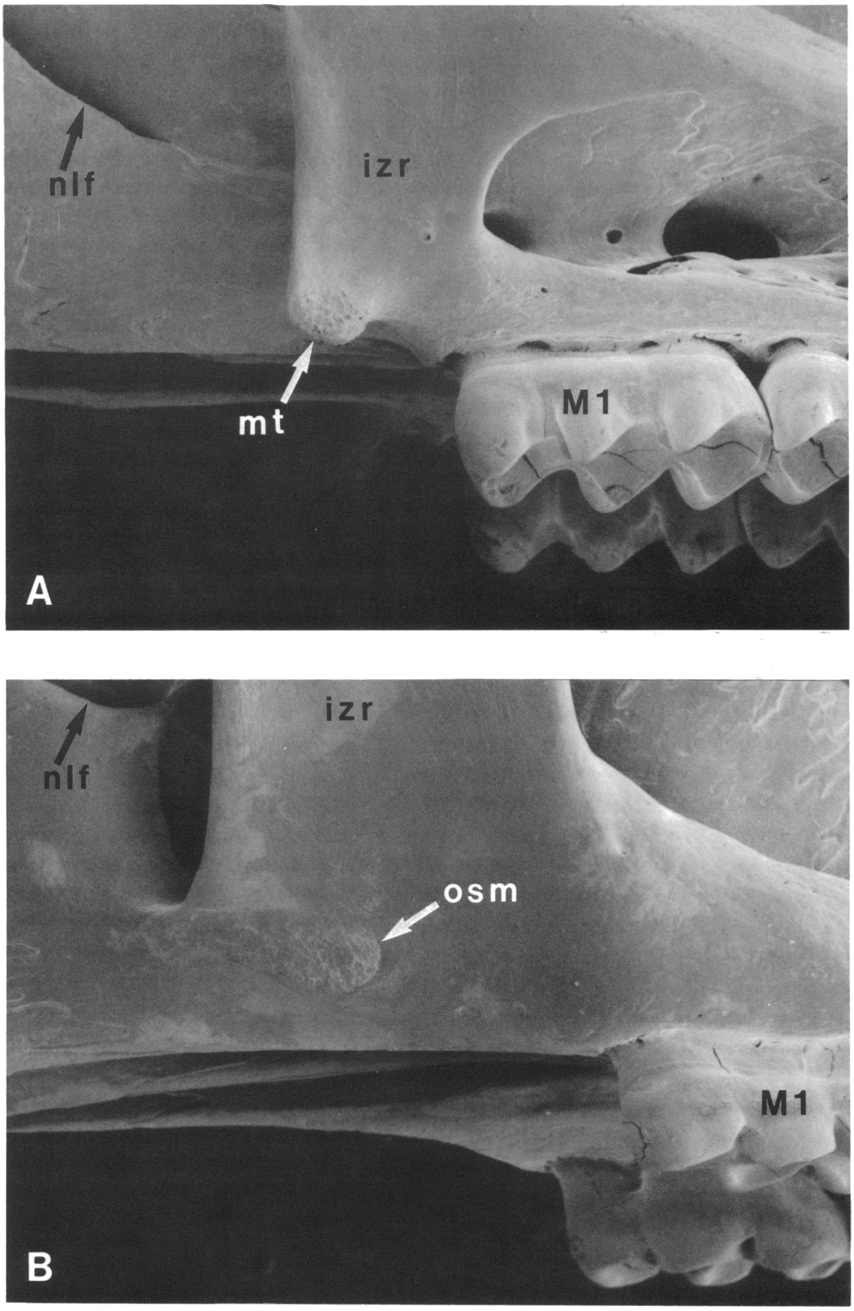


Fig. 12. Origin of the superficial masseter. **A,** *Rheomys thomasi* (MVZ 98805); **B,** *Podomys floridanus* (AMNH 219436). **izr,** inferior zygomatic root; **M1,** first maxillary molar; **mt,** masseteric tubercle; **nlf,** nasolacrimal foramen; **osm,** origin of superficial masseter.

with the broad zygomatic plates of other sigmodontines, but there is also substantial variation among ichthyomyines in the width and position of this element. In species with slender incisors and large molars (*Anotomys leander, A. trichotis, Rheomys mexicanus,* and *R. underwoodi*), the inferior zygomatic root is very slender and its posterior edge is lo-

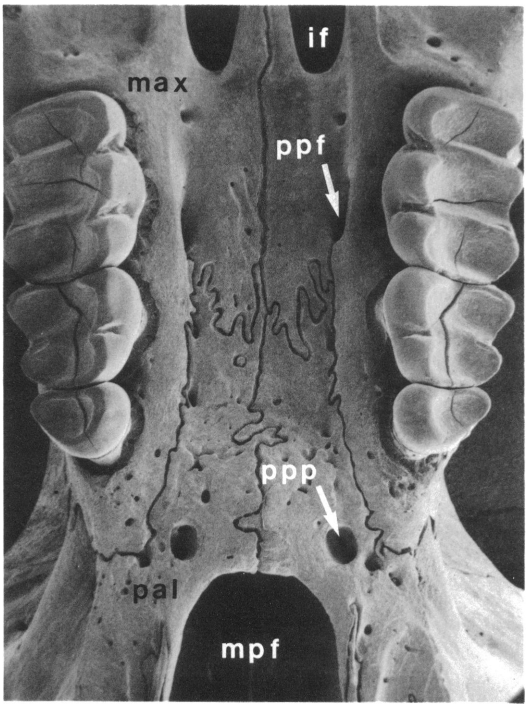


Fig. 13. Palatal bridge of *Ichthyomys hydrobates tweedi* (UMMZ 155787). **if,** incisive foramen; **max,** maxillary; **mpf,** mesopterygoid fossa; **pal,** palatine; **ppf,** posterior palatine foramen; **ppp,** posterolateral palatal pit.

cated above the anterocone of M1. By contrast, in some ichthyomyines with large incisors and small molars (*Ichthyomys, Daptomys peruviensis, D. oyapocki*) the inferior zygomatic root is broader and its posterior edge lies anterior to the first molar. Ichthyomyines with dental proportions that fall between these two extremes have intermediate morphologies of the inferior zygomatic root.

The bony palate between the molar rows (the so-called palatal bridge) exhibits considerable morphological variation among muroids. The ichthyomyine palate (fig. 13) conforms to the "long-wide" morphotype described by Hershkovitz (1962): the width of the palate between the first maxillary molars equals or exceeds the individual length of those teeth, and the mesopterygoid fossa does not penetrate anteriorly between the third molars (i.e., the palate is produced posteriorly behind the molar rows). The palatal bridge of ichthyomyines is smooth and uncomplicated by comparison with the deeply furrowed and grooved configuration of this structure in other muroid groups. The posterior margin of the hard palate (the anterior limit of the mesopterygoid fossa) may be smoothly squared or concave posteriorly, or a small median postpalatal process may be present, but a strong median spine is never produced.

Behind the molar rows and to either side of the mesopterygoid fossa are the parapterygoid fossae (fig. 9, ppf) within which the internal pterygoid muscles originate. The parapterygoid fossae of ichthyomyines are narrow and their anterior limits merge almost imperceptably with the posterolateral corners of the palate. Ichthyomyine parapterygoid fossae do not resemble the deeply excavated concavities from which the internal pterygoids originate in sigmodontines with hypsodont, flat-crowned molars.

The unpaired bones that comprise the basicranial axis (presphenoid, basisphenoid, and basioccipital) are exposed along the ventral midline from the anterior limit of the mesopterygoid fossa to the ventral margin of the foramen magnum. In *Anotomys leander* and *A. trichotis* these three bones lie approximately in one plane and the basicranial axis is nearly straight, but the ventral angle between the basisphenoid and basioccipital bones is substantially greater than 180° in adult specimens of most other ichthyomyine species. The latter configuration results from an ontogenetic rotation of the two bones about a transverse axis passing through the sphenoccipital suture. Thus, while the basicranial axis is straight or nearly so in juvenile *Daptomys, Ichthyomys, Neusticomys,* and *Rheomys* species, the ventral angle between the basisphenoid and basioccipital bones increases with growth. Sphenoccipital kyphosis, as the process and result of this ontogenetic rotation of bones about the synchondrosis may be called, is most conspicuous in adult specimens of *Ichthyomys.*

Cranial Foramina and Fenestrae: The cranial foramina of mammals provide a rich source of information about sensory adaptations and a useful collection of characters by which species and higher taxonomic categories can be discriminated. The nomenclature of rodent cranial foramina used herein follows Wahlert (1974, 1985), but statements about the contents of foramina are based upon my own dissections except where other authorities are cited.

The incisive foramina (fig. 9, if) of ichthyomyines are long, but not unusually so by muroid standards; the ratio of incisive foramina length (LIF) to the length of the diastema (LD; see Materials and Methods for definitions of these measures) varies from .67 to .76 (mean = .72) among ichthyomyine populations for which adult measurements are available. Ichthyomyine incisive foramina may extend posteriorly to or just between the anterocones of the first maxillary molars, but do not penetrate so deeply between the molar rows as in *Akodon, Phyllotis* and allied genera. The shape of the incisive foramina exhibits some limited variation among ichthyomyines.

The posterior palatine foramina (fig. 13, ppf) are inconspicuous perforations in the bony palate located one on either side of midline at or near the maxillary-palatine sutures. These foramina do not exhibit, within the tribe, the unusual configurations that they may assume in other muroid groups (Carleton, 1980).

The posterolateral palatal pits (fig. 13, ppp) consist of one or a few small, simple holes in each palatine bone at the posterolateral corners of the hard palate. In other sigmodontines (e.g., *Nectomys* and members of some of the subgenera of *Oryzomys*) complex posterolateral palatal pits may be recessed in large, distinct fossae.

The myomorph infraorbital foramen (fig. 14) divides the maxillary root of the zygomatic arch into superior and inferior rami and transmits nerves, muscle, blood vessels, and the nasolacrimal duct from the orbital fossa to more anterior regions on or in the rostrum. In most muroids, the lumen of the infraorbital foramen consists of a wide dorsal portion and a slitlike, narrow ventral moiety. In all ichthyomyines, however, the foraminal lumen is as wide ventrally as dorsally, and appears oval in frontal view; the shape of this foramen constitutes one of the most conspicuous osteological peculiarities of the tribe. Winge (1891, 1941) attributed the expanded ventral part of the infraorbital foramen of *Ichthyomys* to the enlarged bundles of trigeminal sensory neurons passing through it

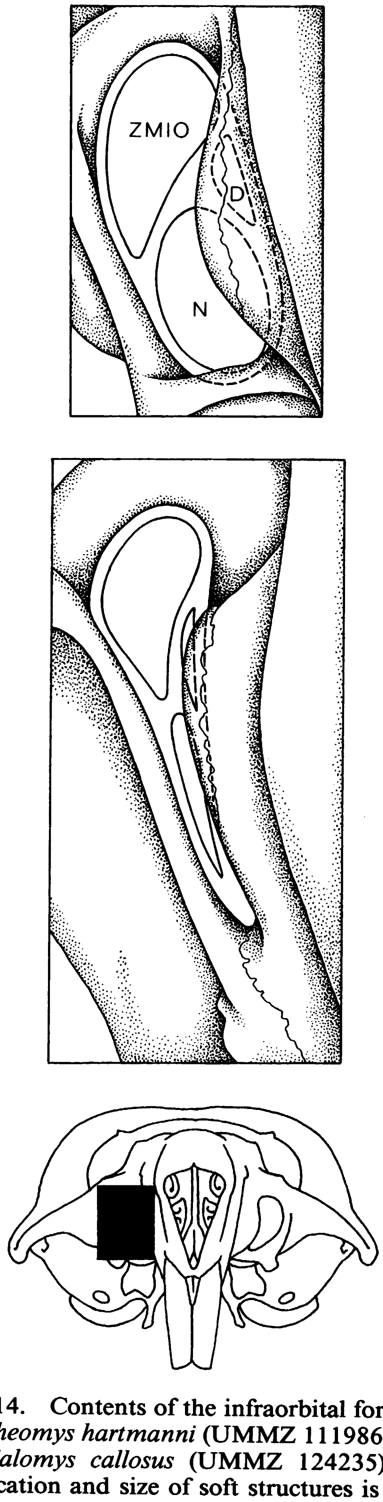


Fig. 14. Contents of the infraorbital foramen. **Top:** *Rheomys hartmanni* (UMMZ 111986). **Bottom:** *Calomys callosus* (UMMZ 124235). The identification and size of soft structures is based on dissections of other fluid-preserved specimens as well. **D**, nasolacrimal duct; **N**, infraorbital nerve; **ZMIO**, infraorbital part of zygomaticomandibularis muscle.

from the stiff and numerous mystacial vibrissae. De Winton (1896: 512), however, remarked, "I am unable to throw any light on the cause of the large infraorbital foramen [of *Ichthyomys*], but I can say that no muscles pass through it, and that the nerve seemed very small when relaxed after it [in the head of the holotype of *I. soderstromi*] reached the Museum in a dry state."

My dissections of fluid-preserved material provide unequivocal support for Winge's observations. In all ichthyomyines that I have dissected (including a specimen of *I. hydrobates soderstromi*), the dorsal part of the foramen transmits the infraorbital slip of M. zygomaticomandibularis (fig. 14, ZMIO) and, closely applied to the side of the rostrum, the membranous nasolacrimal duct (fig. 14, D) that provides an open passage from the orbit to the nasal cavities. These two structures, together with the small infraorbital blood vessels that supply the soft tissues of the muzzle, do not differ appreciably in relative size between ichthyomyines and most other muroids. By contrast, the nerve that traverses the ventral part of the foramen is conspicuously larger in ichthyomyines (fig. 14, top, N) than in the typical muroid condition (fig. 14, bottom). This bundle contains exclusively sensory neurons, from the second division of the fifth (trigeminal) cranial nerve, that pass to the mystacial vibrissae and surrounding integumentary structures (Greene, 1935). This nerve is a flat sheet of small fibers in all nonaquatic muroids that I have dissected, but in ichthyomyines it resembles a thick cable composed of many separate strands whose individual connections to vibrissal follicles is easily demonstrated. This is the "infraorbital nerve" of Hill (1935) and the combined "external nasal" and "superior labial" branches of the maxillary nerve of Greene (1935). The anterior superior alveolar nerve (another branch of the trigeminal) also passes through the infraorbital foramen to supply the upper incisor root, but this small nerve (not shown in fig. 14) does not appear to differ in size among muroids.

The nasolacrimal foramen (fig. 8, 10, 11, nlf) is a slitlike, posterodorsal opening in the nasolacrimal capsule on each side of the rostrum. The foramen admits the nasolacrimal duct and the anterior superior alveolar nerve into the rostrum. In some muroids the nasolacrimal foramen is hidden from lateral view behind the inferior zygomatic root, but in all ichthyomyines it is exposed.

Medial to the inferior zygomatic root, the thin lateral wall of the rostrum is extensively fenestrated in many muroids—portions of the turbinals and the upper nasal chambers are exposed through a wide vacuity bounded dorsally by the lacrimal bone and ventrally by the maxilla. In all ichthyomyines, however, the lateral wall of the rostrum is complete and unfenestrated (although small, unossified fissures occasionally separate the lacrimal and maxillary bones). In *Ichthyomys* the lacrimal is small and it is sometimes lost when the skull is cleaned, but the resulting hole is an obvious artifact of preparation and is not to be confused with the fenestra described above.

A sphenopalatine foramen perforates the ventromedial wall of each orbit above the molar rows in all ichthyomyines; occasionally it appears fused with the dorsal palatine foramen. Both foramina appear highly variable within species, however, and do not appear to differ from their common appearance among most other sigmodontines. A single ethmoid foramen (fig. 10, ef) penetrates the frontal bone in the medial wall of the orbit.

The optic foramen (fig. 10, of) is conspicuously smaller in ichthyomines than in other muroids of equivalent body size. The diminutive ichthyomyine optic foramen transmits a correspondingly small optic nerve and suggests a greater reliance on other senses than sight.

The anterior alar fissure (sphenoidal fissure of Hill, 1935) contains the anterior opening of the alisphenoid canal in rodents (Wahlert, 1983, 1985); it is a wide, roughly oval cleft (fig. 10, aaf) in the posterior wall of the orbital fossa, bounded by the alisphenoid, orbitosphenoid, and palatine bones. The supposed large size of this fissure in ichthyomyines (according to Winge, 1941) is perhaps more apparent than real because of its close proximity to the tiny optic foramen.

A small perforation in each frontal bone above and a little behind the eye is present in all muroid rodents I have examined but it is not named by Hill (1935) or Wahlert (1974); it is illustrated for *Peromyscus*, but not labeled or discussed, by Klingener (1968: fig. 1). Thomas (1893) named this pair (one on each side) of tiny holes the supraorbital foramina in order to describe their unusual position in species of *Ichthyomys.* The supraorbital foramina transmit small blood vessels from the dorsal region of the orbital fossa to the venous system surrounding the olfactory lobes of the brain (Greene, 1935: fig. 221). In all muroids (except *Ichthyomys*) that I have examined for this character, the supraorbital foramina occupy the lateral surface of the frontals beneath the supraorbital margins; the foramina therefore lie within the orbits (e.g., figs. 8, 10, sof). In large adult specimens of *Ichthyomys,* however, the supraorbital foramina are located between the orbits on the dorsal surface of the frontals (fig. 15, bottom). In younger specimens of *Ichthyomys,* the supraorbital foramina are located at or near the supraorbital margins, close to the position that they occupy in other genera (fig. 15, top). The dorsal location of the foramina in adult rats of this genus is therefore the result of ontogenetic remodeling of the interorbital region.

The buccinator and masticatory nerves of ichthyomyines are usually separated by an internal bony septum but leave the braincase together through a common buccinator–masticatory foramen (fig. 10, bmf). The buccinator–masticatory foramen can be identified by twin grooves on the lateral surface of the alisphenoid that mark the exit of these nerves. This foramen is separated from the more posterior foramen ovale accessorius (fig. 10, foa) by a vertical strut of the alisphenoid bone. In many other sigmodontines the buccinator and masticatory foramina are confluent with the foramen ovale and the foramen ovale accessorius is absent.

The sphenopalatine vacuities are large fenestrae that perforate the dorsolateral walls of the mesopterygoid fossa in many muroids (see Carleton, 1980: fig. 8). In ichthyomyines, the bony roof and walls of the mesopterygoid fossa are substantially complete, and the sphenopalatine vacuities, if present, are only narrow slits to either side of the basisphenoid–presphenoid suture (fig. 9, spv).

Anterior to the auditory bulla is a large unossified region in the floor of the braincase; this unossified area may also include the foramen ovale which, when discrete, is small.

Above the auditory bulla the lateral wall of the braincase of most sigmodontines is

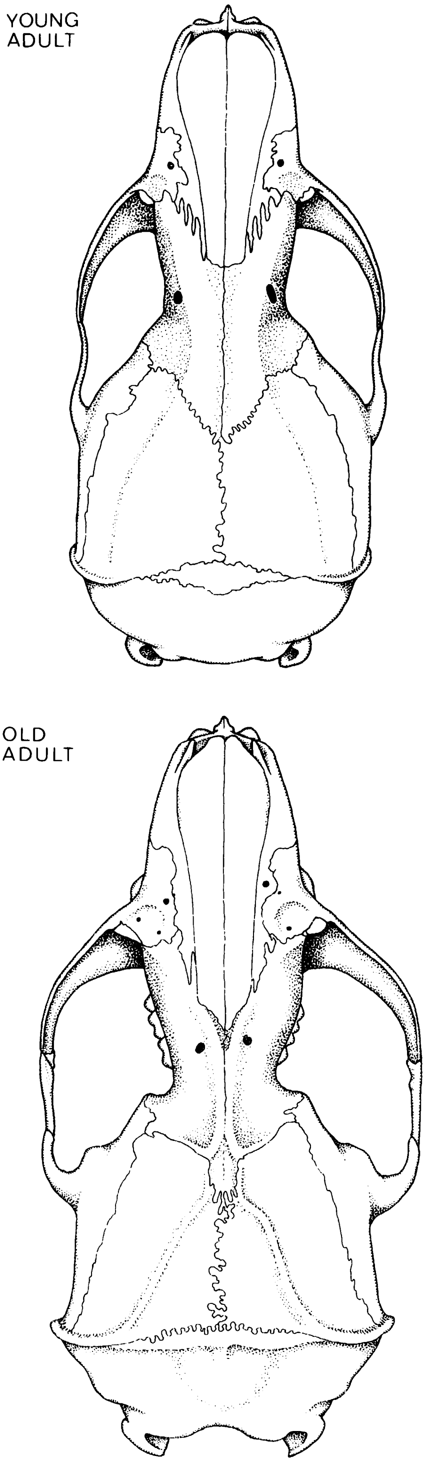


Fig. 15. Supraorbital foramina in *Ichthyomys pittieri.* **Top:** young adult (4/c/a; MBUCV I-2803). **Bottom:** old adult (6/f/a/; MBUCV I-2776).

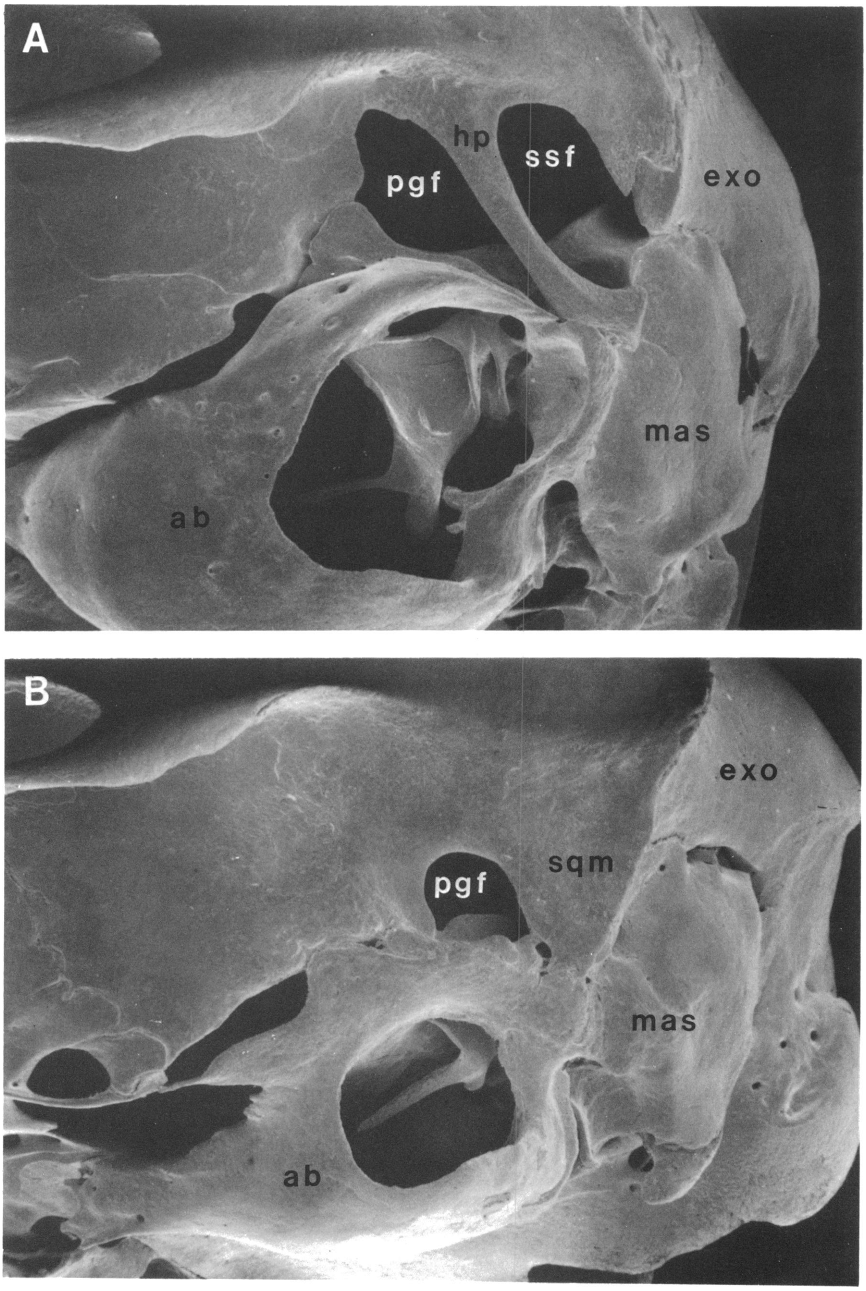


Fig. 16. Left lateral view of bullar region. **A**, *Podomys floridanus* (AMNH 219436). **B**, *Rheomys thomasi* (MVZ 98805). **ab**, auditory bulla; **exo**, exoccipital; **hp**, hamular process of squamosal; **mas**, mastoid; **pgf**, postglenoid foramen; **sqm**, squamosal; **ssf**, subsquamosal foramen.

perforated by two openings, the postglenoid foramen and the subsquamosal fenestra, separated by a slender hamular process of the squamosal bone (fig. 16A). The transverse sinus, a major component of the cerebral venous system, exits the braincase through the postglenoid foramen (Greene, 1935: fig. 223), passing along a groove in the floor of that opening between the dorsal lip of the ectotympanic bulla and the anterior lamina of the

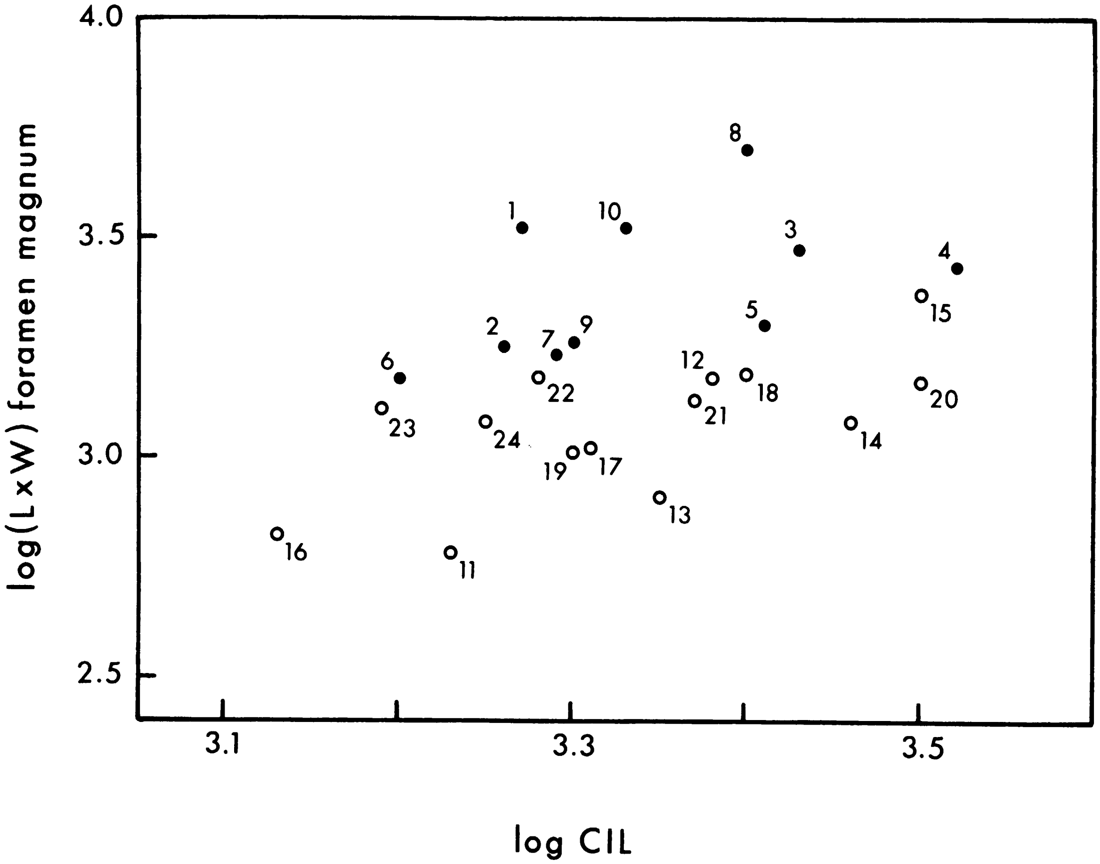


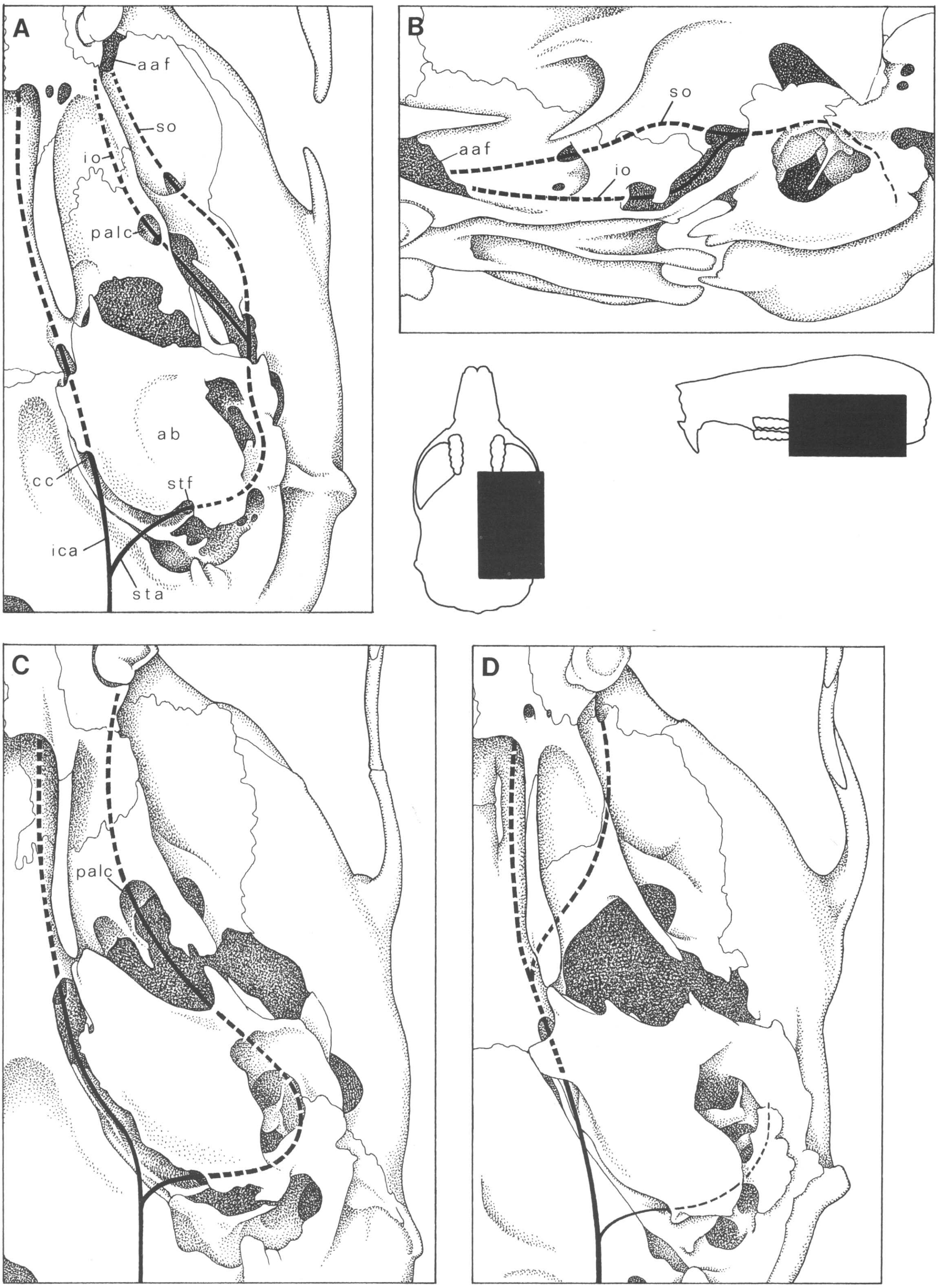
Fig. 17. Scatterplot of mean adult foramen magnum area (estimated as the product of foramen height and width) and condyloincisive length (both transformed to natural logarithms) for ichthyomyines (solid symbols) and other Sigmodontinae (open symbols). **1,** *Anotomys leander* (N = 4); **2,** *A. trichotis* (4); **3,** *Ichthyomys hydrobates soderstromi* (4); **4,** *I. h. tweedii* (5); **5,** *I. pittieri* (5); **6,** *Neusticomys monticolus* (5); **7,** *Rheomys hartmanni* (4); **8,** *R. mexicanus* (5); **9,** *Rheomys thomasi* (5); **10,** *R. underwoodi* (3); **11,** *Akodon mollis* (5); **12,** *Bolomys lasiurus* (5); **13,** *Calomys callosus* (5); **14,** *Delomys sublineatus* (5); **15,** *Graomys griseoflavus* (5); **16,** *Oryzomys albigularis* (5); **17,** *O. nigripes* (5); **18,** *O. talamancae* (5); **19,** *Phyllotis andinum* (5); **20,** *Rhipidomys macconnelli* (5); **21,** *Sigmodon hispidus* (5); **22,** *Sigmodontomys alfari* (5); **23,** *Thomasomys laniger* (5); **24,** *Zygodontomys brevicauda* (5).

petrosal. The subsquamosal fenestra dos not transmit anything in muroids.[1] Ichthyomyines possess postglenoid foramina, but lack subsquamosal fenestrae; the hamular process of the squamosal is therefore absent, and that bone is in solid contact with either the occiput or the mastoid along its entire posterior margin (fig. 16B). Small foramina are sometimes present between the mastoid and the occiput and between the squamosal and the mastoid but these minute perforations exhibit considerable intraspecific variability.

The foramen magnum is unusually large in

---

[1] My dissections confirm Hill's (1935) observation that the muroid subsquamosal fenestra (Hill called it the subsquamosal foramen) transmits no vessel or nerve. Musser (1982) suggested that the subsquamosal fenestra is homologous with the squamosomastoid foramen (first named by Wahlert, 1974), a small hole in the squamosal-mastoid suture that transmits a vein in many rodent taxa. Musser (1982: 39) hypothesized that the subsquamosal fenestra represents a "further erosion of the squamosal by the [squamosomastoid] foramen," but since the fenestra transmits no vein this is not a convincing description of ontogenetic process or a compelling argument for homology even if the two openings are indistinguishable on a cleaned skull.


A
aaf
so
io
palc
ab
cc
stf
ica
sta
B
so
aaf
io
C
palc
D

ichthyomyines by comparison with nonaquatic sigmodontines (fig. 17). The foramen magnum transmits accessory nerves and vertebral and spinal arteries but the medulla oblongata (myelencephalon) fills most of the foraminal lumen. At the level of the foramen magnum the medulla oblongata contains a number of cranial nerve nuclei and their fiber tracts together with ascending and descending neuronal systems that connect the spinal cord with other parts of the central nervous system (Zeman and Innes, 1963). Enlargement of the medulla oblongata among other semiaquatic mammals is correlated with hypertrophy of the spinal trigeminal nucleus and reflects increased vibrissal sensitivity (see fig. 72 and citations in accompanying text).

The periotic capsule of the mastoid bone (figs. 9, 10, per) is fenestrated in some muroids. Small mastoid fenestrae are present in some individuals of several ichthyomyine populations, but these perforations do not appear to be a consistent feature of the periotic capsule.

The sphenofrontal and stapedial foramina together with the carotid and alisphenoid canals are osteological features associated with the carotid arterial supply discussed below.

The transverse canal and the stylomastoid, jugular, and hypoglossal foramina are present in all ichthyomyines (fig. 9); they do not vary appreciably among members of the tribe and their anatomical relationships resemble those illustrated for *Peromyscus* by Klingener (1968: fig. 2, but note that the transverse canal is labeled as the basisphenoid canal).

CAROTID ARTERIAL SUPPLY: Patterns of carotid arterial supply differ among ichthyomyine species, and these differences are reflected in the presence, absence, and relative sizes of foramina and in the presence or absence of grooves on the internal and external surfaces of the braincase. Patterns of vascular supply that I inferred from such osteological features and from dried fragments of vessels adhering to incompletely cleaned skulls were later confirmed by dissections of fluid-preserved heads. Three major conformations of the internal carotid artery and its derivatives were discovered (fig. 18). Names of vessels used below follow Bugge (1970); foraminal names follow Wahlert (1974 and 1985).

1. In species of *Daptomys* and *Neusticomys* (fig. 18A, B) and in *Anotomys trichotis*, the common carotid artery bifurcates behind the auditory bulla to form the external and internal carotid arteries. The internal carotid promptly gives rise to the stapedial artery and then enters the braincase through the carotid canal between the bulla and the basioccipital bone.

After its departure from the internal carotid, the stapedial artery enters the bulla via the stapedial foramen, passes through the stapes, and exits the middle ear by a cleft in the roof of the bullar capsule. The stapedial artery passes rostrally within the braincase to the anterior margin of the bulla where it divides into infraorbital and supraorbital branches. The supraorbital branch continues rostrally in a shallow groove along the inner surface of the squamosal and alisphenoid bones and exits the braincase through a sphenofrontal foramen (not illustrated) or the anterior alar fissure. The supraorbital branch of the stapedial artery supplies the eyeball and surrounding soft tissues in the orbit, comprising the ophthalmic circulation.

From the anterior edge of the bulla the infraorbital branch of the stapedial artery passes rostroventrally and enters the posterior opening of the alisphenoid canal; inside the braincase, the vessel courses rostrally along the inner surface of the alisphenoid below the supraorbital branch and emerges onto the floor of the orbit through the anterior alar fissure. The infraorbital branch of the stapedial artery supplies the deep tissues of the upper face, comprising the internal maxillary circulation.

---

←

Fig. 18. Ichthyomyine carotid circulation patterns. **A** and **B**, *Neusticomys monticolus* (UMMZ 155606); **C**, *Anotomys leander* (UMMZ 126294); **D**, *Rheomys hartmanni* (UMMZ 111986). **aaf**, anterior alar fissure; **ab**, auditory bulla; **cc**, carotid canal; **ica**, internal carotid artery; **io**, infraorbital branch of stapedial artery; **palc**, posterior opening of alisphenoid canal; **so**, supraorbital branch of stapedial artery; **sta**, stapedial artery; **stf**, stapedial foramen.

The supraorbital branch of the stapedial artery supplies the ophthalmic circulation in all of the species assigned to this carotid pattern but the internal maxillary circulation may be supplied directly by the internal carotid artery rather than by the infraorbital branch of the stapedial in occasional specimens of *Neusticomys monticolus* and *Anotomys trichotis.*

2. The pattern of carotid supply in *Anotomys leander* (fig. 18C) differs from the preceding by the absence of the supraorbital branch of the stapedial artery. After exiting the bulla as before, the stapedial artery passes rostroventrally, without dividing, over the roof of that capsule, crosses the unossified region anterior to the bulla, and passes entire into the posterior opening of the alisphenoid canal wherein its course resembles that of the infraorbital branch described above. The vessel emerges into the orbital fossa via the anterior alar fissure and presumably supplies both the internal maxillary and the ophthalmic circulations.

3. In species of *Ichthyomys* and *Rheomys* (fig. 18D) the stapedial artery supplies only the middle ear; the supra- and infraorbital branches described above are both absent. The ophthalmic and internal maxillary circulations are, instead, both supplied by a different vessel that departs from the internal carotid artery inside the braincase, passes obliquely over the roof of the parapterygoid fossa and enters the orbit through the anterior alar fissure.

The principal osteological features associated with the different carotid circulation patterns can be summarized as follows: *A large stapedial foramen* accommodates the large stapedial artery in species with circulatory patterns 1 and 2; the stapedial foramen is smaller in species with pattern 3 circulation. *The posterior opening of the alisphenoid canal is huge* when it accommodates the undivided stapedial artery that passes through it in circulatory pattern 2; the posterior opening of the alisphenoid canal is present, but less conspicuous, in species with carotid pattern 1 where only the infraorbital branch of the stapedial artery is transmitted. The posterior opening of the alisphenoid canal is absent altogether from species with carotid pattern 3. *A conspicuous anteroposterior groove on the inner surface of the squamosal and alisphenoid bones* usually marks the passage of the supraorbital branch of the stapedial artery along the lateral wall of the braincase in species with circulatory pattern 1. In species with circulatory pattern 3 *the floor of the braincase on either side of the mesopterygoid fossa bears an internal, oblique groove* that is externally visible through the thin bone forming the roof of each parapterygoid fossa; this groove marks the passage of the branch of the internal carotid that passes rostrolaterally to the anterior alar fissure.

AUDITORY BULLAE AND OSSICLES: Ichthyomyine auditory bullae are small, flask-shaped, or globular capsules that are widest posterolaterally and taper anteromedially to short, bony eustachian tubes. Each bulla is composed of a ventrolateral, bubble-shaped ectotympanic element that forms the eustachian tube and encloses the tympanic membrane, and a petrosal element that forms the dorsal roof and part of the medial wall of the capsule. Unlike the inflated bullae of some sigmodontines in which only the globose ectotympanic portion is visible, the petrosal part of the ichthyomyine bulla is always exposed between the ectotympanic and the basioccipital. The petrotympanic fissure, an obvious seam between the two bullar elements, contains the carotid canal and the stapedial foramen on the posteromedial surface of the capsule.

All living sigmodontines except ichthyomyines have a tympanic membrane that is divided into two functionally distinct and anatomically separate parts (fig. 19A): a large, anteroventral pars tensa and a smaller, posterodorsal pars flaccida (also called the membrana Shrapnelli, see van der Klaauw, 1931; the pars flaccida of sigmodontines is not homologous with the accessory tympanum of gerbils according to Lay, 1972). The pars tensa is a taut, cone-shaped membrane attached along its semicircular anteroventral margin to the inside of the ectotympanic bulla. The posterodorsal margin of the pars tensa is formed by the arcus terminalis, a narrow band of connective tissue attached along the gracile process of the malleus and anchored posteriorly to a bony spur on the posterior rim of the external auditory meatus. Above the arcus terminalis is the pars flaccida, a roughly

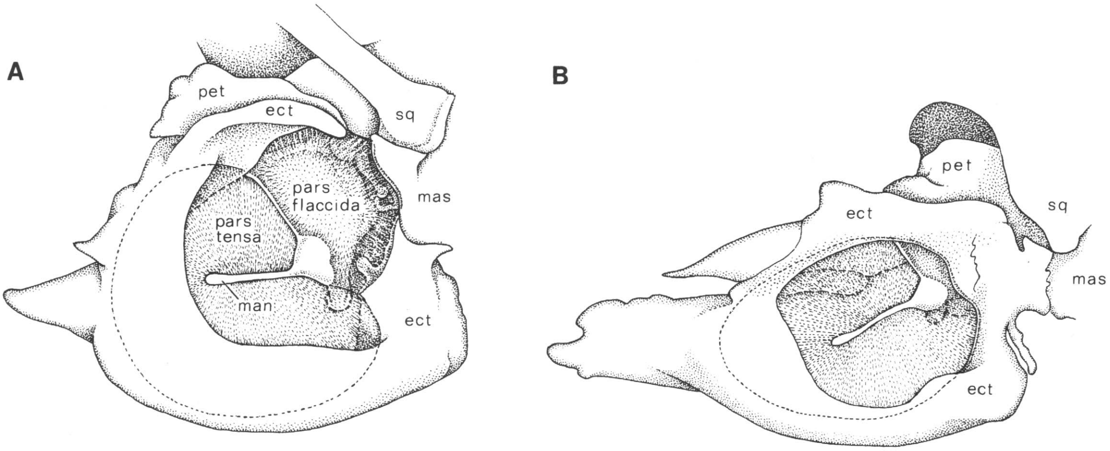


Fig. 19. Muroid auditory membranes. **A,** *Podomys floridanus* (based on AMNH 218050 and 219433); **B,** *Rheomys thomasi* (MVZ 98807 and 132002). The crescentic dotted line marks the attachment of the pars tensa inside the ectotympanic bulla. **ect,** ectotympanic part of auditory bulla; **man,** manubrium of malleus; **mas,** mastoid; **pet,** petrosal; **sq,** squamosal.

semicircular membrane through which the stapes, the incus, and the head and cephalic peduncle of the malleus are revealed to lateral view. The bony margins of the pars flaccida are formed by the ascending anterior and posterior horns of the incomplete ectotympanic ring and by the mastoid.

All ichthyomyines lack a well-developed pars flaccida (fig. 19B). Broad anterior and posterior laminae of the ectotympanic are joined above the pars tensa to form the posterodorsal border of that membrane, and these bony plates conceal the stapes, incus, and the proximal parts of the malleus from lateral view through the external auditory meatus.

Cockerell et al. (1914) described and figured the auditory ossicles of *Ichthyomys hydrobates*; I have been able to confirm and extend their observations only for the malleus, the single middle ear bone readily visible without dissection of scarce osteological material.

The malleus of most sigmodontines (Carleton, 1980; Cockerell et al., 1914) is characterized by (1) a large, knoblike orbicular apophysis that projects posteroventrally from the base of the manubrium opposite the gracile process, and (2) a cephalic peduncle whose long axis is bent approximately perpendicular to the shaft of the manubrium. In most ichthyomyines, the orbicular apophysis is present as a small but distinct knob or spur (fig. 20B, oa), but in *Anotomys trichotis* and *Daptomys venezuelae* the orbicular apophysis is absent (fig. 20A). The cephalic peduncle of the malleus appears relatively shorter in ichthyomyines than in other sigmodontines, and it is also less conspicuously reflected rostrally with respect to the long blade of the manubrium.

MANDIBLE AND HYOID: Ichthyomyine dentaries (see illustrations accompanying the taxonomic accounts, below) resemble those of many other sigmodontines and lack the derived mandibular characteristics of Gerbillinae and Arvicolinae (Repenning, 1968; Carleton, 1980). In all ichthyomyines the coronoid process is well developed and falciform, and the sigmoid notch between the coronoid and condyloid processes is correspondingly deep; this condition contrasts with the diminutive coronoid process and shallow sigmoid notch of many phyllotines (illustrated by Hershkovitz, 1962). A bony capsule that contains the root of the lower incisor is discernable but not prominent on the lateral surface of the mandible below the base of the coronoid process. The angular process lies approximately in the same plane as the condyloid process (ascending ramus).

Variation in mandibular morphology

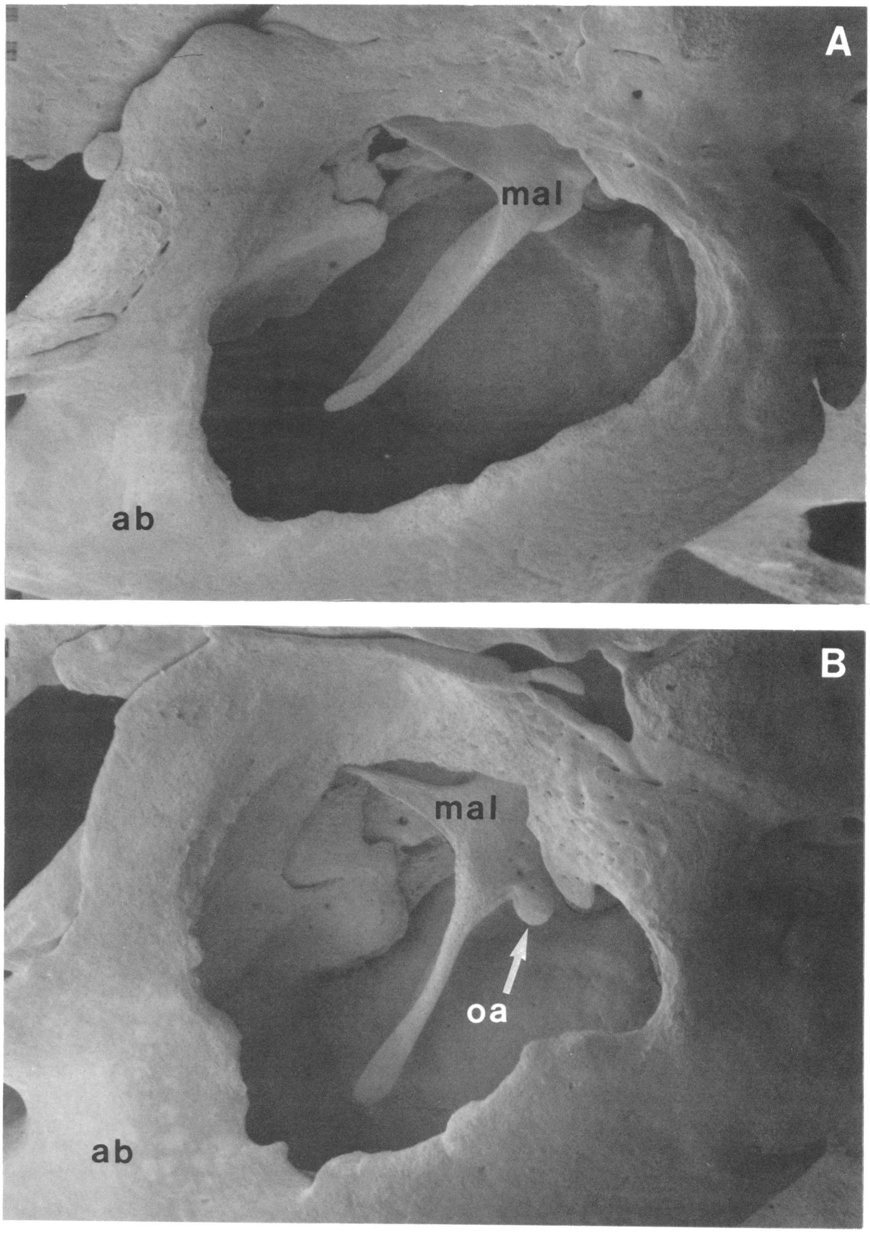


Fig. 20. Malleus of ichthyomyines. **A,** *Anotomys trichotis* (MBUCV I-2795); **B,** *Neusticomys monticolus* (AMNH 64646). **ab,** auditory bulla; **mal,** malleus; **oa,** orbicular apophysis.

among ichthyomyines is chiefly associated with dental characteristics. In species with slender incisors and large molars (*Anotomys leander, A. trichotis, Rheomys mexicanus,* and *R. underwoodi*), the angular process is not produced posteriorly beyond the condylar process; when the mandible is oriented with the molar occlusal plane horizontal, the tip of the angular process in these species is anterior to or just below the articular condyle. In addition, the depth of the mandible from the dorsal edge of the coronoid process to the ventral edge of the angular process is small relative to mandibular length (from condyle to incisor tip). By contrast, in those ichthyomyines with broad incisors and small molars (e.g., *Daptomys peruviensis* and *Ichthyomys* species), the tip of the angular process is produced behind the articular condyle and the mandible is deep from coronoid to angular process relative to its length. Ichthyomyines with intermediate dental proportions have intermediate mandibular morphologies.

Since I used dermestid beetles to prepare skeletal specimens, only the ossified elements of the hyoid apparatus were recovered. All ichthyomyine hyoids examined (including representatives of all genera) conform to a common morphotype. The basihyal is straight (not strongly arched) and lacks an entoglossal process (see Sprague, 1941, and Carleton, 1980, for descriptive terminology); thyrohyals are ⅓ to ¾ as long as the basihyal, with or without trochanters and laterally deflected tips; hypohyals could not be determined with certainty and may be co-ossified with thyrohyals or the basihyal; ceratohyals are long or short but always straight and simple.

## EXTERNAL AND POSTCRANIAL SKELETAL PROPORTIONS

Ichthyomyines vary in external and postcranial skeletal proportions and some postcranial proportions serve to distinguish ichthyomyines from other New World muroids. Additionally, patterns of morphological integration in the ichthyomyine postcranial skeleton provide evidence for locomotor adaptations similar to those previously reported for other groups of semiaquatic mammals.

External and Postcranial Skeletal Measurements: External dimensions, Head-and-Body Length (HBL), Length of Tail (LT), and length of Hind Foot (HF) were obtained by standard procedures (see Materials and Methods). Measurements of the humerus (HUM) and femur (FEM) were each taken from the head to the medial condyle of those bones (see Greene, 1935, for illustrations). Dimensions of the radius (RAD) and tibia (TIB) are greatest lengths.

Samples and Within-Sample Variation: Table 2 presents ranges and means of the seven external and postcranial skeletal dimensions described above for samples of 10 ichthyomyine taxa, and table 3 presents similar data for a comparative collection of 12 other sigmodontine species. Ichthyomyine measurements summarized in table 2 are of adult specimens as determined by toothwear (TWC = 3–6); ichthyomyine epiphyses rarely appear fused, even in obviously old individuals, so that this conventional criterion of skeletal maturity could not be used. Measurements of other sigmodontine species (table 3) are derived from the largest skeletons available within local population samples; I used this expedient because toothwear classes cannot be meaningfully equated among dentitions with grossly different occlusal morphologies.

Sample sizes for most species are small (reflecting the scarcity of specimen preparations other than traditional skins-and-skulls), but the results of previous studies suggest that average deviations from mean values within populations are likely to be much less than the interspecific differences of interest here. Measurements of long bones (humerus, radius, femur, and tibia) typically exhibit coefficients of variation ranging from 3 to 5 within homogeneous population samples of adult mammals (Latimer and Riley, 1934; Clark, 1941; Yablokov, 1974; Miller and Anderson, 1977). Ratios of long bone measurements are less variable still, with typical coefficients of variation from 1 to 3 for placental mammals (e.g., Hildebrand, 1961; Thorington, 1972). The situation is less satisfactory for two external measurements, Length of Head-and-Body and Length of Tail; these dimensions typically exhibit higher coefficients of variation within populations of small muroids, from 4 to 6 and 5 to 8, respectively; the length of the hind foot is usually much less variable, with coefficients of 2 to 4 (e.g., Clark, 1941). A sample of ten adult (TWC 3–5) specimens of *Anotomys leander* from Papallacta, Ecuador, that I measured in the field exhibits coefficients of variation for HBL, LT, and HF of 5.8, 7.4, and 3.3, respectively. Despite the fact that HBL and LT are so variable, however, their ratio is much less so; for the sample of *A. leander* just described, the index LT/HBL had a coefficient of variation of just 3.8.

Comparisons: Table 4 provides numerical values of four ratios calculated from sample

TABLE 2

**The Mean and Range (in parentheses) of External and Postcranial Skeletal Measurements (in millimeters) for Ten Ichthyomyine Species Samples**

| Species, locality,[a] and sample size[b] | Measurements[c] | | | | | | |
|---|---|---|---|---|---|---|---|
| | HBL | LT | HF | HUM | RAD | FEM | TIB |
| *Anotomys leander* | 115 | 142 | 36 | 13.5 | 15.8 | 16.8 | 27.6 |
| (Ecuador, Papallacta, 6) | (101–122) | (125–153) | (34–37) | (13.0–14.0) | (15.1–16.2) | (15.9–17.4) | (25.9–28.4) |
| *A. trichotis* | 117 | 130 | 32 | 13.4 | 14.5 | 16.4 | 26.0 |
| (Venezuela, Buena Vista, 3) | (113–120) | (126–133) | (32–33) | (13.1–13.8) | (14.0–14.8) | (15.9–16.6) | (25.1–26.5) |
| *Ichthyomys h. hydrobates* | 139 | 145 | 34 | 16.4 | 14.0 | 19.7 | 27.4 |
| (Venezuela, Mérida, 1) | (130–150) | (134–150) | (30–36) | | | | |
| *I. h. tweedii* | 162 | 152 | 36 | 17.9 | 14.5 | 22.9 | 29.2 |
| (Ecuador, Mindo, 4) | (155–171) | (141–170) | (33–38) | (17.0–19.1) | (14.1–15.2) | (21.6–24.7) | (27.7–30.9) |
| *Neusticomys monticolus* | 112 | 109 | 26 | 13.5 | 13.0 | 16.8 | 23.8 |
| (Ecuador, Guarumal, 4) | (105–119) | (104–114) | (25–26) | (13.0–13.9) | (12.8–13.2) | (16.2–17.3) | (23.2–24.3) |
| *Rheomys hartmanni* | 118 | 108 | 28 | 14.2 | 12.6 | 18.0 | 23.2 |
| (Costa Rica, San Isidro, 2) | (110–124) | (105–115) | (27–29) | (14.1–14.2) | (12.6) | (17.7–18.2) | (23.0–23.4) |
| *R. mexicanus* | 132 | 160 | 39 | 15.5 | 15.6 | 20.0 | 28.9 |
| (Mexico, San José L., 1) | (121–140) | (154–168) | (35–41) | | | | |
| *R. thomasi stirtoni* | 129 | 126 | 33 | 14.9 | 14.4 | 19.2 | 26.0 |
| (El Salvador, Los Esesmiles, 5) | (120–134) | (110–140) | (30–35) | (14.0–16.0) | (13.3–15.2) | (17.4–20.4) | (24.2–27.8) |
| *R. t. thomasi* | 115 | 122 | 31 | 14.1 | 13.4 | 18.2 | 24.9 |
| (El Salvador, Cerro Cacaguatique, 4) | (102–136) | (109–137) | (30–33) | (13.3–14.8) | (12.8–14.2) | (17.1–19.4) | (23.5–26.5) |
| *R. underwoodi* | 138 | 153 | 38 | 15.0 | 15.6 | 18.8 | 28.6 |
| (Costa Rica, Volcán Poás, 2) | (135–142) | (148–158) | (37–39) | (14.9–15.1) | (15.5–15.8) | (18.6–19.0) | (28.2–28.9) |

[a] Country, followed by Gazetteer reference.

[b] Sample size refers to numbers of postcranial skeletons measured. External dimensions are usually represented by larger series.

[c] Abbreviated as explained in text.

means[2] for the 10 ichthyomyine taxa of table 2. Ichthyomyine tails average slightly greater in length than heads-and-bodies, but may be a little shorter (*Ichthyomys hydrobates tweedii*; *Rheomys hartmanni*) or a good deal longer (*Anotomys leander*; *Rheomys mexicanus*). Hindfeet average about one-fourth of head-and-body length, but may be nearly as little as one-fifth (*I. h. tweedii, N. monticolus*) or nearly as much as one-third (*A. leander, R. mexicanus*) of that dimension. The brachial index (RAD/HUM) averages close to unity among ichthyomyines, but in some species the radius may be substantially shorter or longer than the humerus. The average value of the crural index (TIB/FEM), by contrast, reflects the fact that the ichthyomyine tibia is consistently longer than the femur by a generous (but variable) fraction.

Table 5 presents values of the same ratios calculated from mean values for the 12 sigmodontine species of table 3. Variation within this collection of non-ichthyomyines is most conspicuous in lengths of tails relative to heads-and-bodies, with observed values that broadly overlap the range of relative tail lengths among ichthyomyines. Relative length of the hindfoot (HF/HBL) also exhibits some overlap between ichthyomyines and non-

---

[2] The ratio of means does not exactly equal the mean ratio, but it is close enough for present purposes and is necessitated anyway by the incomplete materials available for most ichthyomyine specimens.

TABLE 3
**The Mean and Range (in parentheses) of External and Postcranial Skeletal Measurements (in millimeters) for 12 Sigmodontine Species Samples**

| Species, | Measurements[c] | | | | | | |
|---|---|---|---|---|---|---|---|
| locality,[a] and sample size[b] | HBL | LT | HF | HUM | RAD | FEM | TIB |
| *Akodon cursor* | 120 | 91 | 26 | 14.8 | 16.0 | 20.0 | 25.0 |
| (Paraguay, Itapúa, 10) | (110–127) | (82–99) | (25–27) | (14.2–16.2) | (15.4–17.2) | (19.1–21.9) | (24.2–26.6) |
| *Calomys callosus* | 109 | 73 | 20 | 14.4 | 13.7 | 19.8 | 21.2 |
| (Paraguay, Chaco, 3) | (99–118) | (71–75) | (19–20) | (14.3–14.5) | (13.3–13.9) | (19.6–20.1) | (20.5–21.5) |
| *Chelemys macronyx* | — | — | — | 16.8 | 16.8 | 22.6 | 26.0 |
| (Argentina, Río Negro, 2) | | | | (16.5–17.2) | (16.6–17.0) | (22.2–23.1) | (25.7–26.2) |
| *Graomys domorum* | 146 | 154 | 30 | 19.0 | 18.7 | 26.3 | 30.4 |
| (Bolivia, Tarija, 3) | (131–166) | (144–161) | (29–31) | (18.8–19.2) | (18.2–19.2) | (25.6–26.8) | (30.1–30.6) |
| *Holochilus brasiliensis* | 173 | 172 | 43 | 22.6 | 21.4 | 32.4 | 35.8 |
| (Paraguay, Pres. Hayes, 2) | (165–188) | (162–177) | (39–46) | (21.9–23.2) | (20.7–22.2) | (31.6–33.3) | (35.1–36.6) |
| *Nectomys squamipes* | 228 | 212 | 55 | 27.2 | 26.6 | 39.5 | 46.4 |
| (Paraguay, Paraguarí, 1) | | | | | | | |
| *Oryzomys albigularis* | 139 | 162 | 32 | 19.2 | 19.3 | 25.2 | 31.3 |
| (Bolivia, Santa Cruz, 3) | (131–145) | (158–166) | (31–33) | (18.7–19.6) | (18.7–19.9) | (24.0–26.0) | (30.2–32.0) |
| *O. caliginosus* | 106 | 87 | 24 | 15.6 | 14.3 | 19.6 | 23.8 |
| (Ecuador, Imbabura, 4) | (101–117) | (76–97) | (22–25) | (15.0–16.6) | (13.7–14.9) | (19.0–20.2) | (22.5–25.2) |
| *O. nigripes* | 106 | 129 | 26 | 13.6 | 13.6 | 19.1 | 23.5 |
| (Paraguay, Paraguarí, 4) | (103–114) | (119–141) | (24–27) | (13.2–14.2) | (13.0–14.2) | (18.3–19.8) | (22.8–24.6) |
| *Oxymycterus delator* | 157 | 97 | 27 | 18.1 | 17.8 | 25.3 | 26.3 |
| (Paraguay, Canendiyu, 5) | (152–165) | (94–102) | (26–28) | (17.8–18.6) | (17.2–18.2) | (23.9–26.4) | (25.7–26.8) |
| *Rhipidomys couesi* | — | — | — | 25.4 | 22.2 | 33.0 | 34.0 |
| (Trinidad, Cumaca, 2) | | | | (24.1–26.6) | (21.6–22.8) | (31.4–34.6) | (32.6–35.4) |
| *Sigmodon hispidus* | 156 | 117 | 32 | 19.9 | 18.3 | 28.4 | 29.4 |
| (United States, Oklahoma, 6) | (146–174) | (110–129) | (31–34) | (19.1–21.6) | (17.7–20.0) | (27.0–31.2) | (28.0–31.6) |

[a] Country, and next-largest political unit.

[b] Sample sizes refer to numbers of postcranial skeletons measured. External dimensions are sometimes represented by larger series.

[c] Abbreviated as explained in text.

ichthyomines, although ichthyomyine hindfeet average relatively longer. The range of ichthyomyine variation in the brachial index brackets the maximum and minimum values of that ratio among these non-ichthyomyines, but there is no overlap between ichthyomyines and sigmodontines represented here in the crural index: all ichthyomyines have longer tibias, relative to femurs, than any other sigmodontines I have measured.

Even a casual inspection of table 4 suggests patterns of association among ichthyomyine external and postcranial skeletal proportions, and this is confirmed in table 6 where product–moment correlation coefficients are presented for all pairwise combinations of the four ratios. All correlation coefficients among ichthyomyine body proportions (below the diagonal in table 6) are large and positive: ichthyomyines with tails that are long relative to heads and bodies also have relatively large hindfeet as well as distal limb bones that are long relative to more proximal elements. It is of considerable interest that this pattern of correlations is evidently not a constant feature of all muroid external and postcranial skeletal comparisons, since an identical analysis of proportions for 10 other sigmodontines (above the diagonal in table 6) reveals only one substantial coefficient, and that be-

TABLE 4
**External and Postcranial Skeletal Proportions of 10 Ichthyomyine Species**

| Species | Ratios[a] LT/HBL | HF/HBL | RAD/HUM | TIB/FEM |
|---|---|---|---|---|
| *Anotomys leander* | 1.23 | 0.31 | 1.17 | 1.64 |
| *A. trichotis* | 1.11 | 0.27 | 1.08 | 1.58 |
| *Ichthomys h. hydrobates* | 1.04 | 0.24 | 0.85 | 1.39 |
| *I. h. tweedii* | 0.94 | 0.22 | 0.81 | 1.28 |
| *Neusticomys monticolus* | 0.97 | 0.23 | 0.96 | 1.42 |
| *Rheomys hartmanni* | 0.92 | 0.24 | 0.89 | 1.29 |
| *R. mexicanus* | 1.21 | 0.30 | 1.01 | 1.44 |
| *R. thomasi stirtoni* | 0.98 | 0.26 | 0.97 | 1.35 |
| *R. t. thomasi* | 1.06 | 0.27 | 0.95 | 1.37 |
| *R. underwoodi* | 1.11 | 0.28 | 1.04 | 1.52 |
| Minimum | 0.92 | 0.22 | 0.81 | 1.28 |
| Maximum | 1.23 | 0.31 | 1.17 | 1.64 |
| Mean | 1.06 | 0.26 | 0.97 | 1.43 |

[a] Calculated from sample means of table 2.

TABLE 5
**External and Postcranial Skeletal Proportions of 12 Sigmodontine Species**

| Species | Ratios[a] LT/HBL | HF/HBL | RAD/HUM | TIB/FEM |
|---|---|---|---|---|
| *Akodon cursor* | 0.76 | 0.22 | 1.08 | 1.25 |
| *Calomys callosus* | 0.67 | 0.18 | 0.95 | 1.07 |
| *Chelemys macronyx* | — | — | 1.00 | 1.15 |
| *Graomys domorum* | 1.05 | 0.20 | 0.98 | 1.16 |
| *Holochilus brasiliensis* | 0.99 | 0.25 | 0.95 | 1.10 |
| *Nectomys squamipes* | 0.93 | 0.24 | 0.98 | 1.17 |
| *Oryzomys albigularis* | 1.16 | 0.23 | 1.00 | 1.24 |
| *O. caliginosus* | 0.82 | 0.23 | 0.92 | 1.21 |
| *O. nigripes* | 1.22 | 0.24 | 1.00 | 1.23 |
| *Oxymycterus delator* | 0.62 | 0.17 | 0.98 | 1.04 |
| *Rhipidomys couesi* | — | — | 0.87 | 1.03 |
| *Sigmodon hispidus* | 0.75 | 0.20 | 0.92 | 1.04 |
| Minimum | 0.62 | 0.17 | 0.87 | 1.03 |
| Maximum | 1.22 | 0.25 | 1.08 | 1.25 |
| Mean | 0.90 | 0.22 | 0.97 | 1.14 |

[a] Calculated from sample means of table 3.

tween two ratio variables that share the same denominator and could be spuriously correlated for reasons discussed by Pearson (1897).

The strong correlations among ichthyomyine external and postcranial skeletal ratios described above suggest that those proportions may be integrated to conform with some consistent requirement of biomechanical design. Because of statistical difficulties that are often associated with the analysis of ratio data (Atchley et al., 1976; Atchley and Anderson, 1978), however, such a hypothesis is more convincingly supported by multivariate analysis of the original dimensions. I extracted principal components from the variance/covariance matrix of $\log_e$-transformed measurements (following the recommendations of Jolicoeur, 1963, and Morrison, 1976) separately for the 10 ichthyomyine species of table 2 and for the 10 other sigmodontines with complete data in table 3.

The first and second principal components together account for 97–98 percent of the total variance in external and postcranial measurements among ichthyomyines and non-ichthyomyines alike (table 7). The first principal component for the ichthyomyine data accounts for 77 percent of the total variance, but the second vector is also large, accounting for fully 20 percent of the total (and 89% of the residual) variance. For the non-ichthyomyine data, the proportions of total variance associated with the first and second components are quite different, 91 and 7 percent, respectively, reflecting a substantially greater range in absolute size.

The first principal component of each data set, in addition to accounting for most of the total variance, also has variable loadings that are all large and positive. Such positive leading eigenvectors are commonly encountered in analyses of morphometric correlation or covariance matrices and are conventionally interpreted as reflecting the common dependence of all measured dimensions on general size. The term "general size" is here intended in a purely descriptive sense for these static data because the ontogenetic information that would be necessary for more biologically explicit interpretation (Cock, 1966) is unavailable. The observation that loadings are not equal for all variables on each first principal component suggests that static allometric (static-size-correlated) variance in shape is also represented by these large vectors (Jolicoeur, 1963). Of considerable interest is the similarity in patterns of static allometry im-

TABLE 6

**Coefficients of Product–Moment Correlation[a] Among External and Postcranial Skeletal Proportions of Ichthyomyines (Below Diagonal) and Non-Ichthyomyines (Above Diagonal)**

| | | | | |
|---|---|---|---|---|
| LT/HBL | — | .74 | .18 | .60 |
| HF/HBL | .94 | — | .06 | .62 |
| RAD/HUM | .78 | .86 | — | .56 |
| TIB/FEM | .82 | .79 | .92 | — |
| | LT/HBL | HF/HBL | RAD/HUM | TIB/FEM |

[a] Calculated from data in tables 4 and 5. The relative magnitude of homologous correlations, not statistical significance, is the appropriate basis for inference here. N = 10 for all calculated correlations.

TABLE 7

**Results of Principal Component Analysis of External and Postcranial Skeletal Measurement Data**

| | Ichthyomyines[a] | | Non-Ichthyomyines[b] | |
|---|---|---|---|---|
| | *PC* 1 | *PC* 2 | *PC* 1 | *PC* 2 |
| % Variance | 77.4 | 20.1 | 91.4 | 6.8 |
| Loadings: | | | | |
| HBL | .399 | −.438 | .355 | .414 |
| LT | .533 | .282 | .479 | −.794 |
| HF | .477 | .357 | .438 | −.050 |
| HUM | .294 | −.447 | .320 | .264 |
| RAD | .231 | .388 | .315 | .188 |
| FEM | .304 | −.482 | .358 | .302 |
| TIB | .311 | .135 | .351 | .011 |

[a] N = 10; components extracted from the variance-covariance matrix of $\log_e$-transformed sample means (table 2).

[b] N = 10; components extracted as above using only those samples with complete data in table 3.

plied for ichthyomyines and non-ichthyomyines: the largest loadings of both first components are for length of hindfoot and length of tail, the smallest loadings for forelimb elements, and loadings of intermediate magnitude for head-body length and hindlimb elements. General size therefore appears similarly represented by homologous components for each data set.

The second principal component calculated from the ichthyomyine data (table 7, second column) displays large, positive coefficients for measurements of the tail, hindfoot, tibia and radius, but large, negative coefficients for length of head-and-body, humerus, and femur. Inspection of the matrix of residual covariances (those remaining after extraction of the first principal component; table 8) reveals the pattern of pairwise associations among variables for which the ichthyomyine second principal is the best-fitting linear expression. Lengths of tail, hindfoot, radius, and tibia covary positively with one another but negatively with lengths of head-and-body, humerus, and femur. Relative to the trunk and more proximal limb bones, therefore, ichthyomyines with larger hindfeet also have longer tails and distal limb bones, the same proportional associations suggested earlier by ratio correlations but now shown to be a pattern independent of general size (table 9). Interestingly, none of the components elicited by analysis of the non-ichthyomyine data (the second principal component is provided for inspection in table 7, fourth column) resembles this nexus of size-independent morphometric dependence.

The pattern of morphological integration in ichthyomyine external and postcranial skeletal dimensions demonstrated here will be familiar to many students of mammalian comparative anatomy. Semiaquatic mammals usually have proportionately shorter proximal limb bones, longer distal limb bones, and larger hindfeet than related, terrestrial species; in addition, semiaquatic mammals that swim with alternate strokes of enlarged hindfeet usually have longer (or more laterally compressed) tails than terrestrial kin (Dobson, 1883; Howell, 1930; Savage, 1957; Hildebrand, 1961; Tarasoff, 1972; Bou et al., 1987). Enlargement of the hindfoot doubtless serves to increase the effective propulsive surface, while side-to-side oscillations of a long tail may balance the asymmetrical thrust of alternate kicks (Howell, 1930; Fish, 1982). Reduction in length of proximal limb elements may function to draw knee and elbow joints as far as possible into a generally fusiform body outline, but could also relate (together with simultaneous elongation of distal

TABLE 8

**Matrix of Residual[a] Variances and Covariances (×100) Among Log$_e$-Transformed External and Postcranial Skeletal Measurements of Ichthyomyines**

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| HBL | .362 | | | | | | |
| LT | −.212 | .164 | | | | | |
| HF | −.273 | .144 | .250 | | | | |
| HUM | .313 | −.198 | −.267 | .339 | | | |
| RAD | −.266 | .162 | .224 | −.295 | .275 | | |
| FEM | .316 | −.239 | −.260 | .353 | −.308 | .425 | |
| TIB | −.089 | .070 | .059 | −.100 | .094 | −.118 | .044 |
| | HBL | LT | HF | HUM | RAD | FEM | TIB |

[a] After extracting the first principal component.

limb bones) to mechanical aspects of aquatic limb function hypothesized by Savage (1957) and Tarasoff (1972). Among related mammalian species differing in degree of aquatic specialization, therefore, tail length, hindfoot length, and lengths of the distal long bones should positively intercorrelate, but correlate negatively with lengths of the proximal limb bones and length of the head-and-body. The signs and magnitudes of variable loadings on the ichthyomyine second principal component clearly conform to this anticipated pattern.

Similarity or difference with respect to size-independent external and postcranial proportions described by the ichthyomyine second principal component is readily visualized by inspection of species scores on that vector. Figure 21 displays such results for ten ichthyomyine species and for five species of cursorial non-ichthyomyines included to serve as a basis for comparisons. The numerical score for each ichthyomyine and non-ichthyomyine species is calculated as the sum of the products $a_i \log_e x_i$, $i = 1–7$, where the $x_i$ are species measurement means from tables 2 or 3 and the $a_i$ are the respective variable coefficients from the second column of table 7.

TABLE 9

**Coefficients of Product–Moment Correlation Between Ichthyomine External and Postcranial Skeletal Ratios and Species Scores on the First and Second Principal Components**

| | Species scores[b] | |
|---|---|---|
| Ratios[a] | *PC*1 | *PC*2 |
| $\frac{\text{LT}}{\text{HBL}}$ | .33 | .90 |
| $\frac{\text{HF}}{\text{HBL}}$ | .19 | .93 |
| $\frac{\text{RAD}}{\text{HUM}}$ | −.12 | .97 |
| $\frac{\text{TIB}}{\text{FEM}}$ | .02 | .94 |

[a] From table 4.

[b] Calculated as the sum of the products $a_i \ln x_i$, $i = 1–7$, where the $x_i$ are species' measurement means from table 2 and the $a_i$ are the corresponding variable coefficients from columns 1 or 2 of table 7.

If ichthyomyines evolved from an ancestor with external and postcranial skeletal proportions similar to those of extant cursorial sigmodontines, then the sequence of ichthyomyine species along the horizontal axis of figure 21 represents a series of morphologies more derived and specialized for aquatic locomotion in proportion to their distance from the cluster of terrestrial species to the left. I therefore interpret the short tails, small hindfeet, long proximal, and short distal limb bones of *Rheomys hartmanni* and those *Ichthyomys* species included in figure 21 to be more primitive and less modified for aquatic locomotion than the long tails, large hindfeet, short proximal, and long distal limb bones of *Anotomys leander, A. trichotis, Rheomys mexicanus,* and *R. underwoodi.*

## QUALITATIVE CHARACTERS OF THE POSTCRANIAL SKELETON

AXIAL SKELETON: Table 10 summarizes numerical variation in the elements that comprise the axial skeletons of 13 ichthyomyine taxa. Most specimens of most species

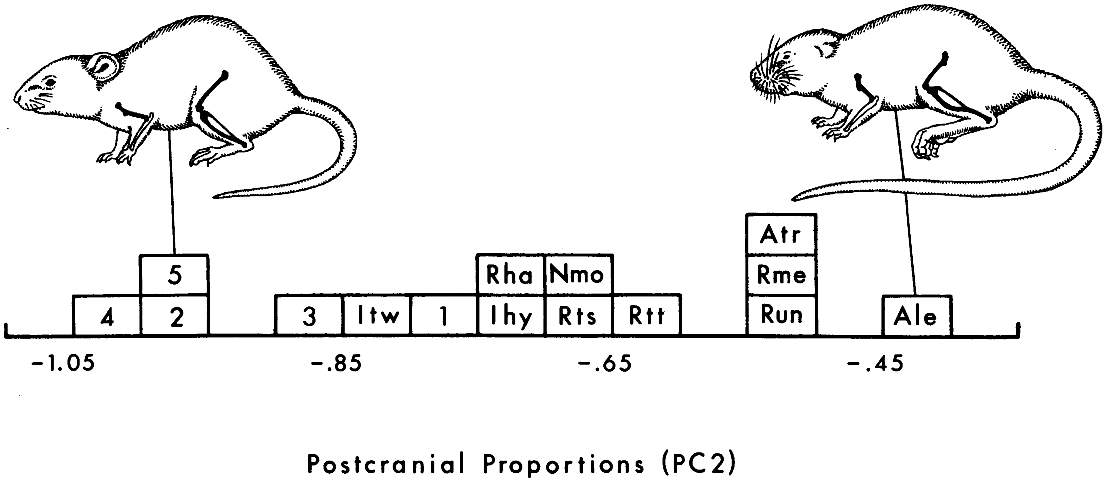


Fig. 21. Size-independent variation in external and postcranial skeletal proportions. Ten ichthyomyine taxa and five species of terrestrial sigmodontines are represented by their scores on the ichthyomyine second principal component (see text for explanation). **Ale,** *Anotomys leander*; **Atr,** *A. trichotis*; **Ihy,** *Ichthyomys hydrobates hydrobates*; **Itw,** *I. h. tweedii*; **Nmo,** *Neusticomys monticolus*; **Rha,** *Rheomys hartmanni*; **Rme,** *R. mexicanus*; **Rts,** *R. thomasi stirtoni*; **Rtt,** *R. t. thomasi*; **Run,** *R. underwoodi*; **1,** *Akodon cursor*; **2,** *Calomys callosus*; **3,** *Oryzomys caliginosus*; **4,** *Oxymycterus delator*; **5,** *Sigmodon hispidus.*

have 13 ribs, 19 thoracicolumbar vertebrae, and 4 sacral vertebrae. *Anotomys leander* departs most conspicuously from these modal counts with 14 ribs, 20 thoracicolumbar vertebrae, and 5 or 6 sacral vertebrae. *A. trichotis* and *Daptomys venezuelae* may usually have 14 ribs as well, but sample sizes for these species are small. Occasional specimens of two species of *Rheomys* also have 14 ribs and 20 thoracicolumbar vertebrae. The number of caudal vertebrae varies widely among ichthyomyines.

Ichthyomyines share the axial skeleton counts of table 10 with many other muroids. Carleton (1980) showed that 13 ribs and 19 thoracicolumbar vertebrae are widespread counts for these elements among muroids, and he hypothesized that these numbers are

TABLE 10
**Counts of Axial Skeletal Elements for 11 Ichthyomyine Species Samples**

| Species | N | Ribs | | Thoracicolumbar vertebrae | | Sacral vertebrae | | | Caudal vertebrae | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 13 | 14 | 19 | 20 | 4 | 5 | 6 | <30 | 30–33 | >33 |
| *Anotomys leander* | 8 | | 8 | | 8 | | 6 | 1 | | 6 | |
| *Anotomys trichotis* | 4 | 1 | 3 | 4 | | 3 | | | | 3 | |
| *Daptomys venezuelae* | 2 | | 2 | 2 | | 2 | | | | 1 | |
| *Ichthyomys h. hydrobates* | 2 | 2 | | 2 | | 2 | | | | 1 | |
| *Ichthyomys h. tweedii* | 4 | 4 | | 4 | | 4 | | | | 1 | |
| *Ichthyomys pittieri* | 1 | 1 | | 1 | | 1 | | | | 1 | |
| *Neusticomys monticolus* | 10 | 9 | | 9 | | 8 | | | 3 | 4 | |
| *Rheomys hartmanni* | 4 | 4 | | 4 | | 4 | | | | 3 | |
| *Rheomys mexicanus* | 11 | 8 | 1 | 7 | 1 | 2 | | | | | 1 |
| *Rheomys thomasi* | 14 | 12 | 2 | 13 | 1 | 12 | | | | 2 | 1 |
| *Rheomys underwoodi* | 3 | 3 | | 3 | | 2 | | | | 1 | |

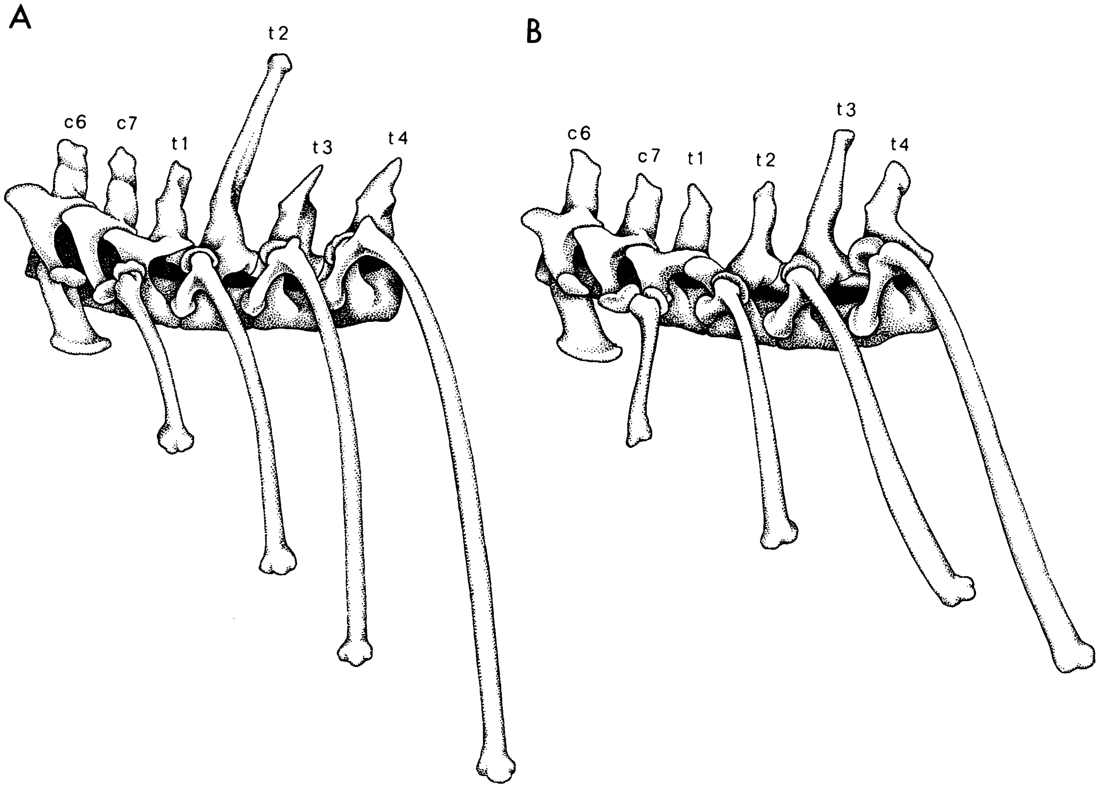


Fig. 22. Attachment of the nuchal ligament. The nuchal ligament attaches to the enlarged neural spine of the second thoracic vertebra of *Podomys floridanus* (**A**, AMNH 218074). In *Rheomys thomasi* (**B**, MVZ 98805) the nuchal ligament attaches to the third thoracic vertebra. **c6, c7,** the last two cervical vertebrae; **t1–t4,** the first four thoracic vertebrae.

primitive for the superfamily. Thirty to 33 caudals are likewise common among other sigmodontines, although a smaller count might be primitive (Carleton, op. cit.). Carleton and Musser (1984) report the frequent occurrence of four sacral vertebrae throughout the superfamily Muroidea.

The neural spine on the second thoracic vertebra of most muroids is much longer than the spines on adjacent vertebrae (fig. 22A) and provides the site of attachment for the nuchal ligament, a stout tendon from which two large muscles (M. splenius and M. rhomboideus) of the neck and shoulder regions originate (Rinker, 1954). Carleton (1980) discovered that this osteological feature is taxonomically widespread—among the muroid groups he surveyed only arvicolines were found to lack an enlarged neural spine on the second thoracic vertebra. In all ichthyomyines that I have dissected, however, the nuchal ligament is attached to the third thoracic vertebra, and in all available skeletons of adult ichthyomyines it is this vertebra and not the second that bears a longer neural spine (fig. 22B).

The head of the first rib articulates with the transverse processes of both the first thoracic and the seventh cervical vertebrae in all ichthyomyines, a condition that is encountered among many other sigmodontines as well (Carleton, 1980: fig. 15).

The muroid sternum consists of an anterior manubrium, several sternebrae, and a posterior xiphoid process (Howell, 1926: fig. 25; Greene, 1935: fig. 31). Most ichthyomyines have four sternebrae, but *Anotomys leander* has five, the single existing skeleton of *Ichthyomys pittieri* has three, and one of four skeletons of *Rheomys hartmanni* also has three.

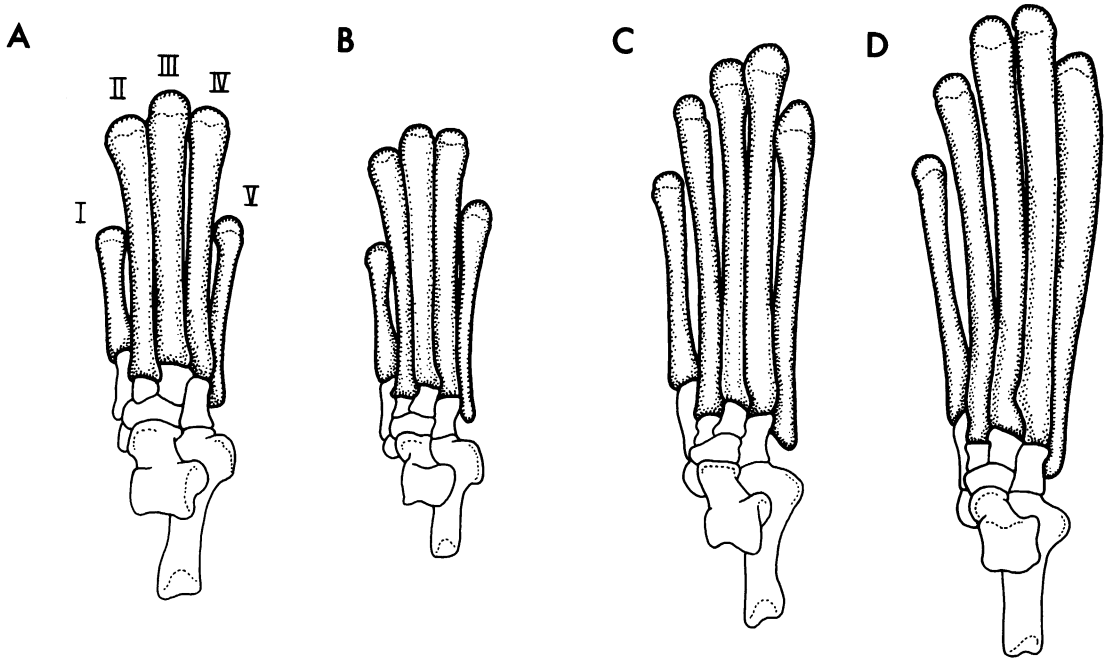


Fig. 23. Metatarsal configurations. **A,** *Sigmodon hispidus* (UMMZ 158049); **B,** *Neusticomys monticolus* (UMMZ 155789); **C,** *Ichthyomys hydrobates* (UMMZ 156375); **D,** *Rheomys mexicanus* (AMNH 205320).

APPENDICULAR SKELETON: The proximal elements of the ichthyomyine pectoral skeleton resemble their homologs among other sigmodontines; clavicles are always present and scapulas lack the third fossa that is present in some Gerbillinae (Carleton, 1980). Ichthyomyines uniformly lack the entepicondylar foramen, a conspicuous perforation through the medial epicondyle at the distal end of the humerus that communicates the median nerve and brachial artery in many mammals (Landry, 1958). The entepicondylar foramen is sporadically absent throughout Muroidea (Carleton, 1980). The deltoid tuberosity of the humerus is large and distinct in all ichthyomyines. The radius and ulna are not remarkable.

The bones of the manus exhibit no appreciable variation in size, position, or number among ichthyomyines. Scaphoid and lunar bones are fused, but the cuneiform, centrale, and the four distal carpals are all separate. Large and well-developed pisiform and falciform bones are also present. Metacarpal and phalangeal proportions as well as the number and distribution of sesamoids resemble those illustrated and described for *Mus musculus* by Romankowowa (1955). In osteological features the ichthyomyine manus appears indistinguishable from the hand skeletons of most other small muroids (see Tullberg, 1899; Howell, 1926; and Greene, 1935 for representative illustrations).

I observed no qualitative differences among ichthyomyines in the proximal elements of the hindlimb. The tibia and fibula are fused distally for 37–49 percent of the length of the former bone, proportions that are not unusual among other sigmodontines (Carleton, 1980).

Ichthyomyine calcanea grossly resemble those of many other muroids (see Stains, 1959, and Romankowowa, 1963, for illustrations and descriptive terminology). Separate and distinct posterior, medial and anterior articular surfaces provide dorsal contact with the astragalus, and the caudal edge of the trochlear process is about level with the cranial limit of the posterior articular surface. The remaining tarsals, consisting of separate astragalus, navicular, cuboid, three cuneiforms, and a single large sesamoid (the

TABLE 11
**Metatarsal Configurations in Living Ichthyomyines and a Hypothetical Ancestor, Arranged in Primitive-to-Derived Sequence**

| Sequence | Taxa | Metatarsals in order of decreasing length |
|---|---|---|
| 1 | hypothetical ancestor | III > II = IV ≫ V > I |
| 2 | *Neusticomys monticolus*<br>*Daptomys venezuelae* | III ≥ IV > II ≫ V > I |
| 3 | *Ichthyomys* sp.<br>*Rheomys hartmanni* | IV > III > II > V > I |
| 4 | *Anotomys trichotis*<br>*Rheomys thomasi* | IV > III > II = V > I |
| 5 | *Anotomys leander*<br>*Rheomys mexicanus*<br>*Rheomys underwoodi* | IV > III > V > II > I |

"medial tarsal" of Hildebrand, 1978), do not appear to differ appreciably among ichthyomyine species or between ichthyomyines and nonaquatic sigmodontines. Instead, the distinguishing osteological features of ichthyomyine hindfeet concern the next most distal series of bones, the metatarsals.

In cursorial muroids such as *Sigmodon hispidus* (fig. 23A) the three middle metatarsals (II–IV) are much longer than the lateralmost (V) and medialmost (I) bones, metatarsal III projects beyond metatarsals II and IV (which are of about equal length), and the tip of metatarsal V projects slightly beyond the tip of I. The three middle metatarsals are closely joined proximally; metatarsal III is straight, but II and IV splay to either side distally. Metatarsals I and V articulate less firmly with adjacent elements, and obviously possess some independence of movement relative to the three ankylosed middle bones.

Among ichthyomyines, *Neusticomys monticolus* (fig. 23B) and species of *Daptomys* retain the metatarsal proportions described above with only minor differences. The three middle metatarsals are still much the longest elements, but metatarsal IV is almost as long as III and a little longer than II; metatarsal V is also conspicuously longer than I.

Members of all of the remaining species and genera of ichthyomyines have metatarsal proportions that are unique among living sigmodontines: metatarsal IV is the longest bone, followed by III, II, and/or V, and I. Metatarsal II is longer than V (the primitive condition) in *Rheomys hartmanni* and species of *Ichthyomys* (fig. 23C); II and V are of roughly equivalent length in *R. thomasi* and *Anotomys trichotis,* but V is longer than II in *A. leander, R. mexicanus* (fig. 23D) and *R. underwoodi.* Table 11 summarizes these changes of metatarsal proportions in a progressive sequence from a hypothetically primitive condition resembling that of *Sigmodon hispidus* and most other terrestrial sigmodontines to the clearly derived morphology represented by *A. leander* and the two large species of *Rheomys.*

There are other changes in the morphology of the metatarsals that accompany the progressive alterations in relative lengths detailed above. As it lengthens, metatarsal V comes to be tightly appressed to the ventrolateral surface of IV, and both of these elements, together with III, acquire a pronounced curvature. Metatarsal III remains closely applied to IV for most of its length, but II and I are largely freed of their contacts with adjacent bones. These two medialmost metatarsals are also straighter and less robust than the three stout, curved, and conjoined lateral elements.

The evident result of these alterations in metatarsal morphology is to transform a primitively narrow, mesaxonic, cursorial foot into an effective organ of aquatic propulsion. The surface area of the foot is increased by lengthening the outer bones and perhaps also by the separation of the two medial metatarsals from the close conformation of the lateral three elements. The overlapping of metatarsals IV and V may serve to strengthen the lateral margin of the foot, and their curvature to reduce resistance of this edge to the flow of water as it is drawn forward in the recovery stroke of swimming. Whether the details of this hydrodynamic interpretation are correct or not, other small mammals that forage for arthropod prey in running waters (see table 51 and accompanying text) have metatarsal morphologies that closely resemble those of ichthyomyines, and some functional correlation with aquatic habits is surely indicated.

## HYOID MUSCULATURE

I surveyed 36 muscles of the head, throat, and neck regions in representatives of every ichthyomyine genus except *Daptomys* (for which only fluid-preserved trunks were available). The morphology of the mandibular adductors is described in a subsequent section; the present account describes only those features of the hyoid musculature that have received systematic attention in other rodent taxa.

THE HYOID SUSPENSION: Two different anatomical arrangements by which the hyoid apparatus is suspended from the basicranium have been discovered among sigmodontine rodents. In the genera *Neotoma, Onychomys, Peromyscus,* and *Reithrodontomys* a cartilaginous stylohyal is present and the anterior cornu is anchored to the petromastoid by a ligament that attaches to the posterior extremity of the stylohyal cartilage and passes into the stylomastoid foramen together with the facial nerve (Sprague, 1941, 1942). Rinker (1954) described the anatomical relationships of the four muscles that attach to the stylohyal in *Peromyscus* and *Neotoma*: (1) Fibers of M. stylohyoideus originate from the stylohyal (some superficial fibers originate also from the paroccipital process in *Neotoma*) and insert onto the posterior portion of the thyrohyoid bone. (2) Fibers of M. jugulohyoideus originate from the paroccipital process and insert onto the stylohyal. (3) M. styloglossus originates from the stylohyal (a few fibers attach to the rim of the external auditory meatus) and inserts into the lateral part of the tongue. (4) M. stylopharyngeus originates from the stylohyal and inserts into the pharynx. This arrangement also occurs in dipodoid rodents for which Klingener (1964) provides illustrations of exceptional clarity.

In *Hodomys, Oryzomys,* and *Sigmodon* the stylohyal cartilage is absent (Sprague, 1941). In *Sigmodon hispidus* and *Oryzomys palustris,* the only sigmodontines with this hyoid morphology whose musculature has hitherto been described (Rinker, 1954), M. stylohyoideus, M. styloglossus, and M. stylopharyngeus originate from a broad aponeurosis that covers the ventral surface of the auditory bulla and attaches to the ventral margin of the external auditory meatus and to the paroccipital process. M. jugulohyoideus is greatly reduced in these species and passes from the paroccipital process to a small cartilage, embedded in the bullar aponeurosis, that Rinker (1954) believed to represent a vestigial stylohyal. Klingener (1964) reported a similar hyoid morphology for *Mesocricetus* and *Microtus.*

All ichthyomyines that I have dissected, including *Anotomys leander, A. trichotis, I. hydrobates, Neusticomys monticolus,* and several species of *Rheomys,* lack a stylohyal cartilage; the attachments of M. stylohyoideus, M. styloglossus, and M. stylopharyngeus among these taxa resemble those described by Rinker for *Sigmodon* and *Oryzomys.* I was unable to consistently demonstrate the existence of a very small jugulohyoid muscle. Klingener (1964) provided cogent arguments for the primitive presence of a stylohyal cartilage among myomorph rodents.

M. OMOHYOIDEUS: The omohyoid is a narrow, strap-shaped muscle that originates from the cranial border of the suprascapular notch and inserts onto the ventral surface of the basihyal deep to M. sternohyoideus. The omohyoid is present in all ichthyomyines that I dissected (including examples of all genera) with the exception of *Anotomys leander* and *Rheomys mexicanus* in which it is absent. The omohyoid is present in all other myomorphs for which published dissections are available (Greene, 1935; Rinker, 1954; Sharma and Sivaram, 1959; Klingener, 1964), but its absence among some hystricomorph genera has been documented by Parsons (1894) and Woods (1972).

## ALIMENTARY CANAL

This section describes the soft anatomy of the alimentary canal as well as some adjacent viscera. From a purely functional perspective, the dentition and the muscles of mastication might also be included here, but the former is traditionally accorded special status in mammalian systematics and the latter is a system of considerable anatomical complexity in its own right; they are treated in other sections.

ORAL CAVITY: Ichthyomyines lack the internal cheek pouches that are sometimes present as small evaginations of the oral mucosa (Rinker, 1963) or as large sacs provided with retractor muscles (Ryan, 1986) in other muroid groups.

Palatal rugae are transverse ridges of cornified epithelium overlying the hard palate that function together with the tongue to control the intraoral movement of food particles (Kutuzov and Sicher, 1952; Weijs, 1975); the shapes and number of such rugae exhibit considerable variation among muroids (Tullberg, 1899; Eisentraut, 1976; Carleton, 1980). Ichthyomyines have three diastemal rugae and three to four intermolar rugae. The anteriormost diastemal ridge is fused to the posterior aspect of the incisive papilla, a pyramidal mound of epithelium that contains the paired openings of the nasopalatine ducts (Quay, 1954). The second and third diastemal rugae are separate; usually these rugae are complete, but in occasional specimens one or both may be divided into right and left segments that remain closely approximated at midline. Four incomplete intermolar rugae are present in *Ichthyomys hydrobates hydrobates* (N = 1), *I. h. soderstromi* (1), *I. h. tweedii* (3), *I. pittieri* (1), *Neusticomys monticolus* (4), *Rheomys hartmanni* (2), *R. mexicanus* (1), and *R. underwoodi* (1). There are only three intermolar rugae in *Anotomys leander* (4), *A. trichotis* (1), *Daptomys venezuelae* (1), and *R. thomasi thomasi* (1). Though the number of palatal rugae often appears to be constant within muroid species, the shapes of individual rugae vary within and among conspecific populations.

Ichthyomyine tongues grossly resemble those of most other muroid rodents (see Tullberg, 1899; Sonntag, 1924; and Vorontsov, 1979, for reviews), and conform in most details with the careful description of the tongue of *Rattus norvegicus* provided by Fish et al. (1944). The ichthyomyine tongue fills the mouth closely when the molars are near occlusion; its width at the level of the intermolar prominence is about one-third its greatest length (from the apex of the organ to the anterior lip of the epiglottis). A shallow median sulcus creases the dorsal surface of the distal ⅓ of the tongue, and an indistinct semilunar sulcus defines the anterior limit of the intermolar prominence (torus linguae). Filiform papillae, produced superficially as tough, horny denticles, are densely spaced over the whole lingual dorsum from the tip to a short distance anterior to the epiglottis; these papillae have a simple conical form anterior to the intermolar prominence, but posterior to the semilunar sulcus they are truly filiform with bifid or complex tips. Fungiform papillae are largely dermal, subsurface structures whose presence is difficult to determine without injection of dyes or maceration of the epidermis, but their presence may be inferred by the absence of filiform papillae from small patches on the lingual surface; ichthyomyine tongues appear to have few fungiform papillae, perhaps 12 or fewer per tongue. A single circumvallate papilla is located on the dorsal midline of the tongue a short distance anterior to the epiglottis; it consists of a large, rounded or elongate-ovoid fleshy tubercle recessed in a deep, semicircular furrow. Behind the circumvallate papilla the dorsal surface of the tongue is smooth and devoid of filiform papillae, but a few small, pimplelike structures that appear to correspond to the lenticular papillae described by Vorontsov (1979) are consistently present. Foliate papillae (the "lateral organs" of Sonntag, 1924, and other authors) occur as one to six indistinct vertical slits arranged in a single series on each side of the tongue behind the intermolar prominence. The number of foliate papillae may differ on opposite sides of the same tongue, however, and sample sizes are insufficient to evaluate possible species differences in this feature. No other variation was evident among the tongues of the ichthyomyine species I dissected.

STOMACH: The most widespread type of stomach among sigmodontines is the uniloc-

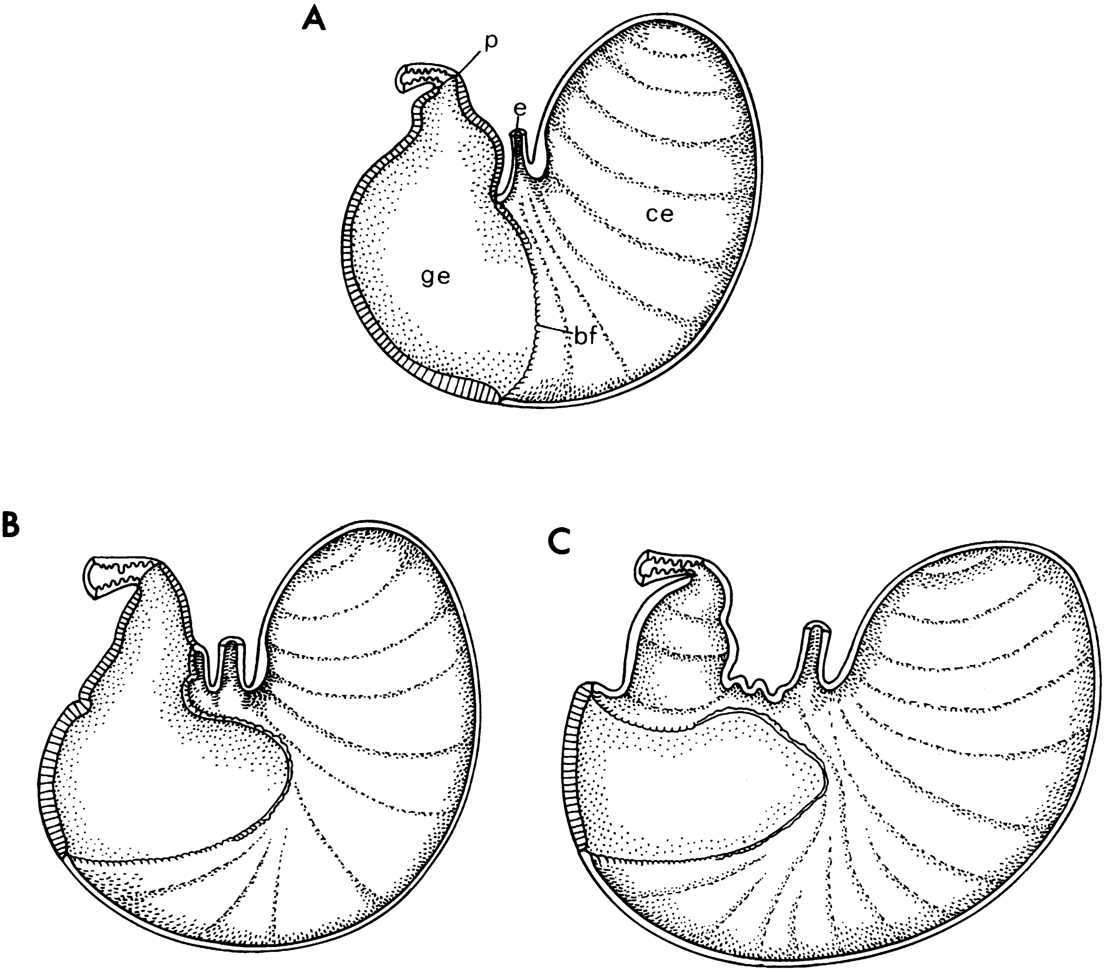


Fig. 24. Ventral view of stomachs in frontal section to show distribution of gastric glandular epithelium (after Carleton, 1973). **A**, *Nyctomys sumichrasti* (UMMZ 113525); **B**, *Daptomys venezuelae* (AMNH 69908); **C**, *Rheomys hartmanni* (UMMZ 111987). **bf**, bordering fold; **ce**, cornified epithelium (on left side of stomach); **e**, esophagus; **ge**, glandular epithelium (on right side of stomach); **p**, pylorus.

ular–hemiglandular morphology (fig. 24A) described by Carleton (1973): the gastric lumen is undivided by deep infoldings of the stomach wall (thus, unilocular) and the gastric mucosa consists of glandular epithelium to the right of the esophagus but cornified squamous epithelium to the left (hence, hemiglandular). The juncture between glandular epithelium and cornified squamous epithelium is marked by a prominent ridge, the bordering fold. In stomachs that conform to the unilocular–hemiglandular type, the bordering fold extends from the incisura angularis (the dextral gastroesophageal angle) to a point almost directly opposite on the greater curvature.

Ichthyomyines all have unilocular stomachs, but the zone of gastric glandular epithelium is less extensive than in the hemiglandular condition described above. In *Anotomys trichotis*, *Daptomys venezuelae* (fig. 24B), and *Neusticomys monticolus* the bordering fold intersects the lesser curvature of the stomach between the esophagus and the pyloric sphincter and does not contact the incisura angularis. In *Anotomys leander* and in all species of *Ichthyomys* and *Rheomys* (fig. 24C) for which material is available, how-

TABLE 12
**Means and Ranges (below, in parentheses) of Hindgut Measurements (in millimeters) for Six Ichthyomyine Species**

| Species | N | Length of small intestine | Length of caecum | Length of large intestine | Total length of hindgut |
|---|---|---|---|---|---|
| *Anotomys leander* | 10 | 595 | 24 | 50 | 670 |
| | | (521–703) | (21–28) | (40–58) | (598–781) |
| *Anotomys trichotis* | 3 | 546 | 13 | 54 | 613 |
| | | (497–602) | (11–15) | (43–59) | (551–675) |
| *Ichthyomys h. tweedii* | 5 | 763 | 26 | 84 | 873 |
| | | (733–807) | (20–32) | (59–99) | (848–915) |
| *Neusticomys monticolus* | 5 | 549 | 19 | 61 | 629 |
| | | (505–571) | (16–22) | (52–70) | (590–651) |
| *Rheomys hartmanni* | 2 | 612 | 24 | 68 | 704 |
| | | (545–680) | (22–25) | (65–70) | (632–775) |
| *Rheomys underwoodi* | 2 | 742 | 42 | 78 | 866 |
| | | (720–775) | (40–43) | (75–80) | (835–898) |

ever, the region between the esophagus and the pyloric sphincter is entirely lined with cornified squamous epithelium; glandular epithelium is restricted to a broad band that crosses the greater curvature on the right-hand side of the stomach. Carleton (1973) drew attention to apparent differences between *Daptomys venezuelae* and *Neusticomys monticolus* in the position of the bordering fold with relation to the esophagus and pyloric sphincter, but the apparently interspecific difference he described is matched by variation within the larger series (N = 16) now available for *N. monticolus.*

GALL BLADDER: The median (or cystic) lobe of the liver is divided into right and left halves by a deep furrow that contains a large, saccular gall bladder in all ichthyomyines except members of the genus *Ichthyomys.* All specimens of *Ichthyomys* that I have examined, including representatives of *I. hydrobates hydrobates, I. h. soderstromi, I. h. tweedii,* and *I. pittieri,* lack any trace of a gall bladder. The presence and absence of gall bladders are both widespread conditions among muroid rodents (Greene, 1935; Howell, 1926; Vorontsov, 1979; Carleton, 1980).

HINDGUT: The ichthyomyine hindgut is distinctive in the anatomical simplicity and relative dimensions of the segments that constitute it.

The small intestine is very long, averaging 86–89 percent of the total length of the hindgut. It is a simple tube, folded and involved with mesenteries, and there is no gross anatomical feature to mark the transition between duodenum and jejunum-ileum. The caecum, by contrast, is small, averaging only 2–5 percent of the total length of the hindgut. The ichthyomyine caecum is slender and vermiform (Thomas, 1893: pl. XXIX, fig. 6), devoid of proximal swellings (ampullae) or sacculations (haustra). Internally, the caecum lacks plications and other sculpture and the lumen is undivided by septa. There are no valves between the caecum and either the small or large intestines.

The large intestine is also short and simple in ichthyomyines; it averages only 7–10 percent of the total length of the hindgut and lacks internal septa or plicae. Although it is folded within the abdominal cavity, the large intestine of ichthyomyines does not form the tight colonic coils that have been described for other muroid species (Vorontsov, 1979).

Table 12 provides means and ranges of length measurements for the hindgut segments of six ichthyomyine species. Soft and elastic even in preservative, hindguts are difficult to measure repeatably; segment lengths are doubtless subject to the usual sources of ontogenetic and individual variation, as well as to unknown artifacts of preservation. Measurements summarized in table 12 are therefore derived only from adult (TWC 3–6) animals that were known to have been fixed in

TABLE 13

**Hindgut Segments as Proportions of Total Length of Hindgut for 14 Species of Muroid Rodents**

(Ichthyomyine proportions calculated from means provided in table 12)

| Species | Small intestine / Hindgut | Caecum / Hindgut | Large intestine / Hindgut | Source[a] |
|---|---|---|---|---|
| Ichthyomyines | | | | |
| *Anotomys leander* | .89 | .04 | .07 | 1 |
| *Anotomys trichotis* | .89 | .02 | .09 | 1 |
| *Ichthyomys h. tweedii* | .87 | .03 | .10 | 1 |
| *Neusticomys monticolus* | .87 | .03 | .10 | 1 |
| *Rheomys hartmanni* | .87 | .03 | .10 | 1 |
| *Rheomys underwoodi* | .86 | .05 | .09 | 1 |
| Herbivorous muroids | | | | |
| *Sigmodon hispidus* | .70 | .10 | .20 | 6 |
| *Neotoma albigula* | .59 | .20 | .21 | 6 |
| *Microtus ochrogaster* | .44 | .21 | .35 | 2 |
| *Otomys irroratus* | .42 | .18 | .39 | 4 |
| Carnivorous muroids | | | | |
| *Onychomys leucogaster* | .74 | .06 | .20 | 6 |
| *Oxymycterus nasutus* | .85 | .05 | .10 | 6 |
| *Scotinomys teguina* | .81 | .04 | .15 | 3 |
| *Hydromys chrysogaster* | .88 | .02 | .10 | 5 |

[a] Sources: (1) this study; (2) Barry, 1977; (3) Hooper and Carleton, 1976; (4) Perrin and Curtis, 1980; (5) Tullberg, 1899; (6) Voronstov, 1979.

10 percent formalin and thereafter stored in 70 percent ethanol. I measured hindguts after cutting the binding mesenteries and extending each segment until it was approximately straight. Despite these precautions, the ranges of measurements provided in table 12 reveal considerable variation within samples. Coefficients of variation for length of the small intestine, caecum, and large intestine were 10.0, 9.5, and 12.3, respectively, in a sample of ten adult *Anotomys leander* from Papallacta, Ecuador.

Nevertheless, calculated means of hindgut proportions are similar among ichthyomyine species, and many other muroids exhibit such widely divergent hindgut morphologies that useful comparisons are possible even when sample sizes are so small. Table 13 provides the relative lengths of hindgut segments for six ichthyomyines and for eight other muroid taxa chosen to exemplify two extremes of muroid hindgut proportions that correlate broadly with diet. Muroid species that are presumed to rely on plant structural carbohydrates for a substantial fraction of their caloric requirements (*Sigmodon hispidus, Neotoma albigula, Microtus ochrogaster,* and *Otomys irroratus* are examples) usually have relatively short small intestines but large and elaborate caecae and large intestines (Vorontsov, 1979; Perrin and Curtis, 1980); cellulose degradation and partial resorption of the degradation products (chiefly volatile fatty acids) apparently occur in the latter two posterior segments (Yang et al., 1969). By contrast, muroids that regularly consume large quantities of animal protein but little plant matter (*Scotinomys teguina, Onychomys leucogaster, Oxymycterus nasutus,* and *Hydromys chrysogaster*) usually have much longer small intestines but diminutive (and simple) caecae and large intestines. Consistent with their known dietary habits, ichthyomyines are clearly more similar in their hindgut proportions to the latter, animalivorous category than to the former, herbivorous group.

## MALE REPRODUCTIVE TRACT

ACCESSORY GLANDS: All ichthyomyines for which fluid-preserved adult male specimens are available (including representatives of all

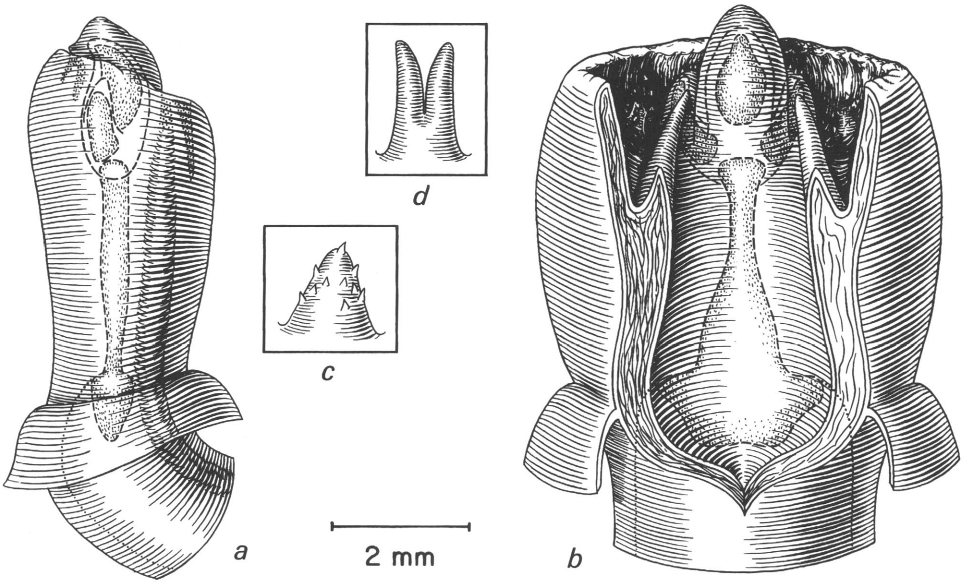


Fig. 25. Glans penis of *Rheomys hartmanni* (UMMZ 112301) in lateral view (**a**) and incised midventrally (**b**), with enlargements of the dorsal papilla (**c**) and the bifurcate urethral flap (**d**). From Hooper and Musser's (1964) figure 7.

five genera) exhibit the complete complement of accessory reproductive glands believed to be primitive for muroid rodents (Voss and Linzey, 1981). This consists of one pair each of preputial, bulbourethral, dorsal and anterior prostate, vesicular, ampullary, and at least one pair of ventral prostate glands. All ichthyomyines except *Anotomys leander* and possibly *A. trichotis* have two well-defined pairs of ventral prostates. As previously reported (by Voss and Linzey, op. cit.), *A. leander* possesses an undifferentiated mass of ventral prostatic tubules that cannot be separated into distinct lateral and medial glands. Only a single proximal male tract is available from *A. trichotis*; I could not confidently distinguish lateral and medial glands in this specimen, but as the animal (UMMZ 156376) is a young adult, it is possible that these glands might be discernable in more mature examples.

SPERMATOZOA: I examined the unstained spermatozoa of 11 ichthyomyine species (including representatives of all five genera) at 1250 diameters magnification using phase contrast optics. All ichthyomyine spermatozoa were found to have flattened heads, roughly oval in outline, armed with a single, large acrosomal hook. Ichthyomyine male gametes are similar in these respects to the sperm of *Peromyscus* (sensu stricto) described by Linzey and Layne (1974), but discrimination of finer details of gametic structure was not possible with the crudely fixed preparations available.

GLANS PENIS: The phalli of all ichthyomyines except *Anotomys leander* resemble the common South American cricetine bauplan described by Hooper and Musser (1964) in the following shared characteristics (see fig. 25): (1) The penis is a roughly cylindrical organ that swells from a narrow, dorsoventrally flattened base at the ventral flexure to a maximum diameter and rounder cross section near the terminal crater; distally, the glans may be divided by shallow longitudinal folds into six indistinct lobes. (2) Small epidermal spines, recessed in fleshy pits, densely invest the whole exterior of the glans except for a folded band of naked skin encircling the base of the organ just distal to the prepuce, and for a narrow strip of soft, crenulated tissue that forms the rim of the terminal crater. (3) A capacious terminal crater contains the urinary meatus, three centrally located bacular mounds, one dorsal papilla, and a bifurcate

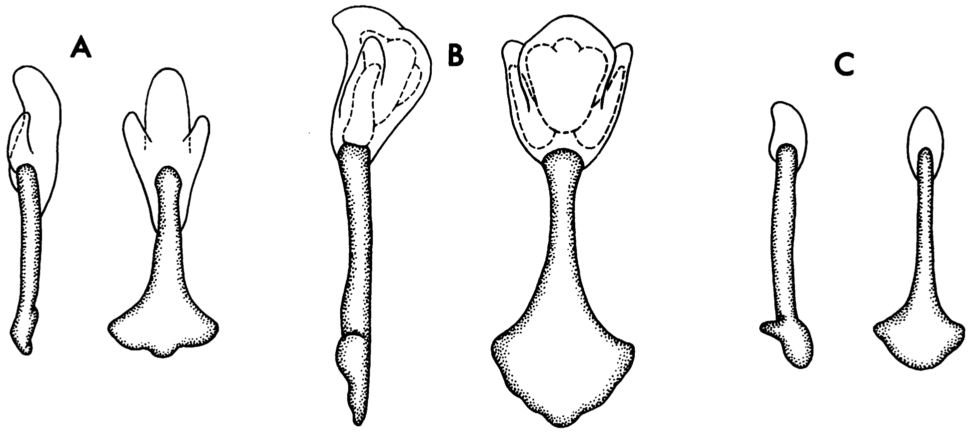


Fig. 26. Ichthyomyine bacular morphology. **A,** *Ichthyomys hydrobates tweedii* (UMMZ 155787); **B,** *Rheomys mexicanus* (AMNH 205313); **C,** *Anotomys leander* (AMNH 244607). Each baculum is shown in lateral and ventral view. The internal calcifications of the distal cartilage of *R. mexicanus* are shown in broken outline.

urethral flap; the epithelium that lines the crater orifice is soft and naked except for small clusters of epidermal spines (similar to those on the exterior of the glans) that may be present on the tips of papillae and the lateral bacular mounds. (4) The baculum consists of a proximal bone with a broad, spatulate base from which arises an elongate shaft that terminates in a rounded distal process; surmounting the bony shaft of the baculum is a trifid cartilaginous mass whose fingerlike processes underlie the three fleshy bacular mounds.

All ichthyomyine phalli also exhibit a pair of spinous papillae recessed in the lateral walls of the crater, one to either side of the baculum. Among the 43 South American cricetine species surveyed by Hooper (1962) and Hooper and Musser (1964), lateral crater papillae were discovered only in *Rheomys hartmanni* (the single ichthyomyine species sampled by those authors) and in species of the genus *Sigmodon* (including *Sigmomys*).

Differences in phallic morphology among the ichthyomyines whose glands conform to the characterization provided above (*Anotomys leander* alone is excluded) consist chiefly in features of the distal bacular cartilage. In all species of *Rheomys* (figs. 25, 26B) the medial bacular mound is very large, filling the lumen of the terminal crater and protruding distally well beyond the crater margins; the cartilaginous digit underlying this large mound is grossly swollen, invariably contains a calcified core, and greatly exceeds the lateral digits in size—a bacular configuration quite unlike those encountered among other South American cricetine taxa (Hooper and Musser, 1964). In *Anotomys trichotis, Daptomys, Neusticomys,* and *Ichthyomys* (fig. 26A) the medial bacular digit is relatively much smaller than in *Rheomys,* does not contain internal calcifications, and more nearly resembles homologous structures among other sigmodontines with complex phalli.

The penis of *Anotomys leander* exhibits several unique features. By comparison with the stouter, faintly hexalobate glandes of other ichthyomyines, the phallus of *A. leander* is slender and plain in external appearance. The dorsal margin of the crater is produced distally beyond the ventral crater lip so that the crater orifice is directed ventrally and the bacular mound is concealed from lateral view. The crater contains two spinous lateral papillae and a bifurcate urethral process, as described above for the other ichthyomyine taxa, but the remaining crater contents are unique to *A. leander.* There are two spine-bearing papillae set closely side by side high on the dorsal wall of the crater in the position occupied by the single dorsal papilla of all other South American cricetines (fig. 27A, B). In addition, *A. leander* has only a single, fingerlike bacular mound that is armed with two large epidermal spines set dorsolaterally, one

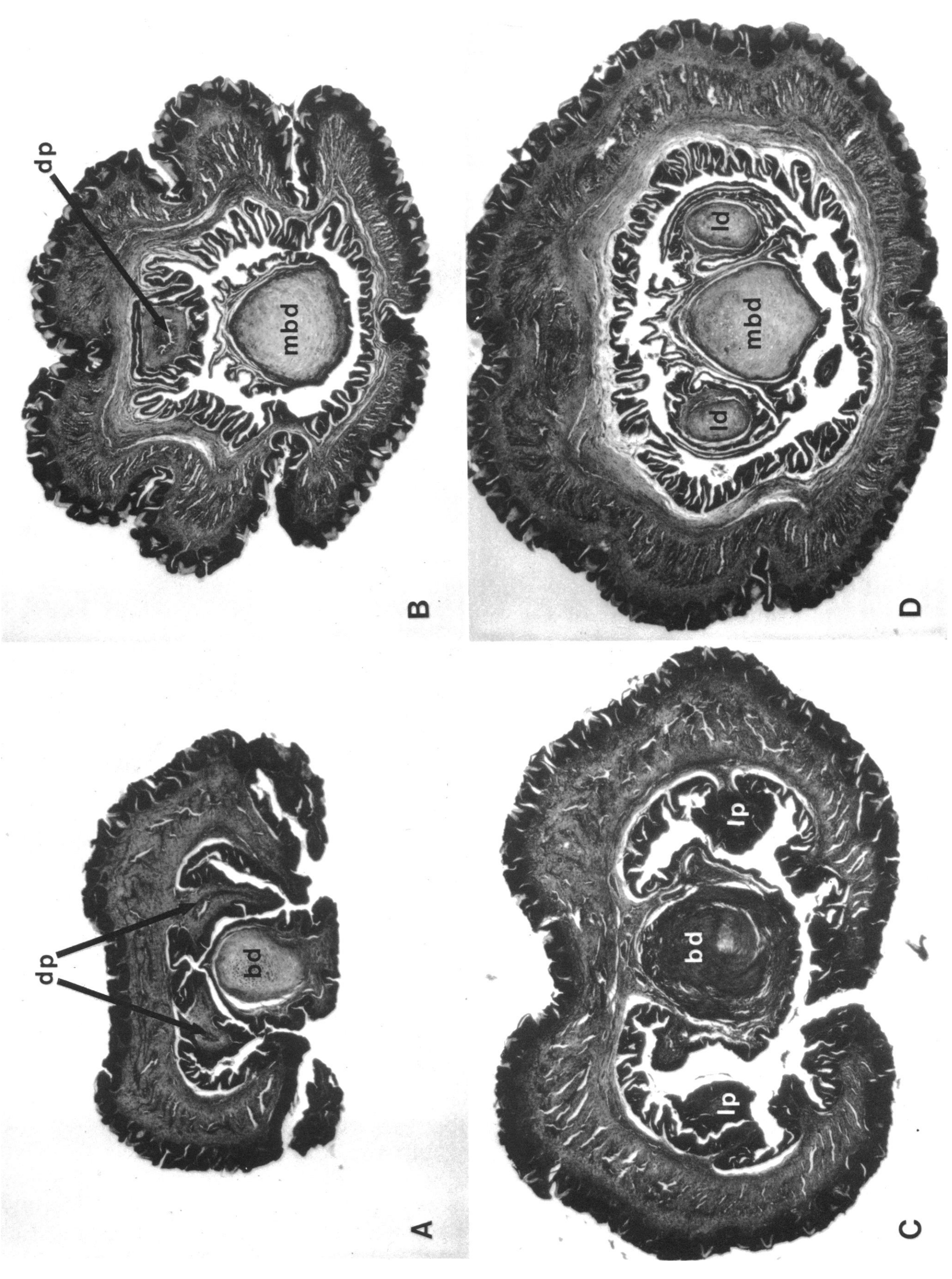


Fig. 27. Transverse sections through the glans penis of *Anotomys leander* (**A, C**) and *Neusticomys monticolus* (**B, D**). Sections A and B pass through the tip of the glans; sections C and D pass through the middle of the crater. Dorsal is toward the top of each section. **bd,** single cartilaginous bacular digit; **dp,** dorsal papilla(e); **ld,** lateral digits of bacular cartilage; **lp,** lateral crater papillae; **mbd,** medial digit of bacular cartilage.

on either side. The mound is supported by a correspondingly simple bacular cartilage; unlike the trifid distal cartilage of other ichthyomyines, the bacular cartilage of *A. leander* consists of a single digit (fig. 26, 27C, D). The two large dorsolateral spines on the medial bacular mound are unsupported by internal cartilaginous processes.

# TAXONOMY

The morphological characters described above provide the basis for the diagnoses and descriptions that follow. The principal purpose of these accounts is to define ichthyomyine taxa in terms of anatomical similarities and differences so that unambiguous identifications can be made; the accounts also serve to summarize information about geographical distributions and to discuss hypotheses about biological species limits. One new name is proposed here, and several names are placed in synonymy, in order to maximize the correspondence between taxonomic categories and observed patterns of character variation. The phylogenetic interpretation of such patterns, however, is deferred to a subsequent section of this monograph.

Available samples are inadequate for satisfactory revision of species limits within several ichthyomyine genera, but I have tried to achieve a species-level classification that is at least comparable from genus to genus by recognizing only phenotypically distinctive populations or groups of populations for which hypotheses of reproductive isolation can be tested by future collecting efforts. These accounts make no pretense to be definitive: there is every reason to believe that new ichthyomyine species will be discovered and that new material from critical localities may suggest changes in the taxonomic arrangements proposed here.

## TRIBE ICHTHYOMYINI VORONTSOV, 1959

SYNONYMS: None.

TYPE GENUS: *Ichthyomys* Thomas, 1893.

CONTENTS: Fourteen species in five genera as arranged and described below.

KNOWN DISTRIBUTION: From San José Lachiguirí in Estado Oaxaca, Mexico, southeastward in mountainous regions and adjacent foothills through Guatemala, El Salvador, and Costa Rica to Cerro Pirre in eastern Panama; in South America, from northern Colombia southward to central Peru and eastward to French Guiana (maps in Appendix). Specimens are unknown from Belize, Honduras, Nicaragua, Surinam, and Brasil but this probably reflects inadequate collecting in appropriate habitats. Ichthyomyines are known from localities near sea level to an elevation of 4000 m.

DIAGNOSIS: Ichthyomyines are small to medium-size, semiaquatic, carnivorous muroid rodents that can be distinguished from all other living members of the superfamily by the following combination of morphological features.

Pinnae small, rounded, and well haired or absent; mystacial vibrissae stiff and abundant, the hairs of the tumid upper lip ventrally recurved; genal vibrissae absent; mammae six, in postaxial, abdominal, and inguinal pairs; pes with a continuous comb of stiff hairs along the plantar margins (weakly developed in some species); hypothenar pad of pes absent or indistinct; tail well haired, the underlying epidermal scales absent or inconspicuous; ventral caudal hairs much longer and denser than hairs of the caudal dorsum.

Incisors opisthodont but approaching the orthodont condition; molars 2/2 or 3/3, rooted, biserial, the left and right maxillary series parallel; labial and lingual cusps arranged in strictly opposite pairs; M1 anterocone always with two functional cusps but the anteromedian flexus shallow, indistinct, or absent; mesoloph(id)s, anteroloph(id)s, posteroloph(id)s, and other accessory enameled structures of the molar crowns small and inconspicuous or absent; M3/m3 small or absent; M1–2 with three roots apiece, m1–2 with two roots each.

Zygomatic notches completely absent; interorbital margins rounded, without beads or sharp edges; braincase smooth in lateral aspect, without conspicuous temporal ridges; gnathic process of premaxillae well developed, projecting conspicuously between upper incisors; inferior zygomatic roots slender, without platelike anterior projections or dorsal spines; masseteric tubercles near base of inferior zygomatic roots well developed; hard palate smooth between the molar rows and produced posteriorly beyond M3; parapterygoid fossae narrow, not deeply excavated; incisive foramina long but not penetrating deeply between molar rows; posterolateral palatal pits few and simple; infraorbital foramen large and ovoid, as wide ventrally as dorsally; lateral wall of rostrum complete behind inferior zygomatic root, not fenestrated; optic foramen very small; buccinator–masticatory foramen separated from foramen ovale accessorius by stout vertical strut of the alisphenoid; sphenopalatine vacuities absent or present only as narrow slits, the bony roof and walls of the mesopterygoid fossa substantially complete; subsquamosal fenestra absent; stapedial foramen always present but sometimes small; auditory bullae small, flask-shaped or globular; tympanic membrane pars flaccida absent.

Neural spine on third (not second) thoracic vertebra enlarged for attachment of nuchal ligament; head of first rib articulates with transverse processes of seventh cervical and first thoracic vertebrae; entepicondylar foramen absent; cheek pouches absent; tongue with one circumvallate papilla; stomach unilocular with glandular epithelium variously reduced from hemiglandular condition; small intestine very long; large intestine very short, simple, without colonic loops; caecum short, simple and vermiform; complete muroid complement of accessory glands present; heads of spermatozoa oval with a single apical hook; glans penis spinous externally with deep terminal crater containing dorsal papilla(e), bacular mound(s), two spinous lateral papillae, and a bifurcate urethral process.

COMMENTS: Ichthyomyini was first proposed as a family-group name by Vorontsov (1959) to include the genera *Anotomys, Daptomys, Ichthyomys, Neusticomys,* and *Rheomys* but was not otherwise defined or diagnosed. Previous and subsequent authors (e.g., Gyldenstolpe, 1932; Cabrera, 1961) consistently treated the ichthyomyine genera together but provided no formal designation for the assemblage. Tribal rank is a conservative assignment for the group since character states that distinguish ichthyomyines from other muroids are at least as numerous as those serving to diagnose most currently recognized subfamilies of Muridae (see Carleton and Musser, 1984).

## KEY TO THE ICHTHYOMYINE GENERA

1a. Carotid circulation pattern 1; five plantar pads on manus (the hypothenar and third interdigital pads separate); stomach with glandular epithelium between esophagus and pyloric sphincter .................... 2

1b. Carotid circulation pattern 2 or 3; five or fewer plantar pads on manus; stomach with glandular epithelium restricted to an oval patch on the greater curvature ........ 3

2a. Hindfoot narrow with weakly developed fringe of stiff hairs; claw of digit V of pes extends to but not beyond first interphalangeal joint of IV; ears plainly visible above unruffled fur of head; philtrum present; tail just equal to or less than combined length of head and body .................... *Neusticomys*

2b. Hindfoot broad with well-developed fringe of stiffened hairs; claw of digit V of pes extends to second interphalangeal joint of IV; ears buried in fur of head, not visible above unruffled surface; philtrum absent; tail longer than combined length of head and body . ............. *Chibchanomys,* new genus

3a. Adult dorsal pelage dull gray-black when fresh (but fading with age to dull rust color); pinnae absent; tufts of pure white fur over external auditory canal; philtrum absent; superciliary vibrissae present; carotid circulation pattern 2 ......... *Anotomys*

3b. Adult dorsal pelage glossy and grizzled-brownish; pinnae present; ear region without conspicuous tufts of white fur; philtrum present or absent; superciliary vibrissae absent; carotid circulation pattern 3 ..... 4

4a. Manus with five plantar pads (the hypothenar and third interdigital pads separate); nasal bones short, truncated anteriorly to reveal nasal orifice in dorsal view; supraorbital foramina on dorsal surface of frontals between the orbits in large adult specimens; occipital condyles produced posteriorly well behind the rest of the occiput; gall bladder absent .................. *Ichthyomys*

4b. Manus with four or fewer plantar pads (the hypothenar and third interdigital pads always fused); nasal bones long, concealing nasal orifice in dorsal view; supraorbital foramina open laterally within the orbits; occipital condyles not produced posteriorly much behind the rest of the occiput; gall bladder present .............. *Rheomys*

## THE MOUSE FROM CUNDINAMARCA

Thomas (1897) described *Ichthyomys trichotis* on the basis of a single specimen collected by G. D. Child in Departamento Cundinamarca, Colombia. Thomas compared the new species with *Ichthyomys hydrobates, I. soderstromi,* and *I. stolzmanni,* the only other ichthyomyines known at that time, noting that *I. trichotis* differed from those "... by the extreme hairiness of its ears, the restriction of the white of the undersurface to the chest and center of belly, and by the slenderness of its incisors" (Thomas, 1897: 221). In 1906, however, Thomas removed *trichotis* from *Ichthyomys* and placed it in a new genus, *Rheomys,* based on characters of the ears, incisors, and muzzle that *trichotis* shared with *R. underwoodi,* the type species. Handley (1976) subsequently identified as *Anotomys trichotis* a single ichthyomyine specimen collected in the Táchira Andes of Venezuela. That the generic membership of *trichotis* should be so open to interpretation is due both to the state of preservation of the type and to the unique combination of morphological features possessed by the species it represents.

The type of *trichotis* (BMNH 97.7.2.2) is a very young animal, sex unknown, with newly erupted and unworn third molars. The specimen consists of a stuffed skin and parts of the head skeleton. The skin is in poor condition with fur missing from the corners of the mouth, the mystacial vibrissae burnt short on the right side, and the pelage coming loose in patches elsewhere. Skeletal fragments consist of the complete left mandible and a fragment of the right bearing the incisor and m1–2, a fragment of the left maxilla and premaxilla bearing M1–3 and the incisor, and a bit of the right maxilla with M1. Despite these meager materials, sufficient characters remain to establish *trichotis* as an animal distinct from species of *Ichthyomys, Rheomys,* or any other named form of ichthyomyine: (1) The pelage is soft, dense and wooly, devoid of buffy-banded awns, and composed exclusively of wool hairs and long, fine guard hairs. (2) No trace of a philtrum is present on the hairy upper lip below the rhinarium. (3) There are five separate plantar pads on the manus; the hypothenar and third interdigital pads are not fused. (4) The pinnae are very small and entirely buried in the fur of the head. (5) The metatarsal margins and digits of the pes are densely fringed with stiff hairs. (6) m3 is extremely small, about half the size of m2 and lacks a distinct posterior cusp.

Since Thomas's (1897) description, seven additional specimens exhibiting this combination of character states have been collected in the Andes of eastern Colombia and western Venezuela and in the Cordillera Carpish of Peru. These specimens appear to represent the same biological species as the type of *trichotis,* and the character states listed above together with other features revealed by study of this new material suggest that *trichotis* is a form sufficiently distinctive to warrant generic recognition.

## ***Chibchanomys*, new genus**

(Figures 4–6, 20, 28, 29)

SYNONYMS: None.

TYPE SPECIES: *Ichthyomys trichotis* Thomas, 1897, based on the British Museum of Natural History specimen (BMNH 97.7.2.2) described above, collected by G. D. Child at some time prior to 1897 in "W. Cundinamarca," Colombia. Thomas (1897: 220) stated that the type had been collected "... in low country near to Magdalena R.," but Thomas's handwritten label attached to the type skin does not provide this information. Since Child's original specimen label is missing (it was probably removed by Thomas and subsequently discarded), the sole remaining source of information is the Mammal Section's accessions register for the year 1897. The first entry for July 2 is the type of *Peramys adustus* whose locality is recorded on two lines as "Hot country/W. Cundinamarca." The second entry for July 2 is the type of *Ichthyomys trichotis,* the locality for which is recorded by ditto marks beneath the lower (second) line of the habitat entry for *Peramys*

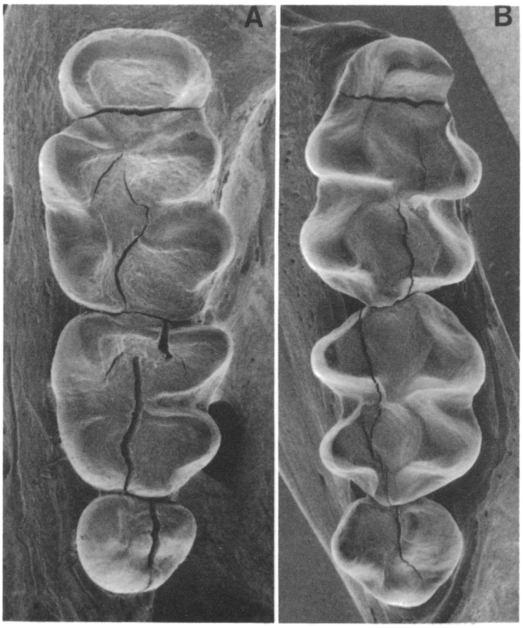


Fig. 28. Molar dentition of *Chibchanomys trichotis* (MBUCV I-2795). **A,** left maxillary molars; **B,** right mandibular molars. About ×16.

*adustus.* The western half of Departamento Cundinamarca consists chiefly of the warm lowlands of the Río Magdalena valley, but judging from the known habitats of all subsequently collected specimens of *trichotis,* it seems more likely that the type was obtained in a montane situation, perhaps in the Cordillera Oriental of eastern Cundinamarca near Bogotá from which Child sent many other mammal specimens to the British Museum in the 1890s.

Contents: Only one described species, *C. trichotis,* is included.

Known Distribution: The uncertain type locality aside, *Chibchanomys* has been collected only at elevations above 2400 m in (1) the Cordillera Oriental of Colombia, (2) the Táchira Andes of western Venezuela, and (3) the Cordillera Carpish of Departamento Huánuco, Peru.

Etymology: Named for the Chibchan, Pre-Hispanic inhabitants of the Cordillera Oriental of Colombia. The first specimens of the new genus were collected within the ancient borders of the Chibchan kingdom.

Diagnosis: Ichthyomyines with dull, gray-black dorsal pelage; small pinnae buried in the fur of the head; philtrum absent; tail longer than combined length of head and body; manus with five separate plantar pads; hindfoot long and broad with well-developed fringing hairs; nasal bones long; supraorbital foramina open laterally within orbits; carotid circulation pattern 1; orbicular apophysis of malleus absent; stomach with glandular epithelium between esophagus and pyloric sphincter; gall bladder present; bacular cartilage tridigitate.

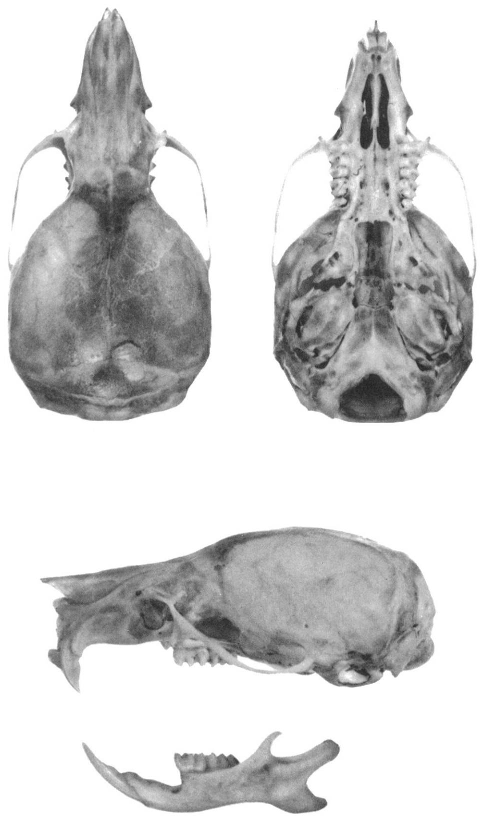


Fig. 29. Cranium and mandible of *Chibchanomys trichotis* (UMMZ 156376). All ×2.

Description: Adult head-and-body length 113–125 mm; HF/HBL = .26–.28; LT/HBL = 1.05–1.15; pelage soft, dense, wooly, composed exclusively of underfur and long, fine guard hairs; color above dull gray-black when fresh (fading with age to brownish hues); venter paler, washed with silvery white (but the bases of the hairs dark gray) over midthoracic, abdominal and inguinal regions; tail unicolored, dark; pinnae very small, concealed beneath fur of head; supraorbital vibrissae absent; rhinarium pigmented (black when dry); philtrum absent in most specimens; manus with three separate interdigital and two separate carpal pads; sole of pes pigmented (black when dry); hypothenar pad of pes absent, thenar elongate, 4th interdigital opposite 2nd and extending to base of 3rd; hairy fringe along metatarsal margins and digits of pes well developed, stiff; claw of digit V of pes extends beyond first interphalangeal joint to distal end of phalange 2 of IV; claw of digit I of pes extends just beyond first interphalangeal joint of II.

Molars 3/3; principal cusps tall and sharp when unworn; M1 without anteroloph; M1–2 with or without small mesolophs (projecting from paracones); small posterolophs present on unworn M1–2; M2 with or without small anteroloph; M3 with or without minute conule behind protocone/paracone; m1 with shallow anteromedian flexid dividing anteroconid into small, sharp labial and lingual conulids; m1 with or without small anterolophid; m1–2 with small peglike posterolophids, with or without small mesolophids; m2 with small anterolophid; m3 small, with or without minute conulid behind protoconid/metaconid; upper incisors narrow and delicate, their anterior enameled surfaces not inclined medially; lower incisors slender and procumbent.

Nasals long, concealing incisors and nasal orifice from dorsal view; rostrum narrow, the nasolacrimal capsules fully exposed in dorsal view; interorbital region narrow relative to breadth of braincase (LIB/BB = .35–.36 in TWC 3–5); supraorbital foramina open laterally into orbits, not onto dorsal surface of frontals; braincase inflated, globose, the lambdoidal ridges inconspicuous or absent; occipital condyles not produced posteriorly behind supraoccipital, not visible dorsally; dorsal profile straight above rostrum but frontals rising abruptly over the orbits to rounded, convex braincase; posterior edge of inferior zygomatic root over M1 anterocone; tip of masseteric tubercle above plane of molar alveoli; incisive foramina slightly wider behind the maxillary/premaxillary suture than anteriorly; palate not produced very far posteriorly beyond M3s; carotid circulation pattern 1; bullae not or slightly inflated, bulbous or flask-shaped; orbicular apophysis of malleus absent; basicranium nearly flat with only slight kyphosis at sphenoccipital suture.

Ribs 13–14; thoracicolumbar vertebrae 19; sacral vertebrae 4; metatarsals IV > III > II = V > I; omohyoid muscle present; stomach nearly hemiglandular with gastric glandular epithelium between esophagus and pyloric sphincter; gall bladder present; bacular cartilage tridigitate, the medial digit larger than the lateral two but not grossly swollen and without a calcified core; one dorsal crater papilla present.

COMPARISONS: *Chibchanomys trichotis* is easily distinguished from members of all of the genera it formerly occupied. *C. trichotis* differs from species of *Ichthyomys* by its dull, soft, gray-black pelage, absence of a philtrum, very small pinnae buried in the fur of the head, long nasal bones, supraorbital foramina located within the orbital fossae, carotid arterial supply (pattern 1), absence of an orbicular apophysis of malleus, distribution of gastric glandular epithelium, possession of a gall bladder, and in growth-invariant craniodental proportions (relatively larger molars, slender incisors, more inflated braincase, and broader palate; see Cranial Morphometrics, below). Species of *Rheomys* differ from *Chibchanomys* by their glossy, grizzled-brownish fur, fused hypothenar and third interdigital pads of manus, carotid arterial supply (pattern 3), presence of an orbicular apophysis of malleus, stomach morphology, and shape of the bacular cartilage. *Chibchanomys* compares closely with *Anotomys* in pelage composition, in postcranial proportions, and in growth-invariant aspects of craniodental form (see Craniodental Morphometrics, below), but differs from that genus by its less reduced pinnae, absence of superciliary vibrissae, separate hypothenar and third interdigital pads of manus, carotid arterial supply, absence of an orbicular apophysis, metatarsal configuration, possession of an omohyoid muscle, stomach morphology, and morphology of the bacular cartilage. *Chibchanomys* differs from *Anotomys, Ichthyomys,* and *Rheomys* in other characters that are detailed in the descriptions provided above and below for these genera, but the ones cited here provide the most conspicuous qualitative contrasts. Character states distinguishing *C. trichotis* from species of *Neustic-*

TABLE 14
**Age, Sex, and Measurements (in millimeters) of *Chibchanomys trichotis* from Colombia, Venezuela, and Peru**

| | Colombia | | Venezuela | | | | Peru |
|---|---|---|---|---|---|---|---|
| | BMNH 97.7.2.2[a] | FMNH 71226 | USNM 442606 | UMMZ 156532 | UMMZ 156376 | MBUCV I-2795 | LSU 14406 |
| Age | 1/?/n | 6/f/n | 6/f/n | 5/f/n | 3/o/n | 1/o/n | 1/o/n |
| Sex | ? | male | female | female | female | male | female |
| HBL | – | 125 | 120 | 116 | 113 | 105 | 102 |
| LT | – | 131 | 133 | 133 | 126 | 115 | 123 |
| HF | 30 | 33 | 33 | 32 | 32 | 30 | 31 |
| Ear | – | 8 | 10 | 7 | 7 | 6 | 6 |
| CIL | – | 25.9 | 26.9 | 26.4 | 25.3 | 24.3 | 23.8 |
| LD | – | – | – | 7.0 | 6.2 | 5.7 | 5.7 |
| LM | 4.4 | – | – | 4.3 | 4.4 | 4.5 | 4.2 |
| LIF | – | 5.1 | 5.3 | 5.1 | 4.8 | 4.6 | 4.5 |
| BIT | 1.2[b] | 1.3 | 1.3 | 1.2 | 1.2 | 1.0 | 1.0 |
| BIF | – | 2.4 | 2.0 | 2.1 | 1.9 | 1.7 | 1.9 |
| BPB | – | – | – | 3.4 | 3.1 | 2.7 | 2.6 |
| LN | – | 8.1 | – | 8.9 | 9.5 | 8.5 | 8.5 |
| BN | – | 3.0 | 3.0 | 3.0 | 2.9 | 2.9 | 2.8 |
| LIB | – | 4.9 | 4.5 | 4.8 | 4.8 | 4.8 | 4.3 |
| ZB | – | 13.9[b] | 13.6 | 14.1 | 13.4 | 12.3 | 11.7 |
| BB | – | 13.8 | 13.7 | 13.6 | 13.4 | 13.0 | 12.4 |
| BZP | 1.2 | 1.0 | 1.0 | 1.1 | 1.0 | 1.1 | 1.0 |
| BM1 | 1.5 | – | – | 1.6 | 1.5 | 1.6 | 1.4 |
| HI | – | 5.3 | 5.0 | 4.8 | 4.6 | 4.1 | 3.9 |
| DI | – | 1.2 | 1.4 | 1.4 | 1.3 | 1.1 | 1.0 |
| BOC | – | 7.6 | 7.6 | 7.5 | 7.2 | 7.2 | 7.8 |

[a] The holotype.
[b] Estimated values.

*omys* are provided under the account for the latter genus, below.

VARIATION: The eight known specimens of *Chibchanomys trichotis* consist of two from Provincia Cundinamarca, Colombia, five from Buena Vista (Estado Táchira), Venezuela, and one from Departamento Huánuco, Peru. With such small samples from widely separated localities, it is difficult to judge the biological significance of morphometric differences among specimens (table 14). The Venezuelan series, however, includes both young and old examples and therefore provides some representation of ontogenetic variation. Animals from Colombia and Peru have measurements that are mostly within a few tenths of a millimeter of like-aged specimens in the Venezuelan sample, and differences that exist do not exceed what might be expected of a single species distributed over some 17 degrees of latitude. Although the skull of the type is smashed, another specimen from Cundinamarca (FMNH 71226) compares closely in cranial dimensions to the older Venezuelan individuals (e.g., USNM 442606) and the skins from Colombia and Venezuela are so alike that I see no reason to doubt their conspecificity. The juvenile Peruvian example (LSU 14406), on the other hand, has a markedly less inflated braincase, slightly broader occipital condyles, and somewhat smaller bullae than Colombian and Venezuelan material; in addition, a narrow median crease of sparsely haired epithelium dividing the right and left mystacial pads suggests the presence of an indistinct philtrum. These character differences may indicate that southern populations of *Chibchanomys* are phenotypically distinctive, but more material is required to substantiate this conjecture.

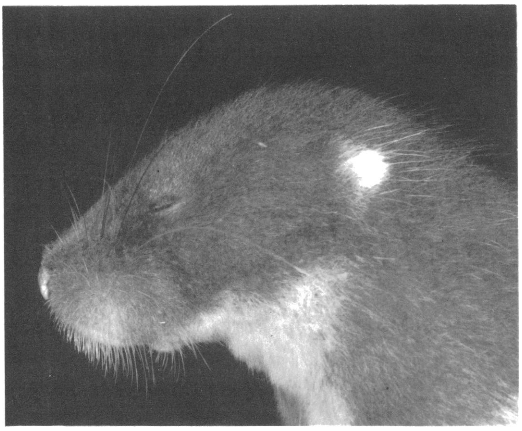


Fig. 30. Head of *Anotomys leander* (AMNH 244606). About ×1.75.

SPECIMENS EXAMINED: *Chibchanomys trichotis* – **Colombia:** Cundinamarca (BMNH 97.7.2.2, the type), San Cristobal (FMNH 71226). **Peru:** Cordillera Carpish (LSU 14406). **Venezuela:** Buena Vista (MBUCV 2795, 2796, UMMZ 156372, 156532; USNM 442606). Total, 8.

### *Anotomys* Thomas, 1906

(Figures 6, 18, 26, 27, 30–32)

SYNONYMS: None.

TYPE SPECIES: *Anotomys leander* Thomas, 1906, based on a British Museum of Natural History specimen (BMNH 5.11.7.1), consisting of the skin, skull, and mandibles of an old (6/f/n) male collected by Ludovic Söderström on 5 August 1905 at an elevation of 11,500 ft (3538 m) on Volcán Pichincha, Provincia Pichincha, Ecuador.

CONTENTS: Only one described species, *A. leander,* is included.

KNOWN DISTRIBUTION: Identifiable localities of the 20 known specimens are all from northern Ecuador, in the western Andes near Volcán Pichincha and Quito (Provincia Pichincha), or in the eastern Andes from the vicinity of Papallacta (Provincia Napo). Recorded elevations range from 2892 to 4000 m.

DIAGNOSIS: Ichthyomyines with dull, gray-black dorsal pelage; pinnae absent; philtrum absent; tail longer than combined length of head and body; manus with only four separate plantar pads; hindfoot very large and broad with well-developed fringing hairs; nasal bones long; supraorbital foramina open laterally into orbits; carotid circulation pattern 2; orbicular apophysis of malleus present; stomach with glandular epithelium restricted to greater curvature; gall bladder present; bacular cartilage with only a single digit.

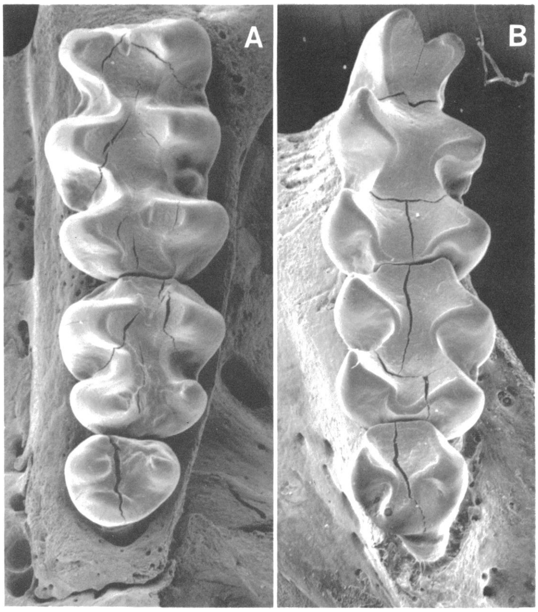


Fig. 31. Molar dentition of *Anotomys leander* (UMMZ 155598). **A,** left maxillary molars; **B,** right mandibular molars. About ×14.

DESCRIPTION: Adult head-and-body length 101–122 mm; HF/HBL = .29–.34; LT/HBL = 1.16–1.32; pelage dense, soft, wooly, composed exclusively of underfur and long, fine guard hairs; color above dull gray-black when fresh (fading with age to brownish hues); silvery-white beneath (but the bases of ventral hairs dark-gray); tail brownish, unicolored; definitive pinnae absent, the external ear reduced to hairy ridges of skin 1 mm or less in height along the dorsal and posterior margins of the external auditory canal, entirely buried in the fur of the head; conspicuous tufts of pure white fur always present over ear region; rhinarium very large, heavily pigmented (black when dry); philtrum absent; small su-

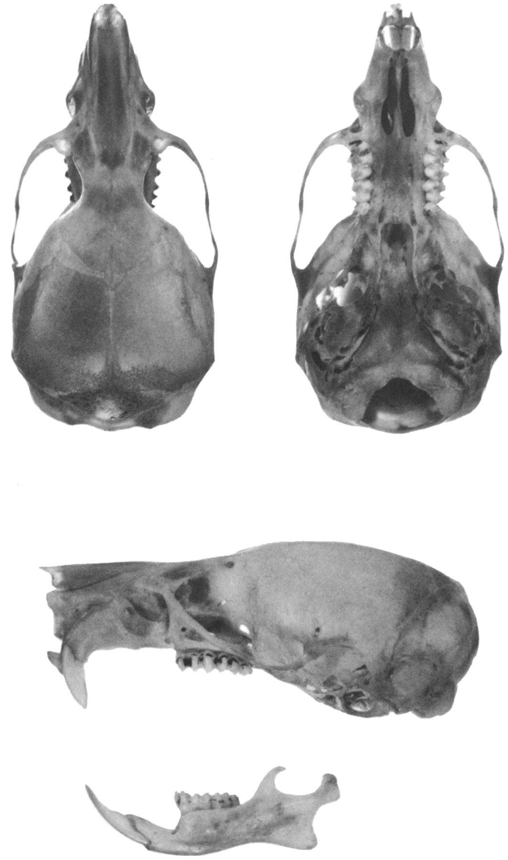


Fig. 32. Cranium and mandible of *Anotomys leander* (AMNH 244605). All ×2.

praorbital vibrissae present; manus with fused hypothenar and 3rd interdigital pads, but the 1st and 2nd interdigital and thenar pads all separate; sole of pes heavily pigmented (black when dry); hypothenar pad of pes absent, thenar pad an elongate ridge, 4th interdigital pad opposite 2nd; hairy fringe along metatarsal margins and digits of pes well developed and conspicuous; claw of digit V of pes extends to base of claw of digit IV, claw of digit I extends to second interphalangeal joint of digit II.

Molars 3/3; principal cusps anteroposteriorly compressed, very tall and sharp when unworn; anterocone of M1 with shallow anteromedian flexus (obliterated with slight wear); M1 without anteroloph, usually with small mesoloph projecting labially from median mure; posteroloph of M1 abuts anteroloph of M2; M2 usually without any vestige of mesoloph; M2 posteroloph small or absent; M3 with tiny posterior conule behind protocone/paracone; m1 anteroconid divided by deep anteromedian flexid into separate, sharp labial and lingual conulids; m1 without anterolophid, with or without small mesolophid; m1 posterolophid abuts m2 anterolophid; m2 with or without small mesolophid, with small peglike posterolophid; m3 small, with diminutive conulid behind protoconid/metaconid; upper incisors delicate and narrow, their anterior surfaces not inclined medially; lower incisors procumbent and very slender.

Nasals long, concealing incisors and nasal orifice from dorsal view; rostrum narrow, the nasolacrimal capsules fully exposed in dorsal view; interorbital region narrow relative to breadth of braincase (LIB/BB = .28–.33 in TWC 3–5); supraorbital foramina open laterally into orbits, not onto dorsal surface of frontals; braincase inflated, globose, the lambdoidal ridges small and inconspicuous; occipital condyles not produced posteriorly beyond supraoccipital, not visible in dorsal view; dorsal profile flat over rostrum and orbits, convex over braincase, the frontals bulging abruptly behind the interorbital constriction; posterior edge of inferior zygomatic root over M1 anterocone; tip of masseteric tubercle above plane of molar alveoli; incisive foramina conspicuously widest behind maxillary/premaxillary suture; hard palate not produced very far behind M3s; carotid arterial pattern 2; bullae flask-shaped, not bulbous or inflated; orbicular apophysis of malleus present; basicranium flat, without obvious kyphosis at sphenoccipital suture.

Ribs 14; thoracicolumbar vertebrae 20; sacral vertebrae 5–6; metatarsals IV > III > V > II > I; omohyoid muscle absent; gastric glandular epithelium restricted to a broad band that crosses the greater curvature on the right-hand side of stomach; gall bladder present; penis with a single bacular mound bearing two large dorsolateral spines and supported by a single cartilaginous bacular digit; two dorsal crater papillae present.

COMPARISONS: *Anotomys leander* possesses a number of morphological attributes that are unique within the Ichthyomyini: the absence of definitive pinnae, the presence of tufts of pure white fur over the external auditory

TABLE 15

**Age, Sex, and Measurements (in millimeters) of Adult *Anotomys leander* from Ecuador**

(The sample mean plus or minus one standard deviation, the range in parentheses, and the sample size are provided in the left-hand column)

| | | Provincia Pichincha (western Andes) | | | |
|---|---|---|---|---|---|
| | Provincia Napo (eastern Andes)[a] | AMNH 66201 | NHRS 6100 | MNHN 1936–2021 | BMNH 5.11.7.1[b] |
| Age | 3–5/c, f/n | 4/f/n | 5/f/n | 6/f/n | 6/f/n |
| Sex | 5 males, 5 females | female | female | female | male |
| HBL | 114.6 ± 6.6 (101–122) 10 | – | – | 120 | – |
| LT | 142.5 ± 10.5 (125–153) 10 | – | – | 150 | – |
| HF | 35.6 ± 1.2 (34–37) 10 | 34 | 33 | 35[c] | 34 |
| Ear[d] | | | | | |
| CIL | 26.0 ± 0.73 (24.2–26.8) 10 | – | 25.3 | 27.0 | 25.2 |
| LD | 6.5 ± 0.31 (6.0–7.1) 10 | 6.4 | 6.7 | – | 6.5[c] |
| LM | 5.0 ± 0.11 (4.8–5.1) 10 | 4.7 | 4.4 | – | 4.6[c] |
| LIF | 4.6 ± 0.13 (4.4–4.9) 10 | 4.4 | 4.4 | 5.0 | 4.7 |
| BIT | 1.2 ± 0.03 (1.1–1.2) 10 | 1.3 | 1.3 | 1.3 | 1.2 |
| BIF | 2.2 ± 0.12 (2.0–2.4) 10 | 2.1 | 2.4 | 2.3 | 2.2 |
| BPB | 3.2 ± 0.29 (2.8–3.7) 10 | 2.9 | 3.5 | – | 3.2[c] |
| LN | 9.8 ± 0.52 (9.1–10.4) 10 | – | – | 9.8 | 9.4 |
| BN | 2.8 ± 0.18 (2.6–3.2) 10 | 3.2 | 3.3 | 3.1 | 3.1 |
| LIB | 4.2 ± 0.20 (4.0–4.6) 10 | 4.1 | 3.6 | 4.0 | 3.8 |
| ZB | 14.4 ± 0.60 (13.2–15.0) 10 | 14.1[c] | – | – | – |
| BB | 13.8 ± 0.22 (13.4–14.1) 10 | 13.5[c] | 13.0 | 13.7 | 13.4 |
| BZP | 0.8 ± 0.07 (0.7–0.9) 10 | 0.8 | 0.8 | 0.8 | 0.8 |
| BM1 | 1.7 ± 0.05 (1.6–1.7) 10 | 1.5 | 1.5 | – | 1.5[c] |
| HI | 4.8 ± 0.29 (4.4–5.3) 10 | 5.6 | 5.0 | 5.0 | 5.2 |
| DI | 1.4 ± 0.06 (1.3–1.5) 10 | 1.5 | 1.4 | 1.4 | 1.4 |
| BOC | 8.1 ± 0.19 (7.8–8.4) 10 | – | 7.6 | 7.9 | 7.5 |

[a] AMNH 244605–244607; UMMZ 126294–126296, 155599–155601, 155603.

[b] The holotype.

[c] Estimated values.

[d] Pinnae not measurable.

canals (fig. 30), the presence of supraorbital vibrissae, carotid circulation pattern 2 (fig. 18C), 20 thoracicolumbar vertebrae and more than 4 sacral vertebrae (table 10), a unidigitate bacular cartilage (fig. 26C) and two dorsal crater papillae (fig. 27). These features, together with the combination of other (nonunique) character states listed in the diagnosis and description, appear more than sufficient to justify generic distinction for this unusual mouse. Morphological differences between *A. leander* and *Chibchanomys trichotis*, a species once placed in *Anotomys* (Handley, 1976), have already been detailed in the account for *Chibchanomys* above; it remains only to compare *Anotomys* with two species of *Rheomys*.

Both Thomas (1906b) and Hooper (1968) remarked similarities between *Rheomys underwoodi* and *Anotomys leander*, resemblances that are also shared with another distinct species, *R. mexicanus*. Together, these three ichthyomyines are characterized by (1) tails longer than head-and-body length, (2) pinnae much reduced (buried in the fur of the head, or absent), (3) absence of a philtrum, (4) fusion of the hypothenar and third interdigital pads of the manus, (5) very large hindfeet, (6) large molars with high, sharp cusps, (7) narrow incisors, slender rostra, and inflated braincases, and (8) glandular epithelium restricted to the greater curvature of the stomach. None of these character states is unique to this species triplet, however, and *A. leander* differs from *R. underwoodi* and *R. mexicanus* in pelage type (dull gray-black versus glossy brownish) and carotid circulation pattern (2 versus 3) as well as by the features unique to the former genus listed earlier.

VARIATION: Twenty specimens of *Anotomys* are available for study. Twelve of these were collected near Papallacta in the eastern Andes of Provincia Napo, Ecuador. Of the remaining eight, two are without adequate locality data; the other six were collected on or in the vicinity of Volcán Pichincha near Quito in the western Andes of Provincia Pichincha, Ecuador. Measurements of adult (TWC 3–6) specimens from Napo and Pichincha are provided in table 15. All of the crania from Pichincha are damaged to a greater or lesser extent, and there are, besides, so few Pichincha specimens that useful statistical comparisons with the Napo series are impossible. Pichincha specimens have consistently smaller molar dimensions (LM, BM1) than Napo examples, but the two geographic samples overlap in all other dimensions and cannot be separated on the basis of nonmetric characters. Since the difference in molar size is not large and other distinctions are wanting, I judge both populations to represent the single described species *A. leander.*

SPECIMENS EXAMINED: *Anotomys leander* – **Ecuador:** Chinchin Cocha (FMNH 53367), La Carolina (NHRS 6100), Papallacta (AMNH 244605–244607; UMMZ 126294–126296, 155598–155603), Volcán Pichincha (AMNH 66201, 66202; BMNH 5.11.7.1, 54.603; MNHN 1936–2021), W. Ecuador (BMNH 34.9.10.176). Total, 20.

### *Ichthyomys* Thomas, 1893

(Figures 3, 4, 6, 11, 13, 15, 23, 26, 33–37)

SYNONYMS: None.

TYPE SPECIES: *Ichthyomys stolzmanni* Thomas, 1893, based on a specimen in the British Museum of Natural History (BMNH 94.8.6.14) consisting of the fluid-preserved carcass, skull, and mandibles of a young (2/o/a) female collected by J. Kalinowski at "Chanchamayo," near Tarma, Departamento Junín, Peru. Thomas (1893: 333) gives the approximate altitude of Chanchamayo as 3000 ft (923 m).

CONTENTS: Eight nominal species have been referred to the genus as follow in chronological order of their description: *I. hydrobates* (Winge, 1891); *I. stolzmanni* Thomas, 1893; *I. soderstromi* de Winton, 1896; *I. tweedii* Anthony, 1921; *I. orientalis* Anthony, 1923; *I. caurinus* Thomas, 1924; *I. nicefori* Thomas, 1924; *I. pittieri* Handley and Mandolfi, 1963. I hypothesize that these represent four biological species whose names should be arranged as follow: *Ichthyomys hydrobates hydrobates, I. h. nicefori, I. h. soderstromi, I. pittieri, I. stolzmanni orientalis, I. s. stolzmanni, I. tweedii* (including *I. caurinus* as a junior synonym). Justification for these changes are provided below.

KNOWN DISTRIBUTION: From the Río Chanchamayo, Departamento Junín, Peru, northward in mountains and adjacent foothills through Ecuador and Colombia to the lowlands of central Panama and the Cordillera de la Costa of northern Venezuela. Recorded elevations range from 300 to 2770 m.

DIAGNOSIS: Ichthyomyines with glossy, grizzled-brownish adult dorsal pelage; pinnae visible above fur of the head; philtrum present and broad; tail longer, equal to or less than head-and-body length; manus with five separate plantar pads; hindfoot short or long relative to head-and-body but proportionately broad with well-developed fringing hairs; nasal bones short, truncated; supraorbital foramina open dorsally between the orbits in large adults; carotid circulation pattern 3; orbicular apophysis of malleus present; stomach with glandular epithelium restricted to greater curvature; gall bladder absent; bacular cartilage tridigitate.

DESCRIPTION: Adult head-and-body length 110–197 mm; HF/HBL = .19–.32; LT/HBL = .76–1.15; adult pelage glossy, grizzled-brownish dorsally due to mixture of buffy-banded awns and dark brown guard hairs in the overfur; venter sharply countershaded, silvery white (but the bases of the hairs dark gray); tail unicolored (dark) or sharply bicolored (dark above, pure white below); ears small but not concealed in fur of head; supraorbital vibrissae absent; rhinarium pigmented (dark brown or black when dry); philtrum present, broad; manus with three separate interdigital and two separate carpal pads; sole of pes pigmented (black when dry);

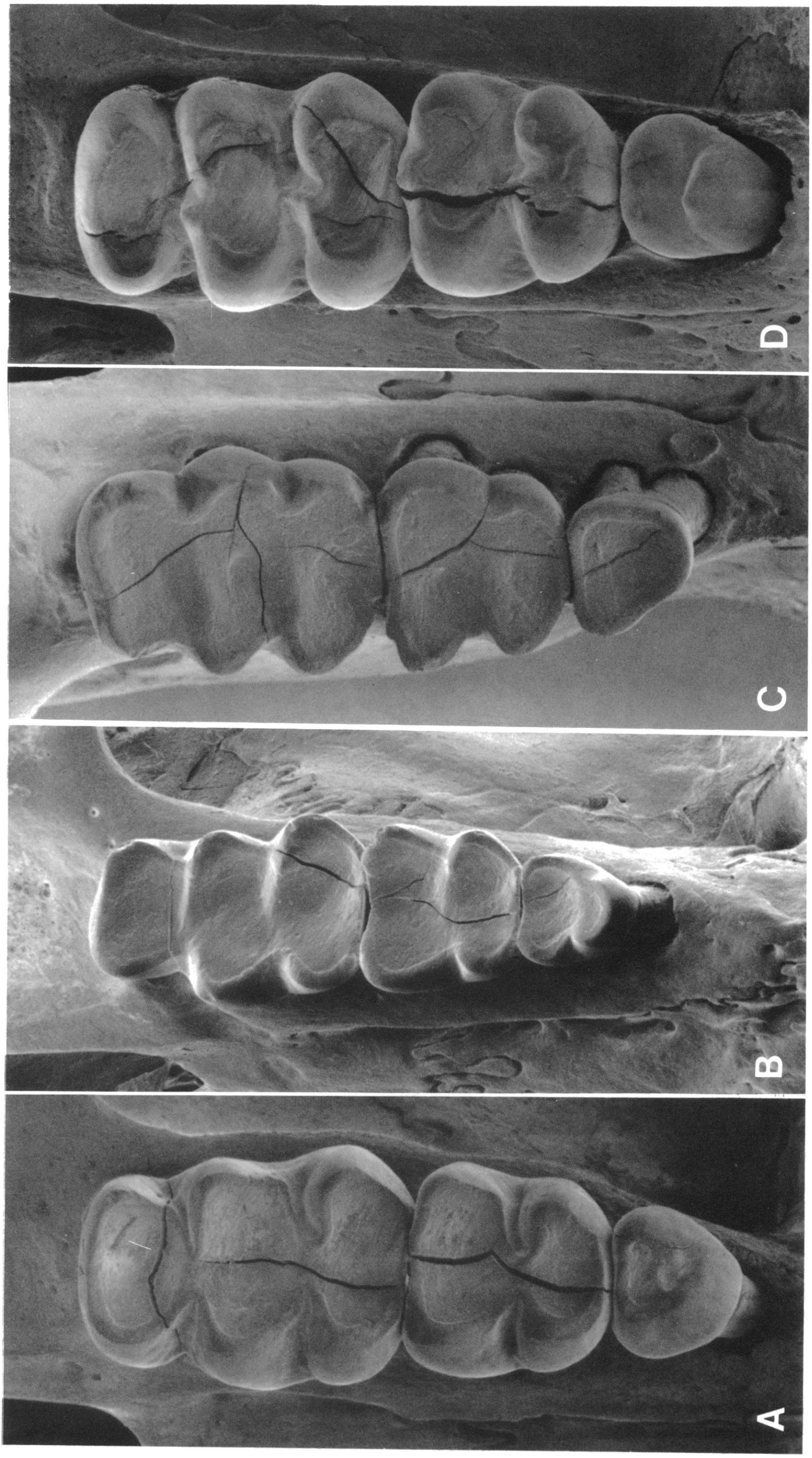


Fig. 33. Maxillary molars of *Ichthyomys* species. **A**, *I. hydrobates soderstromi* (left side, AMNH 46729, LM = 4.3 mm); **B**, *I. pittieri* (left side, CVULA I-0853, LM = 3.7 mm); **C**, *I. stolzmanni orientalis* (right side, AMNH 62382, LM = 4.3 mm); **D**, *I. tweedii* (left side, UMMZ 155784, LM = 4.6 mm).

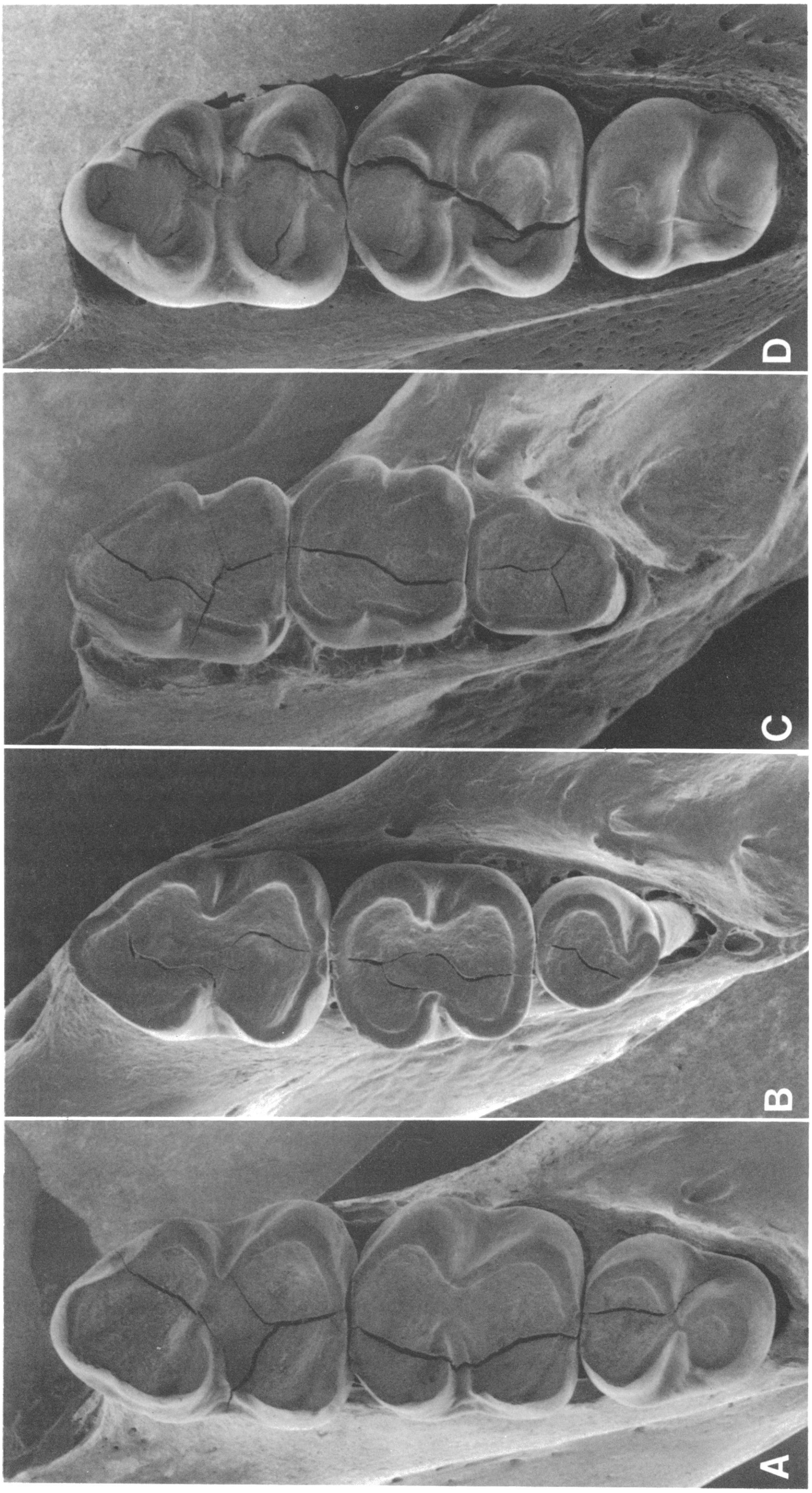


Fig. 34. Right mandibular molars of *Ichthyomys* species. Specimens and magnifications are the same as for figure 33.

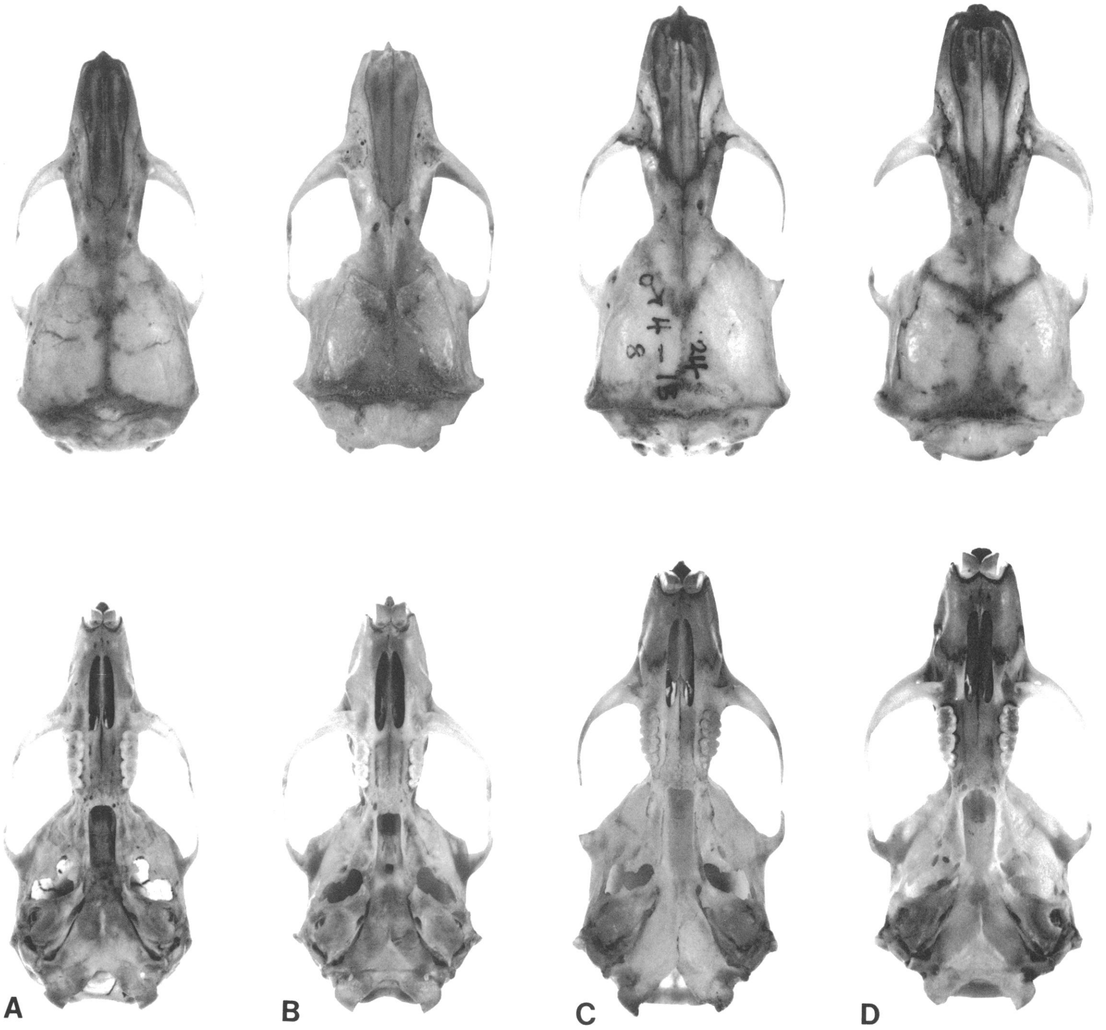


Fig. 35. Dorsal and ventral views of crania of *Ichthyomys* species. **A,** *I. hydrobates soderstromi* (AMNH 64624); **B,** *I. pittieri* (MBUCV I-2776); **C,** *I. stolzmanni orientalis* (BMNH 24.4.18.8); **D,** *I. tweedii* (AMNH 71383). All ×2.

hypothenar pad of pes absent, 4th interdigital pad almost opposite 2nd and extending to base of 3rd; hairy fringe along metatarsal margins and digits of pes well developed; claw of digit V of pes extends beyond first interphalangeal joint almost to the distal end of phalange 2 of digit IV; claw of digit I extends beyond first interphalangeal joint to about half the length of phalange 2 of digit II.

Molars 3/3; cusps not anteroposteriorly compressed, blunt even when unworn and not very tall; newly erupted M1–2 with minute anterolophs and posterolophs, but these obliterated with only slight wear (TWC 2); small mesolophs on M1–2, when present, project posterolabially from paracones; M3 usually with small posterior conule; anteroconid of m1 usually without any vestige of anteromedian flexid, never divided into distinct labial and lingual conulids; m1 without anterolophid; minute anterolophid on m2 and posterolophids on m1–2 obliterated with slight wear (TWC 2–3); mesolophids usually absent; m3 large, with subequal entoconid/hypoconid lobe behind protoconid/metaconid or small, with only a minute posterior

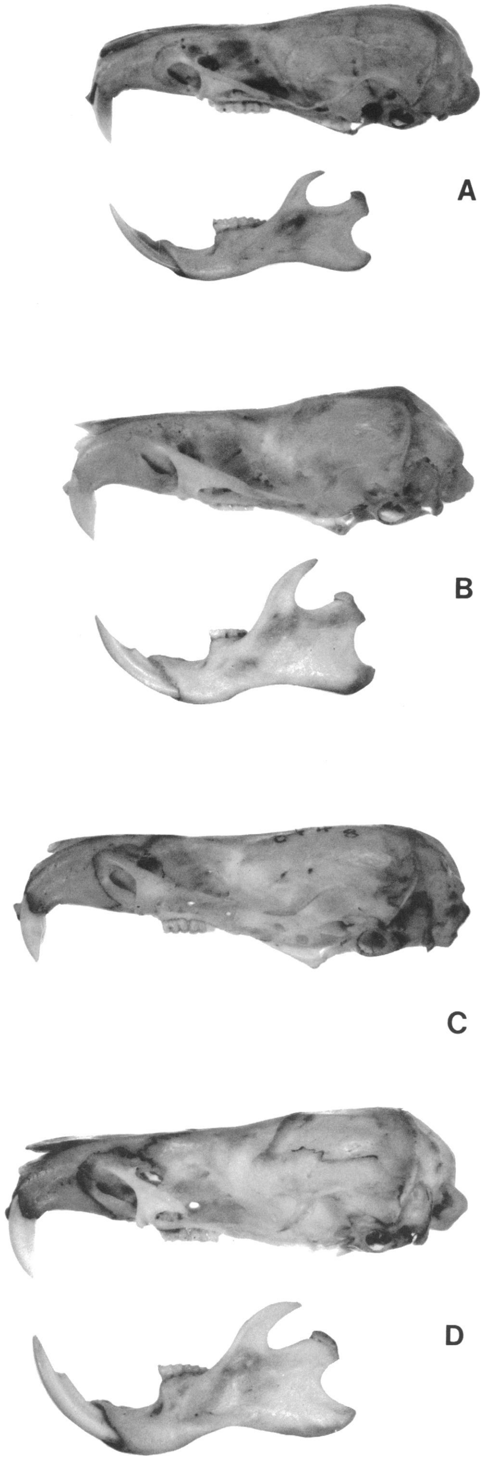


Fig. 36. Lateral views of cranium and mandibles of *Ichthyomys* species. Specimens and magnifications are the same as for figure 35.

vestige of the entoconid/hypoconid (*I. pittieri* only); upper incisors broad and thick, their anterior enameled surfaces inclined medially, the lateral tips of these teeth sharp and well separated; lower incisors strong and recurved, the wear facet on their lesser curvatures notched in some large specimens.

Nasals short, appearing truncated anteriorly to reveal incisors and nasal orifice in dorsal view; rostrum very broad, the nasolacrimal capsules concealed from dorsal view; interorbital region broad relative to breadth of braincase in young animals (TWC 1 and 2) but eroding with age to become more constricted in some old adults (LIB/BB = .33–.39 in TWC 1–2, .28–.38 in TWC 4–6); supraorbital foramina open laterally (near the orbital margins) in young animals but migrate with erosion of the interorbital region onto the dorsal surface of the frontals in most adults; zygomatic processes of maxillae and squamosals stout, broadly flaring from rostrum and braincase in older adults; braincase broad and low, the lambdoidal ridges produced as wide lateral crests in large adults; occipital condyles produced posteriorly well behind supraoccipital, clearly visible in dorsal view; dorsal profile conspicuously flattened, the frontals not rising abruptly behind the orbits; posterior edge of inferior zygomatic root anterior to M1 anterocone; tip of masseteric tubercle above or projecting below plane of molar alveoli; incisive foramina narrow, parallel-sided or nearly so; palate produced posteriorly well behind M3s; carotid circulation pattern 3; bullae flask-shaped, not inflated; orbicular apophysis of malleus present; basicranium with conspicuous kyphosis at sphenoccipital suture, not flat.

Ribs 13; thoracicolumbar vertebrae 19; sacral vertebrae 4; metatarsals IV > III > II > V > I; omohyoid muscle present; gastric glandular epithelium restricted to a broad band that crosses the greater curvature on the right-hand side of the stomach; gall bladder absent; bacular cartilage tridigitate, the medial digit larger than the lateral two but not grossly swollen and without a calcified core; one dorsal crater papilla present.

COMPARISONS: Ellerman (1941) and Hall (1981) suggested that *Ichthyomys* and *Rheomys* lack sufficient diagnostic characters to

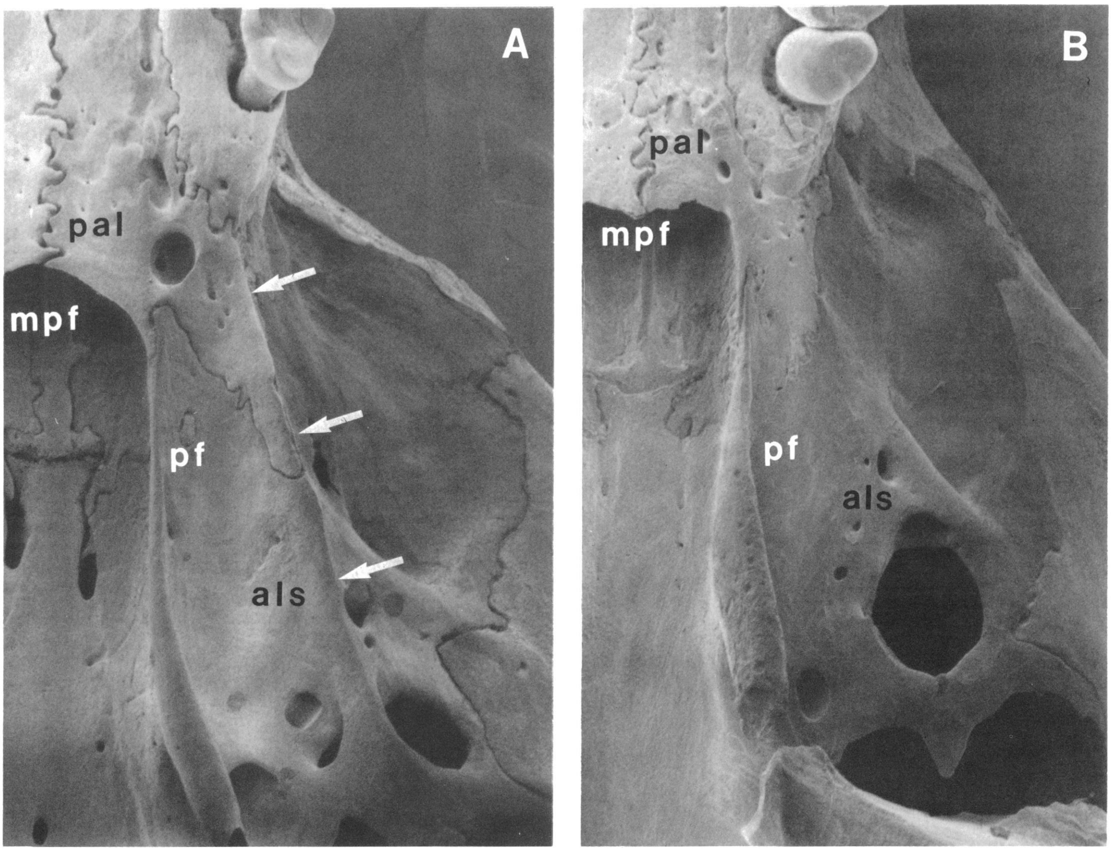


Fig. 37. Parapterygoid region of *Ichthyomys hydrobates* subspecies. **A,** *I. h. hydrobates* (NHRS 6091); **B,** *I. h. soderstromi* (AMNH 24354). Arrows in (A) indicate the bony ridge that forms the lateral edge of the parapterygoid fossa. **als,** alisphenoid; **mpf,** mesopterygoid fossa; **pal,** palatine; **pf,** parapterygoid fossa.

justify their recognition as separate genera, but I believe that these names usefully identify distinctive clusters of species whose assigned rank is consistent with the degree of difference presently recognized among other muroid genera. *Ichthyomys* differs from *Rheomys* by possession of five separate plantar pads on the manus, by the absence of a gall bladder, and in numerous details of cranial morphology: short, truncated nasal bones; supraorbital foramina located dorsally between the orbits; broadly flaring zygoma; well-developed lambdoidal crests; occipital condyles produced well behind the rest of the occiput; and pronounced basicranial kyphosis (see the diagnosis and description of *Rheomys* for alternative states).

Anthony (1929) indicated similarities in cranial morphology between *Daptomys* (=*Neusticomys*) *venezuelae* and *Ichthyomys,* consisting in the overall stoutness of cranial construction and the relative breadth of the rostrum; other ichthyomyines that Anthony studied appeared to him to have less robust crania and slender rostra. Resemblances in size-independent cranial proportions are demonstrable between some species of *Neusticomys* and *Ichthyomys* (see Cranial Morphometrics, below), but differences in qualitative characters between the two genera are so many (as can be seen by comparing their respective diagnoses) that the taxa are not easily confused.

VARIATION: I interpret the variation in available series of skins and skulls of *Ichthyomys* to represent four biological species.

### *Ichthyomys hydrobates* (Winge, 1891)

These are highland populations of rats of small body size and slender rostra (both relative to most other congeners) with bilobed lower third molars and dark, unicolored tails. The species ranges from the vicinity of Mérida, Venezuela, through the Colombian Andes to at least as far south as Quito, Ecuador. The type of *I. h. hydrobates* (UZM 862) consists of the skin, skull, and mandibles of an adult (4/f/a) female collected in the "Sierra de Merida, Venezuela" in 1890; the type was sent to the Copenhagen museum by Witzke, the Danish consul at Maracaibo, but the original collector is unknown. In addition to the type, I have examined 28 skins and skulls of *I. h. hydrobates* collected by S. Briceño between 1895 and 1904 in the vicinity of Mérida at elevations of 1600 to 1700 m. These specimens, together with a single example from the nearby locality of La Mucuy, may be regarded as topotypes; measurements of adults in this series (table 16) exhibit variation equivalent to that commonly observed in samples of better-documented geographic homogeneity.

The type and unique specimen of *Ichthyomys hydrobates nicefori* (BMNH 23.11.13.9) consists of the skin, skull, and mandibles of an adult (4/f/a) male collected by Nicéforo María at "Paime (North of Bogotá)," in August, 1923. *I. h. nicefori* differs from *I. h. hydrobates* in dorsal pelage color (slightly darker in *nicefori*), coloration of the pinnae (the inside of the pinnae are white in *nicefori*, grizzled-brownish in *hydrobates*), and size of the braincase (relatively and absolutely larger in *nicefori*). Except for two measurements spanning the braincase (ZB, BB), cranial dimensions of the type of *nicefori* (table 16) do not depart by more than 0.1 mm from the range of topotypic variation in *I. h. hydrobates*.

The type and 21 topotypes of *Ichthyomys hydrobates soderstromi* were collected by Ludovic Söderström and associates (Tate, 1931) in the vicinity of Guápulo and the Río Machángara, near Quito in Provincia Pichincha, Ecuador. In characters of the skin, the dorsum of *soderstromi* is darker than topotypic *hydrobates* but about as dark as *nicefori*; the pinnae of *soderstromi* average smaller than those either of *nicefori* or of *hydrobates* (table 16); the inside of the pinnae are dark in *soderstromi*, like those of *hydrobates*, not white as in *nicefori*. The ranges of variation in all cranial measurements of adult (TWC 3–5) topotypes of *soderstromi* overlap with those of like-aged topotypic *hydrobates* (table 16). The single qualitative cranial character distinguishing *soderstromi* from *hydrobates* and *nicefori* is the presence or absence of the bony ridge that forms the lateral margin of each parapterygoid fossa (fig. 37). This ridge, produced anteriorly by the palatine bone, but extending posteriorly onto the alisphenoid, is well developed in the latter two taxa (fig. 37A) but is usually absent or just faintly discernable in *soderstromi* (fig. 37B); the parapterygoid fossae themselves are broader in *hydrobates* and *nicefori* than in *soderstromi*.

Although *hydrobates, nicefori,* and *soderstromi* were originally described as distinct species, the small differences diagnostic of each could also be interpreted as intraspecific geographic variation. In effect, each name is the descriptor of a single local population; the only specimens available from intermediate localities are two from the western Andes of Departamento Cauca, Colombia, that resemble typical *hydrobates* in characters of the skin and skull. Since *hydrobates, nicefori,* and *soderstromi* resemble one another in size, in the relative slenderness of their rostra and in the uniform color of their tails, it seems more useful to draw attention to these resemblances by a hypothesis of conspecificity than to emphasize small differences by retaining each as a separate species.

### *Ichthyomys pittieri*
### Handley and Mondolfi, 1963

Four specimens of *Ichthyomys pittieri* are currently available for comparisons, three from the type locality near Rancho Grande (Estado Aragua), and one from the vicinity of Naiguatá (Distrito Federal), Venezuela. Both localities, about 100 km apart, are situated in the forested coastal cordillera that forms the easternmost extension of the Andes.

The type of *I. pittieri* (USNM 324987) consists of the skin, skull, and mandibles of an old adult (6/f/a) male; the skin is in poor condition and all of the molar dentition is

TABLE 16
**Age, Sex, and Measurements (in millimeters) of Adult Specimens of *Ichthyomys hydrobates* Subspecies**
(The sample mean plus or minus one standard deviation, the range in parentheses, and the sample size are provided for each measurement)

| | *I. h. hydrobates* | *I. h. nicefori* | *I. h. soderstromi* |
|---|---|---|---|
| | Holotype and topotypes[a] | BMNH 23.11.13.9[b] | Holotype and topotypes[c] |
| Age | 3–5/o, c, f/a | 4/f/a | 4–5/f/a |
| Sex | 5 males, 12 females | male | 8 males, 4 females |
| HBL | 135 (135) 1 | – | 125 (125) 1 |
| LT | 134 (134) 1 | – | 139 (139) 1 |
| HF | 33.5 ± 1.9 (30–36) 11 | 34 | 33.2 ± 1.3 (31–35) 12 |
| Ear | 9.4 ± 0.5 (9–10) 8 | 10 | 8.6 ± 0.5 (8–9) 12 |
| CIL | 30.4 ± 1.56 (28.3–32.3) 10 | 32.1 | 31.0 ± 0.70 (30.0–32.2) 12 |
| LD | 8.0 ± 0.40 (7.3–8.6) 16 | 8.6 | 8.3 ± 0.29 (7.9–8.8) 12 |
| LM | 4.2 ± 0.09 (4.1–4.4) 16 | 4.2 | 4.2 ± 0.12 (4.0–4.4) 12 |
| LIF | 6.0 ± 0.36 (5.4–6.7) 16 | 6.7 | 5.9 ± 0.24 (5.5–6.3) 12 |
| BIT | 2.0 ± 0.12 (1.8–2.2) 15 | 2.1 | 2.0 ± 0.07 (1.9–2.1) 12 |
| BIF | 2.0 ± 0.15 (1.8–2.2) 15 | 2.1 | 2.0 ± 0.10 (1.9–2.1) 12 |
| BPB | 2.8 ± 0.22 (2.5–3.3) 16 | 2.9 | 3.0 ± 0.20 (2.6–3.3) 12 |
| LN | 10.6 ± 0.76 (9.3–12.0) 9 | 12.0 | 11.6 ± 0.67 (10.4–13.1) 11 |
| BN | 3.4 ± 0.32 (2.9–4.1) 13 | 3.8 | 3.6 ± 0.15 (3.3–3.9) 12 |
| LIB | 4.5 ± 0.28 (4.0–4.9) 16 | 5.0 | 4.7 ± 0.22 (4.2–5.1) 12 |
| ZB | 15.0 ± 0.88 (13.7–16.2) 11 | 16.5[d] | 15.7 ± 0.41 (15.0–16.3) 9 |
| BB | 13.6 ± 0.35 (13.0–14.0) 15 | 14.6 | 13.5 ± 0.13 (13.3–13.7) 12 |
| BZP | 1.3 ± 0.18 (1.0–1.5) 17 | 1.3 | 1.4 ± 0.08 (1.2–1.5) 12 |
| BM1 | 1.4 ± 0.05 (1.4–1.5) 17 | 1.6 | 1.6 ± 0.04 (1.5–1.6) 12 |
| HI | 5.8 ± 0.35 (5.0–6.5) 15 | 5.6 | 5.4 ± 0.19 (5.1–5.7) 12 |
| DI | 1.8 ± 0.16 (1.6–2.1) 17 | 2.1 | 1.7 ± 0.12 (1.5–2.0) 12 |
| BOC | 8.7 ± 0.21 (8.4–9.1) 11 | 8.4 | 8.7 ± 0.20 (8.4–9.1) 9 |

[a] AMNH 24354, 24355; BMNH 97.5.21.1, 98.7.1.32, 99.12.1.36, 99.12.1.37, 13.2.3.14; MNHN 1900-560, one uncataloged specimen; NHRS 6099; RMNH 2148, 2151; UMMZ 156375; USNM 125323, 151288, 172941; UZM 862 (the holotype).

[b] The holotype.

[c] AMNH 46730, 46732, 64624; BMNH 96.1.28.5 (the holotype), 2.9.7.4, 34.9.10.171; NHRS 6089, 6090, 6093; UZM 2083, 2409, 2492.

[d] Estimated value.

missing except left m1 and right m2. Information from the two topotypes and the Naiguatá example, all recently collected, permits critical emendations to Handley and Mandolfi's diagnosis and comparisons based on the aged and incomplete holotype.

*Ichthyomys pittieri* compares closely with *I. h. hydrobates* (the only other described Venezuelan congener) in pelage color, making allowances for the fact that most specimens of *I. h. hydrobates* are now more than 80 years old and seem faded by comparison with recently collected examples (e.g., UMMZ 156375); both species have dark, unicolored tails and dark ears. Measurements of head-and-body and of tail (HBL, LT: table 17) differ conspicuously among the four specimens of *I. pittieri,* but this may be a methodological artifact since I do not know how the collectors of USNM 324987 (the holotype), one topotype (CVULA I-0853), and the Naiguatá example (MBUCV I-2803) measured their specimens. The values for HBL and LT of MBUCV I-2776 (*I. pittieri,* table 17) and of *I. h. hydrobates* (table 16, from UMMZ 156375) are both my determinations from fresh material; if representative of their respective populations, these values suggest that specimens of *I. pittieri* have much shorter tails, relative to head-and-

TABLE 17
**Age, Sex, and Measurements (in millimeters) of Specimens of *Ichthyomys pittieri***

| | Rancho Grande | | | Naiguatá |
|---|---|---|---|---|
| | USNM 324987[a] | MBUCV I-2776 | CVULA I-0853 | MBUCV I-2803 |
| Age | 6/f/a | 6/f/a | 4/f/a | 4/c/a |
| Sex | male | male | female | male |
| HBL | 130 | 156 | 135 | 110 |
| LT | 130 | 118 | 115 | 110 |
| HF | 30 | 30 | 29 | 28 |
| Ear | 10 | 11 | 8 | 9 |
| CIL | 31.2 | 31.5 | 28.0 | 27.5 |
| LD | 8.9[b] | 9.1 | 7.6 | 7.5 |
| LM | 3.6[b] | 3.6 | 3.7 | 3.6 |
| LIF | 6.1 | 6.1 | 5.5 | 5.0 |
| BIT | 2.2 | 2.3 | 2.1 | 2.1 |
| BIF | 2.2 | 2.4 | 2.0 | 1.8 |
| BPB | 3.0[b] | 3.0 | 2.8 | 2.7 |
| LN | 11.4 | 12.2 | 10.4 | 10.2 |
| BN | 3.8 | 4.1 | 3.5 | 3.8 |
| LIB | 4.1 | 4.7 | 4.9 | 5.1 |
| ZB | 15.3 | 16.1 | 14.1[b] | 13.5 |
| BB | 12.6 | 12.6 | 12.5 | 12.8 |
| BZP | 1.7 | 1.7 | 1.4 | 1.4 |
| BM1 | – | 1.2 | 1.2 | 1.1 |
| HI | – | 5.9 | 5.1 | 5.0 |
| DI | 1.8[b] | 2.0 | 1.7 | 1.7 |
| BOC | 8.1 | 8.3 | 7.9 | 7.6 |

[a] The holotype.
[b] Estimated values.

body, than specimens of *I. h. hydrobates.* Hindfeet are smaller in all four specimens of *I. pittieri* than is average for *I. hydrobates* subspecies.

Examples of *I. pittieri* fall within the range of variation of most cranial dimensions for like-aged specimens of *I. h. hydrobates,* with the exception of molar and neurocranial measurements (LM, BM1, BB, BOC). *I. pittieri* has smaller molars than any other described congener and is, in addition, the only member of the genus in which the lower third molar lacks a distinct posterior entoconid/hypoconid lobe (fig. 34B). The narrower braincase of *I. pittieri* together with a broad rostrum and flaring zygoma (fig. 35B) provide additional, visually conspicuous distinctions between this lowland form and highland *I. hydrobates* subspecies with more inflated braincases but slender rostra and delicate zygoma (fig. 35A). Handley and Mondolfi (1963) drew attention to peculiarities of the holotype of *I. pittieri* in characters of the infraorbital foramen, inferior zygomatic root, and upper incisors, but these are less apparent in the topotypes and the Naiguatá specimen and perhaps represent individual variation. The development of temporal ridges and sagittal crests remarked in the holotype of *I. pittieri* by Handley and Mondolfi and also evident in MBUCV I-2776 are not pronounced in younger examples (CVULA I-0853, MBUCV I-2803; see fig. 15).

### *Ichthyomys stolzmanni* Thomas, 1893

The animals referred to this species are large-bodied lowland rats with large hindfeet, sharply bicolored tails, bilobed lower third molars, and narrow skulls. Samples derive from only two localities in the Amazonian foothills of the Andes and comprise a total of seven specimens. I follow Cabrera (1961) in regarding *I. orientalis* Anthony 1923 as no more than subspecifically distinct from *I. stolzmanni.*

The disposition and provenance of the type of *Ichthyomys stolzmanni* have already been described; the fluid-preserved pelage is now much faded, but the color plate provided by Thomas (1893) and reproduced here as figure 3 records the original pigmentation. No other specimens from the type locality are known.

The type of *I. s. orientalis* consists of the skin, skull, and mandibles of an adult (5/f/a) male collected or purchased by Ludovic Söderström, dated 15 September 1921 and labeled "near the river Napo 3000 feet about." In addition to the type, there are five topotypes, all collected (or purchased) by Söderström in June of 1921.

Anthony (1923: 8) provided the following comparison: "*I. orientalis* appears to differ from *stolzmanni* in slightly larger size, coloration less brown, darker forefeet, smaller ears, more flaring zygomata, and greater interorbital constriction." The supposed difference in pelage pigmentation is now difficult to evaluate: while the dorsal coloration of the type and topotypes of *orientalis* is appreciably darker than that illustrated for *stolzmanni* in Thomas's color plate (Thomas, 1893: pl. XXVIII), the type of *stolzmanni* was preserved in fluid for three years prior to illustration and might have faded appreciably. The cited difference in forefoot coloration is conspicuous, however: the type and topotypes of *orientalis* have brownish hairs over the metacarpals while the metacarpal pelage of *stolzmanni,* as illustrated (see fig. 3), is white.

The type of *stolzmanni* is a much younger animal than the type of *orientalis* (TWC 2 versus 5), an observation that plausibly accounts for the differences in cranial dimensions described by Anthony (1923). Growth in *Ichthyomys* is accompanied by increases in most cranial dimensions, with the exception of molar measurements (which do not increase) and of Least Interorbital Breadth (which diminishes as the result of local bone resorption; see Comparative Morphology, above, and Cranial Morphometrics, below). Most measurements of the type of *stolzmanni* fall within the range of topotypic variation in *orientalis* (table 18), and the few that do not provide an inadequate basis for specific distinction.

*Ichthyomys stolzmanni* is the only described member of the genus to have a bicolored tail, and its large size (of which CIL is a convenient cranial index) is matched only by *I. tweedii.* From *I. tweedii, I. stolzmanni* differs in possession of significantly (Student's-*t* comparisons of adult means recorded in the right-hand columns of tables 18 and 19; $p < .01$) larger hindfeet, narrower incisors, shorter nasals, narrower interorbital regions, and narrower zygoma. The absolutely and relatively larger hindfeet of *I. stolzmanni* are immediately evident in visual comparisons with skins of *I. tweedii,* while the differences in cranial proportions indexed by the preceding contrasts in measurement means are striking: crania of *I. stolzmanni* (figs. 35C, 36C) appear narrower and conspicuously more gracile overall than the broad, robust skulls of *I. tweedii* (figs. 35D, 36D). Although conclusive evidence of genetic isolation in sympatry is lacking, both epithets usefully label phenotypically distinctive populations on opposite sides of the Andes.

TABLE 18

**Age, Sex, and Measurements (in millimeters) of Specimens of *Ichthyomys stolzmanni***

(The sample mean plus or minus one standard deviation, the range in parentheses, and the sample size are provided for each measurement in the right-hand column)

| | *I. s. stolzmanni* | *I. s. orientalis* |
|---|---|---|
| | BMNH 94.8.6.14[a] | Holotype and topotypes[b] |
| Age | 2/o/a | 3–5/o, f/a |
| Sex | female | 4 males, 2 females |
| HBL | – | – |
| LT | – | – |
| HF | 40 | 39.3 ± 0.52 (39–40) 6 |
| Ear | 10 | 9.8 ± 0.45 (9–10) 5 |
| CIL | 33.1 | 33.6 ± 1.27 (32.2–35.2) 6 |
| LD | 8.7 | 8.7 ± 0.44 (8.1–9.1) 6 |
| LM | 4.4 | 4.4 ± 0.05 (4.3–4.4) 6 |
| LIF | 6.5 | 6.6 ± 0.19 (6.3–6.8) 6 |
| BIT | 2.1 | 2.2 ± 0.08 (2.1–2.3) 6 |
| BIF | 2.4 | 2.0 ± 0.16 (1.8–2.2) 6 |
| BPB | 2.9 | 3.0 ± 0.21 (2.7–3.3) 6 |
| LN | 11.0 | 11.3 ± 0.44 (10.9–12.1) 6 |
| BN | 4.2 | 3.9 ± 0.23 (3.6–4.2) 6 |
| LIB | 5.0 | 4.4 ± 0.29 (4.0–4.8) 6 |
| ZB | 16.0 | 16.2 ± 0.61 (15.4–17.0) 6 |
| BB | 14.2 | 14.3 ± 0.16 (14.1–14.6) 6 |
| BZP | 1.4 | 1.5 ± 0.15 (1.3–1.7) 6 |
| BM1 | 1.6 | 1.6 ± 0.05 (1.5–1.6) 6 |
| HI | 6.0 | 5.9 ± 0.40 (5.4–6.4) 5 |
| DI | 1.8 | 1.9 ± 0.12 (1.8–2.1) 6 |
| BOC | 9.5 | 9.0 ± 0.17 (8.8–9.2) 4 |

[a] The holotype.

[b] AMNH 62382 (the holotype); BMNH 24.4.18.8, 34.9.10.168–34.9.10.170; NHRS 6098.

### *Ichthyomys tweedii* Anthony, 1921

These large rats have dark, unicolored tails, bilobed lower third molars, and massive skulls with broad rostra and flaring zygomatic arches; specimens are known from the Andean foothills and adjacent lowlands of western Ecuador (Provincias del Oro, Imbabura, and Pichincha) and from central Panama. The species includes *I. caurinus* Thomas 1924 as a junior synonym.

The type of *I. tweedii* (AMNH 47798) consists of the skin, skull, mandibles, and postcranial skeleton of an old adult (6/f/a) male obtained by H. E. Anthony on 16 July 1920 at Portovelo, Provincia del Oro, Ecuador. The elevation of Portovelo is given by Anthony (1921) as 2000 ft (615 m). No other specimens are known from the vicinity of the type locality.

TABLE 19

**Age, Sex, and Measurements (in millimeters) of Specimens of *Ichthyomys tweedii***

(The sample mean plus or minus one standard deviation, the range in parentheses, and the sample size are provided for each measurement in the right-hand column)

| | AMNH 47798[a] | BMNH 24.4.18.7[b] | Series from Pichincha lowlands[c] |
|---|---|---|---|
| Age | 6/f/a | 2/o/a | 3–5/o, c, f/a |
| Sex | male | male? | 13 males, 7 females, 2 unknown |
| HBL | 167 | – | 161.2 ± 6.6 (155–171) 5 |
| LT | 150 | – | 148.2 ± 5.6 (141–155) 5 |
| HF | 36 | 35 | 35.7 ± 1.3 (33–38) 21 |
| Ear | 9 | 9 | 9.7 ± 0.9 (8–11) 21 |
| CIL | 34.9 | 32.2 | 34.4 ± 1.16 (32.4–36.6) 14 |
| LD | – | 8.3 | 9.1 ± 0.44 (8.4–9.7) 20 |
| LM | – | 4.4 | 4.4 ± 0.11 (4.3–4.6) 18 |
| LIF | 6.5 | 6.4 | 6.7 ± 0.41 (5.8–7.5) 20 |
| BIT | 2.5 | 2.3 | 2.5 ± 0.18 (2.1–2.8) 21 |
| BIF | 2.1 | 2.0 | 2.2 ± 0.18 (1.9–2.5) 19 |
| BPB | – | 3.1[d] | 3.1 ± 0.25 (2.8–3.7) 13 |
| LN | 12.4 | 12.8 | 12.6 ± 0.87 (10.7–14.0) 20 |
| BN | 4.5 | 4.1 | 4.2 ± 0.30 (3.6–4.8) 20 |
| LIB | 4.7 | 4.7 | 4.8 ± 0.28 (4.4–5.4) 20 |
| ZB | 17.9 | 16.1 | 17.3 ± 0.71 (16.4–19.0) 16 |
| BB | 14.3 | 14.3 | 14.4 ± 0.28 (13.9–14.9) 18 |
| BZP | 1.5 | 1.4 | 1.5 ± 0.12 (1.2–1.7) 20 |
| BM1 | – | 1.5 | 1.5 ± 0.07 (1.4–1.6) 21 |
| HI | 6.5 | 5.7 | 6.2 ± 0.52 (5.4–7.1) 19 |
| DI | 2.1 | 1.9 | 2.0 ± 0.13 (1.8–2.2) 22 |
| BOC | 8.3 | 9.7 | 9.1 ± 0.35 (8.5–9.8) 16 |

[a] The holotype of *I. tweedii.*

[b] The holotype of *I. caurinus.*

[c] AMNH 71382–71386, 71388–71391; BMNH 34.9.10.175; MNHN 1932-2950, 1932-2951; NHRS 6094–6097; UMMZ 65183, 126300, 155782, 155785–155787.

[d] Estimated value.

The type of *I. caurinus* (BMNH 24.4.18.7) consists of the skin, skull, and mandibles of a subadult (2/o/a) male purchased by Ludovic Söderström in August 1923; the specimen label bears the locality "near Pechahal below Gualea 2–3000 feet." No other examples of *Ichthyomys* that I have examined bear this exact geographic designation, but 41 specimens from Cacao Cocha, Mindo, Río Blanco, and Río Pachijal sample populations near the type locality within the upper Río Esmeraldas drainage of Provincia Pichincha, Ecuador (see Appendix: Gazetteer for further comments). Unfortunately, the precise geographic origins of Söderström specimens (as the type of *I. caurinus* and most other lowland Pichincha *Ichthyomys*) are often problematic (Chapman, 1926: 10–11) and do not provide a reliable basis for sorting samples. There is, therefore, probably some geographic heterogeneity among the specimens whose measurements are provided in the last column of table 19, but inasmuch as a range of intermediates exist between skulls exhibiting opposite extremes for any measurement in this series, it seems reasonable to provide sample statistics for the whole.

In his diagnosis of *I. caurinus,* Thomas (1924b) remarked only that "Another allied lowland species—*I. tweedii* Anth.,—occurs in southern Ecuador (Provincia del Oro), but is decidedly larger than *I. caurinus.*" The discrepancy in age between the types of *tweedii* and *caurinus,* however, renders such a simple size comparison inadequately diagnostic. Among the 41 other specimens of large lowland *Ichthyomys* from Pichincha there are none that fall into the same toothwear classes as the two holotypes, but the range of variation among Pichincha adults (TWC 3–5; table 19, right-hand column) nevertheless suggests that the metric differences between *tweedii* and *caurinus* do not exceed those that could accompany ontogeny. I have found no qualitative character to distinguish the two holotypes, and what differences exist in cranial proportions resemble those that regularly accompany allometric growth in other congeners. I see no biological justification for retaining *caurinus* as a separate taxon.

From adjoining highland populations of *I. hydrobates soderstromi, I. tweedii* is distinguished by its larger overall size (evident in the crania of figs. 35 and 36, and the measurements of tables 16 and 19), proportionately broader zygoma, broader rostra, less inflated braincase, and wider parapterygoid fossae with well-formed lateral edges (see fig. 37). Comparisons with *I. stolzmanni,* the large species of the Amazon lowlands, have already been provided.

SPECIMENS EXAMINED: *Ichthyomys hydrobates*–**Colombia:** Cerro Munchiquito (USNM 294985); Chisquio (FMNH 90293); Paime (BMNH 23.11.13.9). **Ecuador:** Guápulo (AMNH 39593, 39594, 46729–46733, 64624;

BMNH 96.1.28.5, 2.9.7.3, 2.9.7.4, 34.9.10.171; NHRS 6089–6093; UZM 2083, 2084, 2408, 2409, 2492); Guarumal (AMNH 244610); no other locality data (PANS 12676, 12677). **Venezuela:** La Mucuy (UMMZ 156375); Mérida (AMNH 24354–24357; BMNH 97.5.21.1, 98.7.1.31, 98.7.1.32, 99.12.1.34–99.12.1.37, 10.12.3.3, 10.12.3.4, 13.2.3.14; MCZ 17768; MNHN 1900-560, -561, -562, and one uncataloged specimen; NHRS 6099; RMNH 2148–2152; USNM 125323, 151288, 172941; UZM 862); no other locality data (FMNH 7047; USNM 115315). Total, 60.

*Ichthyomys pittieri* – **Venezuela:** Rancho Grande (CVULA I-0853; MBUCV I-2776; USNM 324987); Naiguatá (MBUCV I-2803). Total, 4.

*Ichthyomys stolzmanni* – **Ecuador:** Río Napo (AMNH 62382; BMNH 34.9.10.168–34.9.10.170, 24.4.18.8; NHRS 6098). **Peru:** Chanchamayo (BMNH 94.8.6.14). Total, 7.

*Ichthyomys tweedii* – **Ecuador:** Cacao Cocha (MNHN 1932-2949, -2950, -2951, -2952, -2953); Gualea (BMNH 24.4.18.7); Mindo (BMNH 34.9.10.172; UMMZ 126300, 155782–155788); Paramba (BMNH 99.11.3.4); Portovelo (AMNH 47798); Río Blanco (MZUP, 3 uncataloged specimens); Río Pachijal (AMNH 71382–71392; BMNH 34.9.10.173–34.9.10.175; MCZ 27347; MZUP, 4 uncataloged specimens; NHRS 6094–6097; UMMZ 65183). **Panama:** Aguacate (USNM 460684, 461078, 461094), Río Trinidad (LACM 43464). Total, 48.

### *Neusticomys* Anthony, 1921
(Figures 6, 18, 20, 23, 24, 27, 38–41)

SYNONYMS: *Daptomys* Anthony, 1929.

TYPE SPECIES: *Neusticomys monticolus* Anthony, 1921, based on an American Museum of Natural History specimen (AMNH 46574) consisting of the skin, skull, and mandibles of a young (2/o/n) female collected by Ludovic Söderström on 16 February 1916 at an altitude of 10,500 ft (3231 m) at "Nono Farm, San Francisco" near Quito, Provincia Pichincha, Ecuador.

CONTENTS: Four species: *N. monticolus* Anthony, 1921; *N. venezuelae* (Anthony, 1929); *N. peruviensis* (Musser and Gardner, 1974); and *N. oyapocki* (Dobust and Petter, 1978). The latter three species were originally described as members of the genus *Daptomys,* here designated a subjective synonym.

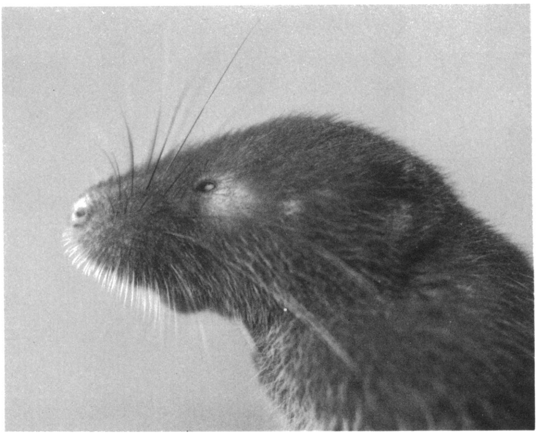


Fig. 38. Head of *Neusticomys monticolus* (UMMZ 155605). About ×1.7.

KNOWN DISTRIBUTION: Andean Ecuador and Colombia (2°S to 6°N) between 1800 and 3750 m elevation (*N. monticolus*); southern French Guiana (*N. oyapocki*); lowland Amazonian Peru (*N. peruviensis*); southern and eastern Venezuela and Guyana between 9 and 1400 m (*N. venezuelae*). Available locality records for *N. oyapocki* (N = 1), *N. peruviensis* (1), and *N. venezuelae* (3) are so few that significant horizontal and vertical range extensions are to be expected with further collecting.

DIAGNOSIS: Ichthyomyines with dull gray-black or glossy brownish adult dorsal pelage; pinnae conspicuous above fur of head; philtrum present; tail only as long as or shorter than head-and-body length; manus with five separate plantar pads; hindfoot narrow with weakly developed fringing hairs; nasal bones long; supraorbital foramina open laterally into orbits; carotid circulation pattern 1; orbicular apophysis of malleus present or absent; stomach with glandular epithelium between esophagus and pyloric sphincter; gall bladder present; bacular cartilage tridigitate.

DESCRIPTION: Adult head-and-body length 101–128 mm; HF/HBL = .22–.25; LT/HBL = .75–1.00; pelage soft, dense, wooly, composed of underfur and fine guard hairs, gray-black when fresh, or short and glossy, grizzled-brownish due to mixture of buffy-

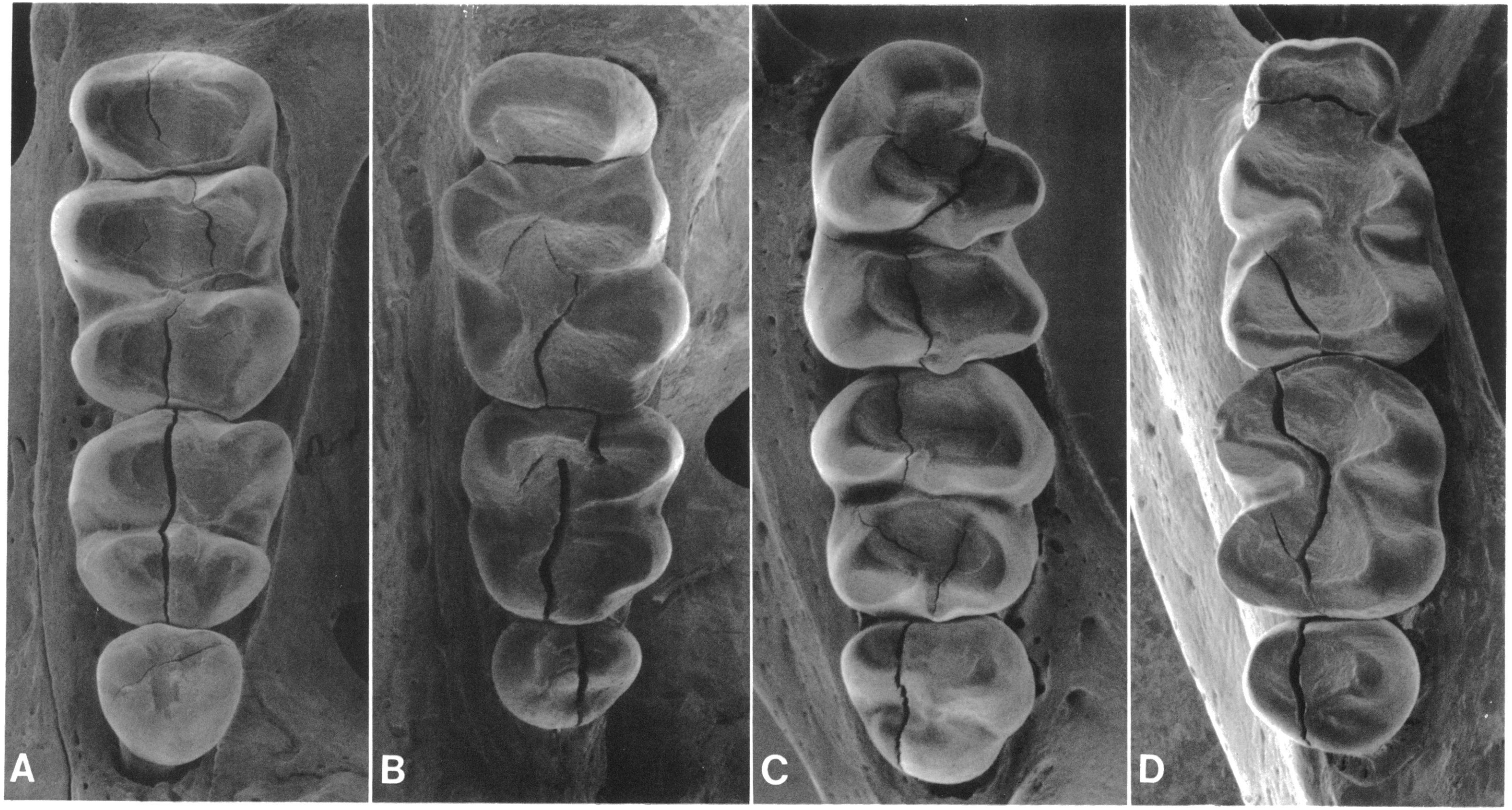


Fig. 39. Left maxillary (**A, B**) and right mandibular (**C, D**) dentition of *Neusticomys monticolus* and *N. venezuelae*. **A, C,** *N. monticolus* (AMNH 64646, LM = 4.1 mm); **B, D,** *N. venezuelae* (AMNH 69908, LM = 4.2 mm).

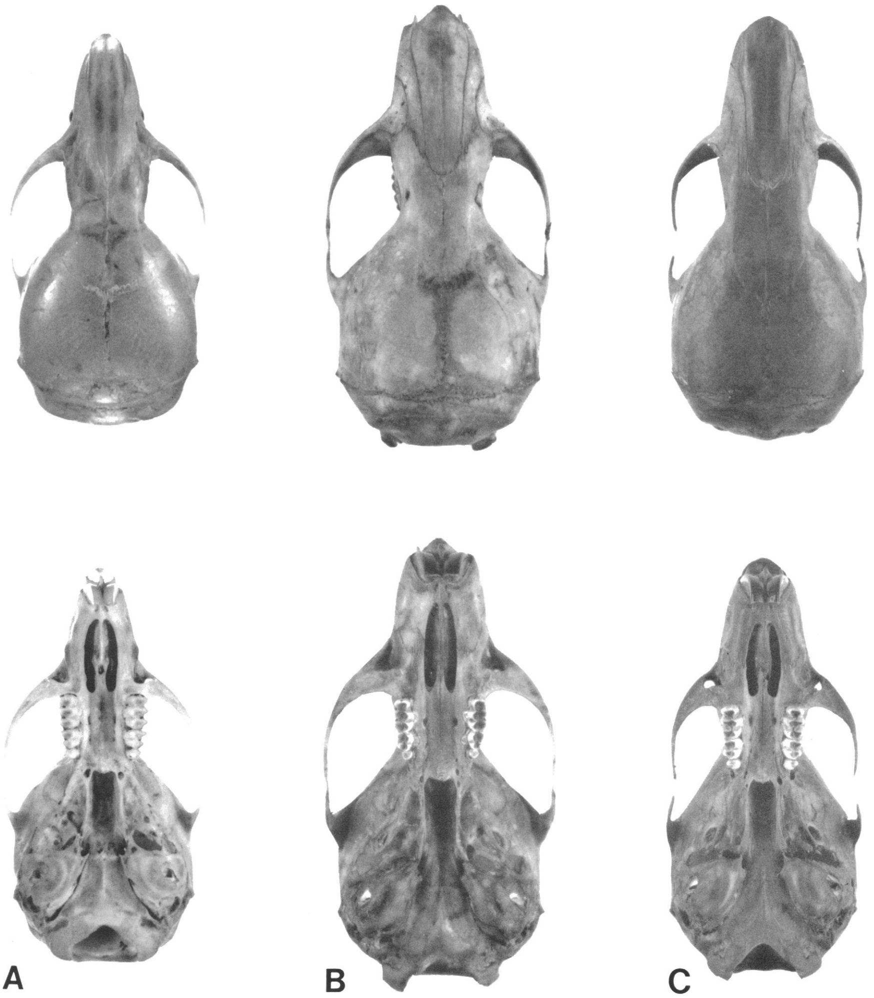


Fig. 40. Dorsal and ventral views of crania of *Neusticomys* species. **A,** *N. monticolus* (AMNH 64627); **B,** *N. peruviensis* (LSU 14407); **C,** *N. venezuelae* (AMNH 69908). All ×2.

banded awns and dark brown guard hairs in the overfur; ventral pelage paler but colored like dorsum, never distinctly countershaded; tail dark and unicolored; pinnae conspicuous, not concealed in fur of head; supraorbital vibrissae absent; rhinarium unpigmented (brown when dry); philtrum present; plantar surface of manus with three separate interdigital and two separate carpal pads, the hypothenar and third interdigital pads not fused; sole of pes not or only slightly pigmented (brown when dry); fourth interdigital pad of pes opposite or distal to first but always well proximal to second; fringing hairs along plantar surface of pes weakly developed, inconspicuous; claw of digit V of pes extends to or just beyond first interphalangeal joint of IV; claw of digit I extends to but not beyond distal end of phalange 1 of II.

Molars 3/3 or 2/2; principal cusps sharp when unworn but not very tall, not anteroposteriorly compressed; M1–2 with or without small anterolophs, posterolophs, and mesolophs; M3 very small, usually without posterior vestige of metacone/hypocone, or absent; m1 anteroconid with or without shallow anteromedian flexid; m1–2 with or without small anterolophids, posterolophids, and mesolophids; m3 small, with or without small posterior conule, or absent; upper incisors

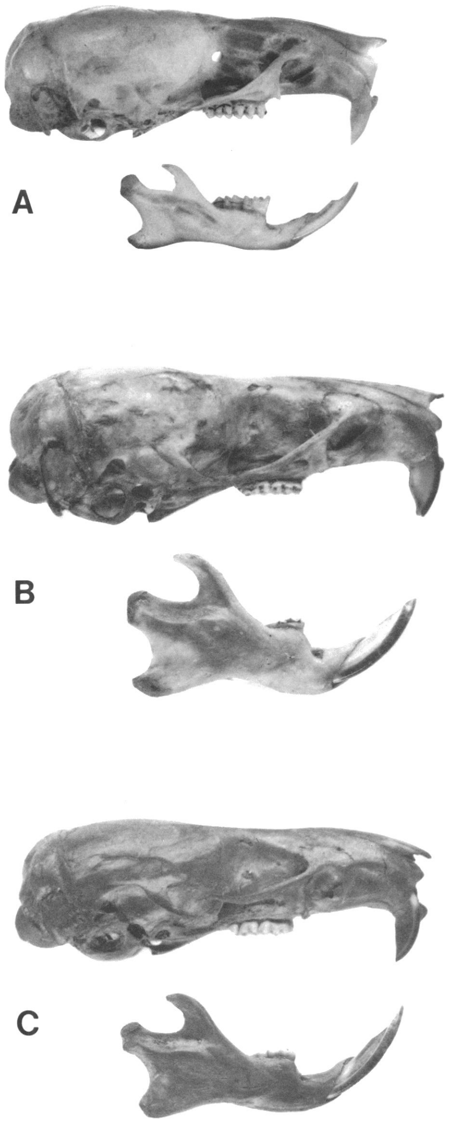


Fig. 41. Lateral view of crania and mandibles of *Neusticomys* species. Specimens and magnifications are the same as in figure 40.

not remarkably broad or narrow, their anterior surfaces inclined slightly medially, or these teeth broad and heavy, their anterior surfaces inclined conspicuously medially; lower incisors moderately procumbent or stoutly recurved.

Nasals long, concealing incisors and nasal orifice from dorsal view; rostrum moderately or very broad, the nasolacrimal capsules not visible in dorsal view or only their tips exposed; interorbital region broad relative to braincase (LIB/BB = .37–.41 in TWC 3–5); supraorbital foramina open laterally within the orbital fossae; zygomatic processes of maxillae and squamosals flaring from sides of rostrum and braincase or not; braincase moderately inflated but not globose; smooth or with small lambdoidal ridges developed in old adults; occipital condyles not or but slightly exposed in dorsal view; dorsal profile almost flat, gently convex over braincase and above maxillary root of zygoma; posterior margin of inferior zygomatic root just above or considerably anterior to anterocone of M1; tip of masseteric tubercle above or below plane of molar alveoli (not developed in the young adult specimen of *N. oyapocki*); lateral limits of incisive foramina convex, usually widest at the premaxillary/maxillary suture; carotid circulation pattern 1; auditory bullae not or but slightly inflated, bulbous or flask-shaped; orbicular apophysis of malleus present or absent; sphenoccipital kyphosis noticeable but not extreme.

Ribs 13–14; thoracicolumbar vertebrae 19; sacral vertebrae 4; metatarsals III ≥ IV > II ≫ V > I; omohyoid present; stomach nearly hemiglandular with gastric glandular epithelium between esophagus and pyloric sphincter; gall bladder present; bacular cartilage tridigitate, the medial digit larger than the lateral two but not grossly swollen and without a calcified core; one dorsal crater papilla present.

COMPARISONS: The four species that I include in *Neusticomys* are easily distinguished as a group apart from other ichthyomyines by the collection of character states provided in the diagnosis above, but *N. oyapocki, N. peruviensis,* and *N. venezuelae* have hitherto been referred to a separate genus, *Daptomys*; the arrangement adopted here therefore requires some comment.

Anthony (1929) remarked similarities in external morphology between *Daptomys* (which then included only *D. venezuelae*) and *Neusticomys* (then including only *N. monticolus*), and apparently based his judgment of generic distinction on differences in cranial proportions alone. Specimens of *N. venezuelae,* together with examples of the other species formerly included in *Daptomys,* contrast with *N. monticolus* by having heavier, more robust crania with proportionately larger incisors and broader rostra, but narrower palates and smaller molars; in addition, the dorsal adult pelage of *Daptomys* is close, glossy and brownish whereas that of *N. monticolus* (when fresh) is dull, wooly, and gray-black. These distinctions are not, however, equivalent to the phenotypic differences that separate other ichthyomyine genera, and useful character information seems more effectively communicated by combining *Neusticomys* and *Daptomys* to form one genus than by retaining each as distinct.

*Neusticomys* uniquely shares carotid circulation pattern 1 and a nearly hemiglandular stomach with *Chibchanomys,* but the two genera differ in many other characters including size of pinnae, presence/absence of a philtrum, length of tail relative to head-and-body, development of fringing hairs on the pes, and metatarsal proportions. Character state differences with other ichthyomyines are sufficiently numerous and obvious that confusion seems unlikely.

VARIATION: Patterns of morphological variation among samples of *Neusticomys* conform plausibly with the four species currently recognized.

### *Neusticomys monticolus* Anthony, 1921

This species is represented by 47 specimens collected at elevations between 1800 and 3754 m in the eastern and western cordilleras of the northern Andes from Pauchi, Provincia Chimborazo, Ecuador (ca. 2°S latitude) to Santa Bárbara, Departamento Antioquia, Colombia ca. 6°25′N). All of these are dull-colored, wooly mice; the fresh pelage is gray-black but older skins fade to rusty-brownish hues. Wrists, ankles, and metapodials are dark, but digits are usually silvery on both manus and pes. The ventral pelage, while not sharply countershaded, is often slightly paler than the dorsum. The oral margins are usually silvery as are at least some of the lowermost mystacial vibrissae. Apparently individual variations in pelage are white tail tips (e.g., AMNH 64625), partially bicolored tails (FMNH 71218), white midpectoral blazes (FMNH 71225), and irregular whitish dorsal spotting (UMMZ 155604) in occasional specimens from populations that do not uniformly exhibit these traits. No geographic variation in external characters is evident.

Variation among populations is apparent in some craniodental dimensions. The holotype, a subadult, was probably collected about 16 km NNE of the summit of Volcán Pichincha (see Gazetteer under Ecuador: Nono Farm "San Francisco"); two specimens (AMNH 64625, 64626) from San Ignacio at 3431 m on the southern flanks of Volcán Pichincha are the only available adult specimens collected reasonably near the type locality (table 20). The extremes of variation among other Ecuadorean populations are represented in table 20 by series from Guarumal and Papallacta (at 2245–2290 m and 3070–3754 m elevation, respectively; see Appendix for information about these and other localities discussed below). The series from Guarumal together with those from nearby Las Machinas and from the Río Pita closely resemble the Volcán Pichincha specimens, but the Papallacta series exhibits some metric differences. Papallacta mice average slightly smaller overall than specimens of comparable age in other Ecuadorean samples (e.g., values for HBL and CIL, table 20), and have narrower incisors, rostra, zygomas, braincases, and occipital condyles. These differences are not large, however, and other distinctive features are wanting. From other Ecuadorean localities (San Antonio, Pauchi, and Sinche) only single specimens are available and none are sufficiently distinctive to warrant comment.

Colombian specimens of *Neusticomys monticolus* are few; those with intact skulls (table 21) consist of two from San Antonio (Departamento Huila) at 2200–2350 m elevation in the headwaters of the Río Magdalena, five from Departamento Antioquia near Santa Bárbara (2700–2800 m) close to the northern terminus of the Cordillera Occidental, and four from Departamento del Valle near Pichindé (1800–1900 m), also in the western cordillera. The specimens from Huila and Valle closely resemble Ecuadorean species, but specimens from Antioquia have conspicuously narrower braincases than any of the Ecuadorean mice. The Antioquia material is also distinctive in the slightly larger size of the entoconid/hypoconid lobe of the

TABLE 20
**Age, Sex, and Measurements (in millimeters) of Selected Specimens of *Neusticomys monticolus* from Ecuador**
(The sample mean and the range in parentheses are provided for the Guarumal and Papallacta samples)

| | | San Ignacio | | Guarumal | Papallacta |
|---|---|---|---|---|---|
| | AMNH 46574[a] | AMNH 64626 | AMNH 64625 | UMMZ 126298, 126299, 155789, 155790, 155793 | AMNH 244608, 244609 UMMZ 155604, 155605 |
| Age | 2/o/n | 3/c/n | 4/c/n | 3–5/f/n | 3–5/c, f/n |
| Sex | female | male | male | 3 males, 2 females | 3 males, 1 female |
| HBL | – | 115 | 113 | 111.2 (105–116) | 104.5 (101–108) |
| LT | – | 105 | 110 | 107.8 (104–111) | 96.8 (92–101) |
| HF | 25 | 26 | 26 | 25.8 (25–26) | 25.0 (24–26) |
| Ear | 10 | 10 | 9 | 10.8 (10–11) | 10.2 (10–11) |
| CIL | 24.2 | 24.7 | 24.5 | 24.8 (24.2–25.7) | 23.6 (23.2–24.1) |
| LD | 5.9 | 5.8 | 6.0 | 6.2 (6.0–6.5) | 5.8 (5.6–6.0) |
| LM | 4.2 | 4.1 | 4.0 | 4.0 (3.9–4.1) | 4.1 (4.0–4.2) |
| LIF | 4.8 | 4.5 | 4.6 | 4.6 (4.5–4.8) | 4.7 (4.3–4.9) |
| BIT | 1.4 | 1.4 | 1.4 | 1.4 (1.4) | 1.2 (1.1–1.3) |
| BIF | 2.2 | 2.1 | 2.1 | 2.1 (2.0–2.2) | 2.1 (2.0–2.2) |
| BPB | 2.6 | 3.1 | 3.1 | 2.9 (2.7–3.1) | 2.8 (2.6–2.9) |
| LN | 9.4[b] | 9.5 | 9.3 | 9.6 (9.4–9.8) | 9.4 (9.2–9.6) |
| BN | 2.8 | 3.1 | 2.9 | 2.8 (2.7–3.0) | 2.6 (2.4–2.7) |
| LIB | 4.7 | 4.8 | 5.1 | 4.8 (4.6–5.0) | 4.6 (4.4–4.9) |
| ZB | 12.4[b] | 13.2 | 13.3 | 13.1 (12.7–13.4) | 12.2 (11.9–12.6) |
| BB | 12.1 | 12.1 | 12.3 | 12.2 (12.1–12.3) | 12.0 (11.9–12.0) |
| BZP | 1.0 | 1.2 | 1.1 | 1.1 (1.0–1.2) | 1.1 (1.1) |
| BM1 | 1.5 | 1.5 | 1.5 | 1.4 (1.4–1.5) | 1.4 (1.3–1.4) |
| HI | 4.5 | 4.5 | 4.7 | 4.8 (4.6–5.1) | 4.4 (4.1–4.7) |
| DI | 1.3 | 1.4 | 1.4 | 1.4 (1.4–1.5) | 1.2 (1.2–1.4) |
| BOC | 7.1 | 7.4 | 7.5 | 7.1 (7.0–7.2) | 6.8 (6.7–6.9) |

[a] The holotype.
[b] Measurements from Anthony (1921).

lower third molar, a dental structure that is usually diminutive in Ecuadorean specimens. Despite such differences, Antioquia specimens are so few and are otherwise so like typical *N. monticolus*, that a new name for them does not seem justified.

### *Neusticomys oyapocki*
### (Dubost and Petter, 1978)
### *N. peruviensis* (Musser and Gardner, 1974)
### *N. venezuelae* (Anthony, 1929)

Originally referred to the genus *Daptomys*, these three species are, as a group, distinguished from *N. monticolus* by their glossy, brownish pelts and more robust crania with broader, blunt rostra and larger incisors but proportionately smaller molars (figs. 40, 41). *N. venezuelae* is known from four specimens; *N. oyapocki* and *N. peruviensis* are known from a single specimen each (table 22). All three holotypes are represented by skins, crania, and mandibles; in addition, fluid-preserved viscera and a partial postcranial skeleton are available from the type of *N. venezuelae.*

Musser and Gardner (1974) discussed variation among the then-known material of *N. venezuelae* (AMNH 69907, 69908; USNM 406123) and the holotype of *N. peruviensis.* Since their discussion, a single additional specimen of *N. venezuelae* (AMNH 142818) from Kartabo, Guyana, has been discovered. The new Guyanese specimen consists of a cleaned cranium and mandibles and a fluid-preserved carcass; the animal is very young with incompletely erupted third molars, and is therefore smaller in most mea-

TABLE 21
**Age, Sex, and Measurements (in millimeters) of *Neusticomys monticolus* from Colombia**
(The sample mean, the range in parentheses, and the sample size are provided for the Valle and Antioquia series)

| | Huila | | Valle | Antioquia |
|---|---|---|---|---|
| | FMNH 71224 | FMNH 71225 | HTC 1373, 2180, 2237, 3365 | FMNH 71218, 71220 71221, 71222, 71223 |
| Age | 4/c/n | 6/f/n | 2–4/o, f/n | 4–5/f/n |
| Sex | male | male | 3 males, 1 female | 5 males |
| HBL | 105 | 108 | 107.0 (98–118) 4 | 106.8 (100–112) 5 |
| LT | 106 | – | 97.5 (92–102) 4 | 102.2 (97–105) 4 |
| HF | 25 | 26 | 25.0 (25) 4 | 24.8 (24–26) 5 |
| Ear | 9 | 9 | 9.0 (8–10) 3 | 9.0 (9) 5 |
| CIL | 23.9 | 24.6 | 24.5 (23.7–25.2) 4 | 23.8 (22.7–24.9) 4 |
| LD | 5.9[a] | 6.3 | 6.0 (5.7–6.2) 4 | 5.8 (5.5–6.1) 5 |
| LM | 4.0 | 4.0 | 4.3 (4.2–4.4) 4 | 4.1 (3.9–4.1) 5 |
| LIF | 4.7 | 5.2 | 4.4 (4.1–4.7) 4 | 4.5 (4.2–4.7) 5 |
| BIT | 1.3 | 1.3 | 1.5 (1.5–1.6) 4 | 1.4 (1.4–1.5) 5 |
| BIF | – | 2.2 | 2.0 (1.9–2.2) 4 | 2.2 (2.1–2.2) 5 |
| BPB | 2.7 | – | 2.7 (2.5–2.8) 4 | 2.9 (2.5[a]–3.3) 5 |
| LN | 8.9 | 10.1 | 9.6 (9.3–10.1) 4 | 9.7 (9.2–10.7) 5 |
| BN | 2.7 | 2.7 | 3.1 (2.9–3.2) 4 | 2.9 (2.7–3.1) 5 |
| LIB | 4.4 | 4.6 | 5.1 (5.0–5.2) 4 | 4.8 (4.6–5.1) 5 |
| ZB | – | 13.0 | 13.1 (13.1) 3 | 12.1 (12.1) 1 |
| BB | 12.5 | 12.2 | 12.2 (11.9–12.4) 4 | 11.4 (11.2–11.5) 4 |
| BZP | 1.1 | 1.1 | 1.3 (1.2–1.5) 4 | 1.0 (0.9–1.1) 5 |
| BM1 | 1.3 | – | 1.4 (1.3–1.4) 4 | 1.4 (1.3–1.6) 5 |
| HI | 4.3 | 4.2 | 4.4 (4.1–4.6) 4 | 4.4 (4.0–4.7) 5 |
| DI | 1.3 | 1.3 | 1.4 (1.3–1.5) 4 | 1.4 (1.4–1.5) 5 |
| BOC | 7.0 | 6.8 | 6.8 (6.6–7.0) 4 | 6.8 (6.6–7.0) 4 |

[a] Estimated values.

sured dimensions than the older Venezuelan specimens (table 22). The smaller size of AMNH 142818 in such precociously maturing structures as the hindfoot, molar dentition (estimated in table 22), and braincase may indicate a significantly smaller adult morphology for Guyanese populations, but in all relevant qualitative characters the Guyana example conforms with the three Venezuelan specimens.

Musser and Gardner (1974) provided a thorough description and diagnosis of *N. peruviensis* that requires no further elaboration here. Dubost and Petter's (1978) description of *N. oyapocki,* however, merits some comment. Dubost and Petter described MNHN 1977-775 (the type) as an adult due to the presence of spermatozoa in the epididymides. The molars of this specimen, however, are but slightly worn (TWC 2) and all basicranial sutures are open; the metatarsal epiphyses appear unfused as well; the pelage is glossy and may be adult, but with no additional material available for comparisons, this ontogenetic inference is uncertain. Dubost and Petter based their diagnosis of *N. oyapocki* on the absence of upper and lower third molars in MNHN 1977-775, and on the smaller size of the remaining molars (see values for LM1-2 and BM1 in table 22). There are, however, additional characters that distinguish the type of *N. oyapocki* from specimens of *N. venezuelae* and/or *N. peruviensis*: (1) Specimens of *N. venezuelae* and *N. peruviensis* all exhibit a small posteroloph (or the worn remnants thereof) on M2, but the type of *N. oyapocki* lacks any trace of a posteroloph on M2. (2) Despite the fact that the type of *N. oyapocki* is slightly larger than, or about equal to specimens of *N. venezuelae* of equivalent age in most nonmolar measurements of the skull, the interorbital region and

TABLE 22
Age, Sex, and Measurements (in millimeters) of *Neusticomys venezuelae*, *N. peruviensis*, and *N. oyapocki*

| | *N. venezuelae* | | | | | |
|---|---|---|---|---|---|---|
| | Venezuela | | | Guyana | *N. peruviensis* | *N. oyapocki* |
| | AMNH 69907[a] | AMNH 69908 | USNM 406123 | AMNH 142818 | LSU 14407[a] | MNHN 1977-775[a] |
| Age | 2/o/i | 2/o/i | 3/f/a | 1/o/i | 4/c/a | 2/o/?a |
| Sex | male | female | female | male | male | male |
| HBL | 131 | 112 | 100 | — | 128 | 114 |
| LT | 105 | 111 | 109 | — | 108 | 82 |
| HF | 28 | 28 | 25 | 24 | 30 | 26 |
| Ear | 10 | 11 | 10 | 10 | 12 | 9 |
| CIL | 26.9 | 26.9 | 26.0 | 23.4 | 28.1 | 27.2 |
| LD | 6.9 | 6.9 | 6.7 | 5.8 | 7.5 | 7.6 |
| $LM^{1-3}$ | 4.1 | 4.2 | 4.0 | 3.9[b] | 3.8 | — |
| $LM^{1-2}$ | 3.5 | 3.5 | 3.3 | 3.2 | 3.2[b] | 3.0 |
| LIF | 4.8 | 4.8 | 5.2 | 4.1 | 5.6 | 5.2 |
| BIT | 2.0 | 1.8 | 1.8 | 1.5 | 2.2 | 1.9 |
| BIF | 2.2 | 2.2 | 2.2 | 1.8 | 2.0 | 2.3 |
| BPB | 2.7 | 2.5 | 2.7 | 2.3 | 3.3 | 3.0 |
| LN | 10.3 | 10.9 | 10.0 | 8.8 | 11.1 | — |
| BN | 3.5 | 3.5 | 3.2 | 3.3 | 3.7 | 3.3 |
| LIB | 5.2 | 5.3 | 5.0 | 5.5 | 5.2 | 4.8 |
| ZB | 13.3 | 12.8 | 13.7[b] | 12.4 | 14.4 | 13.7 |
| BB | 12.5 | 12.5 | 12.5 | 11.6 | 12.8 | 11.2 |
| BZP | 1.1 | 1.2 | 1.3 | 1.3 | 1.3 | 1.5 |
| BM1 | 1.3 | 1.4 | 1.3 | 1.4 | 1.3 | 1.1 |
| HI | 5.1 | 5.0 | 5.1 | 4.0 | 4.9 | 5.2 |
| DI | 1.6 | 1.7 | 1.7 | 1.2 | 1.9 | 1.6 |
| BOC | — | 7.6 | 7.1 | 7.4 | 7.6 | 7.1 |

[a] Holotypes.
[b] Estimated values.

braincase of *N. oyapocki* are conspicuously narrower. (3) Unlike *N. venezuelae, N. peruviensis,* and all other ichthyomyine specimens that I have examined, *N. oyapocki* lacks a distinct bony tubercle for the origin of M. masseter superficialis; instead, the superficial masseter of *N. oyapocki* originates on each side from a small patch of rugose bone below the anterior edge of the inferior zygomatic root. (4) In specimens of *N. venezuelae* the posterior edge of the inferior zygomatic root is located above the anterocone of M1; in *N. oyapocki* (and *N. peruviensis*) however, the posterior edge of the zygomatic root is located well anterior to the M1 anterocone (the anterocone of M1 is fully 1.2 mm behind the inferior zygomatic root in the type of *N. oyapocki*).

While the characters listed here together with others discussed by Musser and Gardner (1974) may not all prove diagnostic when more material of lowland *Neusticomys* becomes available, similarities and differences in these attributes among existing specimens seem usefully indicated by the three species taxa currently recognized.

SPECIMENS EXAMINED: *Neusticomys monticolus* – **Colombia:** Pichindé (HTC 1373, 2180, 2237, 3365); San Antonio (FMNH 71224, 71225); Santa Bárbara (FMNH 71218–71223). **Ecuador:** Guarumal (UMMZ 126298, 126299, 155789–155794); Las Machinas (AMNH 64634–64639); Nono Farm "San Francisco" (AMNH 46574); Papallacta (AMNH 244608, 244609; UMMZ 126297, 155604–155606); Pauchi (AMNH 66848); Río Pita (AMNH 63376, 64627–64633, 64646); San Antonio (AMNH 67548);

San Ignacio (AMNH 64625, 64626); Sinche (AMNH 62920). Total, 47.

*Neusticomys oyapocki* – **French Guiana:** Trois-Sauts (MNHN 1977-775). Total, 1.

*Neusticomys peruviensis* – **Peru:** Balta (LSU 14407). Total, 1.

*Neusticomys venezuelae* – **Guyana:** Kartabo (AMNH 142818). **Venezuela:** Cerro Duida (USNM 406123); Río Neverí (AMNH 69907, 69908). Total, 4.

### *Rheomys* Thomas, 1906

(Figures 5–12, 14, 16, 18, 19, 22–26, 42–48)

SYNONYMS: *Neorheomys* Goodwin, 1959.

TYPE SPECIES: *Rheomys underwoodi* Thomas, 1906, based on a British Museum of Natural History specimen (BMNH 7.5.30.5) consisting of the skin, skull, and mandibles of an adult (5/c/a) male collected by Cecil F. Underwood on 5 May 1905 near Tres Ríos, Provincia Cartago, Costa Rica.

CONTENTS: Seven nominal species and subspecies have been referred to the genus as follow in chronological order of their description: *R. underwoodi* Thomas, 1906; *R. raptor* Goldman, 1912; *R. thomasi thomasi* Dickey, 1928; *R. thomasi stirtoni* Dickey, 1928; *R. hartmanni* Enders, 1939; *R. thomasi chiapensis* Hooper, 1947; *R. mexicanus* Goodwin, 1959. The number of biological species represented among these specific and subspecific epithets is considered below in the section on variation. *Ichthyomys trichotis* (Thomas, 1897) was transferred to *Rheomys* by Thomas (1906b) but is here regarded as a generically distinct form (see account for *Chibchanomys* above).

KNOWN DISTRIBUTION: The genus *Rheomys* is endemic to Central America. Collection localities range from San José Lachiguirí, Estado Oaxaca, Mexico, south and east through the mountains and adjacent foothills of Guatemala, El Salvador, Costa Rica, and Panama. Recorded elevations range from 369 to 2462 m.

DIAGNOSIS: Ichthyomyines with glossy, grizzled-brownish adult dorsal pelage; pinnae visible or not above fur of head; philtrum present or absent; tail shorter, equal to or longer than head-and-body length; manus with four or fewer separate plantar pads; hindfoot short or long relative to head-and-body but proportionately broad with well-developed fringing hairs; nasal bones long; supraorbital foramina open laterally within the orbital fossae; carotid circulation pattern 3; orbicular apophysis of malleus present; stomach with gastric glandular epithelium restricted to greater curvature; gall bladder present; bacular cartilage tridigitate.

DESCRIPTION: Adult head-and-body length 92–142 mm; HF/HBL = .21–.34; LT/HBL = .85–1.33; adult pelage glossy, grizzled-brownish dorsally due to mixture of buffy-banded awns and dark brown guard hairs in the overfur; venter distinctly countershaded, silvery white or pale gray (but the bases of the hairs dark); tail dark and unicolored or bicolored (dark brown-black above, pale gray-brown or white below); ears small but visible above the unruffled pelage of the head or very small and buried in the fur of the head; supraorbital vibrissae absent; rhinarium pigmented (blackish when dry) or not (brown when dry); philtrum present or absent; manus with hypothenar and 3rd interdigital pads fused; hypothenar pad of pes absent, 4th interdigital nearly or completely opposite 2nd; claw of digit V of pes extends to 2nd interphalangeal joint of IV, or beyond 2nd interphalangeal joint almost to base of claw of IV; claw of digit I of pes extends to 1st or 2nd interphalangeal joint of II.

Molars 3/3; cusps anteroposteriorly compressed, tall and sharp when unworn, or not compressed, sharp but not very tall even when unworn; newly erupted M1–2 with small anterolophs, mesolophs and posterolophs but these usually obliterated with slight wear; M3 with or without a minute posterior conule; anteroconid of m1 narrow, divided by anteromedian flexid into distinct, sharp labial and lingual conulids or the flexid shallow or absent and the paired conulids indistinct or absent; newly erupted m1–2 with small anterolophids, mesolophids, and posterolophids; small ectolophids sometimes present; m3 large, with subequal entoconid/hypoconid cusp pair behind protoconid/metaconid, or small, with or without a minute posterior vestige of the entoconid/hypoconid (*mexicanus* only); upper incisors narrow, their anterior enameled surfaces not or but slightly inclined medially or these teeth

Fig. 42. *Rheomys thomasi.* Reproduced from Stirton's (1944) halftone plate 1. Note externally visible pinna.

broad, their anterior enameled surfaces conspicuously turned medially; lower incisors correspondingly narrow and procumbent or stronger, less procumbent.

Nasals long, concealing incisors and nasal orifice from dorsal view; rostrum narrow, the nasolacrimal capsules fully exposed in dorsal view or the rostrum broad, only the tips of the nasolacrimal capsules visible dorsally; interorbital region broad or narrow relative to width of braincase (LIB/BB = .33–.40); supraorbital foramina open laterally into orbits, not onto dorsal surface of frontals; zygomatic processes of maxillae and squamosals neither very strong and broadly flaring nor (except in *underwoodi*) very delicate; braincase inflated or not; lambdoidal ridges not well developed even in large adults; occipital condyles not produced posteriorly beyond the supraoccipital, not visible in dorsal view; dorsal profile concave or flattened over orbits, convex over rostrum and braincase; posterior edge of inferior zygomatic root above M1 anterocone; tip of masseteric tubercle high above molar row on inferior zygomatic root or produced below the plane of the molar alveoli from the base of the root; incisive foramina vary considerably in shape; palate produced posteriorly slightly or well beyond M3s; carotid circulation pattern 3; auditory bullae flask-shaped, not inflated; orbicular

Fig. 43. Head of *Rheomys mexicanus* (AMNH 205313). About ×1.6. Note absence of externally visible pinna.

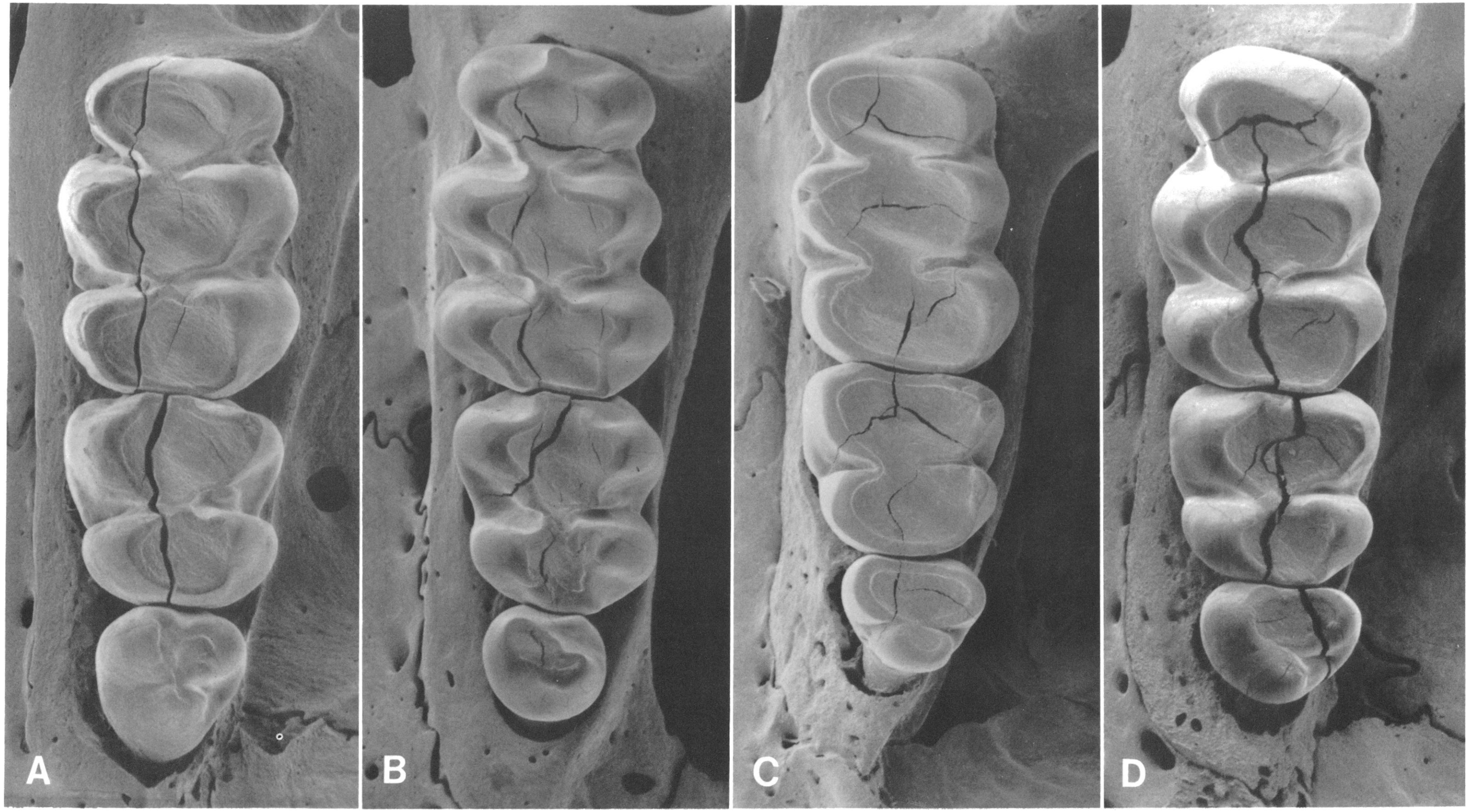


Fig. 44. Left maxillary dentition of *Rheomys* species. **A,** *R. underwoodi* (UMMZ 115459, LM = 5.1 mm); **B,** *R. mexicanus* (AMNH 186922, LM = 4.9 mm); **C,** *R. raptor hartmanni* (UMMZ 112300, LM = 4.6 mm); **D,** *R. thomasi thomasi* (MVZ 98802, LM = 4.3 mm).

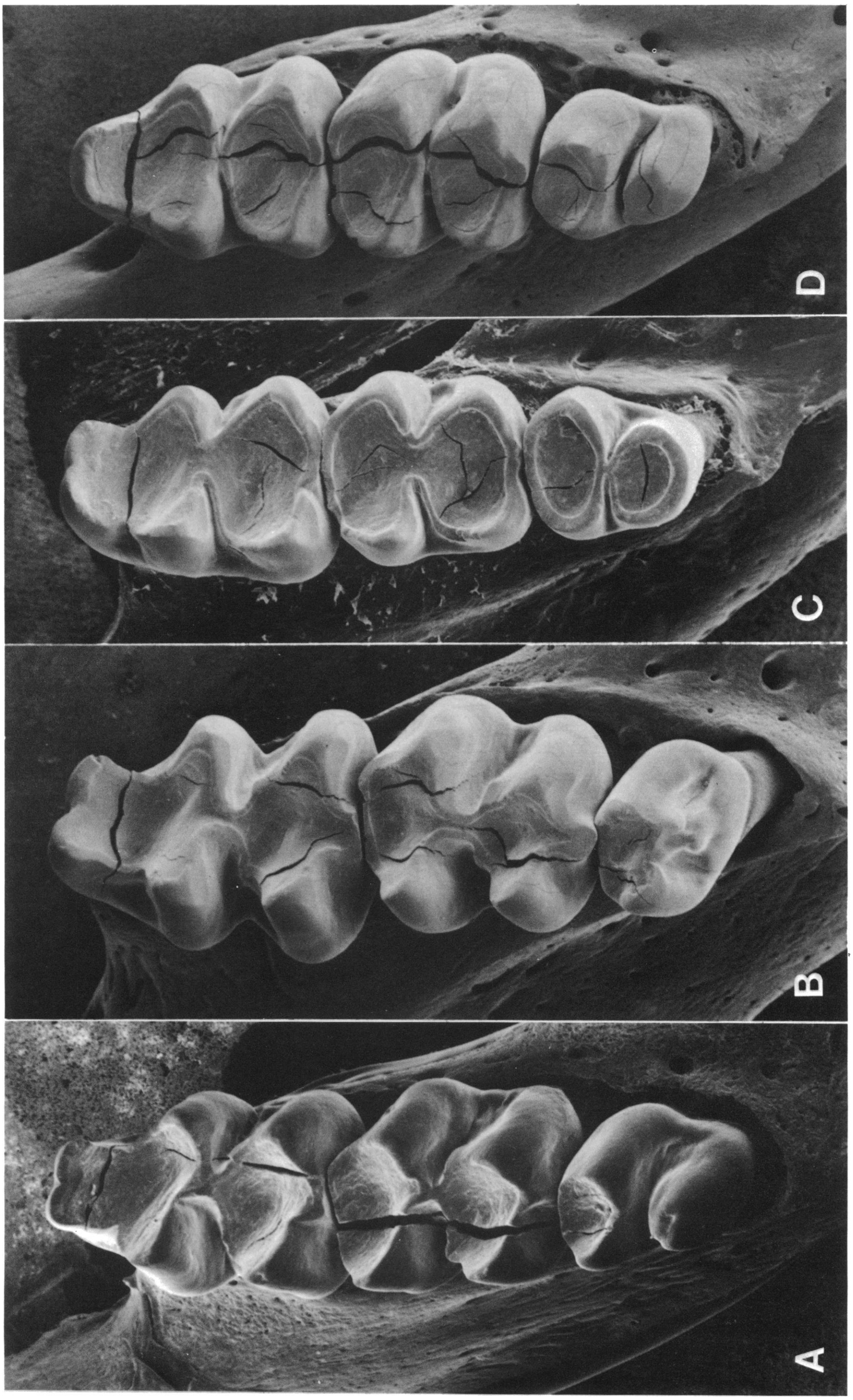


Fig. 45. Right mandibular dentition of *Rheomys* species. Specimens and magnification are the same as for figure 44.

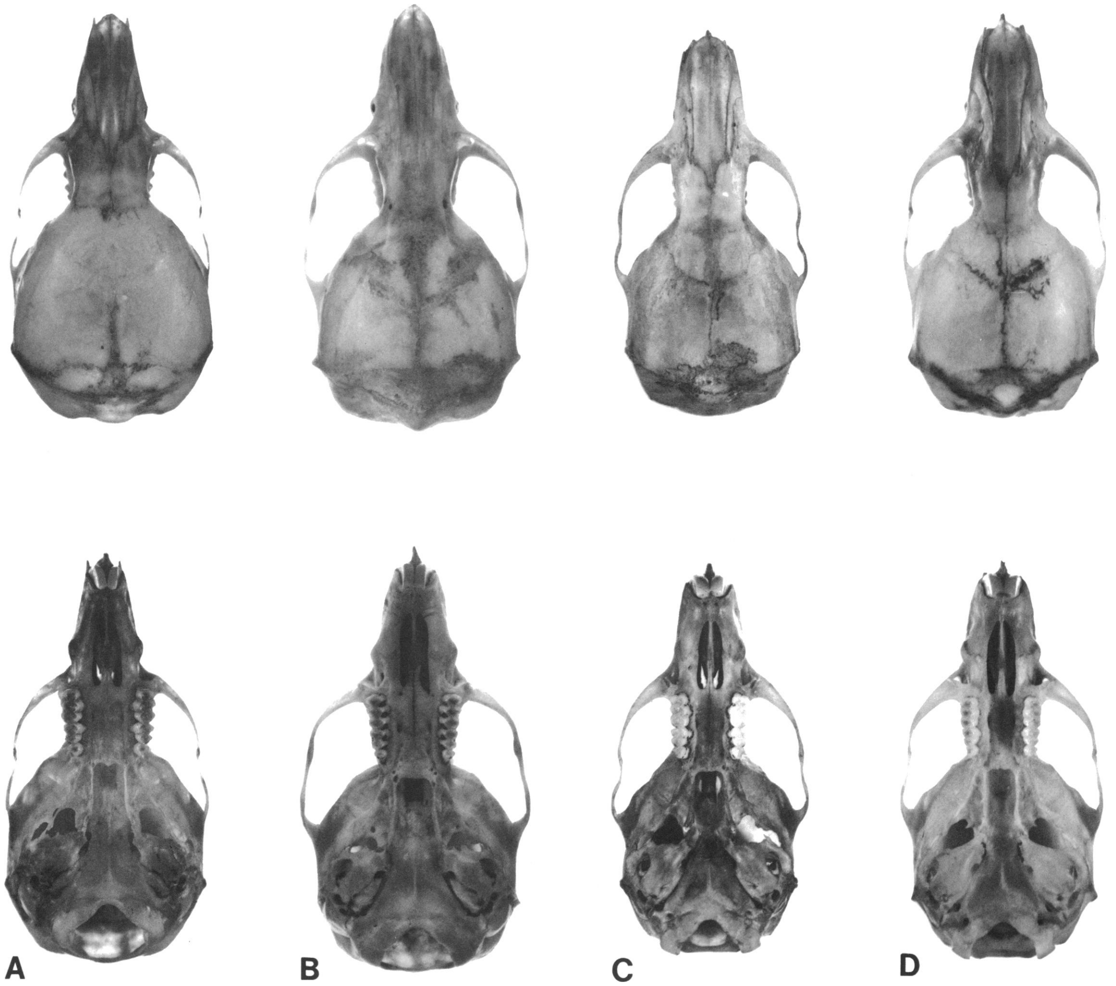


Fig. 46. Dorsal and ventral views of crania of *Rheomys* species. **A,** *R. underwoodi* (USNM 516940); **B,** *R. mexicanus* (AMNH 205320); **C,** *R. raptor hartmanni* (USNM 396586); **D,** *R. thomasi thomasi* (MVZ 98805). Slightly less than ×2.

apophysis of malleus a small spur or knob; sphenoccipital kyphosis noticeable but not extreme.

Ribs 13–14; thoracicolumbar vertebrae 19–20; sacral vertebrae 4; metatarsals IV > III > II ≥ V > I or IV > III > V > II > I; omohyoid muscle present (most species) or absent (*mexicanus* only); gastric glandular epithelium restricted to a broad band that crosses the greater curvature on the right-hand side of stomach; gall bladder present; bacular cartilage tridigitate, the medial digit grossly swollen with a bulbous, calcified core in all adult specimens; one dorsal crater papilla present.

COMPARISONS: Comparisons of *Rheomys* with other ichthyomyine genera have already been provided in the preceding accounts.

VARIATION: The seven named forms of *Rheomys* are easily sorted into two morphologically distinctive groups that may be informally designated by the oldest specific epithet belonging to each.

The two species comprising the *underwoodi* group, *R. underwoodi* and *R. mexicanus,* are large-bodied forms (HBL averages about 130–140 mm for TWC 3–5) with very large and broad hindfeet (HF averages 37–40 mm; TWC 3–5). Tails average conspicuously longer than heads-and-bodies (LT/HBL

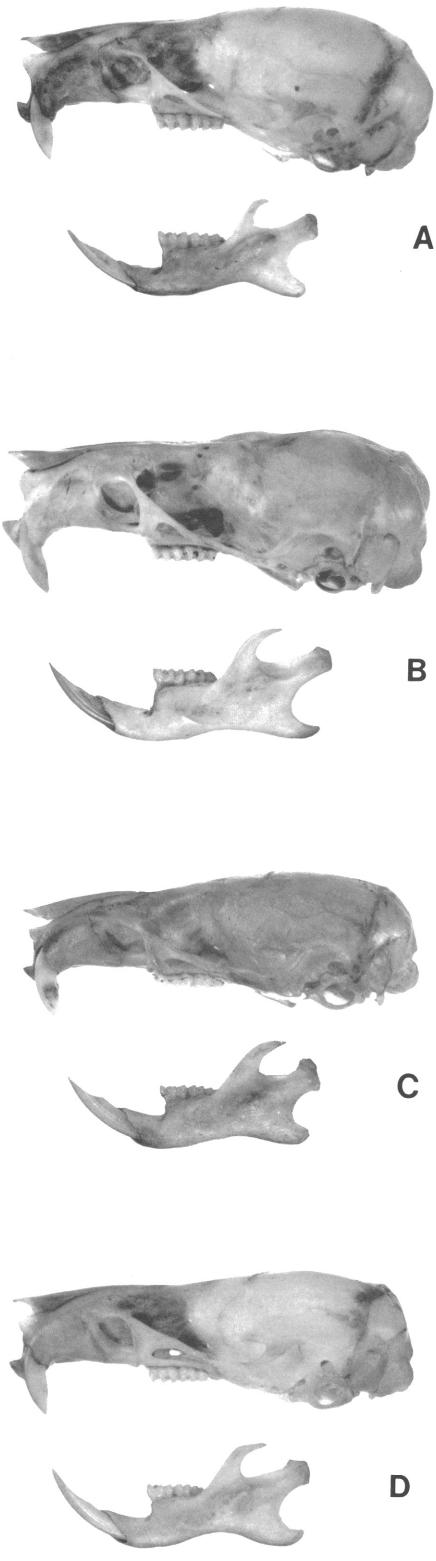
= 1.11–1.21; TWC 3–5) and are distinctly bicolored in adult examples: dark brownish or blackish above and dirty silvery (*underwoodi*) or pure white (*mexicanus*) below. Pinnae are always very small and buried in the fur of the head (fig. 43). The muzzle between the rhinarium and upper lip is entirely hairy and undivided by any trace of a naked philtrum.

Skulls of *Rheomys underwoodi* and *R. mexicanus* (figs. 46A, B, 47A, B) have slender rostra and greatly inflated braincases; inferior zygomatic roots are slender and the hard palate between the molar rows is broad. Upper incisors are long and slender; molars are large (LM averages 4.8–5.0 mm) and broad (BM1 averages 1.6–1.8 mm) with tall, sharp principal cusps separated by wide reentrant folds.

By contrast, members of the *raptor* group (*R. raptor, R. hartmanni,* and *R. thomasi* subspecies) are smaller-bodied forms (HBL averages less than 130 mm for TWC 3–5) with smaller hindfeet (HF averages 28–33 mm; TWC 3–5). Tails average about as long as heads-and-bodies (LT/HBL = .92–1.07; TWC 3–5) and are not distinctly bicolored although the ventral caudal hairs are paler than hairs of the caudal dorsum in occasional specimens. Pinnae are small but always visible above the unruffled fur of the head (fig. 42). A distinct philtrum is usually present.

Skulls of *R. raptor* and *R. thomasi* (figs. 46C, D, 47C, D) have relatively broader rostra and less inflated braincases than skulls of the *underwoodi* group; inferior zygomatic roots are broader and the hard palate between the molar rows is relatively narrower. Upper incisors are comparatively short and broad. Dimensions of the molar dentition are smaller (LM averages 4.2–4.5 mm; BM1 = 1.4–1.5 mm) and the molar cusps are not as tall or separated by such wide reentrant folds as in *R. underwoodi* and *R. mexicanus.*

Some of these morphological differences between members of the *underwoodi* and *raptor* groups were previously remarked by Goodwin (1959) who compared *R. mexican-*



←

Fig. 47. Lateral view of crania and mandibles of *Rheomys* species. Specimens are the same as for figure 46. Slightly less than ×2.

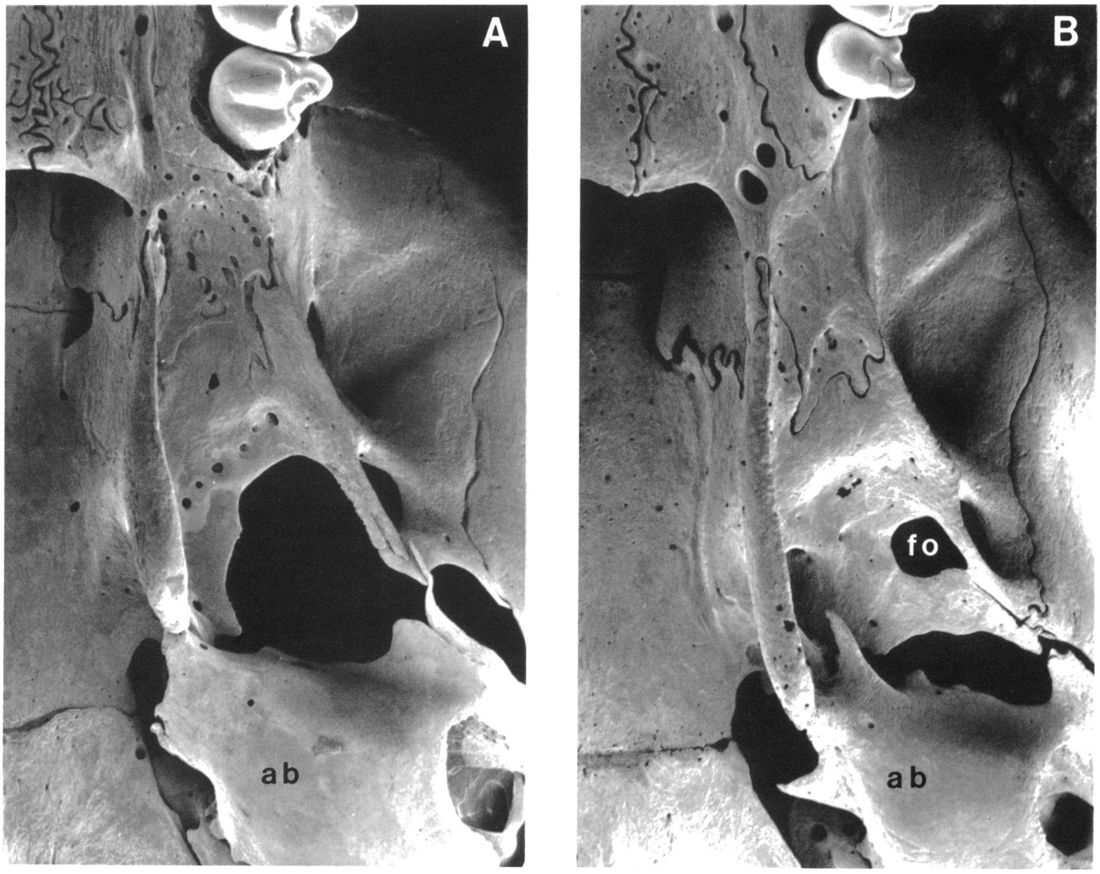


Fig. 48. Ventral view of left parapterygoid region in *Rheomys underwoodi* (**A**) and *R. mexicanus* (**B**). Anterior to the auditory bulla (**ab**) there is a large unossified region in the former species, but in *R. mexicanus* this region is largely ossified and the foramen ovale (**fo**) is always present as a discrete perforation in the floor of the braincase.

*us* with *R. thomasi* and judged the two forms to be so different that he erected the subgenus *Neorheomys* to contain *R. mexicanus.* In doing so, Goodwin apparently assumed that his examples of *R. thomasi* represented the typical morphology of *Rheomys* since he provided no comparisons with *R. underwoodi,* the genotype. *R. mexicanus* and *R. underwoodi* are each morphologically diagnosable, but the number of characters in which they resemble one another and together differ from other members of the genus suggests that any useful subgeneric classification would place both in the nominate subgenus; character differences between *R. mexicanus* and *R. underwoodi* appear insufficient to justify retention of the subgenus *Neorheomys* by any criterion of taxonomic utility.

Hooper (1968) also identified many of the distinctions between the *underwoodi* and *raptor* groups in his comparison of *R. underwoodi* with *R. hartmanni* and pointed out that geographic overlap between those two forms in Panama and Costa Rica is not consistent with Hershkovitz's (1966) suggestion that all named populations of *Rheomys* are conspecific. Although unequivocal evidence from sympatry is wanting, I believe that there is sufficient information to justify recognition of at least four species of *Rheomys.*

### *Rheomys underwoodi* Thomas, 1906

The disposition and geographic origin of the type of *R. underwoodi* have already been provided; no other specimens from the type

TABLE 23
Age, Sex, and Measurements (in millimeters) of ***Rheomys underwoodi*** from Costa Rica and Panama

| | Costa Rica | | | | | | |
|---|---|---|---|---|---|---|---|
| | Tres Ríos | Volcán Poás | | | Panama | | |
| | BMNH 7.5.30.5[a] | UMMZ 115460 | UMMZ 115389 | LACM 28260 | PANS 18328 | USNM 516940 | $\bar{x}$ ± SD[c] |
| Age | 5/c/a | 3/c/i | 4/c/a | 5/f/a | 4/c/a | 4/c/a | |
| Sex | male | male | male | male | female | male | |
| HBL | 130 | 135 | 137 | 142 | 136 | 138 | 136.3 ± 3.9 |
| LT | 150 | 152 | 148 | 158 | 156 | 149 | 152.2 ± 4.0 |
| HF | 36 | 37 | 38 | 37 | 37 | 38 | 37.2 ± 0.8 |
| Ear | 6 | 6 | 7 | 7 | 4 | 6 | 6.0 ± 1.1 |
| CIL | 28.6 | 28.0 | – | 28.3 | 28.6 | 27.5 | 28.2 ± 0.46 |
| LD | 7.9 | 7.6 | 7.2 | 7.6 | 7.6 | 7.4 | 7.6 ± 0.24 |
| LM | 4.9 | 5.1 | 5.0 | 4.9 | 5.0 | 4.9 | 5.0 ± 0.08 |
| LIF | 5.0 | 5.0 | 4.9 | 5.0 | 5.9 | 5.3 | 5.2 ± 0.38 |
| BIT | 1.5 | 1.4 | 1.5 | 1.4 | 1.4 | 1.3 | 1.4 ± 0.08 |
| BIF | 2.1 | 2.2 | 2.3 | 2.1 | 2.4 | 2.1 | 2.2 ± 0.13 |
| BPB | 3.5 | 3.5 | 3.5 | 3.6 | 3.5 | 3.5 | 3.5 ± 0.04 |
| LN | 11.3 | 11.4 | 11.4 | 12.1 | 12.1 | 11.1 | 11.6 ± 0.43 |
| BN | 3.7 | 3.4 | 3.6 | 3.6[b] | 3.6 | 3.5 | 3.6 ± 0.10 |
| LIB | 5.5 | 4.9 | 4.9 | 4.9 | 5.2 | 5.3 | 5.1 ± 0.26 |
| ZB | 15.1 | 15.5 | – | 15.1 | 14.8 | 14.8 | 15.1 ± 0.29 |
| BB | 14.5 | 14.6 | – | 14.4 | 14.7 | 14.5 | 14.5 ± 0.11 |
| BZP | 1.1 | 1.3 | 1.3 | 1.2 | 1.5 | 1.1 | 1.2 ± 0.15 |
| BM1 | 1.7 | 1.7 | 1.8 | 1.8 | 1.7 | 1.7 | 1.7 ± 0.05 |
| HI | 5.4 | 5.5 | 5.6 | 5.1 | 5.4 | 5.4 | 5.4 ± 0.17 |
| DI | 1.5 | 1.3 | 1.4 | 1.3 | 1.4 | 1.5 | 1.4 ± 0.09 |
| BOC | – | 8.8 | – | 8.6 | 8.3 | 8.3 | 8.5 ± 0.24 |

[a] The holotype.
[b] Estimated value.
[c] The mean plus or minus one standard deviation.

locality are known. Additional material of *R. underwoodi* consists of four specimens from Volcán Poás, Costa Rica, and four from the mountains of western Panama (see entries for Candela, Río Chiriquí Viejo, and Velo in the Appendix). Measurements of the type and of adults from Volcán Poas and Panama (table 23) show remarkable metric uniformity. The interorbital region of the type is somewhat broader absolutely, and in proportion to the braincase, than in other adult examples, but additional distinguishing characters among these population samples are wanting. Thomas's (1906b) description of external morphology and pelage color applies equally well to all subsequently collected adults except that tails are more sharply bicolored in other adult skins than in the type; specimens in immature pelage (e.g., UMMZ 115459, 115460, USNM 516939), however, have dark and unicolored tails.

The only species of ichthyomyine other than *Rheomys underwoodi* known to occur in Costa Rica and extreme western Panama is *R. raptor hartmanni.* The characters provided above for the *underwoodi* and *raptor* species groups together with other distinguishing features described by Hooper (1968) permit easy identification of *R. underwoodi* and *R. r. hartmanni* where their geographic ranges overlap. Closest comparisons between *R. underwoodi* and other congeners are with *R. mexicanus.*

### *Rheomys mexicanus* Goodwin, 1959

*Rheomys mexicanus* is represented by 28 specimens from three localities in Estado Oa-

TABLE 24
**Age, Sex, and Measurements (in millimeters) of *Rheomys mexicanus***
(The sample mean, the range in parentheses, and the sample size are provided separately for the San José Lachiguirí and Unión Hidalgo samples)

| | San José Lachiguirí[a] | Unión Hidalgo[b] | $\bar{x}$ ± SD[c] |
|---|---|---|---|
| Age | 3–5/c, f/a | 3–5/o, f/a | |
| Sex | 3 males, 2 females | 7 males, 1 female | |
| HBL | 131.0 (121–140) 4 | 129.0 (105–141) 7 | 129.7 ± 10.5 |
| LT | 158.5 (154–160) 4 | 154.7 (140–171) 7 | 156.1 ± 9.2 |
| HF | 39.4 (38–41) 5 | 39.6 (37–42) 8 | 39.5 ± 1.7 |
| Ear | 8.0 (8.0) 1 | 7.1 (6–8) 7 | 7.2 ± 0.7 |
| CIL | 29.9 (29.1–30.2) 4 | 29.7 (28.1–31.4) 7 | 29.8 ± 1.01 |
| LD | 8.3 (8.1–8.5) 5 | 8.1 (7.4–8.8) 8 | 8.2 ± 0.38 |
| LM | 4.9 (4.7–5.1) 5 | 4.8 (4.6–5.0) 8 | 4.8 ± 0.13 |
| LIF | 5.7 (5.4–6.2) 5 | 5.9 (5.4–6.4) 8 | 5.8 ± 0.31 |
| BIT | 1.5 (1.4–1.6) 5 | 1.6 (1.4–1.6) 8 | 1.5 ± 0.08 |
| BIF | 2.4 (2.0–2.6) 5 | 2.2 (2.1–2.4) 8 | 2.3 ± 0.18 |
| BPB | 3.7 (3.5–3.9) 5 | 3.6 (3.2–3.8) 8 | 3.6 ± 0.19 |
| LN | 11.7 (11.1–12.2) 5 | 12.0 (10.4–13.0) 7 | 11.9 ± 0.74 |
| BN | 3.8 (3.6–3.9) 5 | 3.7 (3.3–3.9) 7 | 3.7 ± 0.20 |
| LIB | 5.1 (4.9–5.2) 5 | 5.1 (4.8–5.3) 8 | 5.1 ± 0.16 |
| ZB | 16.7 (16.5–16.8) 3 | 16.6 (15.6–17.7) 5 | 16.6 ± 0.68 |
| BB | 14.7 (14.5–15.1) 4 | 14.8 (14.5–15.2) 7 | 14.8 ± 0.26 |
| BZP | 1.3 (1.1–1.4) 5 | 1.3 (1.1–1.4) 8 | 1.3 ± 0.12 |
| BM1 | 1.6 (1.6–1.7) 5 | 1.7 (1.6–1.7) 8 | 1.7 ± 0.05 |
| HI | 6.2 (6.1–6.2) 4 | 6.0 (5.4–6.7) 8 | 6.0 ± 0.38 |
| DI | 1.5 (1.5–1.6) 5 | 1.5 (1.4–1.6) 8 | 1.5 ± 0.08 |
| BOC | 8.9 (8.4–9.3) 4 | 8.7 (8.4–9.0) 7 | 8.8 ± 0.28 |

[a] AMNH 179970 (the holotype), 179971, 182138, 205320, 207447.
[b] AMNH 185015, 189291, 205314–205317, 205319, 208256.
[c] The mean plus or minus one standard deviation calculated from combined data.

xaca, Mexico. The holotype and 10 topotypic examples from San José Lachiguirí together with 14 specimens from Unión Hidalgo were obtained by Thomas MacDougall between 1958 and 1964; a single MacDougall specimen (AMNH 205313) lacks locality information. In addition to these, two specimens have recently (in 1978) been collected near Totontepec in the Sierra Mixes (see Appendix). Cranial measurement means of adults (TWC 3–5) from San José Lachiguirí and Unión Hidalgo differ by 0.3 mm or less and comparisons with *R. underwoodi* are therefore reasonably based on mean values from both locality samples combined (table 24). The two Totontepec examples, prepared as skins and skulls in the field, closely resemble specimens from San José and Unión Hidalgo in all metric and qualitative characters save that the dorsal pelage is darker on the fresh Totontepec skins than on skins from the latter two samples which were prepared from fluid-preserved material.

*Rheomys mexicanus* (see Goodwin, 1959, for detailed description) is strikingly similar to *R. underwoodi* in external characters and in fur color with allowances made for the faded pelage pigments of San José and Unión Hidalgo examples of the former species. However, the tails of *R. mexicanus* specimens are more sharply bicolored (pure white below) than those of *R. underwoodi* in which the ventral caudal pelage is pale gray-brown. The apparently smaller mean body size (HBL) of *R. mexicanus* probably reflects shrinkage in alcohol (of the MacDougall specimens) prior to measurement rather than a real difference from *R. underwoodi* (compare mean values in tables 23 and 24). The hindfeet of *R. mexicanus,* however, are significantly larger than those of *R. underwoodi.*

Adults of *R. mexicanus* average slightly larger than *R. underwoodi* adults in most cranial dimensions (tables 23, 24), but have absolutely and proportionately smaller molars. Visual comparisons of crania (figs. 46, 47) suggest a smoother, more inflated, globose braincase and a more slender rostrum in *R. underwoodi,* but two qualitative contrasts provide a less subjective basis for species discrimination: (1) In *R. underwoodi* the unossified fissure in the floor of the braincase anterior to the auditory bullae is confluent with the foramen ovale (fig. 48A); in *R. mexicanus* this region is more extensively ossified and a small, discrete foramen ovale is consistently present behind each parapterygoid fossa (fig. 48B). (2) In *R. underwoodi* (as in both species of the *raptor* group) M3 consists of a large paracone–protocone cusp pair and a small, posterior remnant of the hypocone–metacone pair (fig. 44A); m3 is distinctly bilobed in this species, consisting of an anterior protoconid–metaconid cusp pair and a smaller posterior lobe that constitutes the hypoconid–entoconid (fig. 45A). In *R. mexicanus,* M3 is a simple peglike tooth with no trace of the hypocone–metacone remnant (fig. 44B), and m3 lacks a distinct posterior hypoconid–entoconid lobe (fig. 45B).

*R. mexicanus* and *R. underwoodi* appear to be closely related taxa and could perhaps be regarded as locally differentiated populations of a single, unusually widespread species. Because qualitative characters permit unambiguous discrimination between the two forms, however, it seems useful to continue to recognize them as specifically distinct pending the discovery of populations from geographically intermediate localities.

### *Rheomys raptor* Goldman, 1912

*Rheomys raptor,* the second species of the genus to be described, was named by E. A. Goldman on the basis of three specimens that he collected between 4500 and 5200 ft (1385–1600 m) on Cerro Pirre in extreme southeastern Panama. The type (USNM 179028) consists of the skin (in good condition), skull, mandibles, and postcranial skeleton of an adult (4/o/a) male. The skull of the holotype lacks M1–3 on both sides and the tips of the nasals are broken; the mandibles retain only Rm1-2 and Lm1. A second specimen (USNM 179026) is of a younger animal (3/o/i); both left and right M3 and left m3 are missing; the right bulla and mastoid are detached and the left bulla, mastoid, and squamosal are missing. The third specimen (USNM 179029) consists of a skin in fresh adult pelage together with two large skull fragments and both mandibles but lacking the molar dentition. While this material was sufficient for Goldman (1912) to recognize the distinctiveness of Cerro Pirre specimens from any other ichthyomyine then known, the availability of just these three fragmentary examples (measurements in table 25) makes comparisons with subsequently named populations of small *Rheomys* difficult to evaluate. No other specimens of *Rheomys* from eastern Panama are available.

Enders (1939) described *R. hartmanni* on the basis of two specimens collected near the hot springs of the Río Cotito at 4900 ft (1508 m) on the Pacific slopes of the Chiriquí highlands in extreme western Panama. Two subsequently collected topotypes, together with seven Costa Rican examples, are also referable to this taxon. The Costa Rican material, collected between 1300 and 1600 m on the Pacific slopes of the Cordilleras Talamanca (see San Isidro, Appendix) and Tilarán (Monte Verde), compares closely with the Panamanian series in most qualitative external characters (described by Enders, 1939) and external measurements (table 26). Adult Costa Rican and Panamanian specimens exhibit overlapping ranges in all craniodental dimensions (table 26) and visual inspection of skulls reveals no basis for discriminating between the samples. The terminal 15 mm on the tail of the holotype is tipped with white, but the tails of three topotypes have no more than a terminal tuft of whitish hairs; Costa Rican specimens have entirely dark tails.

The three specimens of *raptor* from Cerro Pirre (table 25) are smaller than average adult *hartmanni* (table 26) in most external and craniodental measurements, but interpretation of these comparisons is difficult due to small sample sizes and because available specimens of *hartmanni* may average slightly older than the three examples of *raptor.* Nevertheless, length of the hindfoot (HF), length of the upper molar row (LM), and breadth of the braincase (BB) are precociously maturing dimensions that typically exhibit less variation within populations than other measurements; comparisons at least in these variables strongly suggest the smaller overall size of *raptor*. Such metric differences do not, however, provide impressive evidence of specific differentiation between montane populations separated by a lowland isthmus and approximately 600 airline kilometers. There are no qualitative characters to distinguish specimens of *raptor* from examples of *hartmanni*.

*R. raptor* and *hartmanni* resemble one another and together differ from *R. thomasi* subspecies in their short and narrow hindfeet (longer and broader in *R. thomasi*); tails that average less than head-body length (LT averages greater than HBL in *R. thomasi*); closer, more finely grizzled dorsal pelage (thicker and more coarsely grizzled in *R. thomasi*); pale gray ventral pelage (venters are more abundantly washed with silver-tipped hairs in *R. thomasi*); and relatively narrower braincases (see account for *R. thomasi* below). Although visual comparisons of mature crania suggest proportional differences between *raptor* and *hartmanni* (smaller rostrum, less flaring zygoma, smoother and more inflated braincase in *raptor*), these are shape differences that regularly accompany growth in muroid cranial ontogeny and are to be expected in comparisons of closely related populations that differ in size; intact skulls of *raptor* (USNM 179026, 179028) have the overall aspect of subadult *hartmanni* (e.g., LACM 25418).

In consideration of the absence of qualitative contrasts between *raptor* and *hartmanni*, their small absolute size difference across a considerable geographic separation, and the shared characteristics that together distinguish them from *R. thomasi* subspecies, it seems more useful to treat these two taxa as subspecies, anticipating that phenotypically intermediate populations may be found between Cerro Pirre and the Chiriquí highlands. A single enigmatic specimen (USNM 520769) of a small *Rheomys* with worn molars but open basicranial sutures and in immature pelage (4/o/i) from the Atlantic slopes of the western Panamanian highlands (Provincia Bocas del Toro, "First Water") is not assignable with certainty to either *R. raptor* or *R. raptor hartmanni*. The small molars of this specimen (LM, 4.0 mm; BM1, 1.3 mm) fall outside the range of variation among available specimens of *R. r. hartmanni* and suggest affinities with *R. r. raptor*, but hindfoot and braincase measurements (HF, 26 mm; BB, 12.5 mm) suggest adult dimensions similar to the western subspecies. Clearly, additional material would be useful.

TABLE 25

**Age, Sex, and Measurements (in millimeters) of *Rheomys raptor raptor* from Cerro Pirre, Panama**

| | USNM 179026 | USNM 179028[a] | USNM 179029 |
|---|---|---|---|
| Age | 3/o/i | 4/o/a | ?/?/a |
| Sex | male | male | female |
| HBL | 92 | 107 | 112 |
| LT | 88 | 94 | 102 |
| HF | 25 | 24 | 26 |
| Ear | 8 | 8 | 9 |
| CIL | 23.7[c] | 24.0 | – |
| LD | 6.3 | 5.9[b] | 6.8[b] |
| LM | 4.2[b] | 4.0[b] | 4.2[b] |
| LIF | 4.4 | 4.6 | 4.7 |
| BIT | 1.4 | 1.6 | 1.8 |
| BIF | 1.9 | 1.9 | 2.0 |
| BPB | 2.4 | 2.5[b] | 2.7 |
| LN | 10.2 | – | 10.6 |
| BN | 3.1 | 3.0 | 3.2 |
| LIB | 4.8 | 4.8 | 4.9 |
| ZB | – | 13.4 | – |
| BB | 12.2[c] | 12.1 | – |
| BZP | 1.2 | 1.2 | 1.4 |
| BM1 | 1.4 | – | – |
| HI | – | 5.1 | 5.3 |
| DI | 1.3 | 1.4 | 1.5 |
| BOC | 7.0 | 6.9 | 7.4 |

[a] The holotype.

[b] Alveolar measurements, probably within 0.2 mm of occlusal equivalents.

[c] Estimated value.

### *Rheomys thomasi* Dickey, 1928

*Rheomys thomasi thomasi* was described by Dickey from material collected in 1925 by R. A. Stirton at 3500 ft (1077 m) on Cerro Cacaguatique El Salvador. Subsequent collections on Cerro Cacaguatique, by Stirton and M. Hildebrand from December, 1941, to January, 1942, increased the total number of specimens available from the type locality to 28. Obtained from both southwestern

TABLE 26
Age, Sex, and Measurements (in millimeters) of ***Rheomys raptor hartmanni*** from Panama and Costa Rica

| | Panama: Cotito Hot Springs | | | Costa Rica: San Isidro | | | | |
|---|---|---|---|---|---|---|---|---|
| | PANS 18329[a] | USNM 396585 | USNM 396586 | UMMZ 111985 | UMMZ 111986 | UMMZ 112300 | UMMZ 112301 | $\bar{x}$ ± SD[b] |
| Age | 5/o/a | 4/c/a | 4/o/a | 5/f/a | 4/o/a | 4/o/a | 5/o/a | |
| Sex | female | female | male | female | male | female | male | |
| HBL | 108 | 124 | 133 | 124 | 121 | 118 | 110 | 119.7 ± 8.6 |
| LT | 104 | 117 | 119 | 106 | 108 | 105 | 115 | 110.6 ± 6.2 |
| HF | 27 | 28 | 28 | 28 | 27 | 28 | 29 | 27.8 ± 0.7 |
| Ear | 11 | 11 | 11 | 11 | 11 | 11 | 11 | 11.0 ± 0.0 |
| CIL | 26.0 | 27.0 | 27.4 | 26.6 | 27.0 | 25.8 | 27.8 | 26.8 ± 0.72 |
| LD | 6.9 | 7.1 | 7.1 | 6.8 | 7.1 | 6.4 | 7.3 | 7.0 ± 0.29 |
| LM | — | 4.5 | 4.4 | 4.4 | 4.5 | 4.6 | 4.4 | 4.5 ± 0.08 |
| LIF | 5.2 | 4.7 | 4.6 | 5.0 | 5.4 | 4.9 | 5.4 | 5.0 ± 0.32 |
| BIT | 1.7 | 1.8 | 1.8 | 1.7 | 1.7 | 1.6 | 1.7 | 1.7 ± 0.07 |
| BIF | 1.8 | 1.8 | 1.9 | 2.0 | 1.8 | 1.8 | 2.1 | 1.9 ± 0.12 |
| BPB | 2.6 | 2.7 | 2.7 | 3.1 | 2.8 | 2.5 | 2.7 | 2.7 ± 0.19 |
| LN | 11.1 | 10.4 | 11.0 | 10.5 | 10.3 | 10.4 | 11.0 | 10.7 ± 0.34 |
| BN | 3.3 | 3.3 | 3.2 | 3.0 | 3.2 | 2.8 | 3.2 | 3.1 ± 0.18 |
| LIB | 4.8 | 4.9 | 5.0 | 5.1 | 5.0 | 4.8 | 5.0 | 4.9 ± 0.11 |
| ZB | 14.2 | 14.0 | 14.6 | 14.7 | 14.4 | 13.5 | 14.5 | 14.3 ± 0.41 |
| BB | 12.4 | 12.4 | 12.7 | 12.8 | 12.9 | 12.1 | 12.6 | 12.6 ± 0.28 |
| BZP | 1.2 | 1.2 | 1.4 | 1.4 | 1.3 | 1.4 | 1.4 | 1.3 ± 0.10 |
| BM1 | 1.5 | 1.4 | 1.5 | 1.5 | 1.5 | 1.5 | 1.5 | 1.5 ± 0.04 |
| HI | 4.9 | 5.2 | 5.5 | 5.0 | 5.2 | 4.6 | 5.0 | 5.1 ± 0.28 |
| DI | 1.5 | 1.6 | 1.7 | 1.6 | 1.5 | 1.5 | 1.6 | 1.6 ± 0.08 |
| BOC | 7.2 | 7.3 | 7.4 | 7.4 | 7.4 | 7.0 | 7.1 | 7.2 ± 0.16 |

[a] The holotype.

[b] The mean plus or minus one standard deviation.

(Depto. San Miguel) and northern (Depto. Morazan) slopes of the mountain (see Stirton, 1944, for descriptions of geography and habitats) but over an altitudinal range of only 370 m, this is an unusually homogeneous series whose descriptive statistics (table 27) provide the most credible summary of individual variation within a local population of any ichthyomyine species.

Along with the nominate subspecies, Dickey (1928) named *R. thomasi stirtoni* on the basis of material collected at 8000 ft (2462 m) in a small range of mountains known locally as Los Esesmiles (Depto. Chalatenango) El Salvador (see Dickey and van Rossem, 1938, and Stirton, 1944). Nine specimens are available from the type locality, of which five were collected by Stirton and Hildebrand after Dickey's description was published.

Finally, Hooper (1947) named *R. thomasi chiapensis* on the basis of a single juvenile (1/o/i) specimen collected at 1100 m near Prusia in the Sierra Madre de Chiapas (Estado Chiapas), Mexico.

Populations referred to *Rheomys thomasi* can be distinguished from those included above in *R. raptor* by the characters listed in the preceding account. While none of those differences alone constitutes sufficient justification for taxonomic separation, they are usefully recognized in the aggregate as evidence of phenotypic differentiation between geographic clusters of populations centered, respectively, in (1) the Chiapas–Guatemalan–Salvadoran highlands and (2) the mountain systems of Costa Rica and Panama. Collections from geographically intermediate montane localities in Honduras and Nicaragua would provide welcome material to test the hypothesis that these are specifically distinct groups.

Specimens of *Rheomys thomasi stirtoni*

from Los Esesmiles are paler and have denser, thicker pelage than topotypic *R. t. thomasi*; *stirtoni* also averages larger in external dimensions (table 28). Dickey (1928: 12) described the skull of *R. t. stirtoni* as "Averaging larger than in *thomasi*, with less flattened profile, and with broader and more inflated braincase; nasals longer and more cuneate posteriorly; anterior palatine foramina wider and less parallel-sided . . . and extending back quite to or beyond the plane of M1; interpterygoid fossa wider than in *thomasi*; M1 slightly broader than in *thomasi* . . . ." The slightly larger overall size of the skulls in *stirtoni* is suggested by comparisons of mean values of CIL with *thomasi*, but intact skulls of *stirtoni* are few and the difference is not statistically significant. Visual comparisons between skulls of the two forms indicate a slightly less flattened dorsal profile and more inflated braincase in *stirtoni*, and the latter difference is also supported by statistical analysis of measurement data. Nasal bones average longer in *stirtoni* (often with more attenuate posterior tips) than in *thomasi* but not significantly so; the supposed differences in mesopterygoid (=interpterygoid) fossa breadth and molar breadth cited by Dickey are not demonstrable with measurements of available material. Incisive foramina are significantly broader and longer in *stirtoni* than in *thomasi* but the differences are small. Burt and Stirton (1961), referring to *R. t. stirtoni* and *R. t. thomasi*, commented that ". . . there is some doubt as to their distinctness," an observation consistent with most of the preceding comparisons.

TABLE 27

**Sample Statistics for Measurements (in millimeters) of Adult (3-5/o, c/a) Topotypes of *Rheomys thomasi thomasi*, and Tests for Differences Between This and Other *Rheomys* Species Samples** (The sample mean plus or minus one standard deviation, the range in parentheses, and the sample size are provided in the left-hand column)

| | | Tests[b] for mean differences from | |
|---|---|---|---|
| | *Rheomys thomasi thomasi*[a] | *R. r. hartmanni*[c] | *R. t stirtoni*[d] |
| HBL | 114.8 ± 11.1 (102–136) 15 | ns | * |
| LT | 122.1 ± 7.5 (109–137) 15 | ** | ns |
| HF | 31.4 ± 1.2 (30–33) 15 | ** | * |
| Ear | 9.3 ± 1.3 (8–12) 15 | na | ns |
| CIL | 26.9 ± 1.00 (25.3–28.5) 12 | ns | ns |
| LD | 7.0 ± 0.38 (6.4–7.6) 14 | ns | ns |
| LM | 4.4 ± 0.10 (4.3–4.6) 15 | ns | ** |
| LIF | 5.0 ± 0.24 (4.6–5.5) 14 | ns | ** |
| BIT | 1.6 ± 0.12 (1.5–1.9) 15 | ns | ns |
| BIF | 2.1 ± 0.12 (1.9–2.4) 14 | ** | * |
| BPB | 3.0 ± 0.23 (2.6–3.3) 14 | * | ns |
| LN | 10.9 ± 0.72 (9.6–11.9) 14 | ns* | ns |
| BN | 3.3 ± 0.17 (3.1–3.6) 15 | * | ns |
| LIB | 4.8 ± 0.15 (4.5–5.1) 13 | * | ns |
| ZB | 14.6 ± 0.67 (13.6–16.1) 13 | ns | ns |
| BB | 13.1 ± 0.26 (12.6–13.5) 14 | ** | ** |
| BZP | 1.4 ± 0.09 (1.2–1.5) 14 | ns | * |
| BM1 | 1.5 ± 0.06 (1.4–1.6) 15 | ns | ns |
| HI | 5.1 ± 0.31 (4.7–5.8) 15 | ns | * |
| DI | 1.6 ± 0.12 (1.5–1.9) 15 | ns | ns |
| BOC | 7.7 ± 0.18 (7.5–8.0) 13 | ** | ns |

[a] MVZ 98798–98801, 98805, 98810, 131998, 132000, 132002, 132004, 132005, 132007, 132008; UMMZ 110889, 110890; 9 males, 6 females.

[b] Results of two-tailed Student's-*t* tests (na = test not applicable, ns = not significant, * $p \leq .05$, ** $p \leq .01$).

[c] Sample statistics provided in last column of table 26.

[d] Sample statistics provided in first column of table 28.

Evidence for the phenotypic distinctness of the third named form, *R. t. chiapensis* is still less satisfactory. The juvenile holotype (UMMZ 88320, table 28), unaccompanied by other material from the same locality, is not a satisfactory basis for inference. Hall (1981) referred Guatemalan specimens from Finca Injerto (Depto. Huehuetenango) to *R. t. chiapensis*, citing Hooper's (1968) discussion. A juvenile specimen (UMMZ 118235) from Finca Injerto does closely match the type of *chiapensis* in all craniodental measurements (table 28) but mature animals from Finca Injerto (e.g., UMMZ 114711, table 28; all of the three adult crania from this locality are broken) are within the range of metric variation among topotypic *R. t. stirtoni* or differ by so little that taxonomic discrimination is hard to justify. Specimens from other localities in Chiapas (AMNH 204261) and Guatemala (TCWC 10637) are juveniles with incompletely erupted third molars and contribute no useful data to the issue.

There are no conspicuous lowland barriers

TABLE 28
**Age, Sex, and Measurements (in millimeters) of *Rheomys thomasi stirtoni* and *R. t. chiapensis* from El Salvador (Los Esesmiles, topotypes), Guatemala (El Injerto), and Mexico (Prusia)**
(The sample mean, the range in parentheses, and the sample size are provided in the first column)

| | El Salvador | | Guatemala | | Mexico |
|---|---|---|---|---|---|
| | MVZ 98811, 98813, 98814, 98815, 131994, 131996 | MVZ 131995 | UMMZ 114711 | UMMZ 118235 | UMMZ 88320[a] |
| Age | 4–5/o, c, f/a | 6/c/a | 5/c/a | 1/o/i | 1/o/i |
| Sex | 5 males, 1 female | female | male | male | male |
| HBL | 127.6 (120–133) 5 | 134 | – | 110 | 94 |
| LT | 125.6 (110–140) 5 | 128 | – | 110 | 114 |
| HF | 33.2 (30–35) 6 | 31 | 34 | 32 | 30 |
| Ear | 9.8 (8–12) 6 | 9 | 10 | 10 | 9 |
| CIL | 27.6 (26.3–28.6) 3 | 28.3 | 29.2[b] | 25.8 | 25.4 |
| LD | 7.4 (6.9–7.7) 4 | 7.6 | 7.5 | 6.4 | 6.4 |
| LM | 4.3 (4.2–4.3) 6 | 4.6 | 4.4 | 4.7 | 4.7 |
| LIF | 5.4 (5.3–5.7) 4 | 5.6 | 5.0 | 4.2 | 4.5 |
| BIT | 1.7 (1.6–1.8) 5 | 1.8 | 1.7 | 1.3 | 1.5 |
| BIF | 2.2 (2.1–2.4) 5 | 2.5 | 2.0 | 2.1 | 2.2 |
| BPB | 3.2 (2.9–3.4) 5 | 3.1 | 3.1 | 2.8 | 2.8 |
| LN | 11.6 (10.8–12.0) 5 | 12.1 | 12.1 | 10.8 | 10.6 |
| BN | 3.2 (3.1–3.5) 5 | 3.3 | 3.4 | 3.1 | 3.0 |
| LIB | 4.8 (4.5–5.0) 5 | 4.8 | 4.8 | 4.8 | 5.0 |
| ZB | 14.5 (14.0–15.1) 5 | – | – | 14.2 | 14.4 |
| BB | 13.5 (13.3–13.8) 5 | – | – | 13.5 | 13.8 |
| BZP | 1.3 (1.2–1.4) 4 | – | 1.3 | 1.4 | 1.2 |
| BM1 | 1.5 (1.4–1.5) 6 | – | 1.5 | 1.5 | 1.6 |
| HI | 5.5 (5.0–6.1) 5 | 5.9 | 6.0 | 5.1 | 5.0 |
| DI | 1.7 (1.5–1.8) 5 | 1.7 | 1.8 | 1.4 | 1.4 |
| BOC | 7.8 (7.4–8.1) 5 | 7.9 | 8.4 | 8.0 | 8.2 |

[a] Holotype of *R. t. chiapensis*.
[b] Estimated value.

to interrupt potential gene flow among populations in the Sierra Madre de Chiapas, the southern Guatemala highlands (Finca Injerto), and the mountains of southwestern Honduras with which Los Esesmiles is continuous (Dickey and van Rossem, 1938). In the absence of phenotypic justification for taxonomic discrimination between *stirtoni* and *chiapensis*, the former name alone seems sufficient to designate the western, larger-bodied *R. thomasi* populations from the smaller-bodied nominate race isolated on Mt. Cacaguatique.

SPECIMENS EXAMINED: *Rheomys mexicanus* – **Mexico:** Totontepec (FWMSH 1952, 1953); San José Lachiguirí (AMNH 175423, 179970–179972, 182137–182139, 186922, 205320, 205321, 207447); Unión Hidalgo (AMNH 185015–185018, 189291, 205314–205319, 208255–208257); locality unknown (AMNH 205313). Total, 28.

*Rheomys raptor* – **Costa Rica:** Monte Verde (UMMZ 116934); San Isidro (LACM 25418; UMMZ 111985–111987, 112300, 112301). **Panama:** Cerro Pirre (USNM 179026, 179028, 179029); Cotito Hot Springs (PANS 18329, 18330; USNM 396585, 396586); First Water (USNM 520769). Total, 15.

*Rheomys thomasi* – **El Salvador:** Cerro Cacaguatique (MVZ 98798–98810, 131997–132008; UMMZ 110889, 110890); Los Esesmiles (MVZ 98811–98815, 131994–131996). **Guatemala:** El Injerto (UMMZ 114711, 118233–118235); Quetzaltenango (TCWC 10637). **Mexico:** Ixhuatán (AMNH 204261); Prusia (UMMZ 88320). Total, 42.

*Rheomys underwoodi* – **Costa Rica:** Tres Ríos (BMNH 7.5.30.5); Volcán Poás (LACM 28260; UMMZ 115389, 115459, 115460). **Panama:** Candela (USNM 516939, 516940); Río Chiriquí Viejo (UMMZ 116935); Velo (PANS 18328). Total, 9.

# CRANIAL MORPHOMETRICS

Even a casual examination of the photographs and tables accompanying the preceding systematic accounts is sufficient to appreciate that ichthyomyine crania vary significantly in size and shape. While verbal descriptions of these cranial differences supplemented by univariate statistical comparisons are usually adequate for simple taxonomic discrimination, more sophisticated inference requires multivariate analysis. For such analysis to provide useful measures of similarity or difference among populations, or to facilitate understanding of the causal processes of form change, prior attention to measurement choice as well as some consideration of the sources of measurement variance and covariance within populations are necessary.

## CHOICE OF MEASUREMENTS

Any quantitative comparison of biological forms is relative to some particular set of measurements. Since an indefinitely large number of dimensions could be measured on objects as complex as mammalian skulls, it is necessary to select some smaller set of metric characters likely to be most useful in the research context. When the intent is just to document or facilitate identifications, any arbitrary collection of operationally defined measurements that permits discrimination among the populations of interest is sufficient. If some biologically interpretable representation of morphology is intended, however, then measurements chosen with attention to the following criteria may maximize the descriptive utility of the resulting data: (1) to be biologically meaningful, measurements must be taken between endpoints that are anatomically homologous from form to form; (2) measurements should diversely sample the form, and not be restricted to just one region or redundantly index one or two visually conspicuous axes of variation; (3) short measurements are to be preferred to long ones because the information they contain is better localized on the form; and (4) a single structure should not serve as the endpoint for many measurements because error or other variation in location of that landmark will thereby be propagated through a whole series of distance measures and be disproportionately represented in the data (Humphries et al., 1981; Strauss and Bookstein, 1982).

Traditional protocols for measuring mammalian skulls rarely satisfy any of the preceding criteria. As corresponding, egregious examples: (1) "Greatest Length of Skull," one of the commoner measurements provided in the taxonomic literature, contains no reference to anatomically defined structures; depending on the species, age, or sex of a measured individual, the posterior limit of this dimension might be the bulging surface of the supraoccipital, one of the occipital condyles, or the nuchal crest. Without homologous endpoints, variation in such a measure is biologically uninterpretable. (2, 3) Conventional sets of mammalian cranial measurements often include two or more long and geometrically redundant samples of the anteroposterior axis (e.g., Basilar Length, Basal Length, Condylobasal Length, Condylobasilar Length, Condyloincisive Length; Thomas, 1905). In addition, the anteroventral, facial part of the skull (consisting of the orbital, rostral, and buccal regions), is often densely measured, but the neurocranium only sparsely so. (4) The incisors (especially in rodent taxonomy) or the posterior margin of the hard palate often serve as limits for a disproportionately large number of measurements. Many such shortcomings of conventional mammalian craniodental measurement schemes could be avoided by thoughtful selection of metric characters with attention to well-defined research objectives, but strict conformance to methodological ideals must often be tempered by practical considerations.

Students of skeletal ontogeny in laboratory rats and in humans often study the skull in midsagittal section where pointlike landmarks can be located on the closed curve of the cranial outline (e.g., Moyers and Bookstein, 1979 and references therein; Vilmann and Moss, 1979). When the shape variation of interest can be adequately represented in this way, one measurement protocol, the truss (Strauss and Bookstein, 1982), ensures even spatial coverage of the form by short measurements, provides proportionate sampling of diverse anatomical axes, and enables reconstruction of the outline from the measurement set. But skulls of muroid rodents exhibit considerable variation in shape that does not lie in the midsagittal plane and, further, many of the cranial structures whose proportions are of interest to systematists are not representable by pointlike landmarks. Dimensions of the braincase, for example, often differ among related muroid species and figure importantly in many taxonomic descriptions, but the braincase is a smoothly curving structure on which the only landmarks are sutural triple-points whose positions are the anatomically arbitrary results of growth processes that have no necessary relationship to the form of the calvarium (Moss, 1954).

The cranial measurements illustrated in figures 1 and 2 and described in Materials and Methods represent my efforts to accommodate some of the suggested ideals of biological mensuration listed above within the limits imposed by available materials and by other considerations. Ichthyomyine skulls are often broken, chipped, or otherwise damaged, so that for every additional dimension added to the measurement protocol, the number of specimens for which complete data are available is diminished. Since sample sizes for these animals are very small to begin with, the fact that I took only 17 measurements of the cranium reflects this practical limitation.

I chose measurements to provide information about craniodental structures or regions whose proportions appeared to exhibit pronounced variation among ichthyomyine species. Many of these measurements are "extremal" in the sense that they are not defined in terms of pointlike anatomical landmarks but as greatest or least distances between parts or across regions. Bookstein (1978) and Moyers and Bookstein (1979) criticize the use of extremal landmarks whose location requires that the measured object be fixed with respect to some arbitrary plane of reference, but the extremal measurements I employ are invariant with respect to spatial orientation. Least Interorbital Breadth, for example, is the smallest distance across the frontal bones between the orbits and requires no fixed plane of reference for its determination. In effect, and so long as comparisons are among ichthyomyines, the extrema of measurements employed here are very small anatomical regions that can reasonably be interpreted as homologous from form to form.

## VARIATION WITHIN POPULATIONS

Sexual Size Dimorphism: Within age classes established on the basis of toothwear (see Materials and Methods), male and female ichthyomyines overlap broadly in all craniodental dimensions and neither the largest nor the smallest individuals in any age class are consistently of one sex or the other. Although sample sizes in this study are too small to test for significantly sex-correlated measurement variance within age classes, the preceding observations together with the frequent absence of appreciable sexual size dimorphism among other sigmodontine species (Hooper, 1952; Pearson, 1958; Packard, 1960; Baker, 1969; Genoways and Jones, 1972; Schmidly, 1972) suggest that any average differences that may exist between the sexes in craniodental dimensions are small enough to be ignored in the context of interspecific comparisons. I combined males and females in all of the analyses reported below.

Growth: Muroid rodents exhibit sustained postweaning growth in many cranial dimensions. This is best demonstrated by longitudinal data (repeated observations of the same animals over time, e.g., Cleall et al., 1968), but is sufficiently obvious also from statistical comparisons of cranial measurements across age classes based on pelage, toothwear, and basicranial suture closure (e.g., Birney, 1973; Genoways and Jones, 1972). Table 29 presents an analysis of 17 craniodental measurements across six toothwear categories for 27 specimens of *Rheomys thomasi thomasi,* and table 30 tabulates the presence or absence of significant correlations among all pairs of craniodental measurements for specimens with complete data (N = 17) in the same sample. Ten of the 17 measured dimensions exhibit statistically significant increases with advancing toothwear consistent with a hypothesis of postweaning growth. In addition, two measurements that do not show significant increases

### TABLE 29
### Analysis of 17 Cranial Measurements by Toothwear Class for a Sample of 27 *Rheomys thomasi thomasi* from Cerro Cacaguatique, El Salvador

(Only the mean value of each measure for each toothwear class is provided)

| | Tooth wear class (and sample size)[a] | | | | | | |
|---|---|---|---|---|---|---|---|
| Measurement | One (1) | Two (5–10) | Three (7–9) | Four (3) | Five (1–3) | Six (0–1) | Statistic[b] |
| CIL | 23.4 | 25.2 | 26.7 | 26.7 | 28.0 | – | 11.86* |
| LD | 5.7 | 6.3 | 6.9 | 6.8 | 7.3 | 7.3 | 15.83** |
| LM | 4.2 | 4.4 | 4.4 | 4.4 | 4.5 | 4.3 | ns |
| LIF | 4.2 | 4.7 | 5.0 | 4.8 | 5.1 | 5.2 | ns |
| BIT | 1.5 | 1.5 | 1.6 | 1.7 | 1.8 | 1.8 | 14.05* |
| BIF | 2.1 | 2.0 | 2.0 | 2.1 | 2.2 | 2.2 | ns |
| BPB | 2.5 | 2.6 | 2.9 | 2.9 | 3.2 | – | 13.01* |
| LN | 9.0 | 10.1 | 10.8 | 10.5 | 11.6 | 11.5 | 12.06* |
| BN | 2.8 | 3.0 | 3.2 | 3.4 | 3.6 | 3.6 | 20.63** |
| LIB | 5.0 | 4.7 | 4.8 | 4.8 | 4.8 | – | ns |
| ZB | 13.1 | 13.5 | 14.4 | 14.4 | 15.6 | – | 14.13** |
| BB | 12.3 | 12.7 | 13.0 | 12.9 | 13.4 | – | 12.05* |
| BZP | 1.2 | 1.3 | 1.4 | 1.3 | 1.5 | 1.4 | ns |
| BM1 | 1.4 | 1.4 | 1.4 | 1.4 | 1.5 | – | ns |
| HI | 4.1 | 4.6 | 4.9 | 5.1 | 5.5 | 5.6 | 17.87** |
| DI | 1.2 | 1.4 | 1.6 | 1.7 | 1.8 | 1.8 | 18.01** |
| BOC | 7.2 | 7.6 | 7.7 | 7.7 | 7.9 | – | ns |

[a] Not all measurements could be determined for all specimens.

[b] Kruskal-Wallis test (see Conover, 1980). One asterisk indicates significant values ($p \leq .05$), two asterisks indicate highly significant values ($p \leq .01$), ns = not significant.

with toothwear in table 29, Length of Incisive Foramina (LIF) and Breadth of the Zygomatic Plate (BZP), nevertheless exhibit significant correlations with most measurements that do (table 30), and I interpret this as evidence that these dimensions are also subject to postweaning growth. Five measurements display no significant increases with advancing toothwear and are also uncorrelated with most growing dimension: Length of Molars (LM), Breadth of the Incisive Foramina (BIF), Least Interorbital Breadth (LIB), Breadth of M1 (BM1) and Breadth of the Occipital Condyles (BOC). Mammalian molars, once erupted, do not grow, so the absence of many significant correlations between measurements of these teeth and the other craniodental dimensions in table 30 is not unexpected. Similarly, Least Interorbital Breadth and Breadth of the Occipital Condyles are measurements that span portions of the central nervous system which, in muroids, completes growth early in postnatal life (Moss and Baer, 1956; King and Eleftheriou, 1960). That Breadth of the Incisive Foramina evidences little postweaning increase, at least within this population sample, is an unexpected observation; ontogenetic changes in this dimension have not previously been investigated.

Toothwear provides, at best, only an approximate index of relative age, and is useful chiefly as a criterion by which comparisons between populations can be grossly standardized. Even if a more accurate measure of absolute (chronological) age were available, however, its usefulness would be compromised by the fact that ontogenetic changes in size and shape are a function not of time but of growth for which an accurate measure would still be required. The ontogeny of two or more anatomical dimensions, however, is more conveniently represented for comparative purposes in terms of relative than absolute growth (Cock, 1966), and multivariate relative growth is most succinctly described by the principal component generalization of the allometric equation proposed by Joli-

TABLE 30
**Matrix of Correlations[a] Among Craniodental Measurements in a Mixed Cross-Sectional Sample of *Rheomys thomasi thomasi*[b]**

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LD | ++ | | | | | | | | | | | | | | | |
| LM | + | ns | | | | | | | | | | | | | | |
| LIF | ++ | ++ | ns | | | | | | | | | | | | | |
| BIT | ++ | ++ | ns | + | | | | | | | | | | | | |
| BIF | ns | + | ns | + | ns | | | | | | | | | | | |
| BPB | ++ | ++ | ns | ++ | ++ | ++ | | | | | | | | | | |
| LN | ++ | ++ | ns | ++ | ++ | ns | ++ | | | | | | | | | |
| BN | ++ | ++ | ns | ns | ++ | ns | ++ | ++ | | | | | | | | |
| LIB | ns | ns | ns | ns | ns | + | ns | ns | ns | | | | | | | |
| ZB | ++ | ++ | ns | ++ | ++ | ++ | ++ | ++ | ++ | ns | | | | | | |
| BB | ++ | ++ | ns | ++ | ++ | ++ | ++ | ++ | ++ | ns | ++ | | | | | |
| BZP | ++ | ++ | + | ++ | ns | ns | + | ++ | ns | ns | ++ | ++ | | | | |
| BM1 | ns | ns | + | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | | | |
| HI | ++ | ++ | ++ | + | ++ | ns | + | ++ | ++ | ns | ++ | + | + | ns | | |
| DI | ++ | ++ | + | ++ | ++ | ns | ++ | ++ | ++ | ns | ++ | ++ | + | ns | ++ | |
| BOC | + | + | ns | + | ns | ns | ++ | ns | + | ns | ++ | ++ | ns | ns | ns | ns |
| | CIL | LD | LM | LIF | BIT | BIF | BPB | LN | BN | LIB | ZB | BB | BZP | BM1 | HI | DI |

[a] A matrix entry of "+" indicates a significant ($p \le .05$) positive value of the calculated product-moment correlation coefficient; an entry of "++" indicates a highly significant ($p \le .01$) positive value; an entry of "ns" indicates a nonsignificant ($p > .05$) correlation.

[b] From Cerro Cacaguatique, El Salvador; N = 17 specimens with complete measurement data; TWC 2–5.

coeur (1963). This method models morphometric ontogeny as a vector, a linear combination of measured dimensions weighted by their relative rates of geometric increase; an estimate of this expression is obtained by extracting the first principal component (see Morrison, 1976, and below) from the matrix of covariances among log-transformed measurements. In order to derive reliable estimates of relative growth when longitudinal data are not available, it is important that the samples from which allometric vectors are calculated be at least mixed cross-sectional (contain individuals of different ages; see Cock, 1966) and be drawn from populations that are not grossly heterogeneous in other respects. Samples from five ichthyomyine species meet these minimal criteria, and the variable loadings on the first principal component extracted from each are provided in table 31.

The fifth column in table 31 provides variable loadings on the first principal component calculated for the sample of *Rheomys thomasi thomasi* discussed earlier. In the multivariate allometric model, isometric growth is indicated by variable loadings (on normalized vectors) equal to the inverse square-root of the number of variables included in the analysis (Jolicoeur, 1963); in the present application this value is $17^{-1/2} = .243$, approximately. Loadings much higher than this value indicate positive allometric growth in the measured variables to which they pertain, while loadings that are much lower than this value indicate negative allometry of the corresponding dimensions. As can be seen, most of the measurements that were hypothesized above to exhibit postweaning growth in *Rheomys thomasi thomasi* have loadings about equal to the isometric value (CIL, LIF, BIT, BN, ZB, HI) or exhibit strong positive allometry (LD, BPB, LN, BZP, DI). By contrast, measurements that are apparently unaffected by postweaning growth have small loadings that denote conspicuous negative allometry (LM, BIF, LIB, BM1, BOC). Breadth of Braincase (BB), a measurement that does increase significantly with advancing toothwear in this sample, nevertheless exhibits negative allometry in relation to growth in overall size.

TABLE 31

**First Principal Components for Mixed Cross-Sectional Samples of Five Ichthyomyine Species and Their Pooled Average**

(see text for further explanation and discussion)

| | *Anotomys leander* | *Ichthyomys h. soderstromi* | *Neusticomys monticolus* | *Rheomys mexicanus* | *Rheomys thomasi* | Pooled |
|---|---|---|---|---|---|---|
| Sample size | 11 | 12 | 8 | 12 | 17 | 60 |
| % Variance | 57.2 | 79.5 | 52.7 | 72.2 | 69.6 | 66.0 |
| loadings: | | | | | | |
| CIL | .167 | .244 | .228 | .220 | .231 | .231 |
| LD | .266 | .397 | .381 | .315 | .339 | .350 |
| LM | .073 | −.126 | −.012 | −.027 | .055 | −.019 |
| LIF | .145 | .301 | .140 | .239 | .278 | .257 |
| BIT | .285 | .315 | .154 | .368 | .219 | .304 |
| BIF | .256 | .109 | −.054 | .167 | .094 | .138 |
| BPB | .423 | .340 | .376 | .320 | .396 | .370 |
| LN | .360 | .396 | .295 | .278 | .338 | .344 |
| BN | .142 | .203 | .148 | .280 | .223 | .233 |
| LIB | −.035 | −.109 | .082 | .029 | .010 | −.013 |
| ZB | .252 | .262 | .208 | .249 | .210 | .247 |
| BB | .114 | .036 | .069 | .091 | .100 | .083 |
| BZP | .462 | .150 | −.230 | .342 | .306 | .284 |
| BM1 | .075 | .052 | −.052 | .011 | .020 | .030 |
| HI | .193 | .273 | .568 | .293 | .261 | .286 |
| DI | .239 | .265 | .272 | .296 | .389 | .316 |
| BOC | .094 | .006 | .018 | .111 | .077 | .072 |

The pattern of variable loadings on the first principal component calculated for each of the other four species samples in table 31 broadly resembles that just described for *Rheomys thomasi,* suggesting that patterns of relative growth in the cranium are similar among these ichthyomyine taxa. Most of the unusually high or low values in table 31 are present in only two columns that represent samples for which the first principal component accounted for rather small fractions of the total variance, 57 percent for *Anotomys leander,* and 53 percent for *Neusticomys monticolus*; available measurement data for these species do not include as broad a representation of age classes as data for the other three, and the deviation exhibited in some variable loadings may therefore reflect sampling error rather than real differences in patterns of relative growth.

Table 32 presents coefficients of vector correlation for all pairwise comparisons among the principal components of table 31. This statistic, calculated as the inner product of the variable loadings, is the cosine of the angle between each vector pair (Morrison, 1976). When two normalized vectors are parallel, their inner product equals unity, and when the vectors are orthogonal, this product is equal to zero. Coefficients of vector correlation therefore serve as indices of similarity among the estimates of multivariate ontogenetic allometry presented in table 31. Most ichthyomyine vectors are nearly parallel, with correlation coefficients among them ranging from .88 to .97; the conspicuous exceptions to these generally high values all relate to the first principal component for *Neusticomys monticolus* whose apparent deviation is plausibly attributable to the small size and limited age representation of that sample.

Because patterns of relative growth in craniodental dimensions appear similar among most of these ichthyomyine populations, it is reasonable to calculate a vector of average multivariate allometry. This is accomplished by subtracting the sample mean from each measurement value and then calculating the

TABLE 32
**Coefficients of Vector Correlation Among the First Principal Components of Table 31**[a]

| | | | | |
|---|---|---|---|---|
| *Iso* | .88 | | | |
| *Nmo* | .60 | .80 | | |
| *Rme* | .94 | .94 | .72 | |
| *Rtt* | .94 | .94 | .76 | .97 |
| | *Ale* | *Iso* | *Nmo* | *Rme* |

[a] Abbreviations: *Ale, Anotomys leander*; *Iso, Ichthyomys hydrobates soderstromi*; *Nmo, Neusticomys monticolus*; *Rme, Rheomys mexicanus*; *Rtt, Rheomys thomasi thomasi.*

first principal component from the pooled (group-centered) data. The resulting vector, presented in the sixth column of table 31 is, in effect, a weighted average of the five within-group estimates to the left.

All of the numerical analyses reported above reflect the common muroid pattern of prolonged postweaning growth (positive allometry) in the facial skull and incisors relative to the precociously maturing braincase and molars (Allen, 1894; Hoffmeister, 1951; Moore, 1966; Cleall et al., 1968; Engels, 1979). Craniodental proportions change significantly through the course of postweaning ontogeny as the result of such differential growth. Thus, young ichthyomyines have braincases and molar dentitions that are large in relation to their small rostra, feeble zygomas, and diminutive incisors. Old adults, by contrast, have braincases and molar rows that seem smaller in relation to their more massive rostra, broader and heavier zygomas, and stronger incisors. The fact that this pattern of differential growth appears very similar across ichthyomyine taxa will be useful in the morphometric analyses of interspecific variation immediately following.

## VARIATION AMONG POPULATIONS

SAMPLES: Analyses of interspecific variation in size and shape should ideally be based on large, mixed cross-sectional samples from all of the populations being compared, but for most ichthyomyines only small series of adult or near-adult specimens are available. Samples from local populations of 15 ichthyomyine species and subspecies were selected for analysis and are identified below. The three-letter abbreviation following each Latin name identifies the taxon in accompanying tables and figures.

*Anotomys leander* (Ale): Ecuador, Papallacta; N = 10, TWC = 3–5.
*Chibchanomys trichotis* (Ctr): Venezuela, Buena Vista; N = 2, TWC = 3–5.
*Ichthyomys hydrobates hydrobates* (Ihy): Venezuela, La Mucuy and Mérida; N = 17, TWC = 3–5.
*Ichthyomys hydrobates soderstromi* (Iso): Ecuador, Guápulo; N = 12, TWC = 3–5.
*Ichthyomys pittieri* (Ipi): Venezuela, Rancho Grande; N = 3, TWC = 4–6.
*Ichthyomys stolzmanni orientalis* (Ior): Ecuador, Río Napo; N = 6, TWC = 3–5.
*Ichthyomys tweedii* (Itw): Ecuador, Mindo, Río Blanco, and Río Pachijal; N = 22, TWC = 3–5.
*Neusticomys monticolus* (Nmo): Ecuador, Guarumal; N = 5, TWC = 3–5.
*Neusticomys peruviensis* (Npe): Peru, Balta; N = 1, TWC = 4.
*Neusticomys venezuelae* (Nve): Venezuela, Río Neverí; N = 2, TWC = 2.
*Rheomys mexicanus* (Rme): Mexico, San José Lachiguirí; N = 5, TWC = 3–5.
*Rheomys raptor hartmanni* (Rha): Costa Rica, San Isidro; N = 4, TWC = 4–5.
*Rheomys thomasi stirtoni* (Rts): El Salvador, Los Esesmiles; N = 6, TWC = 4–5.
*Rheomys thomasi thomasi* (Rtt): El Salvador, Cerro Cacaguatique; N = 15, TWC = 3–5.
*Rheomys underwoodi* (Run): Costa Rica, Volcán Poás; N = 3, TWC = 3–5.

Sample means for the cranial measurements defined and illustrated in Materials and Methods are recorded in table 33 for each of the 15 population samples listed above; other sample statistics, when available, have been provided in tables accompanying the preceding taxonomic accounts.

RESULTS: The first two columns of table 34 provide variable loadings on the first and second principal components extracted from the covariance matrix of $\log_e$-transformed population sample means, and figure 49 displays the 15 ichthyomyine populations in the plane of the first two principal components. The first principal component accounts for 66 percent of the total interspecific variation in adult cranial measurements. Many variable loadings on the first interspecific principal component are large and positive, but three variables (BIF, BPB, and BB) have loadings that are near zero, and two variables (LM and

TABLE 33
**Craniodental Measurement Means (in millimeters) for 15 Ichthyomyine Population Samples**
(Taxa abbreviated as in accompanying text)

| | Samples | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Meas. | *Ale* | *Ctr* | *Ihy* | *Iso* | *Ior* | *Ipi* | *Itw* | *Nmo* | *Npe* | *Nve* | *Rme* | *Rha* | *Rts* | *Rtt* | *Run* |
| CIL | 26.0 | 25.8 | 30.4 | 31.0 | 33.6 | 30.2 | 34.4 | 24.8 | 28.1 | 26.9 | 29.9 | 26.8 | 27.6 | 26.9 | 28.2 |
| LD | 6.5 | 6.6 | 8.0 | 8.3 | 8.7 | 8.5 | 9.1 | 6.2 | 7.5 | 6.9 | 8.3 | 6.9 | 7.4 | 7.0 | 7.5 |
| LM | 5.0 | 4.4 | 4.2 | 4.2 | 4.4 | 3.6 | 4.4 | 4.0 | 3.8 | 4.2 | 4.9 | 4.5 | 4.3 | 4.4 | 5.0 |
| LIF | 4.6 | 5.0 | 6.0 | 5.9 | 6.6 | 5.9 | 6.7 | 4.6 | 5.6 | 4.8 | 5.7 | 5.2 | 5.4 | 5.0 | 5.0 |
| BIT | 1.2 | 1.2 | 2.0 | 2.0 | 2.2 | 2.2 | 2.5 | 1.4 | 2.2 | 1.9 | 1.5 | 1.7 | 1.7 | 1.6 | 1.4 |
| BIF | 2.2 | 2.0 | 2.0 | 2.0 | 2.0 | 2.2 | 2.2 | 2.1 | 2.0 | 2.2 | 2.4 | 1.9 | 2.2 | 2.1 | 2.2 |
| BPB | 3.2 | 3.2 | 2.8 | 3.0 | 3.0 | 2.9 | 3.1 | 2.9 | 3.3 | 2.6 | 3.7 | 2.8 | 3.2 | 3.0 | 3.5 |
| LN | 9.8 | 9.2 | 10.6 | 11.6 | 11.3 | 11.3 | 12.6 | 9.6 | 11.1 | 10.6 | 11.7 | 10.6 | 11.6 | 10.9 | 11.6 |
| BN | 2.8 | 3.0 | 3.4 | 3.6 | 3.9 | 3.8 | 4.2 | 2.8 | 3.7 | 3.5 | 3.8 | 3.0 | 3.2 | 3.3 | 3.5 |
| LIB | 4.2 | 4.8 | 4.5 | 4.7 | 4.4 | 4.6 | 4.8 | 4.8 | 5.2 | 5.2 | 5.1 | 5.0 | 4.8 | 4.8 | 4.9 |
| ZB | 14.4 | 13.8 | 15.0 | 15.7 | 16.2 | 15.2 | 17.3 | 13.1 | 14.4 | 13.0 | 16.7 | 14.3 | 14.5 | 14.6 | 15.3 |
| BB | 13.8 | 13.5 | 13.6 | 13.5 | 14.3 | 12.6 | 14.4 | 12.2 | 12.8 | 12.5 | 14.7 | 12.6 | 13.5 | 13.0 | 14.5 |
| BZP | 0.8 | 1.0 | 1.3 | 1.4 | 1.5 | 1.6 | 1.5 | 1.1 | 1.3 | 1.2 | 1.3 | 1.4 | 1.3 | 1.4 | 1.3 |
| BM1 | 1.7 | 1.6 | 1.4 | 1.6 | 1.6 | 1.2 | 1.5 | 1.4 | 1.3 | 1.4 | 1.6 | 1.5 | 1.5 | 1.5 | 1.8 |
| HI | 4.8 | 4.7 | 5.8 | 5.4 | 5.9 | 5.5 | 6.2 | 4.8 | 4.9 | 5.0 | 6.2 | 5.0 | 5.5 | 5.1 | 5.4 |
| DI | 1.4 | 1.4 | 1.8 | 1.7 | 1.9 | 1.8 | 2.0 | 1.4 | 1.9 | 1.6 | 1.5 | 1.6 | 1.7 | 1.6 | 1.3 |
| BOC | 8.1 | 7.4 | 8.7 | 8.7 | 9.0 | 8.1 | 9.1 | 7.1 | 7.6 | 7.6 | 8.9 | 7.2 | 7.8 | 7.7 | 8.7 |

BM1) have substantial negative loadings. The second interspecific principal component accounts for 19 percent of the total variance or 54 percent of the residual variation (that remaining after the first component is partialed out). Variable loadings on the second component include large positive values (for LM, BPB, and BM1) and also large negative values (for BIT and DI).

While principal components represent the major axes of multivariate dispersion and may suggest empirical interpretations of simple systems (e.g., in the analysis of external and postcranial skeletal dimensions reported earlier), no a priori biological significance can be attributed to their loadings or to the scores of samples projected on them without introducing external information (Wright, 1954). In the immediately preceding analyses of craniodental measurements *within* population samples, a single identifiable process, growth, could be assumed the largest source of morphometric variation among individuals. The within-sample first principal component was then interpretable as a multivariate generalization of the allometry equation, a biological model that carried attendant implications for the component scores (as estimates of growth in size) and variable loadings (as coefficients of relative growth; see Jolicoeur, 1963). In the present analysis of multivariate dispersion *among* populations, however, there is no reasonable a priori expectation that either the first or

TABLE 34
**Variable Loadings on the First and Second Interspecific Principal Components (*PC*1, *PC*2), the Size Factor (*S*), and the Largest Shape Factor (*H*)**

| Measurement | *PC*1 | *PC*2 | *S* | *H* |
|---|---|---|---|---|
| CIL | .225 | .174 | .231 | .052 |
| LD | .280 | .211 | .350 | .064 |
| LM | −.098 | .364 | −.019 | .366 |
| LIF | .289 | .132 | .257 | −.012 |
| BIT | .573 | −.305 | .304 | −.531 |
| BIF | −.005 | .142 | .138 | .135 |
| BPB | −.029 | .331 | .370 | .321 |
| LN | .177 | .154 | .344 | .063 |
| BN | .288 | .156 | .233 | .014 |
| LIB | .009 | −.062 | −.013 | −.054 |
| ZB | .144 | .273 | .247 | .181 |
| BB | .033 | .277 | .083 | .232 |
| BZP | .398 | −.065 | .284 | −.234 |
| BM1 | −.104 | .404 | .030 | .402 |
| HI | .182 | .248 | .286 | .141 |
| DI | .305 | −.172 | .316 | −.289 |
| BOC | .131 | .301 | .072 | .207 |

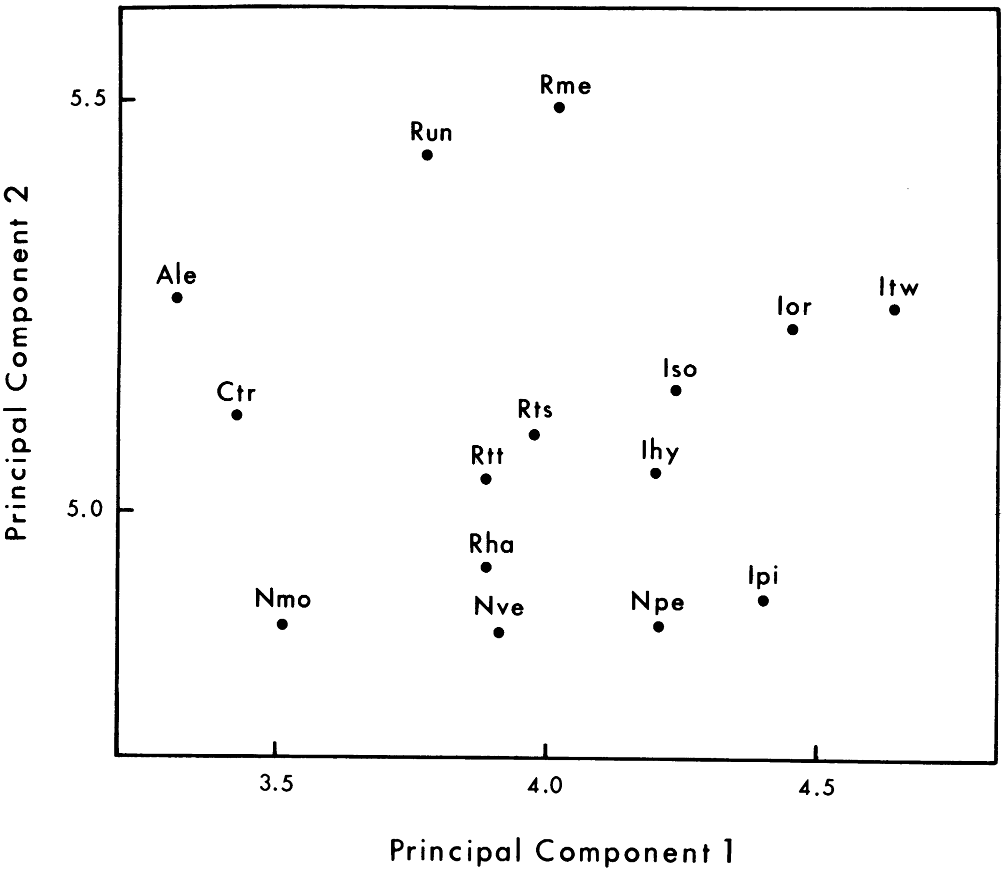


Fig. 49. Fifteen ichthyomyine population samples in the plane of the first and second principal components. Taxonomic abbreviations are explained in the accompanying text.

subsequent principal components will describe variation attributable to any morphogenetic process.

If the variable loadings on the first interspecific principal component (table 34, first column) are compared with loadings on the average within-group first principal component (table 31, last column), the two factors are seen to broadly resemble one another but there are also striking differences. In particular, loadings for BIT and BPB are much larger and much smaller, respectively, on the interspecific vector than on the pooled within-group first principal component or on any of the within-group estimates calculated separately for the five species samples represented in table 31. The first interspecific principal component therefore confounds morphometric variation attributable to growth and its accompanying allometries with shape variation that is not growth-correlated within species. If such conceptually distinct sources of interspecific differences as growth in size and size-independent shape variation are to be distinguished in analyses, they must be modeled explicitly.

I used the pooled within-group first principal component to estimate the fraction of interspecific morphometric variation attributable either to growth (there are minor differences in sample age composition) or to population divergence in genes that parallel growth in their phenotypic effect by altering the lengths but not the slopes or intercepts of ancestral ontogenetic vectors. The third column of table 34 reproduces the coefficients (from table 31) that I used to estimate interspecific size, hereafter, the size factor, *S*. The variance associated with $S$ is just the variance of the sum of products

$$S_j = a_1X_{1j} + a_2X_{2j} \ldots + a_{17}X_{17j} = \sum_{i=1}^{17} a_iX_{ij}$$

where $S_j$ is the score of population $j$ on $S$, the $a_i$ are the 17 variable coefficients for $S$ (third column of table 34), and the $X_{ij}$ are the 17 $\log_e$-transformed measurement means for population $j$. This size factor accounts for 48 percent of the total interspecific variation in adult cranial morphology, substantially less than the 66 percent associated with the first principal component, but the objective here is not to statistically summarize more variance but rather to partition variance more interpretably. Thus, 48 percent of the variation among the ichthyomyine sample means of table 33 can be interpreted as the result of minor variation in sample age composition and of phyletic variation in the duration or overall rate of growth with all else held constant.

After partialing out the variance in $S$ (by regressions of the $\log_e$-transformed measurement means on population size scores) there remains slightly more than 50 percent of the among-population total. Of this residual variation, over half (28% of the total) is accounted for by the leading eigenvector (the "first" principal component) of the residual covariance matrix, the shape factor[3], $H$, whose loadings appear in the fourth column of table 34.

Figure 50 displays the 15 ichthyomyine populations by their scores on the size ($S$) and shape ($H$) factors. The positions of the populations relative to one another are little changed from those earlier displayed in the plane of the first two principal components (fig. 49), but the axes have been rotated some 30–35° counterclockwise, or by an angle approximately equal to that between the pooled within-group and the among-group first principal components (the arc cosine of the inner product of $S$ and $PC1$).

Figure 51 contrasts patterns of variable loadings on the interspecific second principal component and on $H$. The majority of loadings on the second principal component are positive, and the highest positive values represent measurements of the molar dentition (LM and BM1); there are also two significant negative loadings, however, for measurements of the breadth and depth of the incisors (BIT and DI). Variable loadings on H resemble those on the second principal component to the extent that the same pairs of molar and incisor measurements have the highest positive and negative weights, respectively, but the magnitude of the negative loadings for the two incisor measurements are greatly augmented and another measurement, Breadth of the Zygomatic Plate (BZP) is also represented by a significant negative weight. By contrast, many measurements that had substantial positive loadings on the second principal component have less weight on $H$. These include measurements of the nasal bones (BN, LN), incisive foramina (LIF), diastema (LD), incisor height (HI), zygomatic breadth (ZB), and a long measurement of the entire skull (CIL). Breadth of the Occipital Condyles (BOC) and Breadth of the Braincase (BB) have somewhat less weight on $H$ than on the second principal component. Breadth of the Palatal Bridge (BPB) retains a large positive loading.

Because the number of observations from which the covariance matrices of these analyses are estimated is so small, the possibility that variable loadings on calculated factors reflect the unusual morphology of just a single population must be considered. I tested the stability of variable loadings on $H$ by a jackknifing procedure in which I removed each of the 15 ichthyomyine populations singly from the analysis and extracted $H$ from the

---

[3] Despite similar notation, the shape factor of the present analysis is not formally equivalent to the sheared second principal component of Humphries et al. (1981); neither is it strictly growth-invariant in the sense of Burnaby (1966). The largest growth-invariant shape factor is the leading eigenvector of the covariance matrix of adjusted means $X_{ij} - a_iS_j$, where the $a_i$ are the within-group variable loadings on $S$. By contrast, $H$ of the present analysis is the leading eigenvector of the covariance matrix of the residuals $X_{ij} - b_iS_j$ where the $b_i$ are regression coefficients of the population mean $X_i$ on population size ($S_j$); these among-groups coefficients are very nearly the same as their within-group equivalents but account for variation with residuals that seem more appropriately size-independent in this interspecific context.

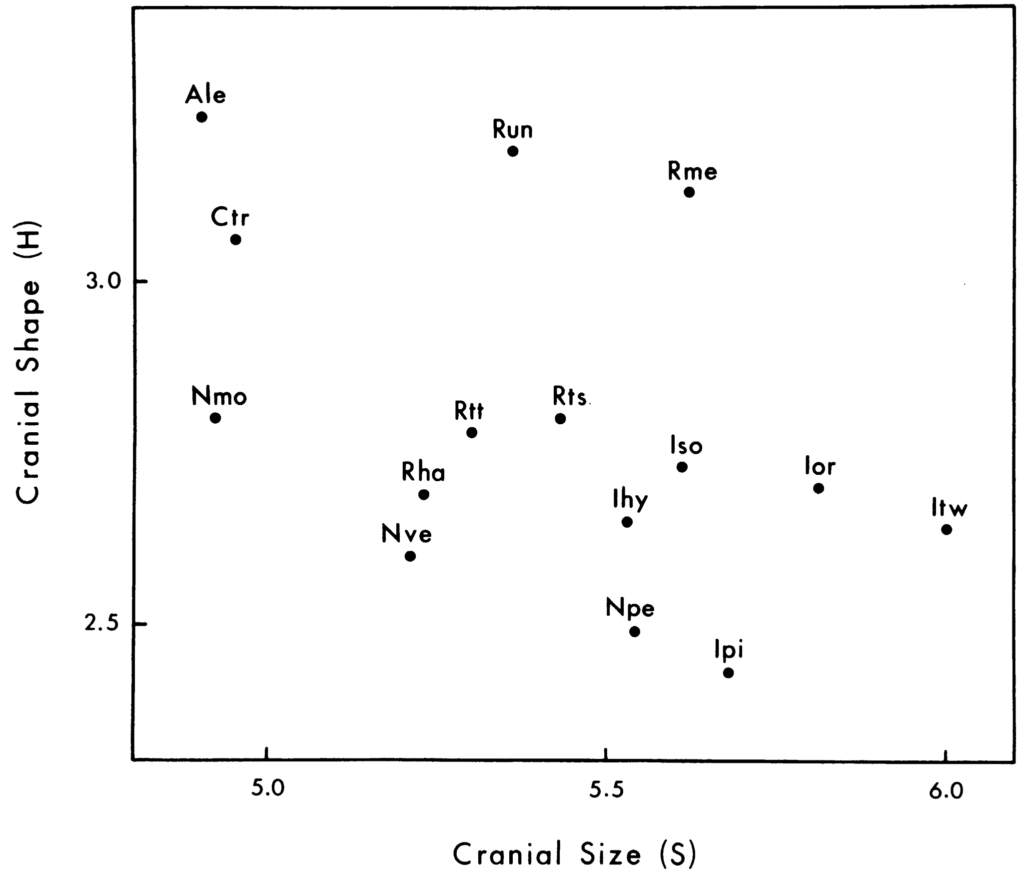


Fig. 50. Fifteen ichthyomyine population samples in the plane of the cranial size and shape factors. Taxonomic abbreviations are explained in the accompanying text.

covariance matrix recomputed for the size-corrected, log-transformed measurement means of the remaining 14 populations. The (absolute) minimum and maximum value for each variable loading obtained by this procedure are recorded in table 35. Clearly, the range of variation for some small loadings (e.g., LIB) is wide, but signs are consistent (except for variables with loadings near zero) and all of the variables that are heavily weighted when $H$ is computed over all 15 populations retain high coefficients in every computation based on 14 populations. By implication, $H$ represents a pervasive pattern of size-independent measurement covariation among ichthyomyines and is not a discriminator of just one deviant population.

The contrasting extremes in ichthyomyine craniodental morphology identified by $H$ can be inferred from the variable loadings. Species with high scores on this factor (*Anotomys leander, Chibchanomys trichotis, Rheomys mexicanus, R. underwoodi*) have relatively larger molars, broader palates, and wider braincases but more delicate incisors and narrower zygomatic roots than species with low scores on this factor (*Neusticomys peruviensis, N. venezuelae,* some species of *Ichthyomys,* and *Rheomys raptor hartmanni*). The crania of *Anotomys leander* and *Ichthyomys tweedii* are illustrated in figures 52 and 53 as examples of species that are widely separated by their scores on $H$. Although *A. leander* is overall the smaller of the pair, it has absolutely longer molar rows, broader first molars, and a wider palate than *I. tweedii*; the incisors of *A. leander* are narrow and delicate, however, and the inferior

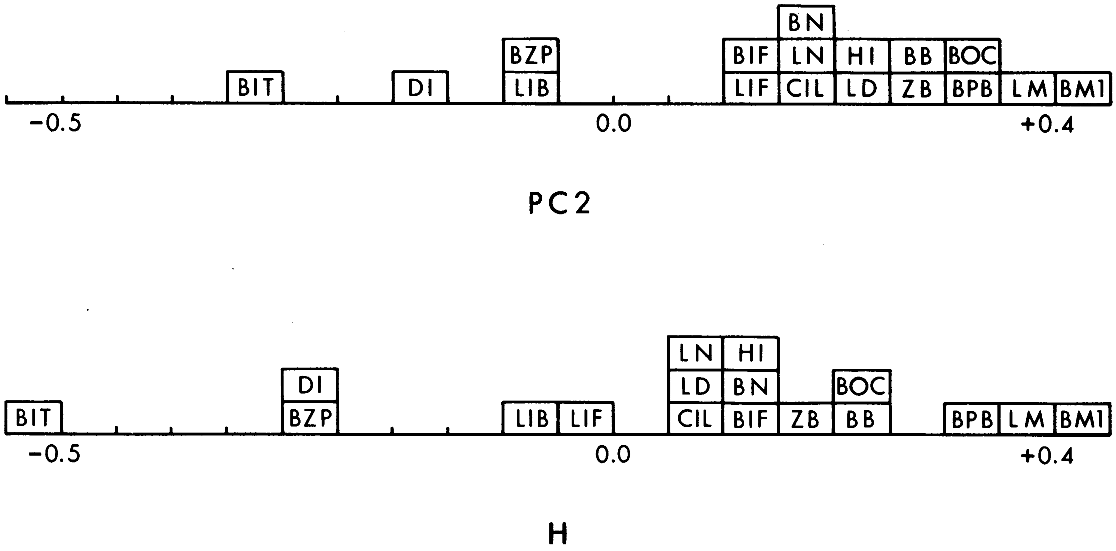


Fig. 51. Variable loadings on the second principal component and the cranial shape factor. Craniodental measurements (abbreviated as explained in Materials and Methods) are distributed along each horizontal axis according to the magnitude of their coefficients (table 34) in the corresponding component or factor expression.

zygomatic root is slender. By contrast, *I. tweedii* has diminutive molars and a narrow palate, but incisors that are disproportionately broader and deeper than those of *A. leander.* The braincase also differs conspicuously between the two species—it is large in relation to the rostrum and zygoma and appears inflated in *A. leander,* but in *I. tweedii* the braincase is much smaller in proportion to the large rostrum and wide zygoma and does not appear inflated.

After partialing out population scores on *S* and *H* from the log-transformed measurements there remains approximately 24 percent of the original variance. I extracted principal components from these residuals, but each accounted for so small a fraction of the total variance (the next-largest component after *H* accounting for only 7.1%) that I feel little confidence in ascribing any biological significance to them. Moreover, jackknifing procedures similar to those employed above to evaluate the stability of variable loadings on *H* reveal that subsequent components of the residual covariance matrix have coefficients that fluctuate considerably in sign and magnitude as individual populations are re-

TABLE 35
**Results of Jackknife Analysis of Variable Loadings on the Principal Shape Factor (*H*)**

| Measurement | Loadings computed for all 15 populations | Loadings computed for 15 sets of 14 populations each[a] | |
|---|---|---|---|
| | | Minimum[b] | Maximum |
| CIL | .052 | .033 | .093 |
| LD | .064 | .050 | .084 |
| LM | .366 | .327 | .389 |
| LIF | −.012 | −.002 | −.041 |
| BIT | −.531 | −.464 | −.565 |
| BIF | .135 | .061 | .173 |
| BPB | .321 | .261 | .391 |
| LN | .063 | .019 | .079 |
| BN | .014 | −.004 | .059 |
| LIB | −.054 | .003 | −.144 |
| ZB | .181 | .159 | .200 |
| BB | .232 | .219 | .252 |
| BZP | −.234 | −.132 | −.352 |
| BM1 | .402 | .350 | .483 |
| HI | .141 | .104 | .158 |
| DI | −.289 | −.198 | −.332 |
| BOC | .207 | .181 | .239 |

[a] See text for explanation.

[b] Minima and maxima tabulated as absolute values regardless of sign.

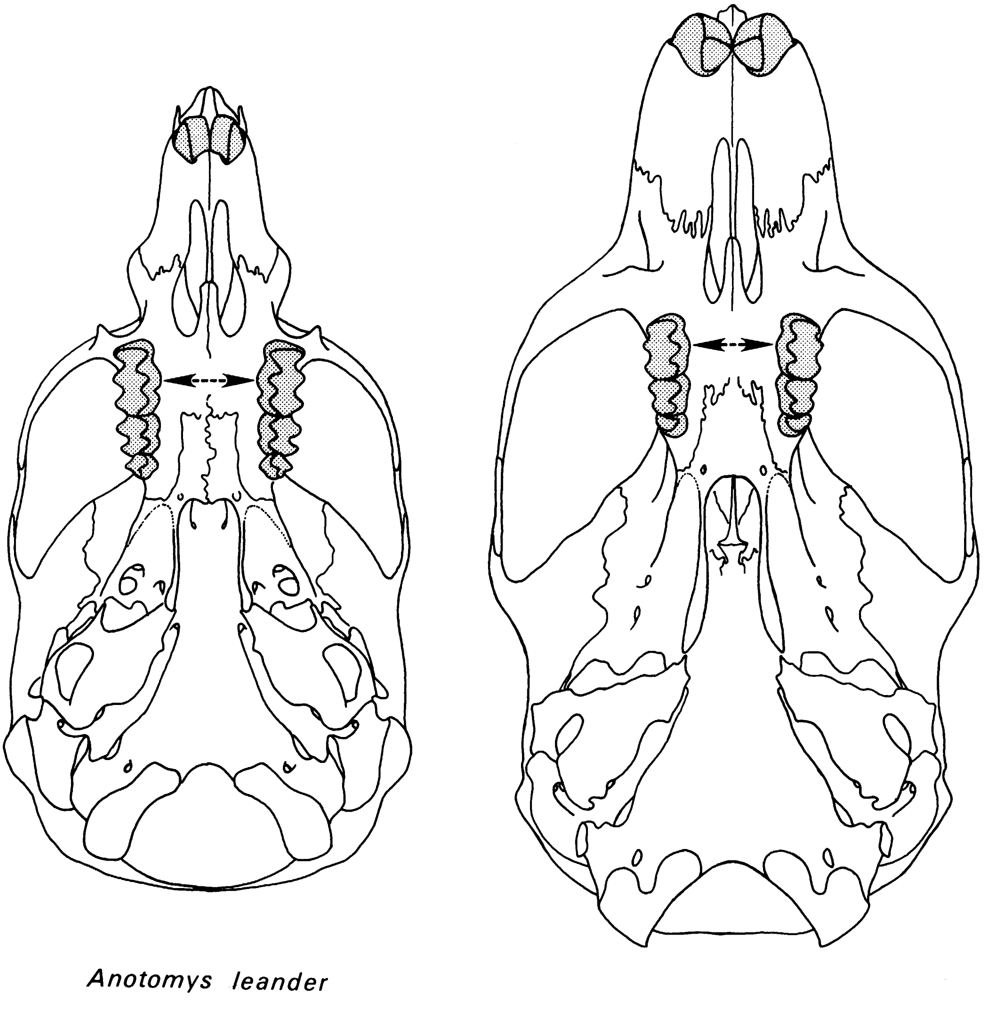
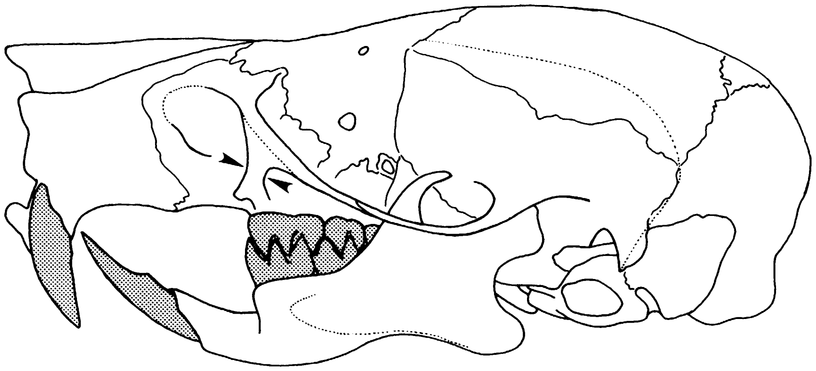


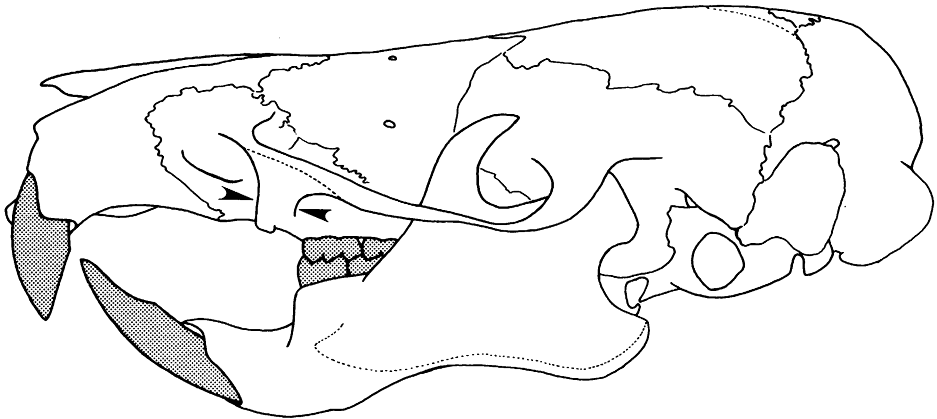
Fig. 52. Ventral view of crania of two ichthyomyine species with divergent scores on the principal shape factor (*H*). Note contrasts in relative incisor and molar size, palatal breadth, and braincase volume.

moved from the analysis. Therefore, while these smaller factors may each serve to identify the morphological peculiarities of one or a few populations, it is unlikely that they represent general patterns of size-independent morphometric covariance. Rather than labor over a complete (but biologically trivial) accounting for each of these minor discriminators, it seems more appropriate to attempt a preliminary interpretation of the biological significance of the principal shape factor, *H*.

BIOLOGICAL INTERPRETATION OF *H*: Interpretation of the empirical significance of factors usually proceeds by inspection of the variable loadings, but additional insights may be gained by examining the pairwise associations among variables within the matrix from which the factor was extracted. Table 36 reproduces a subset of the residual covariance matrix (*S* partialed out) consisting of variances (along the diagonal) and covariances (the off-diagonal elements) for the eight measurements with highest loadings on the principal shape factor and on all jackknifed estimates of *H*. Within this portion of the residual covariance matrix, two patterns of



*Anotomys leander*



*Ichthyomys tweedii*

Fig. 53. Lateral view of crania of two ichthyomyine species with divergent scores on the principal shape factor (*H*). Note contrasts in relative incisor and molar size and in breadth of the inferior zygomatic root.

TABLE 36

**Residual[a] Covariances ($\times$100) Among Selected Log$_e$-Transformed Measurements**

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| LM | .818 | | | | | | | |
| BIT | −.844 | 1.545 | | | | | | |
| BPB | .436 | −.921 | .811 | | | | | |
| BB | .426 | −.562 | .334 | .286 | | | | |
| BZP | −.372 | .380 | −.381 | −.336 | 1.042 | | | |
| BM1 | .833 | −.918 | .485 | .479 | −.381 | 1.033 | | |
| DI | −.466 | .812 | −.454 | −.275 | .026 | −.523 | .639 | |
| BOC | .370 | −.451 | .203 | .255 | −.362 | .426 | −.272 | .325 |
| | LM | BIT | BPB | BB | BZP | BM1 | DI | BOC |

[a] Size partialed out by regression of each variable against population scores on the size factor (*S*).

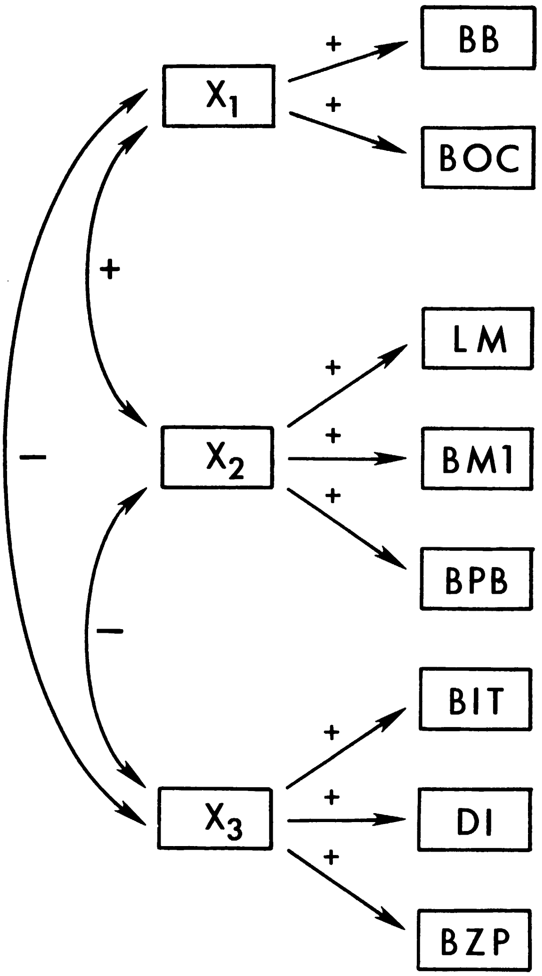


Fig. 54. Path diagram for the principal shape factor: a hypothesis about latent causal relations responsible for observed patterns of size-independent covariation in ichthyomyine craniodental measurements. See the text for further explanation.

TABLE 37

**Craniodental Measurements Means (in millimeters) for Four Carnivorous, Terrestrial Sigmodontine Species**

| | *Onychomys leucogaster*[a] | *Onychomys torridus*[b] | *Scotinomys teguina*[c] | *Scotinomys xerampelinus*[d] |
|---|---|---|---|---|
| CIL | 24.6 | 22.8 | 20.3 | 20.8 |
| LD | 7.0 | 6.3 | 5.8 | 6.0 |
| LM | 4.2 | 3.7 | 3.9 | 4.1 |
| LIF | 5.1 | 4.9 | 4.2 | 4.4 |
| BIT | 1.5 | 1.4 | 1.3 | 1.1 |
| BIF | 2.2 | 1.9 | 1.7 | 1.7 |
| BPB | 3.1 | 2.7 | 2.8 | 2.8 |
| LN | 10.8 | 10.1 | 8.2 | 8.8 |
| BN | 2.9 | 2.8 | 2.5 | 2.5 |
| LIB | 4.8 | 4.5 | 4.3 | 4.5 |
| ZB | 13.8 | 12.6 | 11.6 | 11.7 |
| BB | 12.3 | 11.4 | 10.3 | 10.4 |
| BZP | 2.0 | 1.7 | 1.8 | 1.9 |
| BM1 | 1.3 | 1.2 | 1.0 | 1.1 |
| HI | 4.4 | 4.0 | 3.7 | 3.4 |
| DI | 1.3 | 1.2 | 1.1 | 1.0 |
| BOC | 6.4 | 6.2 | 5.4 | 5.4 |

[a] USNM 202615, 202617, 202618, 202620, 202621.
[b] USNM 24980, 24981, 24983, 24987, 24988.
[c] USNM 396578, 396581, 396582, 396584, 516898.
[d] USNM 324021, 324026, 324027, 324028, 324040.

association are of primary interest: (1) The eight measurements comprise two disjoint sets [LM, BPB, BB, BM1, BOC] and [BIT, BZP, DI] within each of which all covariances are positive and between which all covariances are negative. (2) Five pairwise associations [cov(BIT, LM), cov(BM1, LM), cov(BPB, BIT), cov(BM1, BIT), and cov(DI, BIT)] are conspicuously larger than any others in the matrix, and all of these involve dimensions measured on or between teeth. These patterns are clearly reproduced in the signs and magnitudes, respectively, of the loadings for these variables on $H$ (table 34).

The fact that the variables with highest loadings on $H$ are dental measurements or measurements of interdental spaces suggests that this factor might represent a system of morphological integration within the masticatory apparatus, but the substantial loadings also of two neurocranial dimensions, BB and BOC, argue the participation of other functional influences. Figure 54 diagrams a system of hypothetical causal relations consistent both with the covariance structure described above and with what may reasonably be inferred from independent anatomical considerations. The internal nodes labeled $X_1$, $X_2$, and $X_3$ each represent latent influences hypothesized to exist as the common cause of variation within corresponding sets of morphologically adjacent dimensions connected to them by single-headed arrows. Double-headed arrows connecting internal nodes represent other, possibly reciprocal, relations that must also be postulated in order

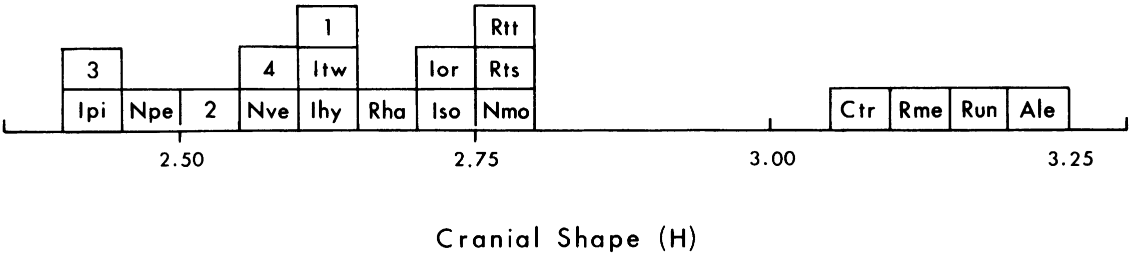


Fig. 55. Scores of 15 ichthyomyine population samples (abbreviated as explained in the text) and four outgroup taxa on the principal shape factor. The outgroup taxa are: **1,** *Onychomys leucogaster*; **2,** *O. torridus*; **3,** *Scotinomys teguina*; **4,** *S. xerampelinus*. See the footnotes to table 37 for outgroup sample composition.

to reproduce the patterns of association observed among measured variables.

Clearly, this formalism is not an empirical interpretation of the principal shape factor, but it does provide a model of the simplest set of functional relationships that such an interpretation could plausibly incorporate. A biologically adequate hypothesis regarding $H$ would minimally require (1) that the nature of the latent influences $X_1$, $X_2$, and $X_3$ as well as the paths of causation among them be made explicit, and (2) that the whole be interpretable in terms of the biology of the species whose morphological differences are reflected in widely divergent scores on the factor. These topics are taken up in subsequent sections of this monograph.

DIRECTION OF ICHTHYOMYINE CRANIAL EVOLUTION: As a quantitative index of size-independent morphometric variation in the head skeleton, the principal shape factor provides an operational basis for inference about the direction of craniodental shape change among ichthyomyines. Subject to the assumption that ichthyomyines evolved from a terrestrial, carnivorous sigmodontine ancestor, the craniodental dimensions of contemporary sigmodontines with terrestrial-carnivorous habits may plausibly suggest the primitive ichthyomyine morphology. The only terrestrial sigmodontines whose carnivorous habits are well documented and whose skulls are not conspicuously specialized in other respects are *Onychomys leucogaster, O. torridus, Scotinomys teguina,* and *S. xerampelinus* (see Horner et al., 1965, and Hooper and Carleton, 1976); mean cranial measurements for representative samples of these species are provided in table 37 and their scores on the principal shape factor in relation to ichthyomyine population samples are illustrated in figure 55. It seems clear from these results that, with regard to those aspects of craniodental shape indexed by *H,* ichthyomyines with low factor scores (*Ichthyomys, Neusticomys,* and some species of *Rheomys*) more closely resemble the four terrestrial-carnivorous sigmodontines chosen for comparison than do ichthyomyines with substantially higher scores (*Anotomys leander, Chibchanomys trichotis, Rheomys mexicanus,* and *R. underwoodi*). Although members of the former cluster, especially *Ichthyomys,* doubtless depart in other aspects from the ancestral cranial configuration, the logic of outgroup comparison together with prior assumptions about ancestral habits suggest that their larger incisors, smaller molars, narrower palates, and less voluminous calvaria are primitive in relation to the delicate incisors, larger molars, broader palates, and inflated braincases of the latter group.

## MASTICATION, DIET, AND CRANIODENTAL FUNCTION

Rodents have traditionally been regarded as herbivores and their distinctive mandibulodental morphology is usually interpreted as an adaptation for mechanically reducing nuts, seeds, stems, roots, and other tough plant materials. Landry (1970) challenged this conventional wisdom by presenting an exhaustive literature review and biomechanical arguments to support his hypothesis that the primitive adaptation of the rodent dentition was for an omnivorous diet. Landry also suggested that the spectacular evolutionary success of rodents might be attributed to the functional versatility of their masticatory apparatus.

Rodents are treated briefly in several general surveys of mammalian masticatory mechanisms (Becht, 1953; Smith and Savage, 1959; Turnbull, 1970) but detailed, function-oriented studies of individual species are few. Several analyses of mastication in laboratory muroids have considered the biomechanical relationships between teeth, masticatory muscles, and jaw movements (e.g., Hiiemae, 1971; Weijs and Dantuma, 1975; Gorniak, 1977), but the reports of Merriam (1895), Lemire (1966), and Kesner (1980) are exceptional for discussing rodent masticatory morphology in relation to natural diets.

The present account describes the occlusal morphology of the teeth and the gross morphology and internal architecture of the mandibular adductor musculature for two ichthyomyine species, *Anotomys leander* and *Ichthyomys tweedii*. I emphasize dental and myological comparisons of presumed functional importance and attempt to relate these to differences in foods eaten. *A. leander* and *I. tweedii* were chosen for comparison because the preceding morphometric analyses revealed conspicuous differences between these species in size-independent aspects of craniodental morphology that might have some interpretable significance for masticatory function. In addition, more is known about the habitats and diets of *A. leander* and *I. tweedii* than about those of most other ichthyomyine taxa.

## INCISORS

The upper incisors of *Anotomys leander* are narrow and delicate by comparison with the broad and robust teeth of *Ichthyomys tweedii*. In frontal view (fig. 56A), the characteristic inverted-V-shaped cutting edge formed by the juxtaposed tips of left and right upper incisors is scarcely developed in *Anotomys*. In *Ichthyomys*, however, the lateral margins of the incisor tips are produced as sharp, divergent points; this morphology is just noticeable in the very young specimen illustrated in figure 56B but becomes increasingly pronounced with age.

In ventral view, the contrast in incisor morphology is more striking. The anterior surfaces of the upper incisors of *Ichthyomys* are inclined medially (fig. 56D) such that the divergent lateral tips described above are produced appreciably beyond the rest of each tooth. In addition, the stout enamel band that forms the broad cutting edge is thickened laterally, effectively reinforcing the sharp lateral points. By contrast, the anterior surfaces of the upper incisors of *Anotomys* (fig. 56B) are not inclined medially; the cutting edges are thin and sharp, but their lateral margins are not reinforced by thicker enamel.

The lower incisors of both species reflect similar contrasts. The mandibular incisors of *Anotomys* are narrow, delicate, and procumbent (fig. 32) while the homologous teeth of *Ichthyomys* are broader, deeper, and (in older specimens) more strongly recurved (fig. 36).

Microscopic examination of the worn surfaces of upper incisors reveals dorsoventrally oriented striae and grooves in the soft dentine of the lingual bevel immediately behind the enamel cutting edge; in addition, transverse gouges are sometimes visible near the posterior limit of the bevel (fig. 56B). The former striae doubtless result from the edge-to-edge apposition of upper and lower teeth that is characteristic of incisor biting in all rodents (see Taylor and Butcher, 1951, for a detailed description); the latter, transverse gouges possibly result from deliberate or reflexive sharpening strokes by the lower incisor tips (Hiiemae and Ardran, 1968).

## MOLAR MORPHOLOGY AND OCCLUSION

While the molars of *Anotomys leander* and *Ichthyomys tweedii* are grossly similar with respect to features shared by all ichthyomyine taxa (see Comparative Morphology: Dentition), the two species differ conspicuously in other details of molar morphology relevant to a discussion of functional occlusion. The occlusal topography of the first and second molars is emphasized in the descriptions that

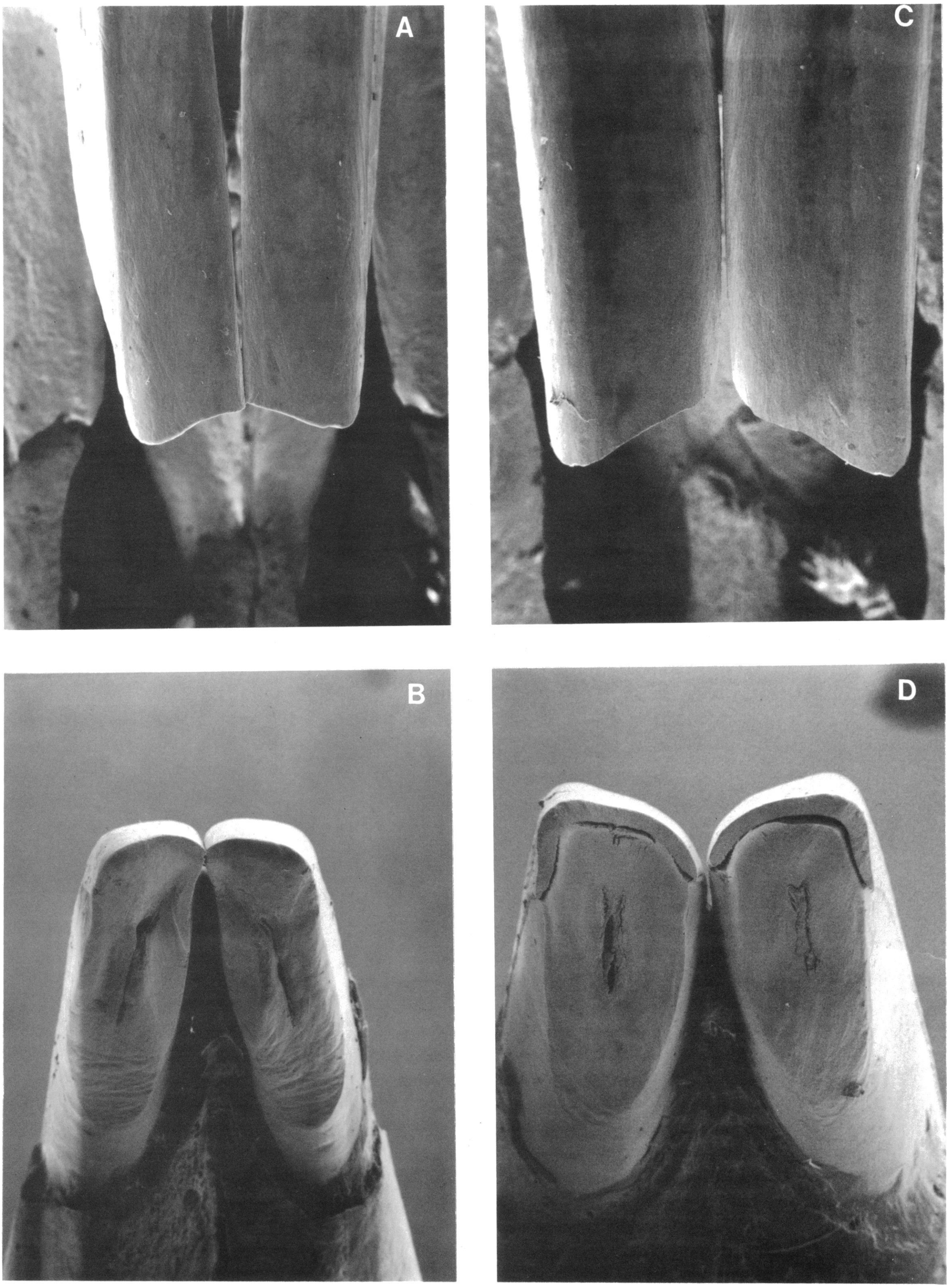


Fig. 56. Upper incisors of *Anotomys leander* (**A, B**; UMMZ 155598) and *Ichthyomys tweedii* (**C, D**; UMMZ 155783).

follow since the morphology of these large teeth is presumed to affect the mechanics of food reduction to a much greater extent than that of the diminutive third molars.

*Anotomys leander*: The unworn principal cusps on the first and second molars of *Anotomys leander* are tall and sharp and appear anteroposteriorly compressed (fig. 57); successive pairs of opposite labial and lingual cusps are separated by deep, wide reentrant folds. On the first two maxillary molars (fig. 57A, C), the cusps slant posteroventrally, and the enamel edge that forms the anterior margin of each cusp stands in higher relief than do the enameled posterior cusp margins. The anterior enamel edges of opposing labial and lingual cusps are, in unworn upper dentitions, almost joined at the midline of the tooth to form sharp, transverse crests divided by shallow median channels of dentine. From an anterolingual perspective (fig. 57A) the maxillary molar row is seen to consist of a serial array of inverted-V-shaped enamel blades. Behind these transverse crests, smooth surfaces of dentine slope away from the high anterior edges and the apices of the cusps toward the midline of the tooth and into shallow troughs that rise from the labial reentrant folds. These worn, predominantly concave surfaces are best seen from a posterolabial perspective (fig. 57C).

The principal cusps of the first and second mandibular molars of *Anotomys leander* (fig. 57B) slant anterodorsally and (except for the anteroconid of m1) have higher posterior than anterior enamel margins. Like the high anterior cusp edges of the upper teeth, the posterior edges of paired labial and lingual cusps on the lower molars are approximated at the midline of the teeth to form an opposing series of high, V-shape transverse crests (fig. 57B); the anteriormost of these notched blades, however, is formed by the anterior edge of the divided anteroconid of m1. In front of the high posterior edges and apices of the mandibular molar cusps are smoothly worn, concave dentinal surfaces that slope away toward the midline of the tooth and into shallow troughs that rise from the lingual reentrant folds (fig. 57D).

The combination of tall, anteroposteriorly compressed cusps and of wide, deep reentrant folds permits considerable interpenetration of the occlusal surfaces of upper and lower molars. In centric occlusion (defined as that position of the mandibular molars resulting in maximal intercuspidation with the maxillary teeth) the divided anteroconid of m1 passes in front of the anterocone of M1, the protoconid/metaconid cusp pairs of m1–2 occupy the reentrant folds and interdental spaces anterior to the paracone/protocone cusp pairs of M1 and M2, respectively, and the hypoconid/entoconid pairs of m1–2 occupy the reentrant folds in front of the metacone/hypocone pairs of M1–2. Intercuspidation in centric occlusion, measured as the vertical distance from the tip of the anteroconid of ml to the tip of the paracone of M1, averaged .61 mm (range, .50–.73 mm) in seven young specimens (TWC 1–4).

The anterior edges of maxillary molar cusps and the posterior edges of mandibular molar cusps exhibit fine, predominantly parallel scratches that have a posteroventral-anterodorsal orientation (fig. 58); manipulation of cleaned skulls and mandibles demonstrates that these dental surfaces can be brought into simultaneous contact as the lower teeth are moved upward and forward into centric occlusion. Hard detrital particles contained in food pressed between these surfaces during such an occlusal movement would leave scratches with the observed orientation. By contrast, the anterior enamel surfaces of mandibular molar cusps and the posterior surfaces of maxillary molar cusps are not marked by parallel scratches, suggesting that high occlusal pressures are not developed between those parts.

The smooth, worn slopes of dentine behind the sharp anterior cusp margins on the upper teeth and in front of the posterior cusp margins on the lower teeth are also scored by parallel scratches (fig. 59), but the marks on these softer dentinal areas have a posterolabial–anterolingual orientation. On the maxillary molars (fig. 59, top), these scratches extend from the labial reentrant folds anteriorly to the tips of the lingual cusps; on the mandibular molars (fig. 59, bottom) the striations extend from the lingual reentrant folds posteriorly to the tips of the labial cusps. Such marks could be scored by a mandibular movement from centric occlusion anteromedially and ventrally, drawing the labial

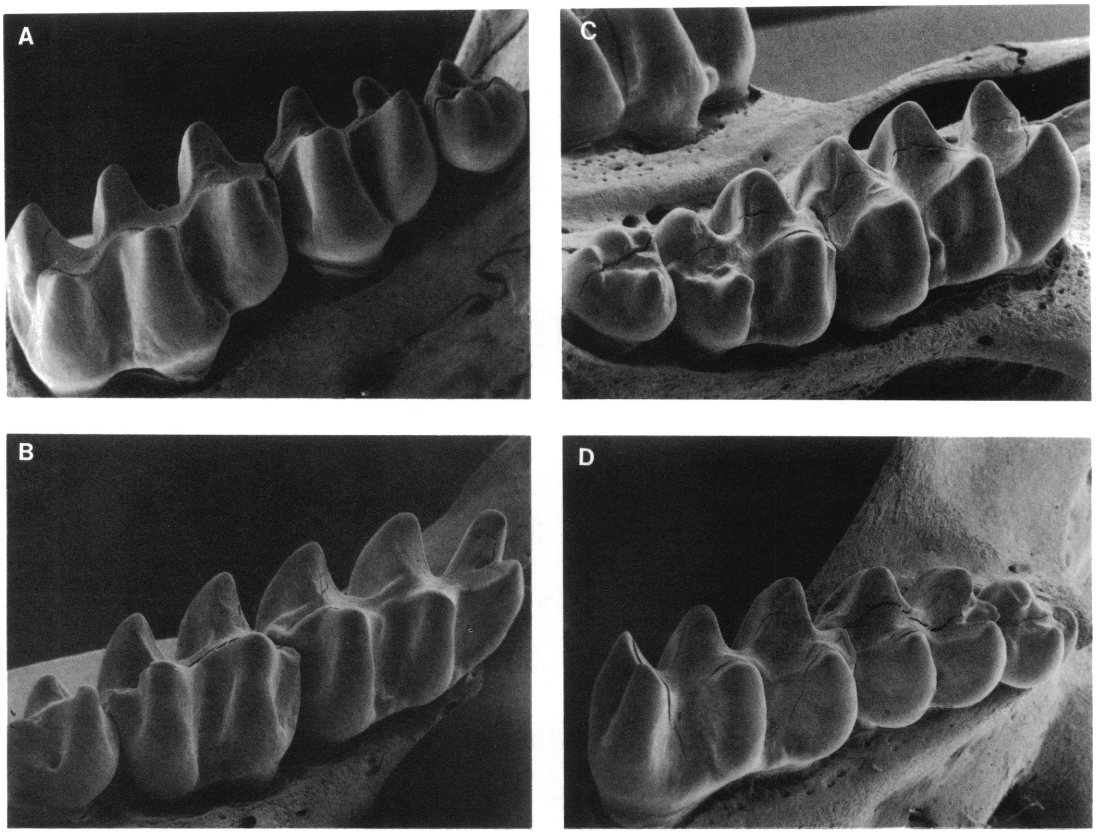


Fig. 57. Molar dentition of *Anotomys leander* (UMMZ 155598). **A,** anterolingual view of left maxillary molars; **B,** posterolabial view of right mandibular molars; **C,** posterolabial view of left maxillary molars; **D,** anterolingual view of right mandibular molars.

cusps of the mandibular teeth out of the labial reentrant folds and across the midline toward the tips of the lingual cusps of the maxillary teeth.

Scratches on dental surfaces produced by detrital particles in food indicate the orientation but not the direction of occlusal movements. Evidence to support the hypothesis of occlusal direction advanced above is as follows: (1) The mandibular teeth might be drawn posteroventrally out of centric occlusion, rather than anterodorsally into the centric position; both movements could account for the observed orientation of scratches on the enameled crests shown in figure 58. However, none of the masticatory muscles (described below) have an orientation appropriate for producing forceful posteroventral mandibular translation. By contrast, several large muscles are obviously oriented to effect powerful mandibular displacement forward and upward. (2) Theoretical models (Rensberger, 1973), comparative data (Kesner, 1980; Krause, 1982), and some quasi-experimental results (Costa and Greaves, 1981) suggest that when food containing abrasive material moves across a dentine surface and over a bordering enamel rim, the softer dentine is eroded below the level of the enamel margin. Movement of food in the opposite direction (i.e., over the enamel and onto the dentine) results in flush enamel-dentine boundaries because the harder enamel protects the immediately adjacent softer tissue from erosion. On worn molars of *Anotomys leander,* flush enamel–dentine boundaries occur within the labial reentrant folds of the upper molars and the lingual reentrant folds of the lower molars, but dentine is eroded below the bordering enamel along labial

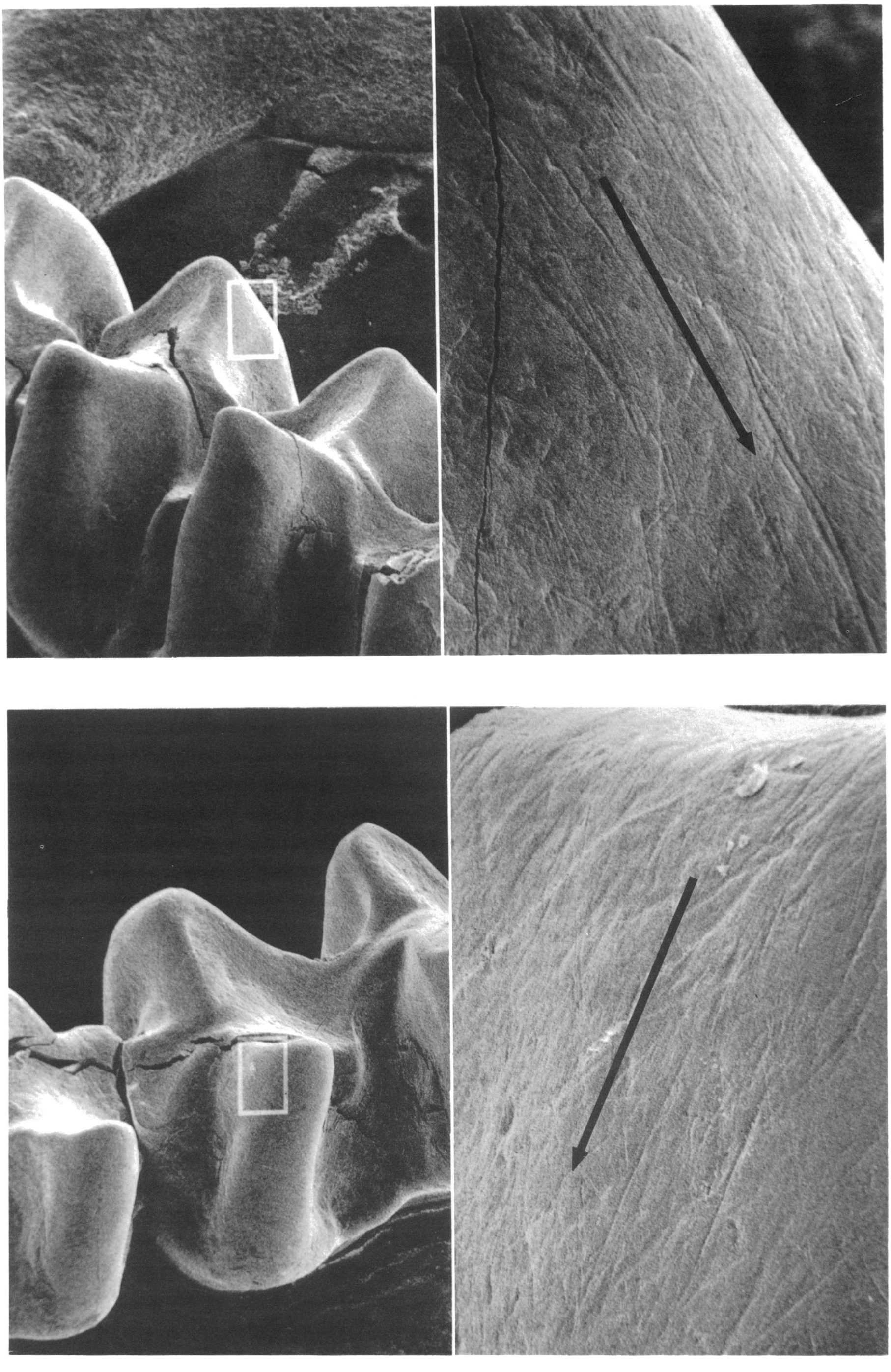


Fig. 58. Detail of wear on occluding molar surfaces of *Anotomys leander* (UMMZ 155602). **Top:** anterolabial views of left M1. **Bottom:** lingual views of left m1. Arrows indicate direction of occlusal movement.

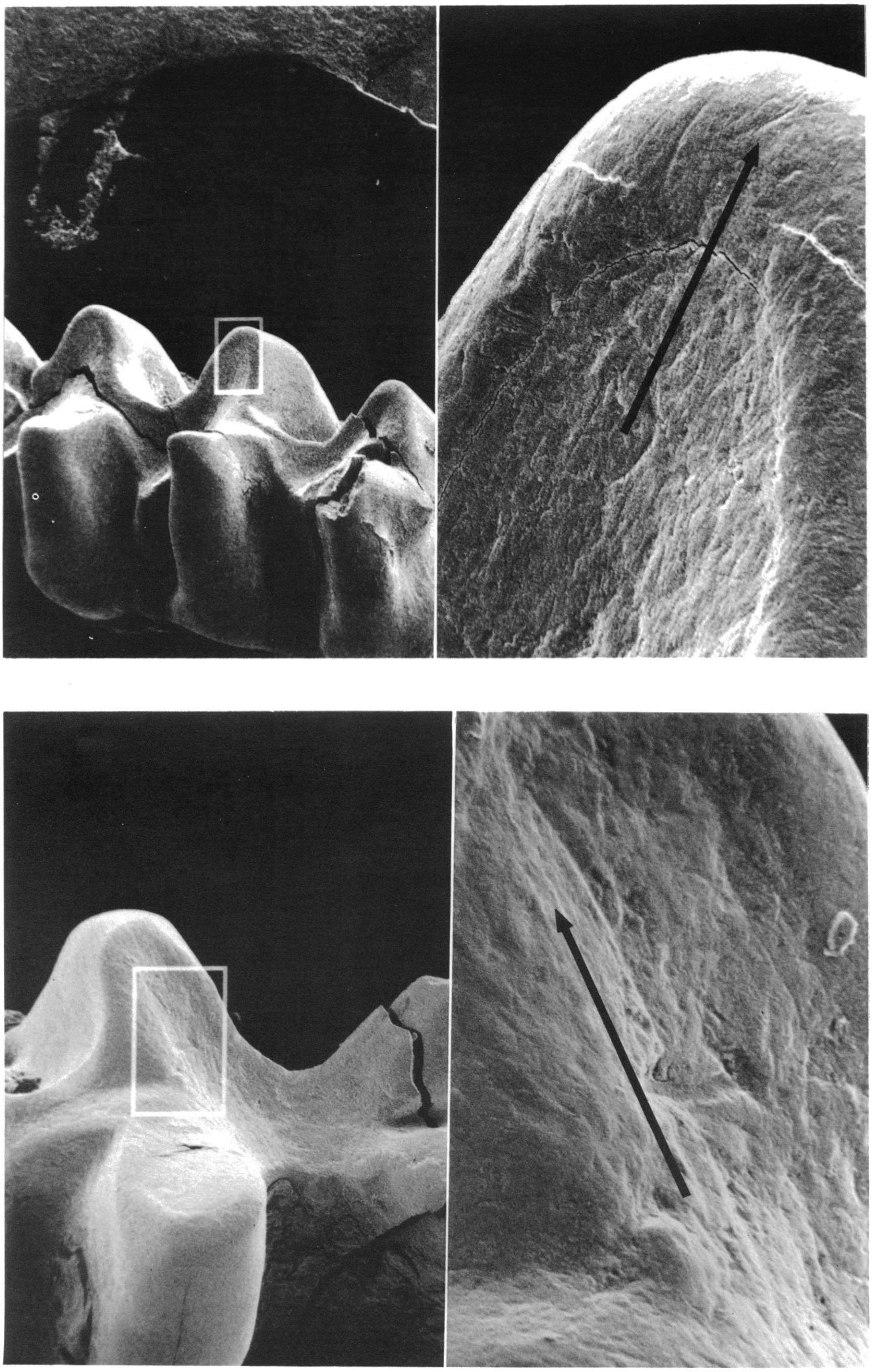


Fig. 59. Detail of wear on occluding molar surfaces of *Anotomys leander* (UMMZ 155602). **Top:** anterolabial views of left M1. **Bottom:** lingual views of left m1. Arrows indicate direction of occlusal movement.

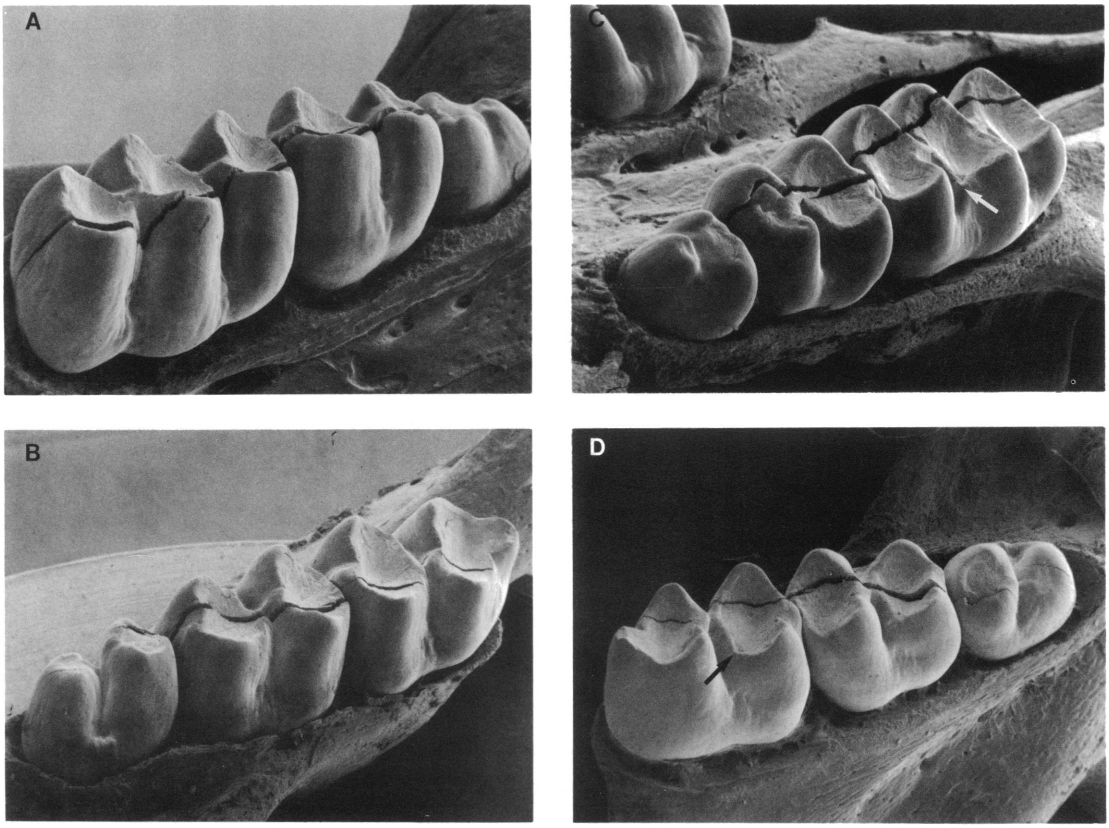


Fig. 60. Molar dentition of *Ichthyomys tweedii* (UMMZ 155783). **A,** anterolingual view of left maxillary molars; **B,** posterolabial view of right mandibular molars; **C,** posterolabial view of left maxillary molars; **D,** anterolingual view of right mandibular molars. Arrows indicate accessory enamel structures described in text.

mandibular and lingual maxillary cusp rims (e.g., fig. 59, top); such patterns of wear are consistent with the anteromedially directed movement of the mandibular teeth out of centric occlusion hypothesized above, but cannot be reconciled with an opposite movement along the same axis of orientation.

Two distinct occlusal phases are thus plausibly indicated during mastication in *A. leander*: (1) an anterodorsal (predominantly vertical) movement of the mandible into centric occlusion, and (2) an anteromedial and ventral mandibular movement out of centric occlusion. Food held between the teeth as the mandible is drawn anterodorsally (Phase 1) would be punctured by the interpenetrating cusps and then sheared as the V-shaped transverse crests on the lower teeth engage the inverted-V-shaped transverse crests on the upper teeth. Food pressed between the teeth in the centric position would subsequently be crushed by the anteromedial and ventral (Phase 2) sliding action of the dentinal surfaces of the mandibular labial cusps over the dentine of the maxillary lingual cusps.

*ICHTHYOMYS TWEEDII*: The molars of *Ichthyomys tweedii* average absolutely smaller than those of *Anotomys leander* despite the fact that *I. tweedii* is, overall, much the larger animal (see measurement data in tables 15 and 19). Differences in molar shape between the two species, however, are even more striking than this contrast in relative size.

The principal cusps on the first and second molars of *I. tweedii* (fig. 60) are, even when quite unworn, low and rounded by comparison with those of *A. leander* (compare with fig. 57); the cusps of *I. tweedii* teeth do not appear anteroposteriorly compressed, and the reentrant folds separating successive pairs of opposite labial and lingual cusps are (again, by comparison with *A. leander*) narrow and shallow.

The raised anterior edges of cusps on the upper molars and the elevated posterior edges of lower molar cusps form low, transverse crests across the teeth (fig. 60A, B), but these appear insignificant by comparison with the high vertical blades formed by the homologous edges in *A. leander* (compare with fig. 57A, B) and do not show the V/inverted-V complementarity of lower and upper molar crests described earlier for the latter species. In addition, the anteroconid of m1 in *I. tweedii* is a diminutive, spade-shaped cusp (fig. 60B) that does not resemble its large, sharp, twin-pointed homolog in *A. leander* (fig. 57B).

Shallow basins of exposed dentine occupy the regions between opposing labial and lingual cusps and comprise most of the occlusal surface of the molars of *I. tweedii.* Unlike the dentinal areas of *A. leander* molars, however, dentine basins on *I. tweedii* teeth do not communicate by worn channels with the floors of the reentrant folds.

Interpenetration of the occluding surfaces of upper and lower molars of *I. tweedii* is not deep, even in very young animals. This is due partly to the anteroposterior thickness of the individual cusps and the consequent narrowness of intervening reentrant folds and interdental spaces noted earlier, but intercuspidation during centric occlusion is also restricted by the early recruitment (with wear) of small, shelflike, accessory enameled structures onto the posterior surfaces of the labial cusps on the maxillary molars, and onto the anterior surfaces of the lingual cusps of the mandibular molars (fig. 60, arrows). These small structures effectively prevent intercuspidation by expanding the horizontal surfaces of the dentine basins while simultaneously reducing the anteroposterior dimensions of the reentrant folds. Thus, in centric occlusion the hypoconid of m1 rests on the shelf formed by the small mesoloph of M1 (fig. 60C, arrow) while the protocone of M1 rests on the mesolophid of m1 (fig. 60D, arrow). Small enameled bumps or spurs sometimes occur within the reentrant folds of *A. leander* molars (a small mesostyle can be seen between the paracone and metacone of M1 in fig. 57C) but are so positioned as not to prevent intercuspidation.

Microscopic examination of the teeth of *I. tweedii* provides no evidence for the presence of a vertical shearing action between the low transverse crests that are present on newly erupted molars: neither the anterior edges of maxillary molar cusps nor the posterior edges of mandibular molar cusps bear anterodorsally–posteroventrally oriented scratches resembling those reported above for the same dental surfaces in *A. leander.* Instead, only the dentinal basins of *I. tweedii* molars show parallel microscopic scratches (fig. 61), and these are oriented along a posterolabial–anterolingual axis. Dentine/enamel boundaries are flush along the posterior margins of the labial cusps on maxillary molars (fig. 61, bottom) and along the anterior margins of the lingual cusps of mandibular molars. Conversely, dentine is worn below bordering enamel rims along the posterior margins of mandibular labial cusps and the anterior margins of maxillary lingual cusps (fig. 61, top). An anteromedially directed scooping action of the labial mandibular cusps across the dentinal basins of the maxillary molars is thus indicated, the initial movement having a slight dorsal component as the mandibular labial cusps move into the inverted maxillary dentinal basins, followed by a ventral movement drawing the mandibular labial cusps over the enamel rims of the maxillary lingual cusps. Such an occlusal stroke would, of course, produce a reciprocal action of the maxillary lingual cusps against the dentinal basins of the mandibular teeth. The low transverse crests wear quickly away (prior to sphenoccipital suture closure) to form low ridges between the dentinal basins; these ridges are marked by scratches with the same orientation as those in the basins and may serve to guide the direction of occlusal movements.

By contrast, then, with the two-phased masticatory stroke in *Anotomys leander,* in which a vertical movement of the mandibular molars into centric occlusion is followed by a transverse sliding action out of the centric position, mastication in *Ichthyomys tweedii,* at least insofar as it marks the teeth,

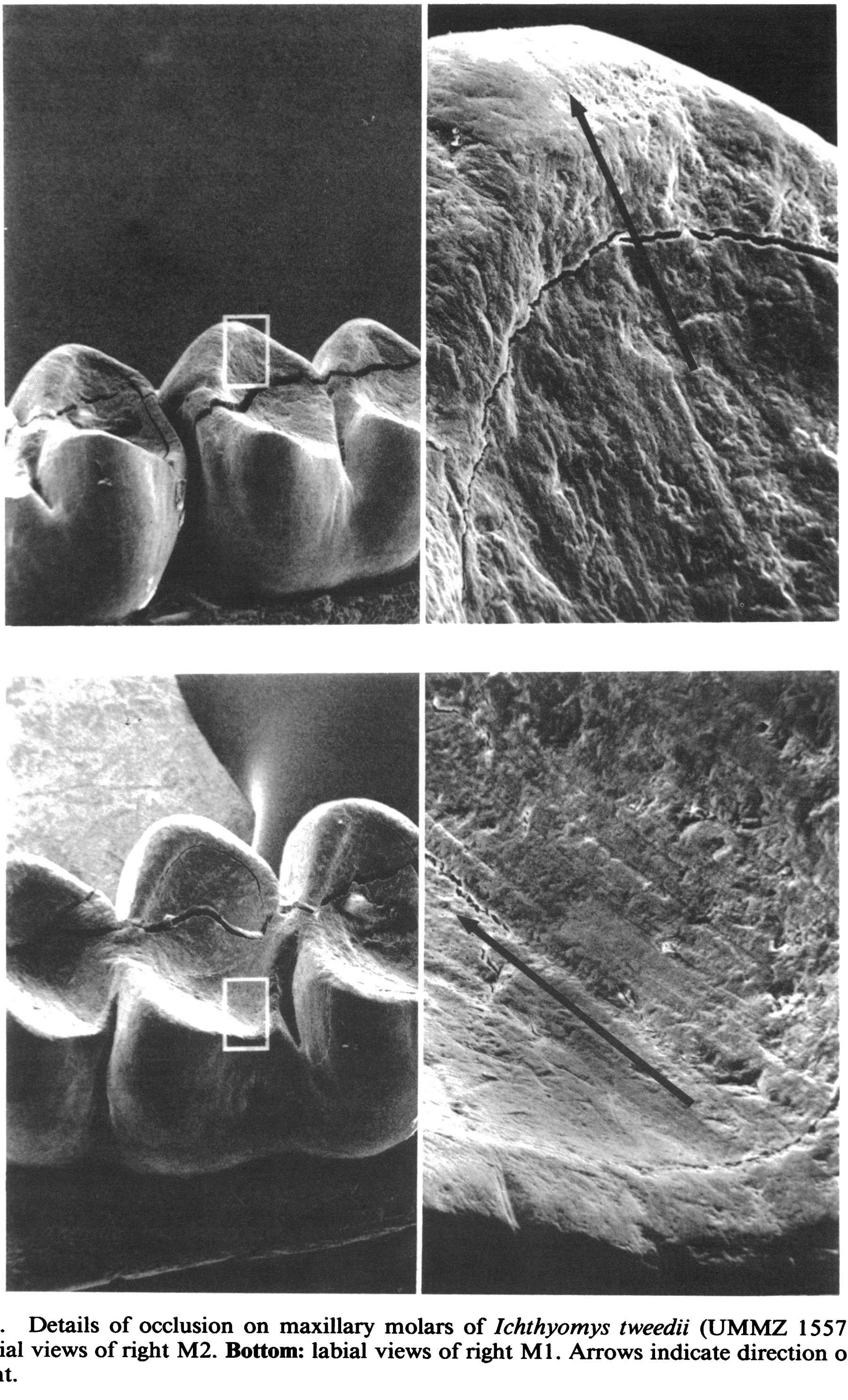


Fig. 61. Details of occlusion on maxillary molars of *Ichthyomys tweedii* (UMMZ 155788). **Top:** anterolabial views of right M2. **Bottom:** labial views of right M1. Arrows indicate direction of occlusal movement.

TABLE 38
Comparison of Nomenclatural Systems for Some Rodent Masticatory Muscles

| This study (after Weijs, 1973) | Gorniak (1977) | Hiiemae and Houston (1971) | Turnbull (1970) | Rinker (1954) (also Kesner, 1980) |
|---|---|---|---|---|
| (1) superficial masseter | superficial head of masseter | superficial masseter | *M. masseter pars superficialis* | *M. masseter superficialis* |
| (2) anterior deep masseter | deep head of masseter (part) | anterior deep masseter (part) | *M. masseter pars profunda* (part) | *M. masseter lateralis profundis pars anterior* |
| (3) posterior deep masseter | deep head of masseter (part) | deep masseter | *M. masseter pars profunda* (part) | *M. masseter lateralis profundis pars posterior* |
| (4) infraorbital part of zygomaticomandibularis | infraorbital head of zygomaticomandibularis | infraorbital part of anterior deep masseter | *M. maxillo-mandibularis* | *M. masseter medialis pars anterior* (part) |
| (5) anterior part of zygomaticomandibularis | anterior head of zygomaticomandibularis | anterior deep masseter (part) | *M. zygomaticomandibularis* | *M. masseter medialis pars anterior* (part) |
| (6) posterior part of zygomaticomandibularis | posterior head of zygomaticomandibularis | suprazygomatic slip of temporalis | not described | *M. masseter medialis pars posterior* |

apparently consists of a single, anteromedial mandibular movement producing a simultaneous scooping action of blunt upper and lower molar cusps into shallow dentine basins on the occluding teeth. A simple crushing or shearing effect on soft food pressed between broad dentinal surfaces moving in opposite directions relative to one another could result from this inferred masticatory action, but high pressures, perhaps suitable for shearing resistant food, might also be developed as the curved enamel rims of the mandibular labial cusps engage the reciprocally concave rims of the maxillary lingual cusps.

## MASTICATORY MUSCLES: ANATOMY

(Figures 62–65)

The mandibular adductor musculature of rodents is complex, homologous muscles vary substantially in their attachments to the skull and mandible among rodent higher taxa, and opinions differ about homologies between rodent and human mandibular adductors. Not surprisingly, several systems of nomenclature have been employed to describe rodent masticatory muscles; that adopted here follows Weijs (1973). Table 38 identifies synonyms among different nomenclatural systems for subdivisions of the masseter and the zygomaticomandibularis complex; there is greater nomenclatural consensus with respect to the temporalis and internal pterygoid. The present account treats only those muscles whose primary action is to adduct the mandible. Other muscles and muscle groups (e.g., the external pterygoid muscle and the occipital and hyoid musculature) may also participate in the mechanical reduction of food but contribute less directly to the development of pressure between occluding dental elements.

SUPERFICIAL MASSETER: The superficial masseter (figs. 62, 63, SM) originates by a thick tendon from a bony process (the masseteric tubercle) at the base of the inferior zygomatic root (fig. 62, apSM). The muscle inserts along the ventrolateral margin and ventral edge of the mandible, and onto the immediately adjacent lateral surface of the posterior deep masseter, from a point below the coronoid process posteriorly to the apex of the angular process; additionally, a discrete slip, the pars reflexa, passes beneath the mandible from the anteroventral margin of the muscle to insert on the medial surface of the dentary below the alveolus of the lower incisor (fig. 62, SMpr).

From its attachment to the maxilla, the tendon of origin passes laterally, around the bulge of the underlying anterior deep masseter, and then spreads posteroventrally to form an extensive superficial aponeurosis; it

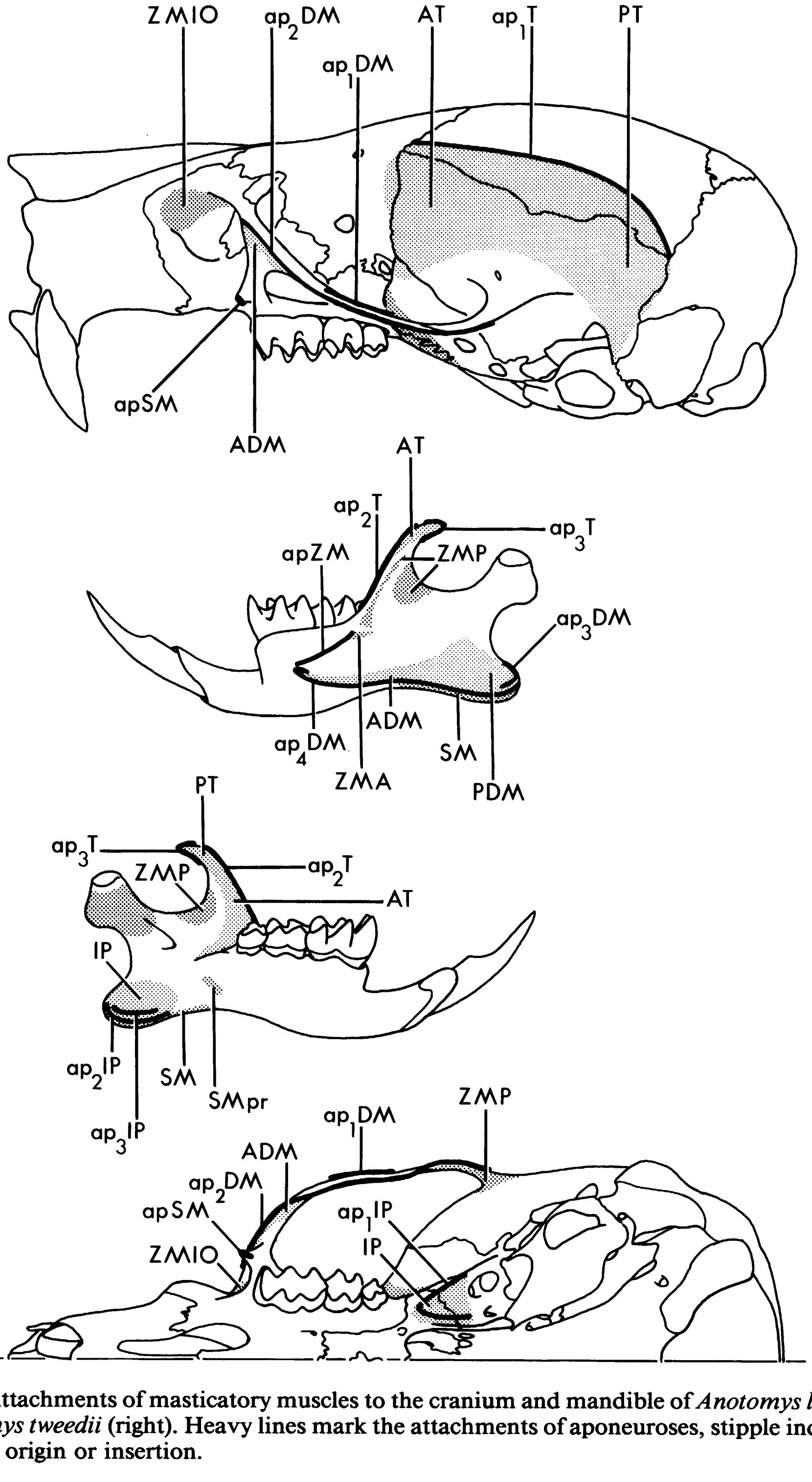


Fig. 62. Attachments of masticatory muscles to the cranium and mandible of *Anotomys leander* (left) and *Ichthyomys tweedii* (right). Heavy lines mark the attachments of aponeuroses, stipple indicates areas of musculous origin or insertion.

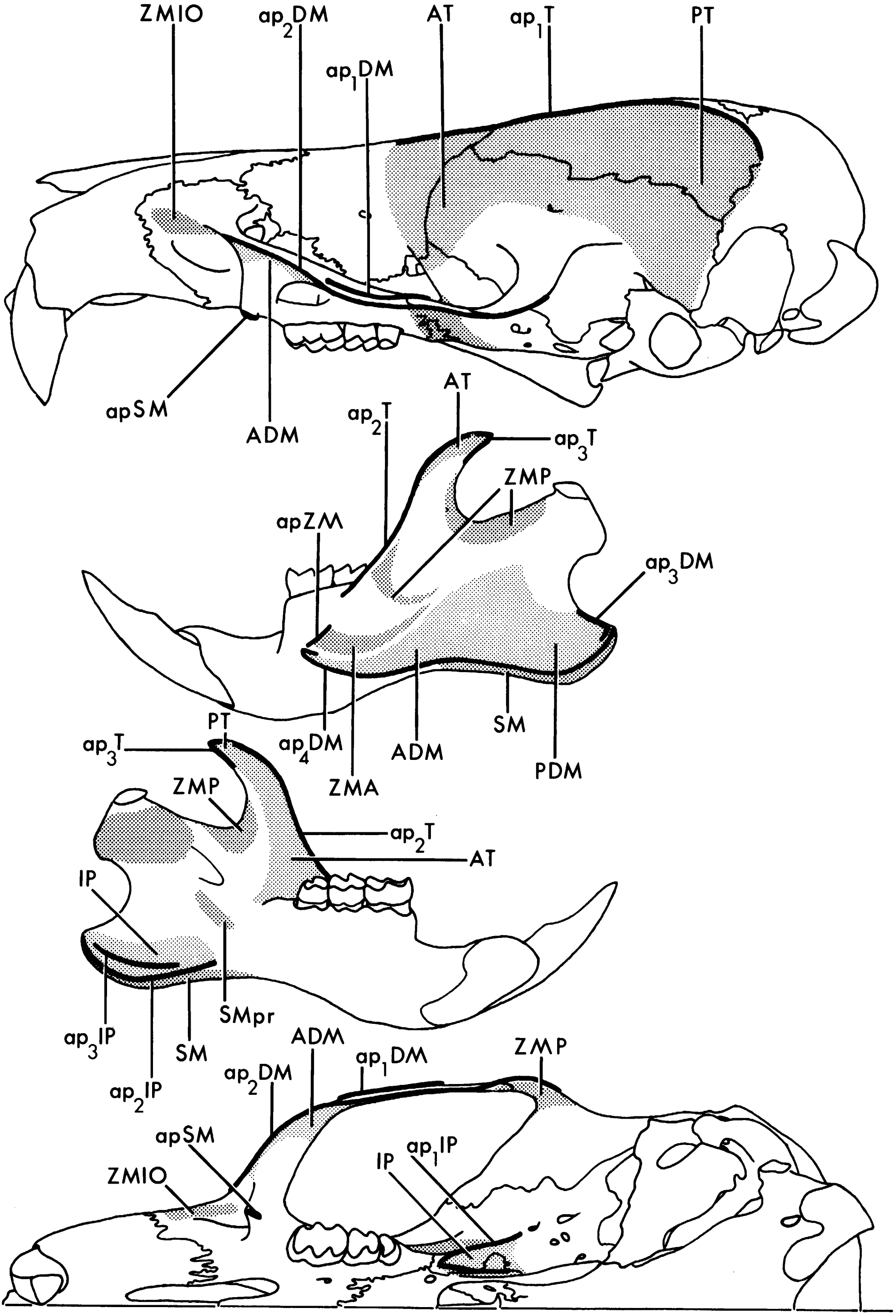


Fig. 62—(Continued). Abbreviations for muscles and aponeuroses are explained in the text. The origin and insertion of the external pterygoid (which is not described in the text) are mapped but not labeled. All elements for both taxa are drawn to the same scale, about ×3.75.

is from the deep side of this connective tissue sheet that the fleshy fibers of the superficial masseter originate. The aponeurosis of origin is dense and opaque over the anterodorsal apex of the muscle (fig. 63), but is thinner and transparent posteroventrally. The fibers of the superficial masseter spread fanwise from their attachments to the aponeurosis: the dorsalmost fibers pass almost directly posteriad while the fibers forming the anterior edge of the muscle have a conspicuously more ventral inclination. Anterior fibers average shorter than posterior fibers in some specimens.

The superficial masseter is of similar relative size in *Anotomys leander* and *Ichthyomys tweedii,* but its origin and insertion are nearer the occluding molar toothrows in the former species. In *A. leander,* the bony tubercle from which the muscle originates is located close to the anterocone of M1, and the posterior limit of muscular insertion (the apex of the angular process) is beneath the articular condyle (fig. 62, left). In *I. tweedii,* the masseteric tubercle is located well anterior to M1 and the angular process is produced behind the articular condyle (fig. 62, right). Because of these positional differences in its attachments to the skull and mandible, the superficial masseter is more vertically oriented, relative to the horizontal plane of molar occlusion, in *A. leander* than in *I. tweedii.*

APONEUROSES OF THE DEEP MASSETER: Four aponeuroses are associated with the complex origins and insertions of the deep masseter in ichthyomyines, but the anatomy of some of these connective tissue sheets is difficult to determine with certainty by gross dissections. Serial sectioning of whole heads is the anatomical technique of choice (Hiiemae and Houston, 1971; Weijs, 1973), but the osteological specimens necessarily sacrificed by such procedures could not be spared. Apparent differences between the aponeurotic arrangements described below and those of *Rattus norvegicus* (as described by Weijs, 1973) must therefore be interpreted with these material and methodological limitations in mind.

1. The external aponeurosis of the zygomatic arch (fig. 62, $ap_1DM$) is attached to the lateral surface of the zygomatic process of the maxilla and to the anterior portion of the jugal. This connective tissue sheet is conspicuous over the anterodorsal part of the posterior deep masseter, and the posterodorsal corner of the anterior deep masseter (fig. 64). The extent of this aponeurosis along the zygomatic arch is relatively greater in *Ichthyomys tweedii* than in *Anotomys leander.*
2. The internal aponeurosis of the zygomatic arch (fig. 62, $ap_2DM$) is attached along almost the entire length of the zygomatic arch from a point above the anterodorsal edge of the inferior zygomatic root caudally to the zygomatic process of the squamosal opposite the glenoid fossa. $Ap_2DM$ is attached along the lateral surface of the zygoma as far posteriad as the attachment of $ap_1DM$, whereupon it bends medially to follow the ventral edge of the maxilla and jugal; the squamosal attachment is again lateral.
3. The aponeurosis of the semilunar incisure (fig. 62, $ap_3DM$) is a feeble, U-shaped aponeurosis, concave anteriorly, attached to the sharp dorsal edge of the angular process and to the lateral surface of the angular process just above the attachment of $ap_4DM$ along the masseteric ridge.
4. The internal aponeurosis of the masseteric ridge (fig. 62, $ap_4DM$) attaches to the lateral surface of the dentary along a gentle biconcave line from a point below m1 to the posterior apex of the angular process. The aponeurosis is exposed where it is reflected back upon itself to form the free anterior margin of the anterior deep masseter, and again, caudally, over the angular process (fig. 64). The attachment of this connective tissue sheet to the mandible is marked by a low, bony scar, the masseteric ridge.

DEEP MASSETER: The deep masseter of ichthyomyines is separated into anterior and posterior parts by a branch of the masseteric nerve that penetrates the fibers of this muscle to supply the superficial masseter. Anterior and posterior parts of the deep masseter also differ in fiber orientation: fibers of the anterior deep masseter have a more vertical orientation than have the more horizontally directed fibers of the posterior part (Rinker, 1954). It is not possible to unambiguously distinguish anterior and posterior parts of the deep masseter on the basis of fiber orientation alone, however, so the position of the masseteric nerve provides a convenient and con-

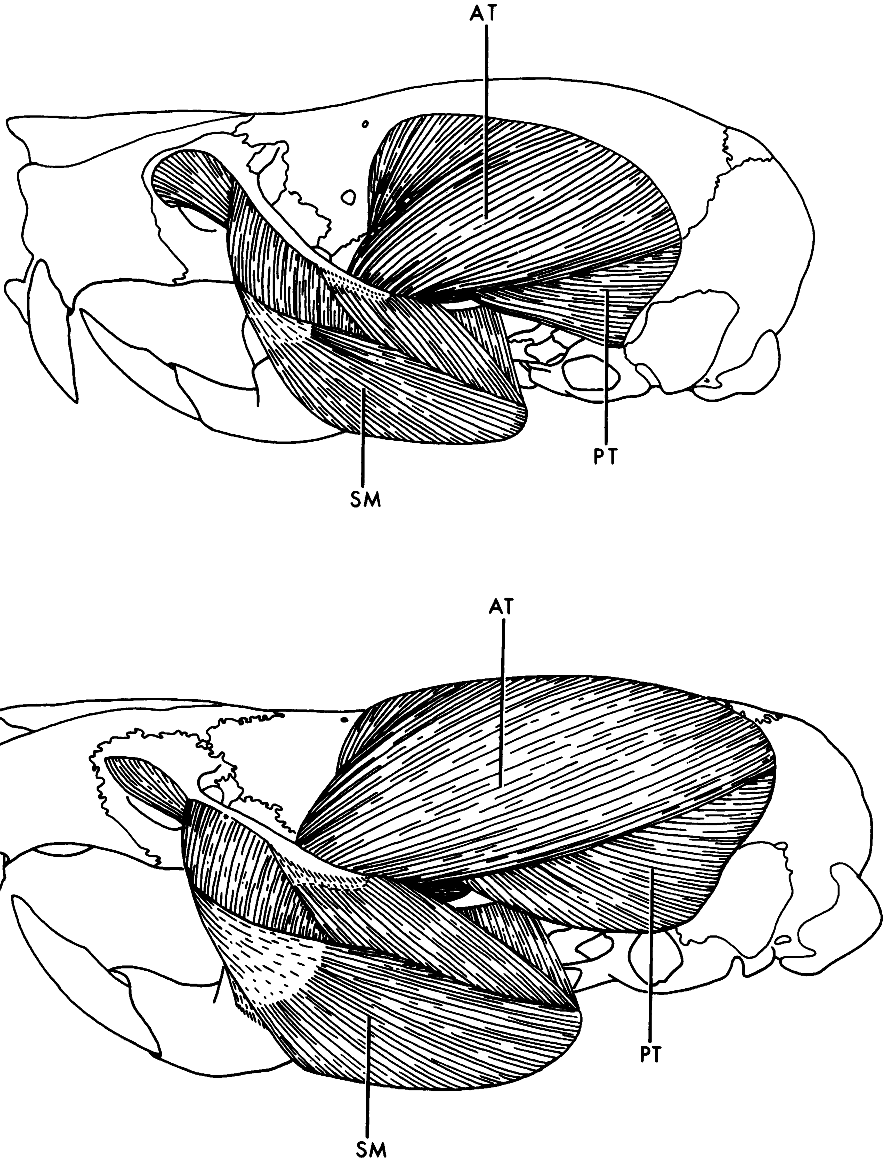
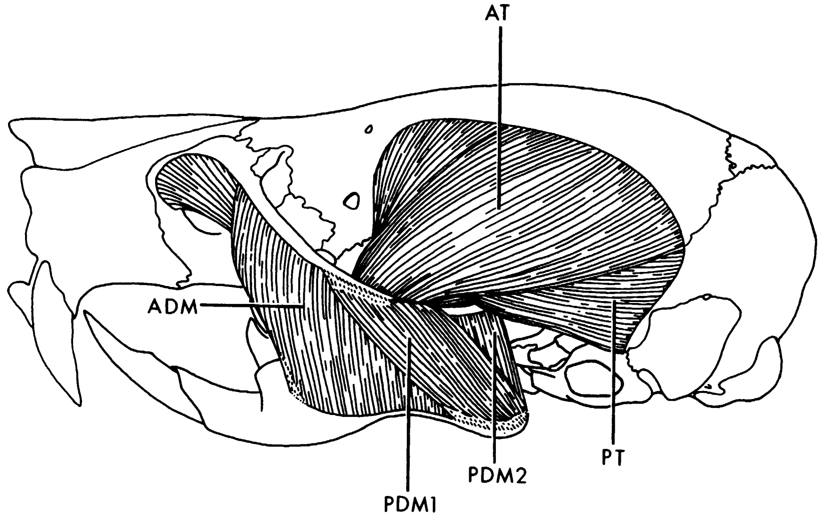


Fig. 63. Superficial aspect of masticatory muscles of *Anotomys leander* (top) and *Ichthyomys tweedii* (bottom). AT, anterior temporalis; PT, posterior temporalis; SM, superficial masseter.

sistent criterion for partitioning this large and complex muscle.

ANTERIOR DEEP MASSETER: The fibers of the anterior deep masseter (figs. 62, 64, ADM) take origin on both sides of $ap_2DM$ from the anterior limit of that aponeurosis above the inferior zygomatic root caudally to the maxillary/jugal suture. In addition, fibers originate musculously from a narrow region below the attachment of $ap_2DM$ on the inferior zygomatic root. Between $ap_1DM$ and $ap_2DM$, where these aponeuroses overlap on the zygomatic process of the maxillary, fibers of the anterior deep masseter anastomose with those of the posterior deep masseter. The parallel fibers of the anterior deep masseter pass almost straight ventrally to insert onto the mandible musculously and by $ap_4DM$ along the anterior ⅔ of the masseteric ridge. Fibers originating from the inferior zygomatic root



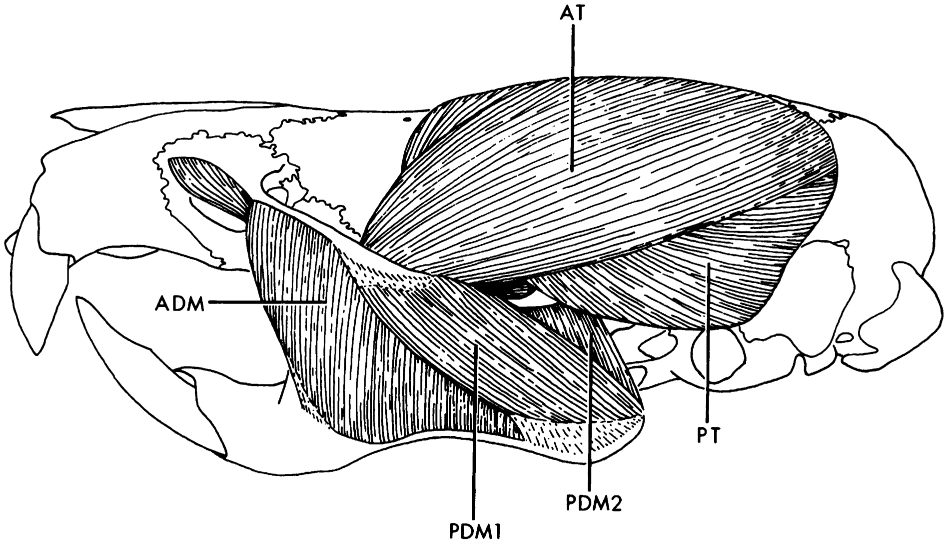


Fig. 64. Masticatory muscles of *Anotomys leander* (top) and *Ichthyomys tweedii* (bottom) with the superficial masseter removed. **ADM,** anterior deep masseter; **AT,** anterior temporalis; **PDM1,** superficial part of posterior deep masseter; **PDM2,** deep part of posterior deep masseter; **PT,** posterior temporalis.

average shorter, in most specimens, than the most posterior fibers that originate from the zygomatic arch.

The limits of origin and insertion are considerably more anterior, with respect to the molar rows, in *I. tweedii* than in *A. leander.* In *I. tweedii,* $ap_2DM$ is produced rostrally beyond M1 by a distance about equal to the entire length of that tooth (fig. 62, right); in *A. leander,* $ap_2DM$ extends rostrally less than one-fifth of that distance beyond the toothrow (fig. 62, left). On the mandible, $ap_4DM$ in *I. tweedii* extends rostrally to a point just beyond the protoconid of m1; in *A. leander,* $ap_4DM$ scarcely extends beyond the hypoconid of that tooth. In consequence, a straight line drawn between the anterior limits of origin and insertion of the anterior deep masseter passes (in sagittal projection) through the occluding first molars of *A. leander,* but anterior to the molar series in *I. tweedii.*

POSTERIOR DEEP MASSETER: The fibers of the posterior deep masseter (figs. 62, 64, PDM) arise from both sides of $ap_2DM$ behind the maxillary/jugal suture and from $ap_1DM$. The fibers originating from $ap_1DM$ constitute a discrete superficial slip (fig. 64, PDM1) with a conspicuously more horizontal course than the fibers of the deeper part (fig. 64, PDM2) that originate from $ap_2DM$. The anteriormost fibers of PDM1 take origin from the deep side of $ap_1DM$, but more posterior fibers arise from both sides of that aponeurosis. The fibers of PDM1 are long and parallel; they pass caudoventrally to insert onto the lateral aspect of $ap_4DM$ above the angular process of the mandible. The fibers of PDM2 are much shorter than those of the superficial part and pass less obliquely caudoventrally to insert musculously on the lateral surface of the dentary, onto the medial side of $ap_4DM$, onto both sides of that part of $ap_3DM$ that parallels the masseteric ridge, and onto the lateral surface of the part of $ap_3DM$ that is attached to the dorsal edge of the angular process.

The superficial oblique part (PDM1) of the posterior deep masseter is more horizontally inclined with respect to the occlusal plane in *I. tweedii* than in *A. leander.* The muscle is otherwise similar between the two species.

ZYGOMATICO-MANDIBULARIS: Deep to the muscles described above are sheets of fibers that originate from the medial aspect of the zygomatic arch, the ventral surface of the squamosal zygomatic process lateral to the glenoid fossa, the roof of the infraorbital canal, and from the side of the rostrum anterodorsal to the nasolacrimal capsules. Collectively, these fibers are here termed the zygomatico-mandibularis following Weijs (1973). Rinker (1954) also grouped these diverse fiber sheets together as M. masseter medialis; other anatomists differ (table 38). The muscle is here described as consisting of three parts: infraorbital, anterior, and posterior.

A single aponeurosis (fig. 62, apZM) is associated with this muscle in ichthyomyines. It is a dense connective tissue sheet that attaches to the mandible from a point just above the reflected anterior fold of $ap_4DM$ and thence posterocaudally in a line toward the base of the coronoid process. Fibers of the infraorbital and anterior parts of the zygomatico-mandibularis insert on the lateral aspect of this aponeurosis, which is considerably more extensive in *A. leander* than in *I. tweedii.*

INFRAORBITAL PART OF ZYGOMATICO-MANDIBULARIS: The fibers of the infraorbital part of zygomatico-mandibularis (figs. 62, 65, ZMIO) originate musculously on the lateral aspect of the rostrum anterodorsal to the nasolacrimal capsules and from the roof of the infraorbital foramen. Passing caudoventrally through the infraorbital foramen they bend abruptly downward over the base of the inferior zygomatic root and attach to the lateral surface of apZM. The fibers of this muscle are neither parallel nor equal in length. The longest fibers (those attaching rostral to the nasolacrimal capsules) pass beneath other fibers that originate more posterodorsally, and insert on apZM deep to shorter fibers originating high on the rostrum and from the roof of the infraorbital canal (this is not easily appreciated in the lateral views of fig. 65).

The infraorbital part of the zygomatico-mandibularis is about the same absolute size in both *Anotomys leander* and *Ichthyomys tweedii,* but relative to the other mandibular adductors it is larger in the former species. In *A. leander* the fibers of this muscle insert into apZM at about the level of the occluding molar rows (fig. 65, top); in *I. tweedii* attachment of the muscle fibers to the aponeurosis is well below the alveoli of the mandibular molars (fig. 65, bottom). The position of the inferior zygomatic root relative to the cheekteeth also affects the position of this muscle. In *I. tweedii,* the infraorbital fibers bend ventrally over the lower zygomatic root and pass just rostral to M1. In *A. leander,* however, these fibers pass downward lateral to the paracone of that tooth.

ANTERIOR PART OF ZYGOMATICO-MANDIBULARIS: The parallel fibers of the anterior part of zygomatico-mandibularis (figs. 62, 65, ZMA) originate musculously from the medial surface of the zygomatic process of the maxilla and pass almost straight ventrally. The anteriormost fibers insert onto the lateral surface of apZM; more posterior fibers insert musculously onto the mandible in a

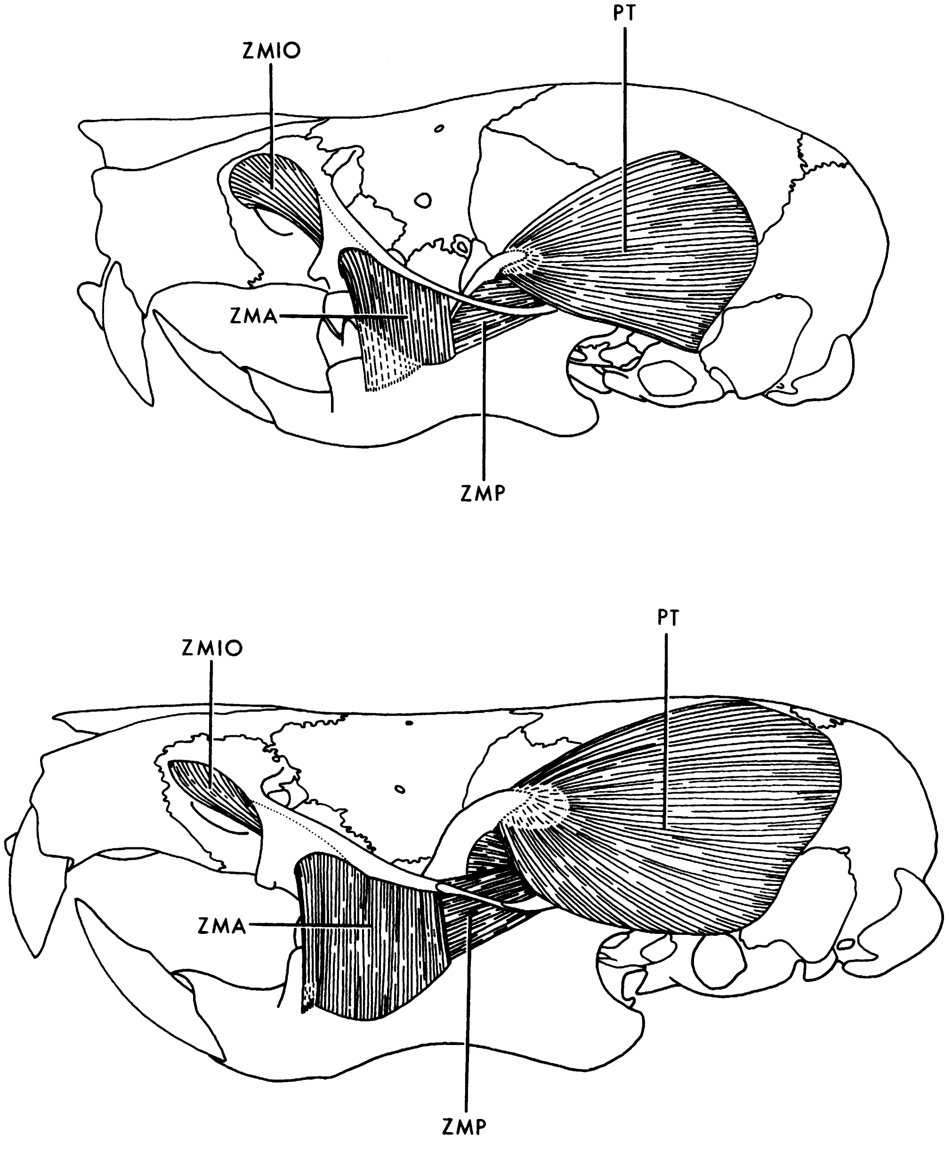


Fig. 65. Masticatory muscles of *Anotomys leander* (top) and *Ichthyomys tweedii* (bottom) with the superficial masseter, anterior and posterior deep masseter and anterior temporalis removed. **PT,** posterior temporalis; **AMA,** anterior part of zygomaticomandibularis; **ZMIO,** infraorbital part of zygomaticomandibularis; **ZMP,** posterior part of zygomaticomandibularis.

crescent-shaped region that extends from apZM caudoventrally toward the articular condyle. The posterior fibers of the anterior part of zygomatico-mandibularis overlap the anterior fibers of the posterior part at nearly right angles.

A much larger proportion of the fibers insert by apZM in *Anotomys leander* than in *Ichthyomys tweedii*; in the latter species, most fibers insert musculously.

POSTERIOR PART OF ZYGOMATICO-MANDIBULARIS: The fibers of the posterior part of zygomatico-mandibularis (figs. 62, 65, ZMP) originate from the medial surface of the jugal and from the zygomatic process of the squamosal lateral to the glenoid fossa.

The fibers pass to two discrete areas of insertion on the mandible (fig. 62). The anteriormost of these, on the lateral surface of the mandible, is a crescent-shaped region extending mostly along the leading edge of the coronoid process (*Anotomys leander*) or from the leading edge of that process caudoventrally beneath the bony capsule that encloses the root of the lower incisor (*Ichthyomys tweedii*). The more posterior area of insertion occupies both medial and lateral surfaces of the mandible within the sigmoid notch (between the coronoid and condylar processes). Because the zygomatic attachments of this muscle are less extensive than its mandibular attachments, the fibers spread fanwise from their origins (fig. 65), the dorsalmost passing straight rostrally, the ventralmost rostroventrally to their insertions.

APONEUROSES OF THE TEMPORALIS: Three aponeuroses are associated with the temporalis complex in ichthyomyines. A fourth, described by Weijs (1973) for *Rattus norvegicus*, appears to be absent in these rodents.

1. The external aponeurosis of origin (fig. 62, $ap_1T$) is a thin and transparent but tough connective tissue sheet that gives origin on its deep side to the superficial fibers of the anterior temporalis. The rostrocaudal extent of this aponeurosis differs greatly between *Anotomys leander* and *Ichthyomys tweedii*. In *A. leander*, $ap_1T$ attaches along a gentle curve on the dorsolateral aspect of the braincase from a point near or at the frontal–squamosal–parietal suture caudoventrally to a point near or at the squamosal–parietal–occipital suture; there is little osteological relief to mark its attachment to the cranium, and the attachments on the right and left sides of the skull are widely separated from one another. In *I. tweedii* the aponeuroses of both sides are joined at dorsal midline just behind the supraorbital foramina and maintain this contact for several millimeters before diverging caudally over the roof of the braincase; the attachments of the aponeuroses sweep caudoventrally to either side of the interparietal and terminate at the lateral nuchal crests where the parietals join the occiput. In adult specimens of *I. tweedii*, the attachment of $ap_1T$ to the skull is marked by a low, bony scar (this is not, however, a distinct temporal ridge as described for *Rattus* and *Sigmodon*; see Weijs, 1973, and Rinker, 1954 respectively).

2. The aponeurosis of the coronoid edge (fig. 62, $ap_2T$) is attached to the leading edge of the coronoid process from a point near the apex of that process rostroventrally to a point just above (*A. leander*) or a little below (*I. tweedii*) the level of the manidbular molar alveoli; at this point the aponeurosis is reflected abruptly medially and caudally to pass between the molars and the base of the coronoid process in the retromolar fossa. Along its attachment to the leading edge of the coronoid process $ap_2T$ is an internal aponeurosis, providing insertion on both sides to fibers of the anterior temporalis; within the retromolar fossa, $ap_2T$ is an external aponeurosis, fibers of the anterior temporalis attaching only to the surface that faces the base of the coronoid process.

3. The aponeurosis of the coronoid tip (fig. 62, $ap_3T$) is distinguished from $ap_2T$ following Weijs (1973) who observed a small discontinuity between the two connective tissue sheets in *Rattus norvegicus*; the discontinuity is difficult to demonstrate in ichthyomyines. $Ap_3T$, exposed for a few millimeters beyond its attachment to the tip of the coronoid process (fig. 65), provides insertion on both sides to fibers of the posterior temporalis. It appears similar in both *Anotomys leander* and *Ichthyomys tweedii*.

TEMPORALIS: The muroid temporalis is a complex muscle and two or more named parts are commonly described by anatomists. Only anterior and posterior parts are here distinguished (superficial and deep parts, respectively, of Rinker, 1954), but even this minimal distinction is difficult to achieve by gross dissection since the two divisions do not have discrete origins on the braincase and fibers from both may anastomose near their insertions to a greater or lesser degree.

ANTERIOR TEMPORALIS: The most superficial fibers of this large muscle (figs. 62, 64, AT) all originate from the deep side of $ap_1T$ and converge rostroventrally to insert on both sides of $ap_2T$ above the leading edge of the coronoid process. Deeper fibers arise from an extensive area of musculous origin on the skull. Fibers originating from the dorsolateral surface of the braincase behind the orbital fossa pass rostroventrally to insert by $ap_2T$

along the leading edge of the coronoid process, or directly onto the tip (lateral side) or distal half (medial side) of that process. These fibers, together with those originating from $ap_1T$, are among the longest of the adductor musculature. By contrast, fibers arising within the orbital fossa are very short and pass almost directly ventrad to insert musculously on the medial aspect of the basal half of the coronoid process and into the retromolar fossa.

This muscle is conspicuously larger in *Ichthyomys tweedii* than in *Anotomys leander* (fig. 64); not only does the area of musculous origin extend over almost the whole dorsal surface of the braincase, but the area of origin within the orbit is more extensive in the former species (fig. 62). It seems likely that increase in the size of this muscle with age is responsible for the considerable erosion of the postorbital region evident in the skulls of old specimens of *Ichthyomys.*

POSTERIOR TEMPORALIS: Fibers of the posterior temporalis (figs. 62, 65, PT) originate musculously on the lateral surface of the braincase and converge rostrally to insert onto the tip of the coronoid process. Most fibers insert by $ap_3T$, but some of the deepest fibers insert musculously on the medial side of the very tip of the coronoid. The most superficial fibers of the muscle are very long; deeper fibers are shorter.

The posterior temporalis is relatively larger in *Ichthyomys tweedii* than in *Anotomys leander* (fig. 65), additional area for origin of the fibers being provided in the former species by the large nuchal crests that form the posterior limits of the squamosal and parietal bones in adult specimens.

APONEUROSES OF THE INTERNAL PTERYGOID: Three aponeuroses participate in the origin and insertion of the internal pterygoid of ichthyomyines.

1. The aponeurosis of origin (fig. 62, $ap_1IP$) is a U-shaped connective tissue sheet, open caudally, that attaches along the lateral margin and the dorsolateral roof of the parapterygoid fossa.
2. The ventral aponeurosis of insertion (fig. 62, $ap_2IP$) attaches to the mandible along the thin, medially inflected ventral edge of the angular process.
3. The dorsal aponeurosis of insertion (fig. 62, $ap_3IP$) attaches to the mandible within the concave medial surface of the angular process above and almost parallel to $ap_2IP$.

INTERNAL PTERYGOID: The internal pterygoid (fig. 62, IP) originates within the parapterygoid fossa, and its fibers pass ventrally, caudally and laterally to insert on the medial aspect and ventral edge of the angular process. The muscle is easily separated into medial and lateral parts (ventral and dorsal parts, respectively, of Rinker, 1954).

The medial part of the internal pterygoid consists of a flat sheet of parallel fibers originating musculously from a narrow region bounded laterally by the internal lamella of $ap_1IP$ and, medially, by the edge of the mesopterygoid fossa; these fibers insert by $ap_2IP$ along the inflected ventral lip of the angular process. In *Ichthyomys tweedii,* some of these fibers also insert musculously along the ventral margin of the mandible where they anastomose with fibers of the superficial masseter.

Fibers of the lateral part of the internal pterygoid originate from both sides of the inner lamella of $ap_1IP$ and from the deep side of the outer lamella of that aponeurosis; fibers also arise musculously from the roof of the parapterygoid fossa between the two lamellae. The fibers of the lateral part of the internal pterygoid insert within the concave medial surface of the angular process musculously and by $ap_3IP$.

## MASTICATORY MUSCLES: WEIGHTS

Some differences in the absolute and relative sizes of muscles between *Anotomys leander* and *Ichthyomys tweedii* are described in the preceding anatomical account and others are evident in accompanying illustrations, but size comparisons are best documented and analyzed quantitatively; muscle size is conveniently quantified by weighing.

The range of variation in muscle wet weights among three duplicate dissections each for *Anotomys leander* and *I. tweedii* (table 39) is small relative to mean values for most muscles with the exception of small parts of the zygomatico-mandibularis. Most masticatory muscles and their constituent parts are absolutely much larger in *Ichthyomys* than in *Anotomys* with the total wet weight of the adductor musculature averaging about four times more massive in the former species.

Functional interpretation of similarities or differences in these weight data is possible only if the quantity of contractile tissue (myofibrils) that actually generates muscular force is a reasonably constant fraction of wet muscle mass. The fraction of dry contractile material composing wet-weighed ichthyomyine masticatory muscle tissue was obtained from acid-digested preparations (see Materials and Methods), but could be determined with confidence only for the larger adductors of *Ichthyomys tweedii*; fluctuations in filter paper weight and other sources of methodological variation prevented acceptably accurate weighing of dried material with a mass less than about 10 mg. The dry weights of contractile material in the superficial masseter, anterior and posterior deep masseter, anterior and posterior temporalis, and internal pterygoid all average 28–32 percent of wet weights with an average range of about 3 percent for homologous values among three specimens of *I. tweedii*. Given this constancy and the similarity of muscle internal architecture between *Anotomys* and *Ichthyomys* detailed above, wet weights probably do represent a nearly constant multiple of myofibril content across muscles and taxa.

TABLE 39

**Absolute Weights (above, in milligrams) and Relative Weights (below, in parentheses) of Wet Masticatory Muscles of *Anotomys leander* and *Ichthyomys tweedii***

| | *Anotomys leander*[b] | | *Ichthyomys tweedii*[c] | |
|---|---|---|---|---|
| Muscle[a] | Range | Mean | Range | Mean |
| SM | 23–24 | 23 | 99–101 | 100 |
| | (.15–.16) | (.15) | (.15–.16) | (.16) |
| ADM | 18–19 | 18 | 62–73 | 67 |
| | (.12–.13) | (.12) | (.10–.11) | (.10) |
| PDM | 20–22 | 21 | 77–97 | 84 |
| | (.14–.15) | (.14) | (.12–.15) | (.13) |
| ZMIO | 5–7 | 6 | 5–7 | 6 |
| | (.03–.04) | (.04) | (.01) | (.01) |
| ZMA | 5–6 | 5 | 22–23 | 22 |
| | (.03–.04) | (.03) | (.03–.04) | (.03) |
| ZMP | 5–8 | 6 | 16–19 | 17 |
| | (.04–.05) | (.04) | (.02–.03) | (.03) |
| AT | 28–31 | 29 | 172–182 | 178 |
| | (.19–.20) | (.20) | (.26–.29) | (.28) |
| PT | 24–29 | 27 | 110–135 | 121 |
| | (.17–.19) | (.18) | (.18–.20) | (.19) |
| IP | 13–14 | 14 | 44–45 | 44 |
| | (.09) | (.09) | (.07) | (.07) |
| Total | 143–157 | 149 | 621–660 | 639 |

[a] Muscle names abbreviated as in the text.

[b] AMNH 244607, UMMZ 126294, 126295.

[c] UMMZ 155782, 155785, 155787.

Muscle wet weights relative to total muscle mass (table 39, parenthetical values) are similar between *Anotomys leander* and *Ichthyomys tweedii* for the superficial masseter (SM), anterior deep masseter (ADM), posterior deep masseter (PDM), anterior and posterior parts of the zygomatico-mandibularis (ZMA, ZMP), posterior temporalis (PT), and internal pterygoid (IP). By contrast, the infraorbital slip of zygomatico-mandibularis (ZMIO), which is of similar absolute size in both species, is relatively much larger in *Anotomys* while the anterior temporalis is relatively larger in *Ichthyomys*. Because *Anotomys leander* and *Ichthyomys tweedii* differ in overall size, however, such proportional differences are difficult to evaluate functionally without some consideration of allometry. An estimate of static allometry in the adductor musculature of ichthyomyines was obtained by extracting the first principal component from the covariance matrix of $\log_e$-transformed muscle wet weights for nine ichthyomyine taxa (table 40). The hypothesis of static isometry for these data (i.e., of constant muscle proportions irrespective of overall size) requires variable loadings all approximately equal to $9^{-1/2} = .333$ (see Jolicoeur, 1963). Most variable loadings on the first principal component (table 41) cluster around this value, but loadings for the infraorbital part of zygomatico-mandibularis (ZMIO) and for the anterior temporalis (AT) suggest strong negative and positive allometry, respectively, for these muscles. Therefore, the relatively larger infraorbital part of zygomatico-mandibularis in *Anotomys leander* and the relatively larger anterior temporalis of *Ichthyomys tweedii* are both consistent with size-correlated proportional variation among other ichthyomyines as well. While this observation does not preclude a functional interpretation of such relative differences, plausible explanations seem likely

TABLE 40
**Absolute Weights (above, in milligrams) and Relative Weights (below, in parentheses) of Wet Masticatory Muscles of Nine Ichthyomyine Taxa**

| Taxa[a] | Muscles[b] | | | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| | SM | ADM | PDM | ZMIO | ZMA | ZMP | AT | PT | IP | |
| *Ale* | 23 | 18 | 21 | 6 | 5 | 6 | 29 | 27 | 14 | 149 |
| | (.15) | (.12) | (.14) | (.04) | (.03) | (.04) | (.20) | (.18) | (.09) | |
| *Ctr* | 17 | 13 | 17 | 4 | 6 | 7 | 24 | 17 | 14 | 119 |
| | (.14) | (.11) | (.14) | (.03) | (.05) | (.06) | (.20) | (.14) | (.12) | |
| *Iso* | 65 | 55 | 55 | 4 | 21 | 17 | 112 | 65 | 26 | 420 |
| | (.16) | (.13) | (.13) | (.01) | (.05) | (.04) | (.27) | (.16) | (.06) | |
| *Ipi* | 131 | 92 | 86 | 6 | 36 | 21 | 209 | 102 | 50 | 733 |
| | (.18) | (.13) | (.12) | (.01) | (.05) | (.03) | (.28) | (.14) | (.07) | |
| *Itw* | 100 | 67 | 84 | 6 | 22 | 17 | 178 | 121 | 44 | 639 |
| | (.16) | (.10) | (.13) | (.01) | (.03) | (.03) | (.28) | (.19) | (.07) | |
| *Nmo* | 32 | 21 | 22 | 5 | 7 | 6 | 41 | 23 | 15 | 172 |
| | (.19) | (.12) | (.13) | (.03) | (.04) | (.03) | (.24) | (.14) | (.09) | |
| *Rme* | 74 | 57 | 61 | 5 | 14 | 21 | 99 | 55 | 36 | 422 |
| | (.18) | (.14) | (.14) | (.01) | (.03) | (.05) | (.24) | (.13) | (.08) | |
| *Rha* | 43 | 30 | 30 | 4 | 15 | 10 | 61 | 34 | 23 | 250 |
| | (.17) | (.12) | (.12) | (.02) | (.06) | (.04) | (.24) | (.14) | (.09) | |
| *Run* | 37 | 35 | 26 | 3 | 9 | 9 | 57 | 28 | 25 | 229 |
| | (.16) | (.15) | (.11) | (.01) | (.04) | (.04) | (.25) | (.12) | (.11) | |

[a] Taxon abbreviations and specimens: *Ale, Anotomys leander* (see footnote b, table 39); *Ctr, Chibchanomys trichotis* (UMMZ 156376); *Iso, Ichthyomys hydrobates soderstromi* (AMNH 64624); *Ipi, I. pittieri* (MBUCV I-2776); *Itw, I. tweedii* (see footnote c, table 39); *Nmo, Neusticomys monticolus* (UMMZ 155789, 155793); *Rme, Rheomys mexicanus* (AMNH 205320); *Rha, R. raptor hartmanni* (UMMZ 111985); *Run, R. underwoodi* (UMMZ 115389).

[b] Muscle names abbreviated as explained in the text.

to invoke size-dependent aspects of masticatory biomechanics rather than the size-independent differences in craniodental morphology whose discovery prompted these comparisons.

The first principal component accounts for 94 percent of the total variance in adult masticatory muscle weights among ichthyomyines (table 41); subsequently extracted components each account for less than 3 percent of the total variance and suggest no biologically comprehensible patterns of covariance. For example, the infraorbital part of zygomatico-mandibularis (ZMIO) is the most heavily weighted variable by a large margin on the second principal component, but this muscle, a mere shred of fibers and tendons, is measured with such a large relative error variance (the standard deviation attributable to error, determined from repeated weighings, is 12–13% of the mean) that its large loading on a component accounting for only 2.6 percent of the total interspecific variation can bear no defensible functional interpretation.

## FOOD AND FEEDING BEHAVIOR

ICHTHYOMYINE DIETS: Following procedures outlined in Materials and Methods, I analyzed the contents of 81 ichthyomyine digestive tracts consisting of the following samples: *Anotomys leander* (N = 14), *Chibchanomys trichotis* (4), *Ichthyomys hydrobates hydrobates* (1), *I. h. soderstromi* (1), *I. tweedii* (8), *Neusticomys monticolus* (23), *N. venezuelae* (2), *Rheomys raptor hartmanni* (2), *R. mexicanus* (19), *R. thomasi stirtoni* (1), *R. t. thomasi* (2), *R. underwoodi* (4). These dissections, together with the published reports of Thomas (1893), Goldman (1920), Stirton (1944), Wagner (1961), Hooper (1968), Goodwin (1969), and Voss et al. (1982) provide direct or indirect information on the diets and feeding behavior of about 100 individuals (Stirton, 1944, did not report his sample sizes, so an exact count is not available). The data are not as extensive as could be wished, but several generalizations seem adequately supported.

Ichthyomyines appear to be almost exclusively carnivorous. Aside from isolated leaflets of moss and other small plant fragments that could have been ingested accidentally, evidence of deliberate vegetable consumption (consisting of several seeds) was present in only one digestive tract of the 81 that I examined. Stirton (1944) reported "a dark pink stained pulp possibly blackberry" and "white starchy pulp" in some of the stomachs of *Rheomys thomasi thomasi* that he dissected, and Wagner (1961) reported "grünen Pflanzenbrei, warscheinlich Brunnenkresse" from one stomach of *R. t. stirtoni,* but microscopic examination of such indeterminate pasty materials in rodent stomachs is necessary to confirm their vegetable origin (Jameson, 1952). As against these few examples of real or apparent herbivory, all of the digestive tracts that I examined and most of those examined by the authors cited above contained abundant animal remains.

Vertebrate material is not common in ichthyomyine guts. Thomas (1893) found the remains of a fish in the stomach of the holotype of *Ichthyomys stolzmanni,* Voss et al. (1982) reported fish bones from the digestive tracts of two *I. tweedii* from Ecuador, Stirton (1944) reported "bones and flesh" of salamanders together with feathers and fur from the stomachs of an unspecified number of *Rheomys thomasi stirtoni* from El Salvador, Hooper (1968) discovered remains of a catfish in the stomach of one *R. t. stirtoni* from Guatemala, and Goodwin (1969) reported fish scales from one *R. mexicanus* stomach from Oaxaca. In addition, I found tetrapod bones in the stomach of another *R. mexicanus* from Oaxaca and a single tadpole in the stomach of an *Anotomys leander* from Ecuador. These are the only records of vertebrate consumption by ichthyomyines. By contrast, all of the digestive tracts I examined, including those with vertebrate bones and integument in them, contained abundant arthropod exoskeletal fragments; Hooper (1968) and Goodwin (1969) also reported arthropods in the stomachs of most of their ichthyomyine specimens.

TABLE 41
**Principal Components Analysis of Muscle Weight Data from Nine Ichthyomyine Species**

| | *PC*1 | *PC*2 |
|---|---|---|
| % Variance | 93.9 | 2.6 |
| Loadings: | | |
| SM | .377 | .086 |
| ADM | .365 | −.138 |
| PDM | .348 | .196 |
| ZMIO | .047 | .702 |
| ZMA | .358 | −.332 |
| ZMP | .288 | −.345 |
| AT | .426 | .002 |
| PT | .373 | .445 |
| IP | .262 | −.119 |

Arthropod prey could be positively identified to order or family (often to genus and sometimes to species) based on macroscopically distinctive fragments (see Materials and Methods) contained in 63 of the ichthyomyine digestive tracts I examined. Of these, all except a single ant, one wasp, and one spider are representatives of the benthic fauna of streams. The following taxa were represented among the identified material: CRUSTACEA, Amphipoda (family undetermined), Decapoda (Pseudothelphusidae); INSECTA, Coleoptera (larval Elmidae and Helodidae), Diptera (larval Blephariceridae, Chironomidae, Simuliidae, and Tipulidae), Ephemeroptera (nymphal Baetidae, Heptageniidae, Leptophlebiidae, and Trichorythidae), Megaloptera (larval Corydalidae), Odonata (one nymph unidentified to family), Orthoptera (aquatic adult Blattidae), Plecoptera (nymphal Gripopterygidae and Perlidae), Trichoptera (larval Calamoceratidae, Hydropsychidae, Leptoceridae, Limnephilidae, and Rhyacophilidae). Some of the unidentified arthropod remains in digestive tracts might represent nonaquatic prey obtained on terra firma, but the diversity of identified aquatic taxa provides substantial evidence that ichthyomyines regularly forage for arthropods in streams. Table 42 documents the diversity of arthropod prey taxa represented in ichthyomyine digestive tracts from four localities.

TABLE 42
**Taxonomic Diversity of Aquatic Arthropods in Ichthyomyine Digestive Tracts**
(Table entries list numbers of genera and species)

| | Predator taxa and sample localities[a] | | | |
|---|---|---|---|---|
| Prey taxa | *Anotomys leander* Ecuador, Papallacta | *Chibchanomys trichotis* Venezuela, Buena Vista | *Ichthyomys tweedii* Ecuador, Mindo | *Neusticomys monticolus* Ecuador, Guarumal |
| CRUSTACEA | | | | |
| Amphipoda | | | | |
| Family indet. | gen. and sp. indet. | | | |
| Decapoda | | | | |
| Pseudothelphusidae | | | gen. and sp. indet. | |
| INSECTA | | | | |
| Coleoptera | | | | |
| Elmidae | 1 gen., 1 sp. | | | |
| Helodidae | | 2 gen., 2 sp. | | 1 gen., 1 sp. |
| Diptera | | | | |
| Blephariceridae | 1 gen., 1 sp. | | | |
| Chironomidae | gen. and sp. indet. | | | |
| Tipulidae | 1 gen., 1 sp. | 1 gen., 1 sp. | | gen. and sp. indet. |
| Ephemeroptera | | | | |
| Baetidae | 2 gen., 2–3 sp. | | 1 gen., 1 sp. | 1 gen., 1 sp. |
| Leptophlebiidae | | 1–2 gen., 2–3 sp. | | 1–2 gen., 1–2 sp. |
| Trichorythidae | | 1 gen., 1 sp. | | |
| Megaloptera | | | | |
| Corydalidae | | | 1–2 gen., 1–2 sp. | |
| Orthoptera | | | | |
| Blattidae | | | gen. & sp. indet. | |
| Plecoptera | | | | |
| Gripopterygidae | 1 gen., 1 sp. | | | |
| Perlidae | | 1 gen., 1–2 sp. | | 1 gen., 1–2 sp. |
| Trichoptera | | | | |
| Calamoceratidae | | | | 1 gen., 1 sp. |
| Hydropsychidae | 1 gen., 1 sp. | | 1 gen., 1 sp. | 1 gen., 1 sp. |
| Leptoceridae | | 1 gen., 1 sp. | | |
| Limnephilidae | 1 gen., 1 sp. | | | |
| Rhyacophilidae | 1 gen., 1 sp. | | | |
| TOTALS: | 11 gen., 11–12 sp. | 7–8 gen., 8–10 sp. | 5–6 gen., 5–6 sp. | 7–8 gen., 7–9 sp. |

[a] Sample sizes: *Anotomys leander,* 12; *Chibchanomys trichotis,* 4; *Ichthyomys tweedii,* 8; *Neusticomys monticolus,* 8.

*Anotomys* and *Ichthyomys*: Twelve digestive tracts of *Anotomys leander* collected from the vicinity of Papallacta, Provincia Napo, Ecuador, contained amphipod crustaceans and representatives of the following insect taxa: COLEOPTERA, Elmidae (larvae of an undetermined genus); DIPTERA, Blephariceridae (larvae of *Blepharicera*), Chironomidae (larvae of an undetermined genus), Tipulidae (larvae of *Limonia*); EPHEMEROPTERA, Baetidae (nymphs of *Baetis* and *Baetodes*); TRICHOPTERA, Hydropsychidae (larvae of *Smicridea*), Limnephilidae (larvae of *Anomalocosmoecus*), Rhyacophilidae (larvae of *Atopsyche* and/or *Cailloma*). All of these are small animals—specimens recovered from stream samples ranged from slightly less than 5 to just over 20 mm (rhyacophilid caddisflies only), but most averaged 5–15 mm.

Eight digestive tracts of *Ichthyomys tweedii* collected in the vicinity of Mindo, Provincia

Napo, Ecuador, contained a less diverse assortment of prey. Taxa identified from stomachs or hindguts included fishes (Characidae), pseudothelphusid crabs, and insects: EPHEMEROPTERA, Baetidae (nymphs of *Baetis*); MEGALOPTERA, Corydalidae (larvae of *Corydalus* and/or *Chloronia*); ORTHOPTERA, Blattidae (genus undetermined); TRICHOPTERA, Hydropsychidae (larvae of *Smicridea*). Of these, fish bones and exoskeletal fragments of mayfly nymphs and caddisfly larvae were sparingly represented in the hindguts of just two specimens. The bulk of material in the digestive tracts consisted of pseudothelphusid crabs, dobsonfly larvae, and aquatic roaches (Blattidae). Pseudothelphusid crabs collected from streams near Mindo range from 10 to 65 mm in measured carapace width, but fragments contained in rat guts suggest that eaten individuals were about 30–35 mm wide in the carapace. Dobsonfly larvae in stream samples range from 15 to 65 mm in length, and fragments from digestive tracts suggest that rats eat larvae of all sizes including the very largest. Blattid roaches range in measured lengths from a little less than 5 to over 20 mm; fragments in rat guts were mostly of large individuals.

The small sample sizes on which these observations are based do not permit elaborate inference about the foods of *Anotomys leander* and *Ichthyomys tweedii*. At most, the data suggest that *A. leander* eats diverse aquatic arthropods of small size, while *I. tweedii* may regularly include much larger prey in its diet. Other lines of evidence, however, combine to support and extend this simple hypothesis.

Figure 66 illustrates the size frequency distribution of arthropods collected from streams in which *A. leander* and *I. tweedii* were trapped (at Papallacta and Mindo, respectively). Arthropods were collected, sorted, and identified following procedures previously explained in Materials and Methods, but two aspects of those procedures require discussion here. Firstly, kickscreening was not an unbiased sampling method because very small or elongate animals were quickly lost through the coarse window-screen mesh that I used. The histograms of figure 66 may therefore underestimate the relative taxonomic diversity of arthropods in the smallest size class. Secondly, stream arthropods were not collected with the intention of using them in the present context; instead, samples were taken to facilitate identification of prey in ichthyomyine stomachs. While a meticulous effort was made to collect representatives of all size classes for each recognizable taxon, not all of the material recovered from kickscreens was preserved, and I cannot altogether rule out the possibility that bias was inadvertently introduced by discarding specimens deemed superfluous.

As against these potential shortcomings, roughly equivalent effort was devoted to sampling stream arthropod communities at Papallacta and Mindo, consisting at each locality of 15–20 carefully sorted screen samples and 6–8 hours devoted to the other explicit sampling procedures described in Materials and Methods. In addition, between 200 and 300 hours were spent working in stream habitats at each locality, wading the streams by day and night, setting traps in shallow water, turning rocks and excavating banks, whereby a strong impression was gained that no large and conspicuous elements of the arthropod fauna were missed. Although both samples represent the arthropods present over just a few weeks at each locality, equatorial stream arthropod communities do not exhibit the marked seasonal fluctuations in taxonomic and ontogenetic composition that are characteristic of streams at higher latitudes (Bishop, 1973; Bottger, 1975; Corbet, 1964; Statzner, 1976; Zwick, 1976). In short, I believe that figure 66 provides comparable size distributions for the commonest arthropod taxa larger than 5 mm that are present year-round in streams at both localities.

In the stream samples from Papallacta, most arthropods were less than 15 mm in length; *Anotomys leander* could take such small items into its mouth entire, and observations from stomach contents suggest that it often does. Much of the material contained in *Anotomys* stomachs consists of whole animals, substantially intact, although punctured, cut, or crushed to a greater or lesser degree and missing legs, cerci, and other fragile appendages (fig. 67). Larval tipulids (*Limonia*), tabanids (*Tabanus*), and rhyacophilids (*Cailloma* and *Atopsyche*) collected at Papallacta sometimes exceed 15 mm in

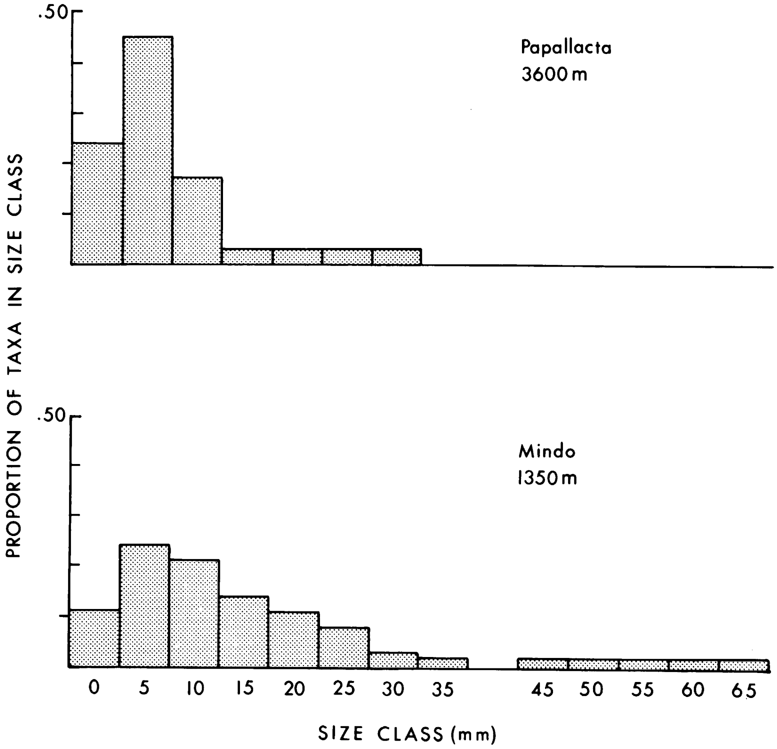


Fig. 66. Size distribution of benthic arthropods collected from streams at Papallacta (14 April 1980) and Mindo (27–28 July 1980). See Gazetteer (Appendix) for geographical information about these Ecuadorean localities.

length (large *Tabanus* may reach 30 mm), but while *Anotomys* would probably have to cut such larger prey into chewable fragments with its incisors, these are soft-bodied organisms whose thin, pliant cuticles would offer little resistance to sharp enamel edges.

At Mindo, the taxonomic diversity of arthropods in the large size classes is greater (members of at least 12 crustacean and insect families are greater than 15 mm in length) and some taxa are huge. Pseudothelphusid crabs, dobsonfly larvae, and aquatic roaches are among the commonest invertebrates in streams near Mindo and were present in almost every kickscreen sample. These animals are eaten by *Ichthyomys tweedii* but they are too large to be chewed entire (fig. 68, top) and must therefore be reduced to ingestible fragments by incisor action. Although no direct observations of the feeding behavior of *I. tweedii* are available, Voss et al. (1982) described and illustrated the feeding behavior of *I. pittieri,* a lowland congener that also eats crabs and dobsonfly larvae. *I. pittieri* uses its large incisors (which resemble those of *I. tweedii*) to dismember crabs (fig. 69) with bites through the limb articulations, and to expose the viscera with bites through the hard carapace and plastron. *I. pittieri* ingests only the soft parts of crabs and does not use its molars to reduce exoskeletal structures. *I. pittieri* also kills dobsonfly larvae and tears them apart into chewable fragments with incisor bites through the hard head capsule and thoracic sclerites and the tough, leathery abdominal integument.

## DISCUSSION

RODENT MANDIBULAR FUNCTION: The procurement and mechanical reduction of food by all rodents minimally involves two distinct behaviors in which force is applied by separate elements of the upper and lower dentitions (Becht, 1953; Hiiemae and Ardran, 1968; Weijs, 1975; Gorniak, 1977). Incisor

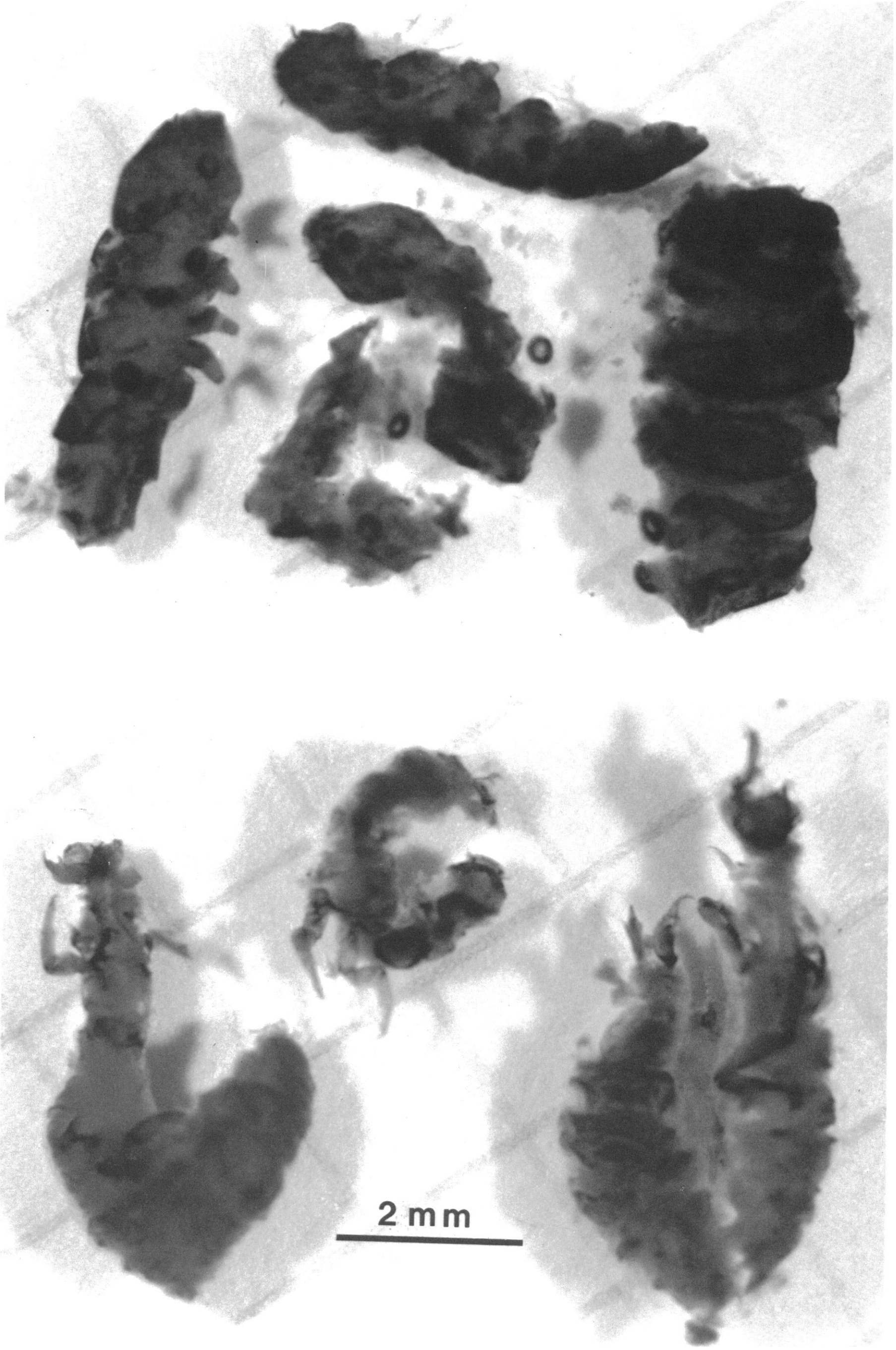


Fig. 67. Prey recovered from stomachs of *Anotomys leander* (AMNH 244607; UMMZ 126295, 155598, 155600). **Top:** larvae of net-winged midges (Diptera, Blephariceridae). **Bottom:** larvae of primitive caddisflies (Trichoptera, Rhyacophilidae). Scale applies to both photographs.

biting is accomplished by anterior translation and depression of the mandibles so that food can be grasped between the tips of the upper and lower incisors. Food particles are sepa-

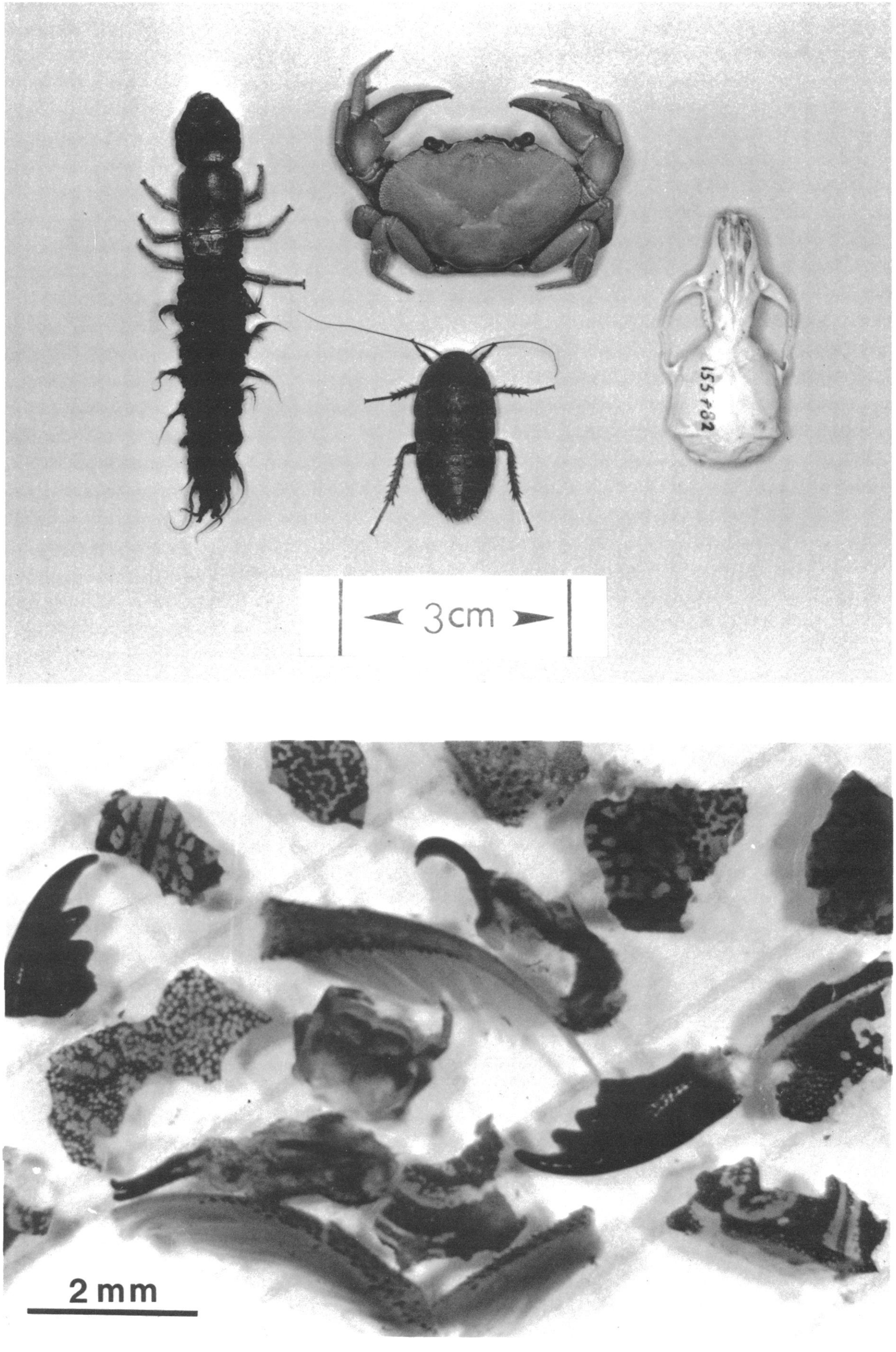


Fig. 68. Prey and stomach contents of *Ichthyomys tweedii*. **Top** (clockwise from right): adult skull of *I. tweedii*; aquatic roach (Orthoptera, Blattidae); dobsonfly larva (Megaloptera, Corydalidae); crab (Decapoda, Pseudothelphusidae). **Bottom:** fragments of dobsonfly larvae from stomachs of UMMZ 155785 and 155786; fragments include mandibles and other mouthparts, pieces of thoracic sclerites, abdominal filaments, and hooked anal prolegs.

Fig. 69. *Ichthyomys pittieri* (MBUCV I-2776) eating a small pseudothelphusid crab.

rated from the bolus (or removed from the substrate) by apposition of the incisor tips and are then transported posteriorly by the tongue and gathered between the molar rows. In order to chew the food particles thus accumulated, the mandible is retracted and elevated in order to bring the upper and lower molars into occlusion and apply pressure to the material held between them.

Because the rodent mandible must be displaced to apply force at each of two points separated along an anterior–posterior axis, the glenoid fossa is a shallow, longitudinal trough without restricting anterior or posterior bony processes and the condyle is free to slide forward and back within the confines of the fossa (Becht, 1953; Smith and Savage, 1959; Risnes, 1973; Weijs, 1975). During incisor biting, the rodent mandibular apparatus works at a mechanical disadvantage with respect to the vertical component of forces developed by the adductor muscles since this must be resisted both at the incisor tips and by the roof of the glenoid fossa (Hiiemae, 1971); the anterior component of the muscular resultant, however, is unresisted at the glenoid because of the sliding action of the joint described above, and is transmitted entirely to food held between the teeth. The effective application of force at the incisor tips is therefore likely to be maximized by a strongly protrusive musculature (Weijs and Dantuma, 1975).

*ANOTOMYS* AND *ICHTHYOMYS*: The preceding descriptive accounts document differences in dental morphology and occlusion between *Anotomys leander* and *Ichthyomys tweedii* that merit summary repetition.

The incisors of *Anotomys leander* are narrow and delicate with thin enamel cutting edges and a fine, tapering bevel; the upper and lower molars, however, are large, with tall, sharp cusps and broad, transverse crests that interpenetrate deeply in centric occlusion. The incisors of *Ichthyomys tweedii* are disproportionately broader and deeper than those of *A. leander,* with stoutly bevelled cutting edges that are turned medially to produce the lateral tips as sharp, divergent points reinforced with thicker enamel; by contrast, the molars of *Ichthyomys* are absolutely and relatively smaller than those of *Anotomys,* with lower, rounded cusps that are not anteroposteriorly compressed and exhibit shallow occlusal interpenetration.

Microscopic evidence of wear indicates that the upper and lower incisors of both ichthyomyine genera occlude by simple apposition of the sharp cutting edges, but the narrowness of the enamel edges and the overall more delicate structure of these teeth in *A. leander* imply some less forceful role in food procurement or reduction than is accomplished by the broader, more robust incisors of *I. tweedii.* Wear striations on the molars provide more direct evidence of differences in dental function. The lower molars of *A. leander* are drawn vertically into centric occlusion, a movement whereby food held between the teeth would be punctured by the tall, interpenetrating cusps and then sheared as the edges of V-shaped transverse crests on the lower teeth engaged the reciprocally inverted-V-shaped edges of transverse crests on the upper teeth. The lower molars of *A. leander* are drawn out of centric occlusion by an anteromedial mandibular movement that could have a crushing effect on food remaining between the teeth in the centric position. There is no evidence for such a two-phase masticatory stroke in *I. tweedii*; chewing is, for this species, apparently accomplished in a single anteromedially directed mandibular movement producing a simultaneous scooping action by blunt upper and lower molar cusps into shallow dentine basins of the occluding teeth. Overall, molar action in *A. leander,* effected by larger teeth with more complex occlusal relationships between formidable cusps and crests, seems better suited to thoroughly triturate resistant food than the less elaborate movements apparently involved in chewing by the smaller, occlusally simpler molars of *I. tweedii.*

Since the morphology of dental surfaces effectively determines the direction of jaw movement when the teeth are near occlusion (Kay and Hiiemae, 1974) and since the occlusal phase of the masticatory cycle is usually when peak muscular forces are developed (Weijs, 1980), the dental contrasts described above between *A. leander* and *I. tweedii* should be accompanied by appropriate differences in the muscles whose contractions produce masticatory movements and forces. The internal architecture of mandibular adductors is almost identical between the two genera, however, and differences in relative weights of muscles appear largely to conform with static allometric trends observed across other ichthyomyine taxa. Instead, functionally interpretable contrasts in mandibular myology between *Anotomys* and *Ichthyomys* consist chiefly of differences in the gross position and orientation of several large adductors.

Figure 70 abstracts the principal contrasts in adductor morphology between *Anotomys leander* and *Ichthyomys tweedii.* The mandibles of both genera are illustrated with the molars in centric occlusion to standardize the comparison; in that position, selected muscles or muscle parts are represented by their working lines, construed as vectors from the center of insertion to the center of origin of each. The muscles and muscle parts illustrated are those whose position and orientation differ strikingly and whose probable working lines could most readily be inferred from maps of origins and insertions (fig. 62) together with consideration of internal fiber arrangements. From superficial to deep, the adductors depicted are (1) the superficial masseter; (2) the rostral portion of the anterior deep masseter (i.e., the wedge-shaped mass of fibers arising musculously or by $ap_2DM$ from the inferior zygomatic root and inserting by the reflected anterior margin of $ap_4DM$); (3) the superficial oblique part of the posterior deep masseter (PDM1); and (4) the internal pterygoid. In *A. leander* the working line of the rostral part of the anterior deep masseter (2) passes through the occluding first molars (in sagittal projection), but in *I. tweedii* the homologous vector passes anterior to those teeth. Intergeneric differences for the superficial masseter (1), the superficial oblique part of the posterior deep masseter (3), and the internal pterygoid (4) consist in

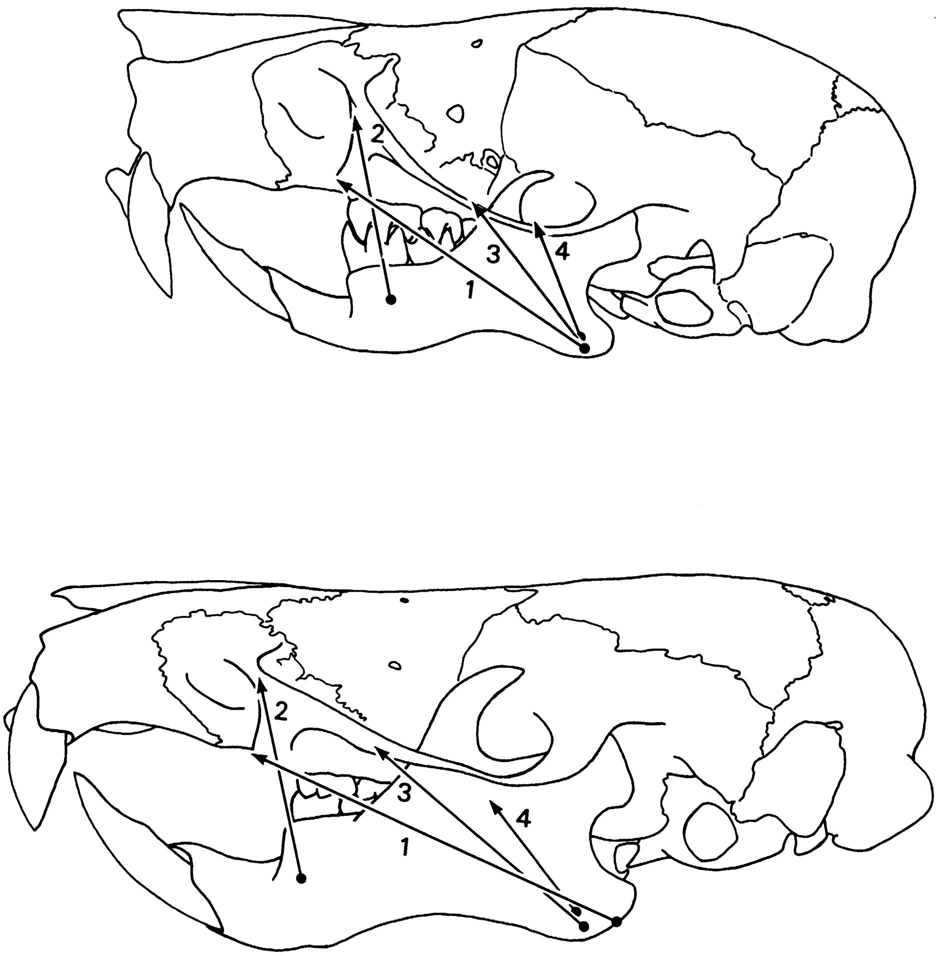


Fig. 70. Working lines of four mandibular adductor muscles for *Anotomys leander* (top) and *Ichthyomys tweedii* (bottom). Differences between the two species are illustrated for the superficial masseter (1), the rostral part of the anterior deep masseter (2), the superficial part of the posterior deep masseter (3), and the internal pterygoid (4). See text for further explanation.

their more protrusive working lines in *Ichthyomys* than in *Anotomys.*

These differences in muscle orientation between the two genera are functionally consistent with the inferences derived earlier from comparisons of dental morphology and occlusion. Mandibular adductors whose lines of action pass through the bite point evoke no reaction in the jaw joint and transmit the entire resultant force of their contraction to food held between the teeth. The position and orientation of the rostral part of the anterior deep masseter in *Anotomys* therefore suggests that effective molar action rather than a strong incisor bite (which would be maximized by longer moments about the jaw joint) is emphasized by the design of the masticatory apparatus of that genus. The working line of the anterior deep masseter parallels the slant of the occluding molar cusps and crests, and the contraction of this muscle is plausibly responsible, at least in part, for the high occlusal pressures that mark those enameled surfaces with parallel vertical scratches. The simultaneous contraction of closing retrusors (such as the posterior temporalis), however, would also be necessary to maintain the molar blades in effective contact as they are drawn vertically into the centric position.

In *Ichthyomys,* the position of the rostral part of the anterior deep masseter in front of the molar rows together with the more protrusive working lines of the superficial masseter and the other adductors illustrated in figure 70 suggest that the masticatory system of that animal emphasizes effective use of its disproportionately large and stout incisors. Relative to a more posterior working line through the molar rows, the position of the anterior deep masseter in *I. tweedii* yields a longer moment about the joint and a correspondingly greater mechanical advantage to development of vertical forces at the incisor bite. The contribution of protrusive muscle arrangements to forceful incisor apposition has already been discussed. None of the muscular alignments in which *I. tweedii* differs from *A. leander* suggests any increased occlusal advantage gained by the diminutive molars of the former species.

The limited dietary data available for *Anotomys leander* and *Ichthyomys tweedii* together with information about the arthropod faunas of the streams that these rodents inhabit suggest possible adaptive explanations for the evident differences in masticatory function revealed by the preceding analyses of dental morphology, occlusion, and mandibular myology. If most of the arthropods available as prey to *A. leander* can be taken into the mouth entire, then the narrow incisors of that species might serve no more forceful role than that of removing adherent organisms from rocky surfaces in the current; most of the needful mechanical partitioning of prey might then be accomplished by the formidable molar dentition. The soft-bodied fly larvae that are the largest members of the stream fauna at Papallacta, if eaten by *A. leander,* probably do not offer appreciable resistance to muscular forces applied at the incisor tips. By contrast, many of the larger arthropods available as prey to *I. tweedii,* including those that are known to be eaten by that rat, cannot be taken into the mouth entire and are protected by heavily sclerotized exoskeletons that must be broken by powerful incisor bites. The size and shape of the incisors of *I. tweedii* together with the orientations of several large adductors are conspicuous design features to enable a strong anterior bite, and the mechanical reduction of prey thus effected might diminish the need for thorough molar trituration.

COMPARISONS WITH OTHER RODENTS: The protrusive musculature required by rodent incisor function can also be exploited for molar chewing with minimal mechanical compromise if the masticatory power stroke is propalinal (posterior to anterior), and this felicitous arrangement is so common in Rodentia that many have assumed it to be universal: "Both gnawing and chewing in rodents involve predominantly anteroposterior (propalinal) movements of the mandible. The characteristic structural modifications of rodent jaws and jaw musculature are all related to this type of movement" (Moore, 1981: 178). The masticatory apparatus of ichthyomyines (and those of many other muroids; see Lemire, 1966, and Gorniak, 1977, for examples), however, differs in important respects from the more familiar morphologies that have prompted such generalizations. Anteroposterior mandibular movements are not possible when cuspidate ichthyomyine molars are near occlusion, and the protrusive muscle alignments required for strong incisor biting are therefore less suitable for effective chewing than in rodents with propalinal masticatory strokes. *Sigmodon hispidus* is an example of the latter, and a comparison of its masticatory apparatus (fig. 71) with those of *Anotomys* and *Ichthyomys* is instructive.

The masticatory musculature of *Sigmodon* (described and illustrated by Rinker, 1954) is strongly protrusive, almost every muscle acting either to draw the mandible forward or back. The most conspicuous osteological features that contribute to this arrangement are the location of the broad zygomatic plate (carrying the origin of the anterior deep masseter) in front of the molar rows, and the production of the angular process of the mandible (carrying the insertions of the superficial masseter and internal pterygoid) well behind the articular condyle. Muscular protrusion of the mandible is obviously necessary to bring the tips of the lower incisors into contact with those of the strongly opisthodont upper teeth, but the power stroke of mastication in this rodent is also protrusive (as evidenced by the worn surfaces of the flat-crowned molars), and the same arrangement of mandibular ad-

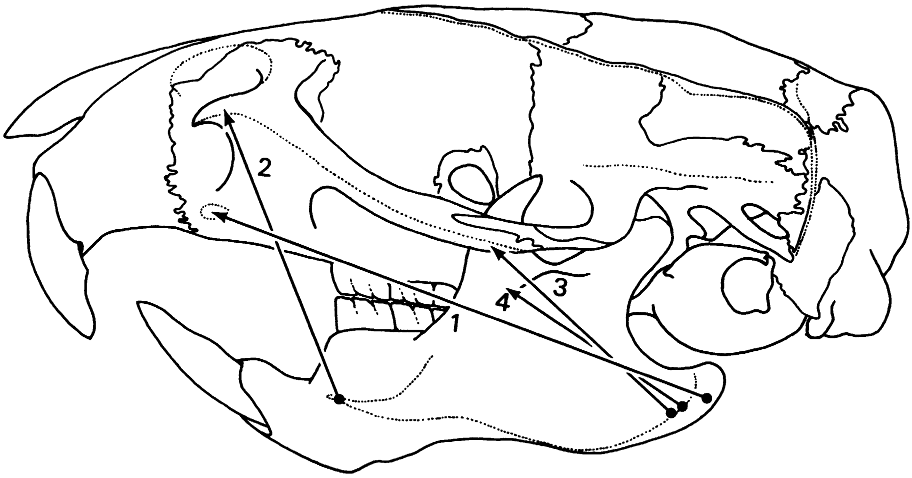


Fig. 71. Working lines of four mandibular adductor muscles for *Sigmodon hispidus*. Numbered vectors represent the same muscles as in figure 70.

ductors that effects forceful incisor apposition also serves to draw the lower molars forward in grinding occlusal contact with the upper teeth.

Ichthyomyine upper incisors are noticeably less opisthodont (posteroventrally recurved) than those of *Sigmodon,* and the anteroposterior distance between the upper and lower incisor tips is less when the molars are near occlusion (compare figs. 70 and 71). To effect incisor biting, ichthyomyines therefore need not protrude their mandibles as far from the position of molar function, and the incisive cutting edges are also aligned to facilitate a less protrusive bite. Correspondingly, the osseous structures providing origins and insertions for mandibular adductors that produce forward translation of the mandible are closer to the occluding molar rows in ichthyomyines than in *Sigmodon,* although *Ichthyomys* exhibits an appreciably more protrusive arrangement of those elements than does *Anotomys.*

The overall impression gained by these comparisons is that ichthyomyine craniodental morphologies are designed to minimize the anteroposterior mandibular displacement necessary to achieve alternate molar and incisor contacts. The transverse mandibular movements involved in ichthyomyine chewing may also serve this end by effecting a relatively large displacement of occlusal surfaces with only minor translatory movements of the condyles. Masticatory mechanisms thus conservative of mandibular translation may permit jaw muscles to work at almost isometric conditions near their resting lengths with little diminution of their contractile force at any functional jaw position (Weijs and Dantuma, 1981).

MASTICATION AND MORPHOMETRICS: Among the results of morphometric analyses presented earlier was the observation that a single pattern of covariances, reflected in the signs and magnitudes of variable loadings on the principal shape factor, *H,* accounts for over half of the size-independent metric variation in craniodental morphology among ichthyomyine species. Variables with the highest (positive or negative) loadings on *H* are measurements of teeth (LM, BM1, BIT, DI) or of spaces between teeth (BPB), and that factor was hypothesized to represent, at least in part, a system of morphological integration within the masticatory apparatus. Data reported in this section provide additional insights about the biological significance of the statistical associations among metric characters that *H* represents.

Contrasts in molar and incisor size between *Anotomys leander* and *Ichthyomys tweedii* are accompanied by differences in occlusion and masticatory musculature that, together with previous functional studies of other rodents, suggest biomechanical interpretations for some observed covariances. Thus, the conspicuous dependence of incisor breadth and depth (BIT, DI) in the residual matrix of table 36 is reasonably explained by the coincident structural requirements of strong incisor biting, a dental function most effectively accomplished by teeth that are wide enough to provide an ample cutting edge and deep enough to resist deforming stresses developed at the tips (Ryder, 1877). Similarly, thorough molar trituration of arthropods is likely effected by teeth with expanded reentrant folds that permit deep interpenetration of cusps and with broad transverse crests that increase the length of shearing blades, design criteria whose functional congruence plausibly explains the strong positive association between LM and BM1.

Within the residual covariance matrix (table 36) from which the principal shape factor was extracted, however, there are also large negative associations among dental measurements. Four of these, cov(LM, BIT), cov(BIT, BM1), cov(BM1, DI), and cov(LM, DI), reflect an inverse relationship between molar and incisor size that would be inexplicable among rodents with propalinal masticatory morphologies (see fig. 71 and accompanying discussion above) in which little or no mechanical compromise between molar and incisor function is evident. The power stroke of ichthyomyine mastication is not propalinal, however, and it is therefore possible that no arrangement of mandibular adductors can simultaneously maximize the efficacy of both incisor and molar function. Molar trituration of arthropods is probably most effective when cusps and crests are tall and interpenetrate deeply, but muscles that facilitate the action of such teeth by alignments adjacent and parallel to the vertical planes of occlusal contact (e.g., the anterior deep masseter of *Anotomys leander,* fig. 70) may do so at the expense of their contribution to forceful incisor biting. Conversely, the protrusive muscle alignments required to forcefully approximate upper and lower incisor tips may not contribute to effective interpenetration of vertical molar cusps or crests, and the longer moments about the jaw joint of muscle working lines that maximize vertical forces at the incisor bite might compromise the fine control of complex molar occlusal movements. The biomechanics of optimal molar and incisor function may therefore be irreconcilable, but both may not be required by carnivorous muroids. Elaborate molar chewing is probably superfluous if suitably subdivided fragments result from incisor action; alternatively, if prey are small enough to be chewed entire, extensive incisor preparation might be equally unnecessary. Size-independent negative covariances between measurements of molars and incisor may therefore reflect the economical distribution of mineralized tissue among dental elements in accordance with the primary or secondary role in food reduction accomplished by each.

Variation in other metric characters with large loadings on *H* may also result from the alternative design requirements of optimal molar and incisor function. Conspicuous among these is BPB, an index of the width of the maxillary palate upon which food is processed and positioned by the tongue during molar trituration (Hiiemae and Ardran, 1968; Kutusov and Sicher, 1952; Weijs, 1975); palatal breadth is also a dimension that must accommodate the medial displacement of molars drawn from centric occlusion during the transverse mandibular movements of ichthyomyine chewing. The positive covariance between BPB and measurements of molar size (LM, BM1) perhaps reflects such requirements for a more spacious oral cavity in species that chew their prey entire. Conversely, negative associations between BPB and indices of incisor robustness (BIT and DI) are consistent with the inferred diminution of molar action in masticatory systems that effect food reduction chiefly with a large anterior dentition.

Breadth of the Zygomatic Plate (BZP) is less heavily weighted on *H* than the other morphological covariates discussed above, and its relationships to masticatory function are correspondingly less obvious. The inferior zygomatic root whose anteroposterior dimension is indexed by this measurement is, however, the only structural element of the skull that could effectively support the anterior portion of the zygomatic arch against the forces developed by mandibular adduc-

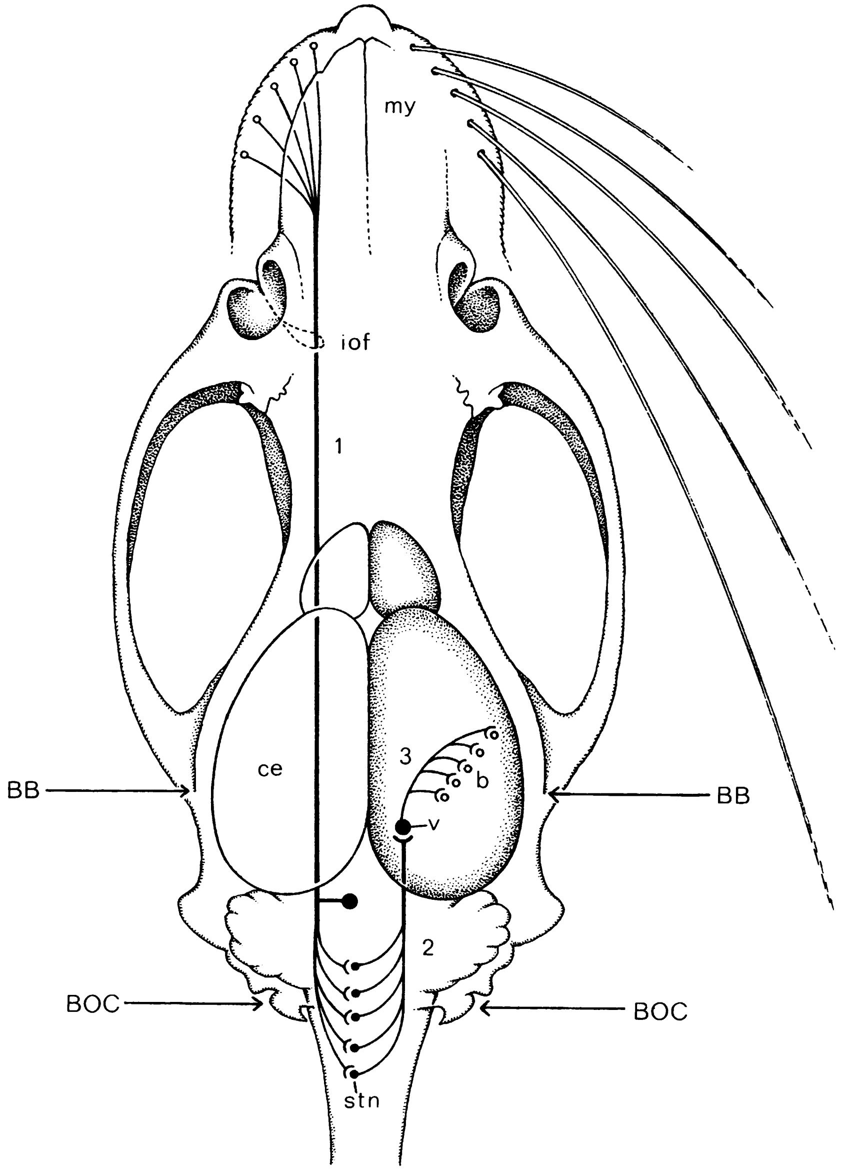


Fig. 72. Trigeminal sensory innervation of the mystacial vibrissae of muroid rodents in relation to the osteological limits of two cranial measurements. See text for further explanation and references. **1**, first-order sensory neurons (with cell bodies in trigeminal ganglion); **2**, second-order sensory neurons (with cell bodies in spinal trigeminal nucleus); **3**, third-order sensory neurons (with cell bodies in ventrobasal complex of thalamus); **b**, neuronal barrels (in cerebral cortex); **BB**, Breadth of Braincase (measurement defined in Materials and Methods); **BOC**, Breadth of Occipital Condyles (measurement defined in Materials and Methods); **ce**, cerebrum; **iof**, infraorbital foramen; **my**, mystacial vibrissae; **stn**, spinal trigeminal nucleus (in medulla oblongata); **v**, ventrobasal complex of thalamus.

tors originating there. Since the rodent mandibular apparatus works at a mechanical disadvantage during incisor biting, the inferior zygomatic root must perhaps be capable of resisting more forceful contractions of the anterior deep masseter in species that accomplish food reduction with the incisors than in species effecting the reduction of equally resistant food by molar action during which almost the entire muscular resultant is probably transmitted to the teeth (Hiiemae, 1971; Weijs and Dantuma, 1975).

As Wright (1968: 325) observed, it is usually easy to suggest a plausible explanation for any single correlation, but it is more difficult to interpret a whole system of correlations in a way that is consistent throughout. The anatomical observations and analyses presented in this section have thus far provided functional interpretations for most of the largest values in the system of size-independent morphometric covariances underlying the principal shape factor, but two neurocranial dimensions (BB and BOC), also have substantial loadings on *H* and remain to be discussed. While the volume of the braincase and the capacity of the foramen magnum indexed by these measures are unlikely to reflect masticatory function in any direct fashion, considerations of sensory neuroanatomy lend credence to the broader adaptive context of the preceding arguments.

Ichthyomyines use their mystacial vibrissae to locate submerged prey (Voss et al., 1982) and the neural pathways of sensory projection from vibrissae to cerebral cortex (determined by anatomical and physiological research on laboratory muroids) link this behavioral specialization with an expected pattern of metric covariance. From the mystacial vibrissae (fig. 72, my) afferent fibers of first-order somatic sensory neurons (1, in the second division of the fifth cranial nerve) pass caudally through the infraorbital foramen (iof) and the anterior alar fissure to terminate in the spinal trigeminal nucleus (stn) of the medulla oblongata. Second-order neurons (2), originating in the ipsilateral spinal trigeminal nucleus, decussate to the opposite side of the brainstem, and ascend via the trigeminal lemniscus (trigeminothalamic tract) to the ventrobasal complex (V) of the thalamus (Zeman and Innes, 1963). Vibrissal sensory representation in both the spinal trigeminal nucleus and in the ventrobasal complex is somatotopically organized with single cellular units in each responding to the stimulation of just one tactile hair (Nord, 1967; Zucker and Welker, 1969; Waite, 1973a, 1973b). From the ventrobasal complex, third-order afferents (3) project vibrissal responses onto "barrels" (b), dense, hollow-columnar concentrations of neurons in layer IV of the somatosensory cerebral cortex (Woolsey and van der Loos, 1970; Welker, 1976; Woolsey, 1978).

Given the demonstrated one-to-one correspondence of vibrissal afferents with cellular units in the spinal trigeminal nucleus (Zucker and Welker, 1969), the exact representation of each vibrissa by one cortical barrel, and a strong correlation between the number of afferents supplying a vibrissa and the size of the barrel to which it projects (Woolsey, 1978), significant phyletic increase in either vibrissal number or sensitivity should be accompanied by volumetric expansion of the medulla oblongata and cerebral cortex. Among many semiaquatic, carnivorous small mammals, conspicuous enlargement of the medulla oblongata and the cerebrum does indeed appear to be consistently correlated with increased vibrissal density and sensitivity (Bauchot and Stephan, 1968; Rehkämper, 1981; Stephan and Kuhn, 1982; Stephan and Dieterlen, 1982). The medulla oblongata and cerebral hemispheres are spanned by measurements of occipital condyle and braincase breadth (fig. 72, BOC, BB), and the substantial loadings of those dimensions on *H* may therefore reflect the finer or coarser tactile discrimination required to locate small or large prey, respectively. This inference is consistent with the observation that ichthyomyine species with narrower incisors and larger molars (*Anotomys leander, Chibchanomys trichotis, Rheomys mexicanus* and *R. underwoodi*) also have denser vibrissal arrays than species with broader incisors and smaller molars (*Ichthyomys* species, some species of *Neusticomys,* other species of *Rheomys*; see fig. 4 and accompanying text).

The preceding functional interpretations can be summarized by labeling the diagram (fig. 54) that was earlier proposed to represent the simplest paths of underlying causal relations that might be responsible for observed patterns of morphometric covariance in the ichthyomyine head skeleton. Identifying latent sources of covariation with specific evolutionary and functional mechanisms (fig. 73) yields an internally consistent biological hypothesis with empirically testable conse-

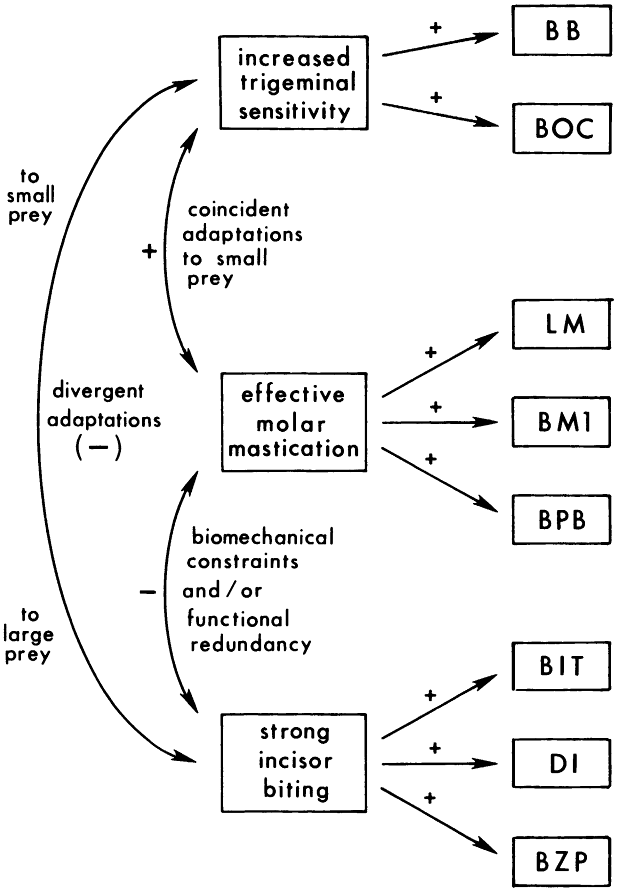


Fig. 73. Labeled path diagram for the principal shape factor. Functional relations and evolutionary processes hypothesized in the accompanying text are here identified with the latent sources of size-independent metric covariation postulated in figure 54.

quences. If size-independent craniodental shape variation among ichthyomyine species results chiefly from dietary adaptations as diagrammed, then the scores of ichthyomyine species on the principal shape factor should be inversely correlated with prey size such that species with high scores on *H* prey on small arthropods while those with low scores on *H* prey on large arthropods. Although adequate information about prey size is not presently available for ichthyomyines other than *Anotomys leander* and *Ichthyomys tweedii,* ecological data summarized in the next section of this monograph suggest that some measurable environmental variables may be useful predictors of stream arthropod size distributions. If ichthyomyine diets can then be assumed to reflect the size distribution of available prey, such predictors may provide the necessary data for evaluating the hypothesis of craniodental adaptation developed here.

## ECOLOGY

Published information about ichthyomyine ecology is almost wholly anecdotal, consisting in large part of observations on the circumstances of a few captures incidental to general faunal survey efforts. Such scattered records do not provide a satisfactory basis for inferences about the ecological context of ichthyomyine evolution, and the present account therefore relies largely on data that I collected in the field from 1978 to 1980. Five individual species accounts are provided to serve as examples of the similarities and differences among habitats upon which subsequent discussions are based; information for other species and localities, when available, is summarized or referenced in the Gazetteer (Appendix).

## HABITAT DESCRIPTIONS

*ANOTOMYS LEANDER*: Twelve specimens of *Anotomys leander* were trapped between 3600 and 3755 m elevation along two streams that descend narrow, south-facing ravines in the watershed of the Río Tambo near the crest of the eastern Andes (Cordillera Oriental), 6.2–8.2 km W (by road) of Papallacta (0°22′S, 78°08′W) in Provincia Napo, Ecuador. The vegetation along the upper reaches of both streams (fig. 74) is cold, wet páramo dominated by dense, wiry bunch grass (to 1 m in height) and scattered thickets of *Polylepis* (Rosaceae). Surrounding hillsides are uninhabited by humans and almost continuously swept by cold, cloud-bearing winds that rise from the valley below. Large terrestrial bromeliads (*Puya* sp.) grow on sheltered slopes and along the stream margins. Low, marshy depressions in the páramo are covered with sphagnum and elastic mats of cushion plants. Ground frost and light snowfalls occur during the local winter (especially July and August) above 3700 m.

Between 3630 and 3660 m, both streams leave the páramo grasslands, pass through a shrubby ecotone, and enter the Subalpine Rain Forest (fig. 75), a low, tangled growth of diminutive trees 5 to 6 m in height. There is no appreciable understory at this elevation but the tangled limbs, sprawling trunks, and twisted roots of trees in this dwarfed forest make foot travel arduous. Palms, bamboos, tree ferns, and epiphytic orchids and bromeliads, common in lowland and lower montane situations, are absent here. Instead, dense, wet mats of mosses, liverworts, and climbing ferns cover branches, tree trunks, exposed roots, prostrate logs, and rocks. Vines are few, thin, and ropelike; woody lianas are absent. A low growth of herbaceous dicots, ferns, and *Equisetum* sparsely covers the forest floor, and the ground is soft and spongy underfoot due to a thick carpet of moss, leaf litter, and matted roots. A deeper, peaty humus layer overlies the volcanic topsoil. Minimum and maximum daily ambient air temperatures that I recorded at streamside beneath the forest canopy at 3600 m from 7 March to 14 April 1980 averaged 6 and 10°C, respectively.

The two streams in which *Anotomys leander* were taken are similar in size (2–4 m in average width; 25–35 cm in average depth) and rush swiftly (90–110 cm/second) over bedrock, boulders, and large cobble. The streambeds are steeply inclined: waterfalls (to 6 m height) and white-water cascades are frequent. The water is cold (6–9°C at 3600 m) and clear. Silt and organic debris accumulate in a few pools or other still, backwater situations. Submerged rocks are slippery with an invisible algal film, and emergent rocks in the streambed are mossy to the waterline. Along the upper, páramo-bordered reaches of both streams the banks are solid bedrock, often thinly overgrown with the matted roots of grasses and of tough, spiny shrubs. Below treeline the banks are of soil and roots, often undercut to form shallow caves that overhang the margins of the stream. In the infrequent absence of fog or clouds, the upper reaches of both streams receive direct sunlight from midmorning to midafternoon. The forest canopy is closed over both watercourses in their lower reaches, however, and little direct sunlight penetrates to the streambeds there.

Benthic invertebrates collected from streams near Papallacta consist primarily of immature aquatic insects, many of which represent taxa that characteristically inhabit cool, swift montane streams (e.g., Blephariceridae, Gripopterygidae, Limnephilidae). I did not observe decapod crustaceans or molluscs in the streams from which *Anotomys leander* was trapped. Among the species of small mammals with which *A. leander* is sympatric near Papallacta (table 43 lists the forest taxa), *Caenolestes fuliginosus, Microryzomys altissimus, M. minutus, Neusticomys monticolus, Reithrodontomys mexicanus, Thomasomys aureus,* and *T. paramorum* were also taken at streamside. Other com-

Fig. 74. Stream habitat of *Anotomys leander* at about 3750 m elevation near Papallacta, Ecuador. Páramo grassland is the natural vegetation bordering streams at this elevation. Photographed 19 April 1980.

mon streamside vertebrates include dippers (*Cinclus leucocephalus*) and the toad *Atelopus ignescens*.

*CHIBCHANOMYS TRICHOTIS*: Four specimens of *Chibchanomys trichotis* were trapped between 2492 and 2584 m elevation along a

Fig. 75. Subalpine Rain Forest at 3600 m elevation near Papallacata, Ecuador. This vegetation borders stream habitats below the páramo grassland shown in figure 74. Note the low, tangled structure of the forest and the thick mats of moss, liverworts, and climbing ferns that cover trunks and branches. Photographed 16 April 1980.

Fig. 76. Upper Montane Rain Forest at about 2500 m elevation near Buena Vista, Venezuela. Note the treeferns and thickets of bamboo in the understory and compare the erect stature of the trees in this forest with those in figure 75. Photographed 14 January 1980.

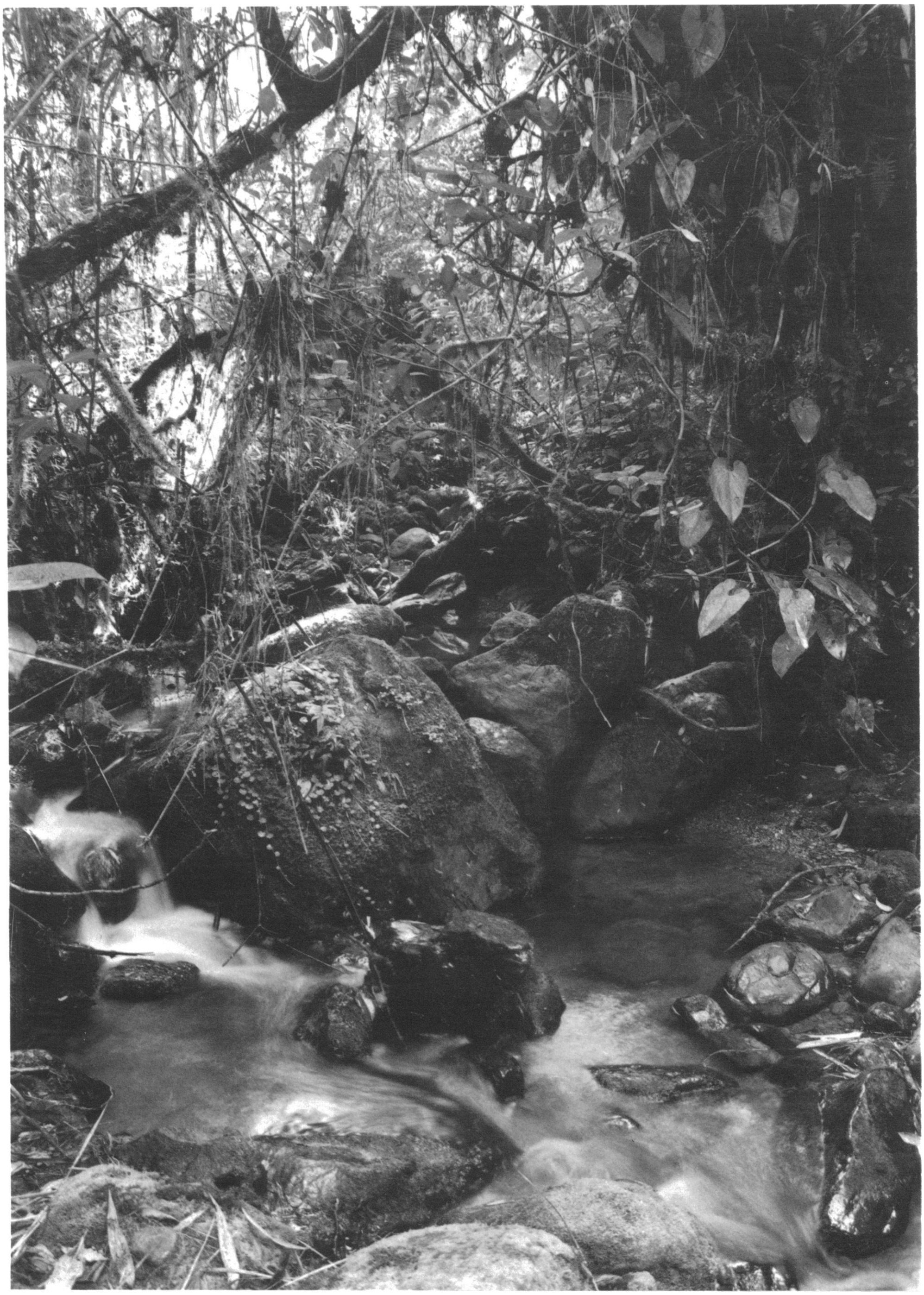


Fig. 77. Stream habitat of *Chibchanomys trichotis* at about 2500 m elevation near Buena Vista, Venezuela. Photographed 14 January 1980.

single stream that descends the forested northwestern slope of Cerro El Cristo, several kilometers south (by trail) of a small community known locally as Buena Vista and 7–

8 km SSE (by air) of Villa Paez, (7°29'N, 72°27'W) in Estado Táchira, Venezuela. The cloud forest (Upper Montane Rain Forest) bordering the stream from 2400 to 2600 m has probably been selectively cut for lumber and firewood for several decades and the undergrowth is penetrated by muddy cattle trails. The forest canopy, 20–25 m in height, is broken and discontinuous (fig. 76). Trees are unbuttressed and their upper branches are laden with epiphytes (chiefly bromeliads) or festooned with thin, rope-like vines (not woody lianas). Tree ferns are abundant in moist situations throughout the forest and scattered palms occasionally emerge to canopy level. The forest understory, including the streambanks, is dominated by dense thickets of bamboo (*Chusquea* sp.) but ferns, herbs, and woody dicots are also common. A superficial litter of logs, branches, twigs, and leaves covers a deep, underlying humus. Minimum and maximum daily ambient air temperatures that I recorded beneath the forest canopy at streamside from 8–15 January 1980 averaged 7 and 12°C, respectively.

The stream in which specimens of *Chibchanomys trichotis* were trapped is a typical Andean brook (fig. 77). In January of 1980, during the local dry season, the stream averaged 1–2 m in average width, 20–30 cm in depth, and flowed with moderate swiftness (30–40 cm/second) over bedrock and cobble and among large boulders. The banks were deeply undercut for a meter or more above water level, however, and it seems likely that considerable fluctuations in discharge occur, perhaps in the form of occasional violent spates or as a regular consequence of the seasonal distribution of rainfall. The water is cold (7–9°C) and clear. Pools (to 1.5 m depth) and small waterfalls (to 3 m height) are abundant. Submerged rock is usually slippery with an invisible algal film and exposed rocky surfaces in the streambed are mossy to about 10–20 cm above the waterline. Mud and organic detritus accumulate at the bottoms of deeper pools and in still, backwater situations. The streambanks are rocky or composed of layered gravel and soil invaded and stabilized by matted roots and overgrown with moss. Streamside vegetation (mostly bamboo) forms a closed canopy over about 50 percent of the streambed but is sufficiently open over the remaining half to admit large sunflecks to the bed from midmorning to midafternoon.

Decapod crustaceans and molluscs were not observed in the streams around Buena Vista; invertebrates collected from the same streams as *Chibchanomys trichotis* were all aquatic insects. Neither reptiles nor adult amphibians were encountered along the stream and tadpoles appeared uncommon. Dippers (*Cinclus leucocephalus*) and tapaculos (*Scytalopus magellanicus*) are abundant along the stream margins and were often caught in traps set for water mice. Among the other small mammals (table 43) with which *Chibchanomys trichotis* is sympatric at Buena Vista, *Caenolestes obscurus, Microryzomys minutus, Oryzomys albigularis,* and *Thomasomys hylophilus* were also taken at streamside.

*ICHTHYOMYS PITTIERI*: The holotype and most subsequently collected specimens of *Ichthyomys pittieri* have been taken between 900 and 1000 m elevation from a single stream immediately adjacent to Estación Biológica Rancho Grande in the Cordillera de la Costa, 14.7 km (by air) NW of Maracay (10°14'N, 67°36'W) in Estado Aragua, Venezuela. The stream (fig. 78) occupies the bottom of a steep-sided, south-facing valley and flows into the Quebrada Guacamaya, a tributary of the Río Limón in the Lago Valencia drainage. The vegetation of the valley slopes and bottom (fig. 79) is wet evergreen forest (Lowland Rain Forest). The forest canopy is 25–30 m in height with only a few emergent palms. Large trees are frequently buttressed and support abundant woody lianas, climbing Araceae, orchids, and bromeliads. The diffuse subcanopy, composed of mixed palms, treeferns, and sapling trees, grades into a sparse understory consisting chiefly of large ferns, seedling and dwarf palms, Cyclanthaceae, Araceae, and shrubby dicots. There is no real humus layer on the forest floor but a thin film of wet, decaying leaves partially conceals the reddish, claylike topsoil. Minimum and maximum daily ambient air temperatures that I recorded beneath the forest canopy at streamside from 18 to 30 November 1979 averaged 19 and 22°C, respectively.

The stream from which *Ichthyomys pittieri* has been taken is narrow (1–2 m average width), shallow (10–15 cm average depth),

Fig. 78. Stream habitat of *Ichthyomys pittieri* at 900 m elevation near Rancho Grande, Venezuela. Photographed 1 December 1979.

cool (20–21°C), and flows with moderate swiftness (30–40 cm/second) over sand, gravel, small cobble, and occasional boulders. Shallow riffles predominate throughout the length of the watercourse, but shallow pools (to 0.5 m depth) with sandy or leafy bottoms occur frequently below small cascades and waterfalls (to 1.5 m height). Packed leaves

Fig. 79. Lowland Rain Forest at about 1000 m elevation near Rancho Grande, Venezuela. A sparse understory and buttressed trees are characteristic of this mature forest. Photographed 3 November 1979.

and loose jumbles of organic debris are common upstream of large rocks and logs and at the bottoms of still-water situations. Submerged rocks are slippery with an invisible algal film and emergent rock in the streambed is thinly covered with moss only above the 10–20 cm floodline formed by short-lived spates that follow heavy afternoon rains. Banks are of gravel or clay, frequently stabilized by matted roots and often undercut near the waterline to form shallow caves. The forest canopy is complete over the streambed and only a few scattered sunflecks penetrate to the water at midday.

Crabs (Pseudothelphusidae), snails (*Pachychilus laevissimus*), tadpoles (unidentified), and the characid fish *Creagrutus beni* are common in the small forest streams around Rancho Grande. The benthic insect fauna is taxonomically diverse. Small adult frogs (especially *Colostethus trinitatus* and *Atelopus cruciger*) and snakes (*Leimadophis zweifeli, Bothrops venezuelensis*) are the most conspicuous diurnal streamside vertebrates. *Chironectes minimus, Didelphis marsupialis, Heteromys anomalus, Neacomys tenuipes,* and *Oryzomys albigularis* are common nocturnal streamside mammals; other sympatric small mammals are listed in table 43.

*ICHTHYOMYS TWEEDII*: Eight specimens of *Ichthyomys tweedii* were collected between 1290 and 1330 m elevation near Mindo (0°03′S, 78°46′W), about 33 km (by air) NW of Quito in Provincia Pichincha, Ecuador. The Mindo region, drained by the Ríos Mindo, Canchupi, and Saguambi, is in the foothills of the western Andes (Cordillera Occidental). Hills and ridge tops are covered with cloud forest (Lower Montane Rain Forest), but the vegetation of adjacent river valleys more closely resembles Lowland Rain Forest. Streams in which *Ichthyomys tweedii* were trapped occupied the latter habitat (fig. 80), much of which probably consists of late successional communities in areas largely deforested only a few decades ago. The canopy in this subclimax forest averages 15–20 m in height. Large trees are buttressed and support moderate loads of vascular epiphytes (chiefly orchids and bromeliads), climbing Araceae, and woody lianas. Tree trunks and branches are covered with a thin moss layer from ground level to a height of about 10 m. Palms and giant bamboo are common canopy emergents. Sapling trees, young palms, tree ferns, and cane form a diffuse subcanopy. The undergrowth (including the streamside vegetation) is dense and consists primarily of woody dicots (many species of Piperaceae and Melastomaceae), Musaceae (*Heliconia*), Zingiberaceae, Cyclanthacae, and dwarf palms. A giant species of *Equisetum* (to 5 m height) is common in the forest undergrowth along riverbanks. A superficial litter of logs, branches, twigs, fruits, flowers, and leaves overlies a thin humus layer and the deeper, clayey topsoil. Minimum and maximum daily ambient air temperatures that I recorded beneath the forest canopy at streamside from 2 to 25 July 1980 averaged 14 and 22°C, respectively.

Forested streams (fig. 81) in the vicinity of Mindo are clear and cool (16–19°C in the early morning, to 21°C by late afternoon), but other physical characteristics vary with the size of the watercourse. Small streams (less than 1 m in average width) are shallow (5–20 cm in depth) and sluggish (10–20 cm/second) with bottoms of sand or mud and are usually heavily overgrown by bordering understory vegetation. Leaf packs commonly accumulate upstream of rocks, logs, or other obstructions in the weak current. Direct sunlight rarely reaches such streams. By contrast, larger streams (2–4 m average width) are deeper (20–30 cm average depth) and swifter (30–50 cm/second) with beds of sand, gravel, large cobble, and scattered boulders; mud, packed leaves, and other organic debris are found only at the bottoms of pools, eddies, and still backwaters. Such streambeds are gently inclined and lack cascades or falls. Stones in the water are slippery with invisible algae and emergent rock in the streambed is sparsely mossy to waterline. Banks are of rocks, gravel, soil, and matted roots. The canopy is sufficiently open over such streambeds to admit large sunflecks from early morning to late afternoon.

Crabs (Pseudothelphusidae) are abundant in streams of all sizes near Mindo but aquatic molluscs are uncommon. The aquatic insect fauna is taxonomically diverse and includes

Fig. 80. Second-growth Lowland Rain Forest at about 1300 m elevation near Mindo, Ecuador. Compare the very dense understory in this subclimax forest with the open understory in figure 79. Photographed 25 July 1980.

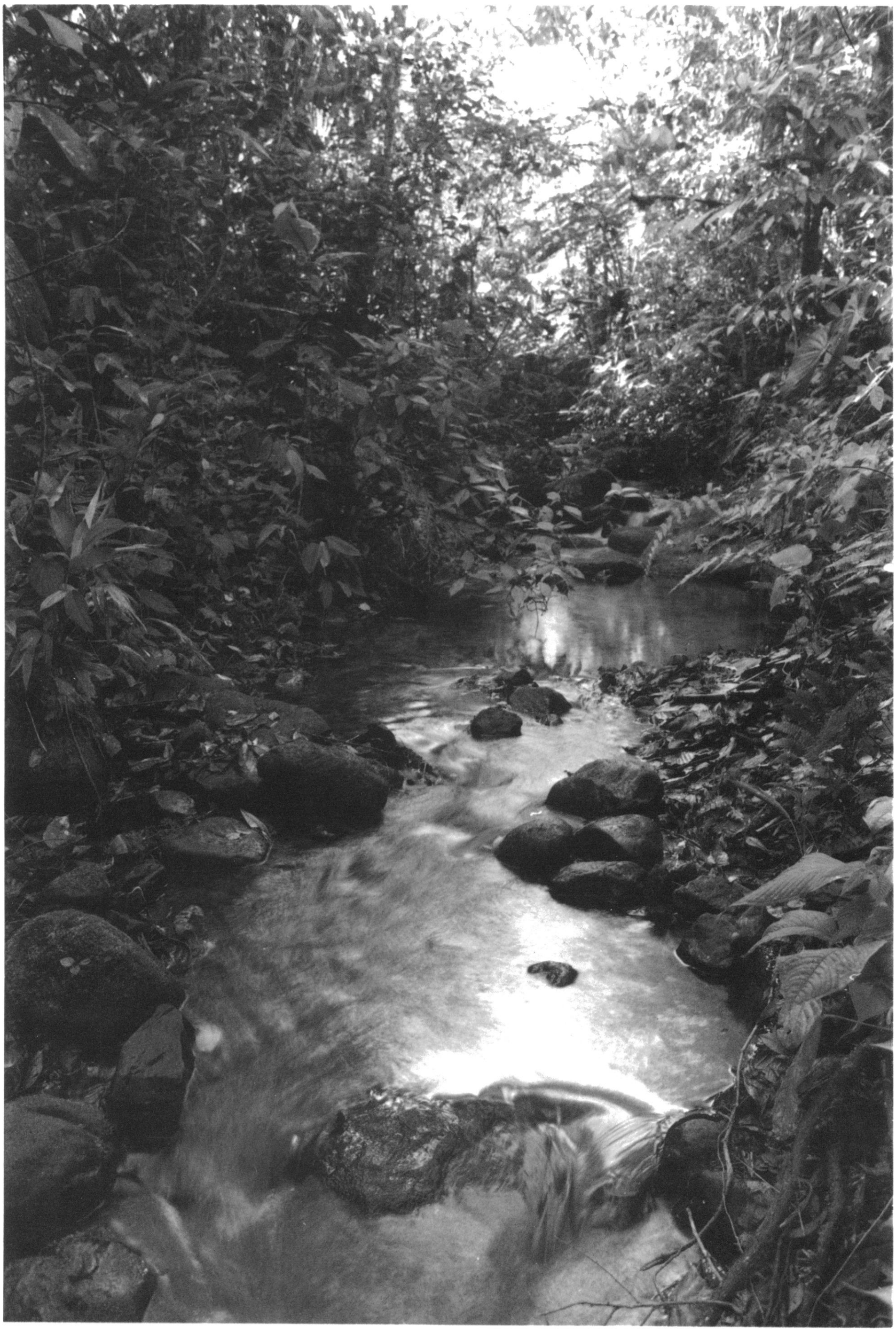


Fig. 81. Stream habitat of *Ichthyomys tweedii* at about 1300 m elevation near Mindo, Ecuador. Photographed 25 July 1980.

an unidentified species of roach (Orthoptera: Blattidae) that is abundant in submerged leafmats and other wet organic debris. Tadpoles, small fishes, adult anurans (*Atelopus* sp., unidentified Hylidae and Leptodactylidae), lizards (*Basiliscus* sp.), and colubrid snakes are also abundant in or along streams. *Chironectes minimus, Didelphis* sp., *Marmosa* sp., *Oryzomys aphrastus, O. hammondi, O. moerex,* and *O. alfaroi* were collected or observed along streams at night.

*NEUSTICOMYS MONTICOLUS*: Eight specimens of *Neusticomys monticolus* were trapped between 2245 and 2290 m elevation on the southwestern slope of Volcán Pichincha in the Cordillera Occidental, 1–2 km (by road) east of Guarumal (0°17′S, 78°43′W) and 17 km (by air) due west of Chillogallo (0°17′S, 78°33′W), Provincia Pichincha, Ecuador. Specimens were collected along two diminutive rivulets that descend narrow ravines on steep, south-facing slopes; both of these tiny watercourses join other small, unnamed streams that empty into the nearby Río Saloya. The bottoms and nearly vertical sides of both ravines are choked with dense, wet, secondary growth composed of small, unbuttressed trees 10–15 m in height, tree ferns, shrubby dicots, Cyclanthaceae, Araceae, terrestrial Orchidaceae, ferns, and herbaceous dicots. Thin, ropelike vines are abundant in the low canopy. Tree trunks, branches, exposed roots, logs, and rocks are covered with a thick growth of wet moss, and the ground is spongy and matted with moss, leaves, and decaying litter. Surrounding slopes are covered with mature cloud forest (Lower Montane Rain Forest) with trees 20–25 m in height bearing luxurious growths of vascular epiphytes, chiefly orchids and bromeliads. A beautiful, silver-leafed *Cecropia* species is a frequent and conspicuous canopy emergent. Tree ferns are common in the subcanopy and the undergrowth is dominated by impenetrable thickets of dwarf bamboo (*Chusquea* sp.).

The watercourses from which *Neusticomys monticolus* were taken near Guarumal are tiny rills, 40–80 cm in mean width and 5–10 cm in mean depth; the water is cool (13–14°C), flowing with moderate swiftness (30–50 cm/second) over coarse sand, gravel and bedrock, and among large cobble. Small waterfalls (to 2 m height) are not uncommon. Packed leaves and other vegetable debris often accumulate upstream of rocks and other obstructions in the current. Submerged rock is slippery with invisible algae and exposed rock in the streambed is mossy to the waterline. The banks are of rock, sand, gravel, and matted roots. The forest canopy is closed over both streambeds to exclude all direct sunlight except for scattered, small sunflecks at midday.

Crustaceans and molluscs were not observed in the streams surrounding Guarumal; collected arthropods were all aquatic insects. Adult and larval anurans were observed but not collected. *Caenolestes fuliginosus, Chilomys instans, Microryzomys minutus, Oryzomys albigularis,* and *Thomasomys silvestris* were also trapped at streamside. A single immature specimen of *Ichthyomys hydrobates* (AMNH 244610) was trapped near the Río Saloya about 100 m downslope from the streams inhabited by *N. monticolus.*

## SIMILARITIES AMONG HABITATS

The accounts provided above, together with information abstracted in the Appendix, supplement previous descriptions of ichthyomyine habitats by Goldman (1920), Tate (1931), Stirton (1944), Goodwin (1959, 1969), Wagner (1961), Hooper (1968), Starrett and Fisler (1970), Musser and Gardner (1974), Handley (1976), and Voss et al. (1982). From these materials, several generalizations readily emerge.

(1) The only definite record of ichthyomyines encountered far from aquatic situations is a series of six *Neusticomys monticolus* collected "... along the bases of moist bluffs often 30 feet from water where they might swim" (unpublished field notes of G. H. H. Tate for 25 September 1923, AMNH Department of Mammalogy archives) at Las Maquinas, Provincia Pichincha, Ecuador (see Appendix). Every other ichthyomyine specimen accompanied by explicit habitat information inked on specimen labels, recorded in fieldnotes or correspondence, or published in the literature (a total of about 200 specimens, representing most known species and

all genera) documents capture in or immediately adjacent to freshwater streams, irrigation ditches, rivers, springs, or swamps. Ichthyomyines have never been collected in the vicinity of salt or brackish water.

(2) In the overwhelming majority of documented cases, ichthyomyines have been captured in or along running water. Tate (1931) reported that the indians of Guápulo, Ecuador, collected specimens of *Ichthyomys hydrobates soderstromi* for Ludovic Söderström by searching for the rodents in swampy fields and turning stones, but this suggestion of a palustrine habitat is not supported by data recorded on Söderström's handwritten labels attached to skins of Guápulo water rats. Habitat information is provided on 14 such labels and indicates that Guápulo *Ichthyomys* were caught by hand in or at the margins of springs or along the rocky banks of the Río Machángara, a nearby stream. Ichthyomyines have not been recorded from lakes.

(3) Ichthyomyines have sometimes been taken in irrigation ditches, canals, culverts, and other artificial watercourses (e.g., Hooper, 1968; Voss et al., 1982) and springs, but most specimens for which information is available have been collected along streams. Ichthyomyines have rarely been taken along watercourses more than a few meters in width or depth. Most photographs and detailed descriptions, published or in manuscript, of ichthyomyine habitats (e.g., Stirton, 1944; Wagner, 1961; Hooper, 1968) depict small, clear streams flowing over predominantly rocky substrates. Such streams are abundant in mountains and their adjacent foothills and skirting piedmonts throughout Central and northern South America. By contrast, ichthyomyines have not been recorded from the turbid, silt-laden "white waters" or from the clear but acid-stained "black waters" that characterize many Neotropical lowland drainage systems (e.g., those described by Carter, 1934 and Fittkau, 1964, 1967).

(4) The natural vegetation bordering streams in which ichthyomyines have been collected is usually evergreen rain forest. Exceptions include the occurrence of *Anotomys leander* and *Neusticomys monticolus* along streams that may be bordered by páramo vegetation at high elevations in the northern Andes (see preceding account for *A. leander* and the Appendix for *N. monticolus* localities), and a few records of other ichthyomyine populations from relatively open and seasonally dry habitats (e.g., Mexico, San José Lachiguirí; Appendix). Typically, however, ichthyomyines are encountered below treeline in regions of high annual precipitation (1600 to more than 3000 mm) whose climax vegetation is rain forest.

The physiognomy of forest growth bordering ichthyomyine streams varies from tall, liana-draped primary Lowland Rain Forest to the dwarfed, mossy tangles of Subalpine Rain Forest. Ichthyomyines are not restricted to undisturbed climax vegetation formations, however, but have also been collected from streams bordered by cultivated coffee and bananas (Stirton, 1944) or by secondary growth succeeding recent deforestation.

## VARIATION AMONG HABITATS

Although members of the tribe Ichthyomyini collectively range from near sea level to at least 4000 m elevation, individual ichthyomyine species have narrower altitudinal distributions. The range in elevation among collection localities for all ichthyomyine specimens with sufficiently precise geographic data provided on labels or in fieldnotes is illustrated in figure 82. Collection localities for *Neusticomys monticolus* reasonably approximate independent samples from the range of one biological species, and the error bars shown for that taxon therefore provide the best available estimate of confidence for calculated mean values of ichthyomyine altitude records. Clearly, some species occur over a considerable range of elevations, but there are also substantial differences among species in their averages.

Most of the conspicuous variation among ichthyomyine habitats appears correlated with altitude. While striking elevational gradients in forest physiognomy are evident from the preceding species accounts and in the manuscript fieldnotes of other collectors, the following discussion chiefly concerns altitude-related differences in stream ecology. This emphasis reflects the distinctive association of ichthyomyines with lotic ecosystems inferred earlier from analyses of diets

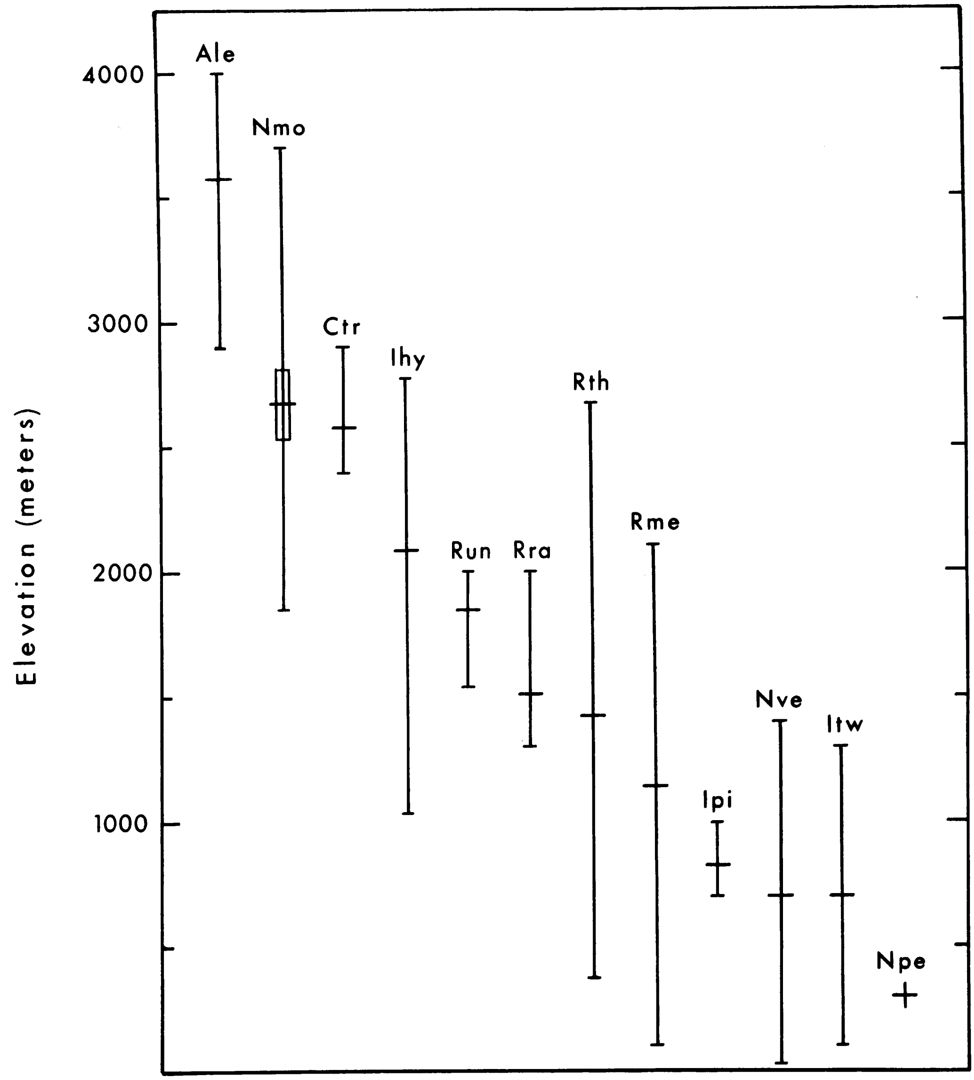


Fig. 82. Altitudinal distribution of ichthyomyine species based on all locality records for which reliable elevation data could be obtained. The range and mean are shown for each species and the standard error of the mean is illustrated for *Neusticomys monticolus.* No accurate elevation data is available from *Ichthyomys stolzmanni* specimens. **Ale,** *Anotomys leander* (6 records); **Ctr,** *Chibchanomys trichotis* (4); **Ihy,** *Ichthyomys hydrobates* (13); **Ipi,** *I. pittieri* (2); **Itw,** *I. tweedii* (8); **Nmo,** *Neusticomys monticolus* (19); **Npe,** *N. peruviensis* (1); **Nve,** *N. venezuelae* (3); **Rme,** *Rheomys mexicanus* (3); **Rra,** *R. raptor* (7); **Rth,** *R. thomasi* (13); **Run,** *R. underwoodi* (5).

and trapping data, but is also necessitated by ignorance of how other aspects of their environment might be important to these rodents.

Streams are complex habitats influenced by many biotic and abiotic factors including precipitation, watershed geomorphology, the particulate structure and lithology of the substrate, slope of the bed, the productivity and physiognomy of bordering vegetation, degree of insolation, water temperature and chemistry, etc. (Macan, 1962; Cummins, 1966; Hynes, 1970). Obviously, many of these factors are interdependent and most are subject to microgeographic and/or seasonal variation. In consequence, a thorough ecological account of even a restricted portion of one watercourse is the labor of years (see Bishop,

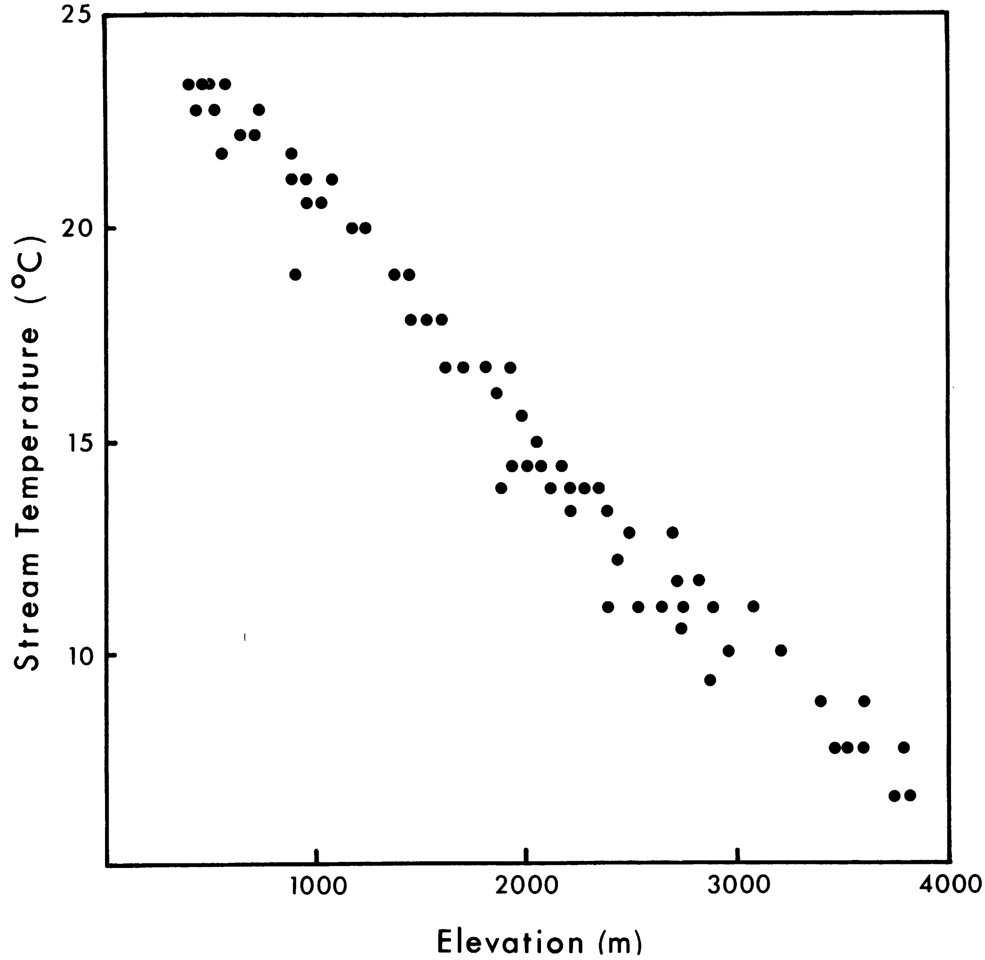


Fig. 83. Water temperature in 65 streams measured between 3808 and 415 m elevation in the eastern Andes of Ecuador (ca. 0°22′ to 1°03′S latitude). See text for additional information.

1973, for a review of such studies and a relevant tropical example) so that any attempt at comparative rhithrolimnology in the present account must be restricted to consideration of just a few relevant aspects of stream biology. Of particular interest in the context of ichthyomyine morphological adaptations is altitude-correlated variation in water temperature, current speed, and benthic arthropod faunal composition.

TEMPERATURE: Water temperatures in small streams usually correspond closely to ambient air temperatures (Macan, 1958; Smith and Lewis, 1975) and therefore vary inversely with altitude following the atmospheric lapse rate. Figure 83 presents data on the temperatures of 65 streams sampled by myself and Paul Kaarakka along an altitudinal transect in the Cordillera Oriental (eastern Andes) of Provincia Napo, Ecuador, from 3808 m near Paso de Guamaní to 415 m at Misahuallí near the Río Napo. All of these data were collected with the same instruments (a pocket mercury-bulb thermometer and a Thommen 2000 altimeter) on 18 and 19 April 1980. Both days were heavily overcast so that any diel variation in water temperature due to direct solar warming was probably minimal. Linear regression of water temperature on elevation for these data yields an estimated coefficient of −5.0°C/1000 m elevation, a value identical to the average lapse rate for free air in the Andes provided by Mani (1968) and within the range of values for lapse rates in the northern Andes provided by Johnson (1976). The estimated intercept (at 0 m elevation) is 25.4°C.

Because measured stream and air temperatures reported in the preceding species accounts and others that I recorded elsewhere correspond reasonably with predictions from the linear model fitted to the data in figure 83, it can be inferred that thermal regimes in ichthyomyine habitats are largely dependent on elevation. Of considerable interest is the very large temperature differential that obtains over the range of elevations inhabited by ichthyomyines, from 6°C near the equator at 4000 m to 25°C at sea level. It is also relevant that water temperature in any single tropical rainforest stream is usually subject to only minor seasonal and daily fluctuation. Tropical mean monthly air temperatures exhibit little variation over the year (less than 3°C at ichthyomyine collection localities for which records are provided by Wernstedt, 1972), and 24-hour variation in air temperatures at streamside is probably minimized by the insulating effect of dense forest canopies (see the daily mean maxima and minima reported in the species accounts above). Ichthyomyines and other sympatric, stream-dwelling organisms must therefore usually experience locally constant temperatures and, in particular, at very high elevations must tolerate persistent cold throughout the year.

CURRENT SPEED: The mean velocity of running water in any stream is a complex function of many factors including the slope of the bed, the geometry of the stream channel in cross section, the roughness of the hard substrate that forms the channel boundaries, and the amount and nature of suspended particulate matter. Empirically, however, stream velocity is roughly proportional to the square of the slope so that, all else being equal, the steeper the bed the faster the stream (Leopold et al., 1964). Inspection of many topographic maps for localities scattered throughout the range of ichthyomyine distribution suggests that streambeds descending the upper, forested slopes of mountains are usually steeper than are streambeds in adjacent foothills and skirting piedmonts. Figure 84 plots the mean slope (vertical descent divided by horizontal distance traversed, both measured in meters) versus altitude (at stream midlength) for all of the 128 first-order (primary, unbranched) permanent streams depicted on a 1:100,000 topographic map of the forested southeastern flanks of the Sierra Nevada in western Venezuela (Hoja 6041, Dirección de Cartografía Nacional, República de Venezuela, 1977). The mapped region includes forested elevations ranging from 3800 to 200 m and appears representative of the gross relief that obtains throughout most of the mountainous New World tropics. The correlation between slope and altitude is obviously significant, and it therefore seems reasonable to expect, on average, faster streams at higher elevations.

Despite such considerations, current velocities encountered by ichthyomyines in their night-by-night activities may not be so predictably altitude-dependent as water temperatures for several reasons. Firstly, the expected relationship between slope and elevation may be disrupted by such local topographic features as the elevated intermontane basins of Andean Ecuador within which slow-moving streams may descend gently-inclined gradients at considerable elevations. Secondly, current velocity varies within streams, being less along the shallow margins and in pools or backwaters than at midstream or over cascades and riffles. By avoiding unfavored microhabitats, ichthyomyines might therefore selectively encounter flow regimes significantly different from the whole-stream average determined by the slope of the bed. Thirdly, current speed is partly dependent on discharge and may therefore vary seasonally with precipitation even in temperature-constant equatorial regions. These sources of regional, behavioral, and seasonal variability compromise the biological relevance of flow measurements made at one place and time and in ignorance of where in the stream ichthyomyines actually spend their time. Figure 84 therefore suggests only a general expectation that may be subject to many exceptions.

ARTHROPOD FAUNAS: Among those factors believed to influence the distribution and abundance of stream benthic arthropods, water temperature, current speed, substrate particle size, and the amount and nature of available food resources are most consistently implicated as important (Ambühl, 1959; Hynes, 1970; Cummins and Klug,

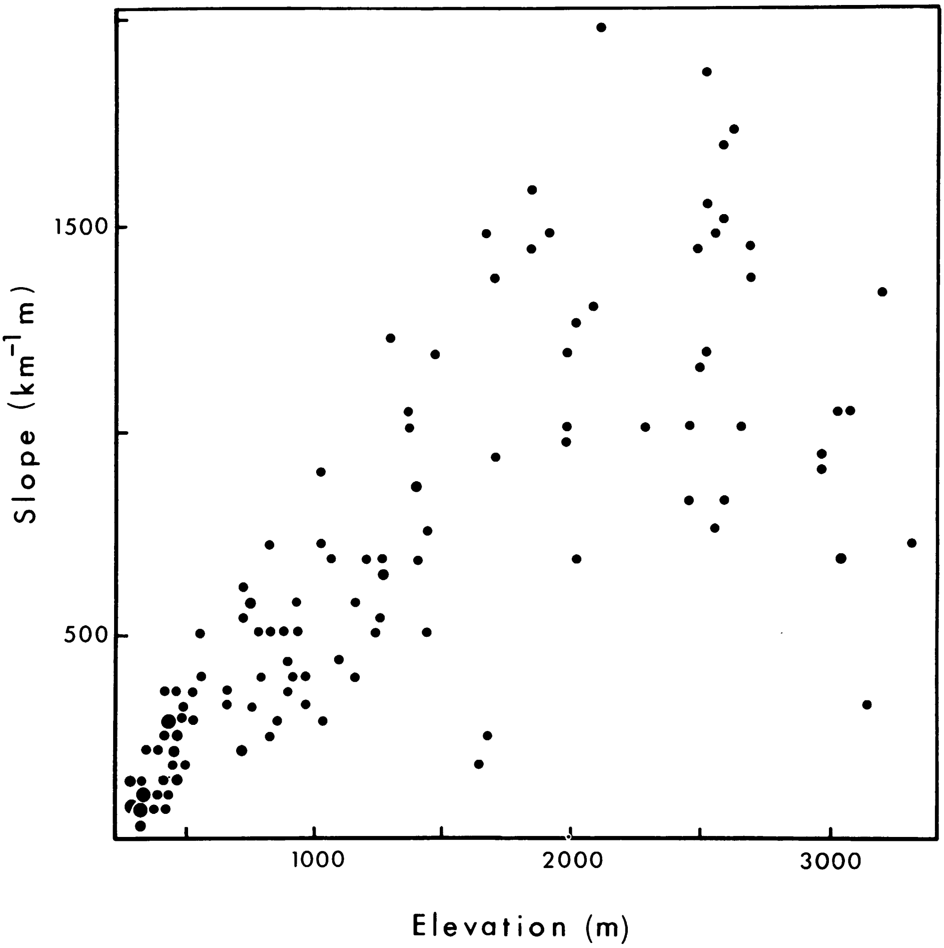


Fig. 84. Mean slope and elevation of 128 first-order streams on the forested southeastern slopes of the Sierra Nevada in western Venezuela (Estado Barinas). See text for other details. Larger dots indicate coincident values of slope and elevation for two or more streams.

1979; Ward and Stanford, 1982; Minshall, 1984). Altitude-correlated variation in these ecological factors is commonly presumed responsible for observed differences (usually discussed only in terms of taxonomic composition) between highland and lowland stream arthropod faunas (e.g., by Dodds and Hisaw, 1925; Williams, 1966; Kamler, 1967; Illies, 1964) and might be causally related to variation in arthropod communities observed among the stream habitats of different ichthyomyine populations.

The differences described earlier between the arthropod faunas of streams inhabited by *Anotomys leander* and *Ichthyomys tweedii* at Papallacta and Mindo, respectively, are represented in other highland-lowland comparisons as well (fig. 85). Thus, the size distribution of stream arthropods sampled at Santo Domingo (3123 m) and Buena Vista (2529 m) resemble the Papallacta fauna (3600 m; fig. 66) in consisting of predominantly small organisms and in lacking any very large species, whereas samples of stream arthropods from the Río Limón (800 m) and Misahuallí (415 m) resemble the Mindo fauna (1350 m; fig. 66) in representing a greater diversity of large species. Altitude-correlated differences in size distributions similar to these stream comparisons have also been documented for terrestrial arthropod faunas. Mani (1968: 58), for example, asserts that "... reduction in the mean body size is one of the most striking characters of high alti-

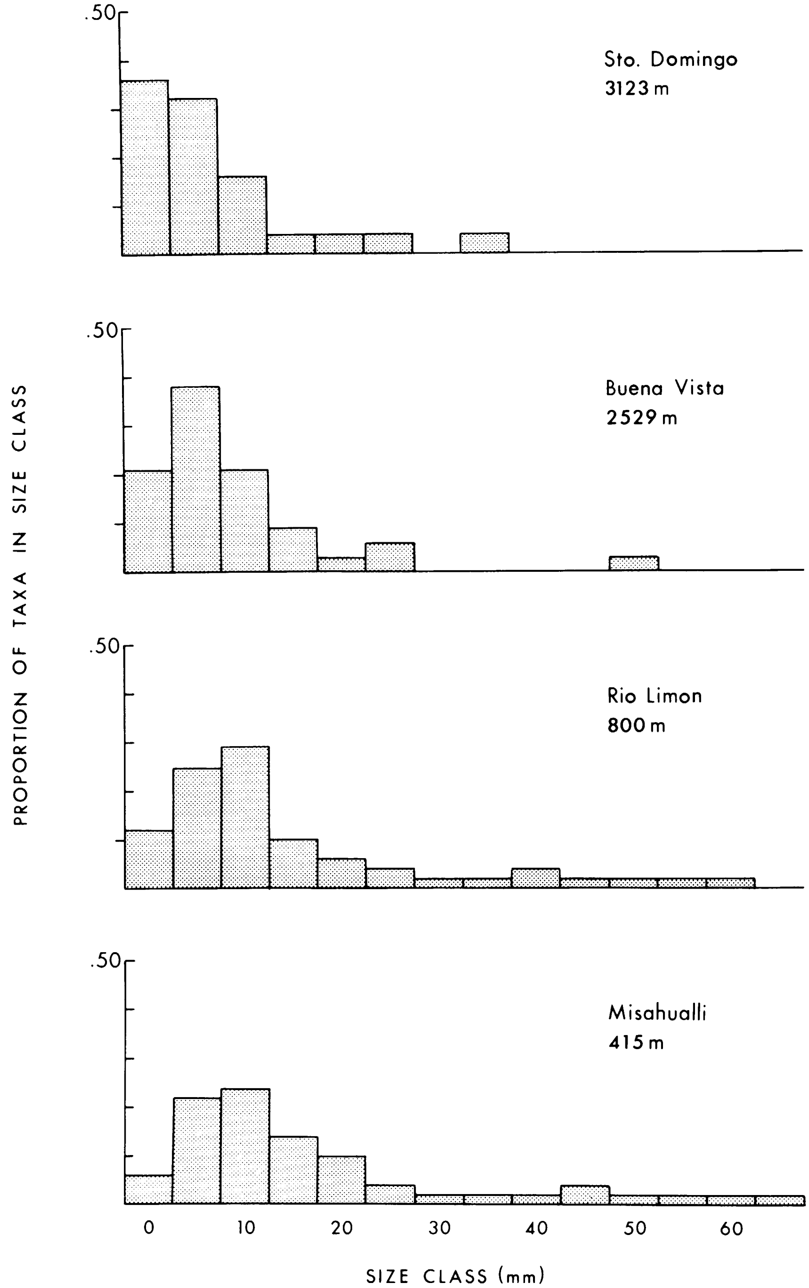


Fig. 85. Size distribution of benthic arthropods collected from streams at four South American localities. Geographical information and dates for the samples are as follows: Santo Domingo (Venezuela, Estado Mérida, 10 km W by road), 29 August 1980; Buena Vista (Venezuela, see Appendix), 15 January 1980; Río Limón (Venezuela, below Rancho Grande, see Appendix), 2 December 1979 and 7 September 1980; Misahuallí (Ecuador, Provincia Napo, ca. 1°03'S, 74°40'W), 2 August 1980.

tude insects. While certainly large or medium-sized insects are not altogether absent on mountains, there is, however, a tendency for reduction in the mean size of the body in most high altitude groups of insects with increase in elevation." Janzen et al. (1976) found no significant variation in mean insect size among sweep samples collected over a 3400 m altitudinal transect of the Venezuelan Andes, but documented a conspicuous decrease in the numbers of large arthropods in samples from higher elevations. The abundance or scarcity of large arthropods did not significantly affect the sample means because an overwhelming majority of individuals at all elevations were very small, but sample medians decreased from 23 mm at 200 m elevation to 10.5 mm at 3600 m.

A tendency to size reduction (whether indexed by the sample mean or median) among high-altitude arthropods in aquatic and terrestrial communities suggests the influence of some ecological factor common to both environments. Water and air temperatures, both lowered at high elevations due to the atmospheric lapse rate, might be responsible for such coincident reductions in arthropod size (Mani, 1962, 1968). Low temperatures diminish insect larval growth rates (Bursell, 1974; Sweeney, 1984), and this direct effect might result in smaller average size if the duration of growth is not lengthened to compensate at higher elevations. Other, indirect influences of the thermal environment on stream arthropod size might be mediated by interactions with the quantity and quality of available food resources (chiefly the diatomaceous periphyton and decomposing organic detritus), both of which may be reduced at low temperatures (Cummins and Klug, 1979; Sweeney, 1984). Because of the seasonal constancy of tropical temperature regimes, aquatic arthropods living at high elevations on equatorial mountains must complete their life cycles in persistently cold water, a situation that rarely obtains at higher latitudes where most streams are summer-warm (Hynes, 1970). Therefore, to the extent that stream arthropod size is influenced by direct or indirect temperature relationships, altitude-correlated trends are likely to be especially pronounced in the tropics.

Other elevation-correlated ecological factors might also be partially responsible for the paucity of large arthropods in high-altitude watercourses. Arthropods living in fast-flowing streams are usually smaller than those inhabiting slower waters (Hora, 1930; Mani, 1968), an association that may result from the influence of current speed on the particulate structure of the mineral substrate and on the local availability of primary food resources. Fast-flowing streams are characterized by well-scoured beds whose mineral substrate consists of bedrock, boulders, and large cobble; slower streams, all else being equal, are usually characterized by beds composed of more diverse substrates that include such finer mineral particles as small cobble, pebbles, gravel, and sand (Leopold et al., 1964). Because leaves and other terrestrial organic litter shed or washed into streams are more likely to be swept away than to sink where the current is swift, and because the large interstitial spaces among the coarse substrate particles of fast-flowing streams do not readily accumulate such detritus (Minshall, 1984), most arthropod primary consumers in torrential streams are either grazers on the microscopic algal film that grows on submerged rock or filter feeders that strain fine particulate matter suspended in the current (Hora, 1930; Nielsen, 1950). Such feeding habits require attachment to exposed surfaces where, perhaps, only those organisms small enough to shelter in the thin boundary layer of static water at the current-substrate interface can avoid being swept away. By contrast, decomposing organic detritus (leaves, fruit, flowers, wood, etc.) is far the most important energy source available to arthropod primary consumers in forested streams wherever gentler currents permit the accumulation of such material in the bed (Anderson and Sedell, 1979; Meritt et al., 1984). Invertebrates inhabiting streams with moderate to slow current speeds may feed on whole leaves and other coarse vegetable particles lodged among the diverse interstices of the rocky substrate, layered at the bottoms of quiet pools or buried in banks of sand or gravel. Arthropod detritivores and predators may attain large size in such sheltered, food-rich microhabitats with few or no mechanical constraints imposed by the current.

SUMMARY: The net effect of these altitude-correlated environmental gradients is that ichthyomyine populations at lower elevations typically inhabit warmer, slower-moving streams with larger resident arthropods available as prey while populations at higher elevations inhabit streams that average colder and faster with smaller resident arthropods. Consistent differences in temperature, water velocity, and arthropod faunal composition undoubtedly exist among streams at any given altitude, but such local variation is demonstrably less than the variation expected between localities that differ greatly in elevation. Since mean elevation records for ichthyomyine species range from over 3000 m to less than 1000 m, these gradients determine conspicuous and predictable interspecific ecological differences. The significance of such differences for ichthyomyine morphological evolution is discussed in the concluding section of this monograph.

## SYMPATRIC COMMUNITIES

The New World tropical rain forests inhabited by ichthyomyines harbor diverse communities of other small mammals, but reliable lists of sympatric species are difficult to obtain. Unlike other vertebrates that can be effectively poisoned, netted, shot, or watched, most small, nonvolant mammals can only be censused by patient trapping which, in tropical forests, may require months or even years of sustained effort to obtain a complete inventory. Table 43 provides species lists for four South American faunas that include ichthyomyines and for which repeated, intensive sampling has resulted in large collections of other nonvolant small mammals as well. Museum specimens are available to document the identification of all species at every locality listed in table 43. There are no comparably complete, verifiable lists of sympatric small mammals available for any Central American fauna that includes ichthyomyines.[4]

Although two ichthyomyine species are sometimes found sympatrically (e.g., *Anotomys leander* and *Neusticomys monticolus* at Papallacta, table 43; *N. monticolus* and *Ichthyomys hydrobates* at Guarumal, Ecuador, see habitat accounts above), ichthyomyines do not co-occur with any other like-sized, semiaquatic-carnivorous mammals. *Nectomys squamipes* is a large lowland rat commonly trapped in or along rainforest streams and is sometimes, perhaps often, sympatric with ichthyomyines (e.g., at Balta, table 43; see also Musser and Gardner, 1974). The diet of free-living *Nectomys squamipes* is not adequately documented in the literature (by analyses of gut contents or feces) but morphological descriptions of its dentition, stomach, and hindgut (see Hershkovitz, 1944; Carleton, 1973; and Vorontsov, 1979, respectively) do not suggest carnivorous specializations. Vorontsov (1979) asserts that *Nectomys* is herbivorous, but captive animals accept a variety of plant and animal food (Ernest and Mares, 1986).

Throughout most of their geographic range, in lowland and foothill habitats to about 1500 m elevation, ichthyomyines co-occur with the water opossum *Chironectes minimus* (e.g., at Rancho Grande and Mindo, see the habitat descriptions provided above for *Ichthyomys pittieri* and *I. tweedii*). The few primary data available on water opossum diets (Mondolfi and Medina, 1957) suggest that fish are preferred but I kill-trapped a water opossum at Mindo which had a small pseudothelphusid crab in its mouth and Mondolfi and Medina (1957) also report an observation of a water opossum eating a crab. Water opossums are much larger than ichthyomyines: lengths of head-and-body vary from 200 to 400 mm and weights from 600 to 800 g (Mondolfi and Medina, 1957; Marshall, 1978). Four-eyed opossums (*Philander*), grisons (*Galictis vittatus*), otters (*Lutra*), and crab-eating raccoons (*Procyon cancrivorous*) are larger carnivorous mammals that also frequent lowland rainforest streams.

---

[4] Wilson (1983) listed the mammals present or expected to be present at several Costa Rican localities. He recorded the expected presence of *Rheomys underwoodi* at Monte Verde between 1500 and 1900 m elevation "on the Pacific slope of the Guanacaste Cordillera" and recorded *R. hartmanni* as "positively identified" from Cerro de la Muerte in the Cordillera de Talamanca between 2800 and 3300 m. The single known specimen of *Rheomys* from Monte Verde (which is located between 1300 and 1500 m in the Cordillera de Tilarán) is an example of *R. raptor hartmanni* (UMMZ 116934). No *Rheomys* have yet been collected from the Cerro de la Muerte or from anywhere in Costa Rica above 2000 m although *R. underwoodi* (not *hartmanni*) might well be expected there. There is at least one conspicuous omission in Wilson's Monte Verde list (*Oryzomys fulvescens*; specimens in UMMZ) and Wilson provided neither published sources for his lists nor the names of museum collections where vouchers are deposited.

TABLE 43

Sympatric Species of Nonvolant Small Mammals[a] at Four Ichthyomyine Collection Localities[b]

| Peru: Balta[c], 300 m | Venezuela: Rancho Grande[d], 900–1100 m | Venezuela: Buena Vista[e], 2400–2600 m | Ecuador: Papallacta[f], 3400–3600 m |
|---|---|---|---|
| MARSUPIALIA | MARSUPIALIA | MARSUPIALIA | MARSUPIALIA |
| Didelphidae | Didelphidae | Caenolestidae | Caenolestidae |
| *Marmosa germana* | *Marmosa cinerea* | *Caenolestes obscurus* | *Caenolestes fuliginosus* |
| *Marmosa murina* | *Marmosa fuscata* | Didelphidae | LIPOTYPHLA |
| *Marmosa noctivaga* | *Marmosa marica* | *Marmosa dryas* | Soricidae |
| RODENTIA | *Monodelphis brevicaudata* | *Marmosa impavida* | *Cryptotis thomasi* |
| Sciuridae | RODENTIA | LIPOTYPHLA | RODENTIA |
| *Sciurus ignitus* | Sciuridae | Soricidae | Muroidea |
| *Sciurus spadiceus* | *Sciurus granatensis* | *Cryptotis thomasi* | *Anotomys leander* |
| Muroidea | Heteromyidae | RODENTIA | *Chilomys instans* |
| *Neacomys spinosus* | *Heteromys anomalus* | Sciuridae | *Microryzomys minutus* |
| *Nectomys squamipes* | Muroidea | *Sciurus granatensis* | *Microxus bogotensis* |
| *Neusticomys peruviensis* | *Akodon urichi* | Muroidea | *Neusticomys monticolus* |
| *Oecomys bicolor* | *Ichthyomys pittieri* | *Chibchanomys trichotis* | *Thomasomys aureus* |
| *Oecomys superans* | *Neacomys tenuipes* | *Chilomys instans* | *Thomasomys boeops* |
| *Oryzomys capito* | *Oecomys bicolor* | *Microryzomys minutus* | *Thomasomys cinnameus* |
| *Oryzomys longicaudatus* | *Oecomys trinitatis* | *Microxus bogotensis* | *Thomasomys erro* |
| *Oryzomys macconnelli* | *Oryzomys albigularis* | *Oryzomys albigularis* | *Thomasomys paramorum* |
| *Oryzomys nitidus* | *Oryzomys fulvescens* | *Oryzomys fulvescens* | *Thomasomys* sp. |
| *Oryzomys yunganus* | *Oryzomys talamancae* | *Rhipidomys fulviventer* | |
| Echimyidae | *Rhipidomys venezuelae* | *Thomasomys aureus* | |
| *Proechimys brevicauda* | Echimyidae | *Thomasomys hylophilus* | |
| *Proechimys simonsi* | *Echimys semivillosus* | | |
| *Proechimys steerei* | *Proechimys guairae* | | |
| *Proechimys* sp. | | | |
| *Mesomys hispidus* | | | |
| *Dactylomys dactylinus* | | | |

---

[a] Taxa with adult weights of several hundred grams or less; lists include all species of sciurid, heteromyid, muroid, and echimyid rodents, lipotyphlans and caenolestids known to occur at each locality but exclude large didelphids, other rodent families, lagomorphs, and carnivores.

[b] See Appendix for geographical information.

[c] Voucher specimens: LSU.

[d] Voucher specimens: AMNH, MARNR, USNM.

[e] Voucher specimens: MBUCV, UMMZ, USNM.

[f] Voucher specimens: Museo de Ciencias Naturales (Quito), UMMZ.

Many small mammals that live in Neotropical rain forests commonly forage along stream margins; some of these species are predominantly insectivorous and others probably eat arthropods opportunistically. Examination of the contents of 154 stomachs of small mammals kill-trapped at Papallacta (Voss, unpublished data) revealed that, in addition to ichthyomyines (*Anotomys leander* and *Neusticomys monticolus*), four other forest-inhabiting small mammals from that fauna are predominantly carnivorous (*Caenolestes fuliginosus, Cryptotis thomasi, Microxus bogotensis,* and *Thomasomys erro*) while stomach samples of the remaining seven species (*Chilomys instans, Microryzomys minutus, Thomasomys aureus, T. boeops, T. cinnameus, T. paramorum,* and *Thomasomys* sp.) all contained at least some arthropod exoskeletal fragments. Nevertheless, only ichthyomyine stomachs were found to contain remains of aquatic arthropods; identifiable arthropod fragments recovered from stomachs of other small mammal species at Papallacta were all of terrestrial origin (chiefly larval Coleoptera and Diptera, spiders, adult beetles, Orthoptera, and Lepidoptera). Analyses of diets of small mammals that cooccur with ichthyomyines at other localities are not available.

These data, few as they are, suggest that ichthyomyines exhibit little trophic overlap with other sympatric mammalian taxa. While *Chironectes minimus* and some carnivorans may eat crabs and perhaps other arthropods in some of the same streams where ichthyomyines forage, the considerable size differences among these mammalian predators seem likely to guarantee some corresponding divergence in the size distribution of crustacean or insect prey that each effectively removes from their common habitat. While competition for terrestrial invertebrate prey may well exist among the many other, smaller mammals that inhabit the tropical rain forests of the New World, there is no evidence that any besides ichthyomyines regularly enter streams to forage for arthropods.

## MISCELLANEOUS TOPICS

Apart from the data on diets, habitats, and communities summarized and discussed above, other aspects of ichthyomyine ecology are obscure.

CIRCADIAN ACTIVITY: Ichthyomyines appear to be chiefly crepuscular or nocturnal but the evidence to document circadian activity is unsatisfactory. Most published or unpublished records imply nocturnal captures, but only Hooper (1968) reports direct observations of an ichthyomyine active at night. In the course of fieldwork in Venezuela and Ecuador I collected 41 ichthyomyines in snap traps and live traps; traps were set or rebaited in the late afternoon and checked at dawn or shortly after. All of the specimens I collected were found in the traps at dawn. Although traps remained open for 24 hours, traps that had been checked at dawn never contained water rats when they were rebaited in the afternoon. While these data are consistent with predominantly nocturnal or crepuscular activity, at least one ichthyomyine specimen (an example of *Ichthyomys pittieri*) has been collected while feeding in the middle of the day (Voss et al., 1982).

REPRODUCTION: Information about ichthyomyine litter sizes is available from only six gravid female specimens (table 44), four with one embryo each and two with two apiece. Plausibly, ichthyomyine litters are small. By comparison, mean litter sizes among other sigmodontine taxa vary considerably, from less than two to more than six, but an average sigmodontine litter is three to four young (M. D. Carleton and R. S. Voss, unpublished review of muroid reproductive data). One near-term ichthyomyine embryo (from UMMZ 156532, *Chibchanomys trichotis*) was naked but had abundant, short mystacial vibrissae, well-clawed and completely separate digits on all feet, and small but unfolded pinnae. The wet weight of this fetus was 5.8 g, its gravid mother weighed 57 g, and a like-aged, nonpregnant female (MBUCV I-2796) collected at the same locality weighed 49 g; neonatal in relation to adult female weight for these specimens is therefore at least 11–12 percent. By comparison, species means of neonatal *Peromyscus* range from 4 to 16 percent of adult female weight (Layne, 1968).

Information about reproduction in relation to seasonality is also scanty. Seasonal variation in temperature is negligible for most, if

TABLE 44
**Data From Six Gravid Female Ichthyomyine Specimens**

| Museum number | Species | Embryos | Locality | Rainfall[a] | Date (and season) |
|---|---|---|---|---|---|
| UMMZ 155599 | *Anotomys leander* | one, large | Ecuador, Papallacta | slightly seasonal | 8 March (late dry) |
| UMMZ 156532 | *Chibchanomys trichotis* | one, near term | Venezuela, Buena Vista | moderately seasonal | 11 January (middle dry) |
| UMMZ 126300 | *Ichthyomys tweedii* | two, newly implanted | Ecuador, Mindo | highly seasonal | 23 May (late wet) |
| AMNH 244609 | *Neusticomys monticolus* | two, large | Ecuador, Papallacta | slightly seasonal | 15 May (early wet) |
| UMMZ 111985 | *Rheomys raptor hartmanni* | one, large | Costa Rica, San Isidro | highly seasonal | 20 July (middle wet) |
| MVZ 131995 | *Rheomys thomasi stirtoni* | one, near term | El Salvador, Los Esesmiles | slightly seasonal | 21 February (middle dry?) |

[a] Seasonal variation in rainfall based on local information and data provided by Wernstedt (1972).

not all, ichthyomyine localities, but monthly mean rainfall exhibits substantial seasonal variation; reproduction is therefore likely to vary with annual rainfall schedules if seasonal trends exist at all. The six gravid ichthyomyine specimens represent both dry and wet season collections (table 44), but are too few even for conjecture. Of 29 immature (TWC 1) ichthyomyine specimens accompanied by date of collection, the following representations by seasonal trimesters are observed: early dry season (N = 3), middle dry season (4), late dry season (11), early wet season (7), middle wet season (2), and late wet season (2). There is thus some suggestion that juvenile recruitment might usually occur in the late dry season and early wet season, but no single locality or species has been adequately sampled throughout the year and these data are obviously subject to many sources of sampling bias.

# PHYLOGENY AND ZOOGEOGRAPHY

The morphology of extant species provides the only basis for inference about the genealogical relationships of ichthyomyines. No fossil ichthyomyines are known and the prospect that they might be discovered in the future is slight because fossiliferous deposits are uncommon in the montane and lowland tropical rain forests where these rodents occur. Exclusive reliance on morphological data for proposing and evaluating alternative hypotheses of ichthyomyine phylogeny is also dictated by the unavailability of adequate materials for karyotypic and biochemical analyses. Much of the discussion that follows is therefore addressed to difficulties arising from the absence of any other source of information about relationships.

Relative recency of common ancestry among organisms cannot be inferred directly from measures of overall resemblance without making restrictive assumptions about the homogeneity of evolutionary rates (Bigelow, 1958). Some systematists (e.g., Colless, 1970) have suggested that such assumptions may not be unrealistic, but Hennig (1966) argued forcibly that primitive and derived similarities are usefully distinguished in phylogenetic analysis. Hennig reasoned that if two (or more) organisms share an homologous attribute that is derived with respect to some more primitive condition, then those organisms must have shared a common ancestor more recently than either (any) did with others exhibiting the more primitive feature. The methodological complexities that accompany most practical applications of this simple axiom result chiefly from evolutionary convergences and reversals that compromise both the correct identification of homologies and the unambiguous determination of directions of change (polarity) in the characters based on those homologies (Kluge and Farris, 1969; Estabrook, 1972, 1978; Meacham, 1980, 1984b).

The phylogenetic discussions immediately following are organized in three parts that separately consider (a) whether ichthyomyines comprise a monophyletic group, (b) to what other sigmodontine taxa ichthyomyines are most closely related, and (c) phylogenetic relationships among ichthyomyine species and genera. The last topic lends itself to treatment by character compatibility analysis and numerical parsimony methods, but the former two topics do not. Every systematist who has attempted to classify living muroids from Tullberg (1899) through Ellerman (1941) to Carleton and Musser (1984) has documented the ubiquity of character convergence and reversal among the higher taxa that provide the context within which hypotheses of ichthyomyine monophyly and outgroup relationships must be evaluated. When homoplasy is so common, neither shortest-tree nor largest-clique criteria (explained in subsequent discussions) are likely to provide maximum-likelihood estimators of phylogeny (Felsenstein, 1978a, 1982, 1983). I therefore elected to treat topics (a) and (b) in a more traditional, non-numerical format.

## ICHTHYOMYINE MONOPHYLY

The survey of comparative morphology presented earlier reveals that ichthyomyines are distinctive in a wealth of anatomical details. Character states that are shared by all ichthyomyines for which appropriate material is available include many features that are either unique among living Sigmodontinae or are exhibited by only a few other taxa: (1) The eye is very small and the foramen that communicates the optic nerve is likewise diminutive. (2) Pinnae are small or absent. (3) Genal vibrissae are absent. (4) Mystacial vibrissae are stiff, abundant, and ventrally recurved on the upper lip and their disposition on enlarged mystacial pads is distinctive. (5) The plantar surface of the pes is fringed with a comb of enlarged hairs. (6) The hypothenar pad of the pes is indistinct or absent. (7) The tail is densely covered with long hairs and the underlying caudal scales are indistinct or absent. (8) The principal labial and lingual molar cusps, arranged in opposite pairs, stand in high relief and most accessory enameled structures of the molar crowns are minute or absent. (9) Zygomatic notches are entirely absent. (10) The gnathic process of the premaxillae is an elongate tab of bone projecting forward well beyond the incisors. (11) Masseteric tubercles are large and well developed. (12) The infraorbital foramen is oval, as wide ventrally as dorsally, and accommodates a greatly enlarged bundle of trigeminal sensory fibers. (13) Subsquamosal fenestrae are absent. (14) A distinct pars flaccida of the tympanic membrane is absent. (15) The nuchal ligament attaches to the third thoracic vertebra. (16) The caecum is vermiform and the large intestine is very short. (17) The glans penis is provided with spinous lateral crater papillae. Ichthyomyines differ in other respects (described in Comparative Morphology, above) from the majority of sigmodontines, but the features listed above provide the best-defined qualitative contrasts.

Of these defining character states, the conformation of the mystacial vibrissae, the complete absence of a zygomatic notch, the presence of large masseteric tubercles, the shape and contents of the infraorbital foramen, the absence of a pars flaccida, and the attachment of the nuchal ligament are unique to ichthyomyines among living Sigmodontinae. The remaining 11 character states are each shared with one or a few other sigmodontine genera, but most sigmodontines among those that I surveyed share no more than one or two of these states with ichthyomyines. For example, *Sigmodon hispidus* has spinous lateral papillae in the crater of the glans penis resembling those of ichthyomyines (Hooper, 1962; Hooper and Musser, 1964) but differs in all other points listed above. Similarly, *Ochrotomys nuttalli* and *Osgoodomys banderanus* lack genal vibrissae but share no other listed attribute with ichthyomyines.

Such patterns of character state distribution document the morphological distinctiveness of ichthyomyines but, in the absence of information about character polarities, do not provide direct support for a hypothesis of ichthyomyine monophyly. Three of the character states listed above were hypothesized by Carleton (1980) or by Carleton and Musser (1984) to be primitive conditions within the superfamily Muroidea; these supposed plesiomorphs include the absence of zygomatic notches, the absence of subsquamosal fenestrae, and the absence of a tympanic membrane pars flaccida.[5] Decisions about the primitive or derived status of such attributes, however, depend on the taxonomic level of analysis and on the consequent choice of outgroup comparisons. If ichthyomyine monophyly is to be evaluated within the Sigmodontinae, then the distribution of character states among other muroid subfamilies permits no unequivocal decisions about polarities: zygomatic notches, subsquamosal fenestrae, and supplementary auditory membranes are present or absent among gerbils, hamsters, murines, and arvicolines and there is no consensus about inter-subfamilial relationships to suggest a more restricted collection of outgroups.

There nevertheless remains an impressive number of character states to support the hypothesis that all ichthyomyines shared a common ancestor more recently than any did with members of other sigmodontine taxa. The disposition of the mystacial vibrissae, well-developed masseteric tubercles, the contents of the infraorbital foramen, and the attachment of the nuchal ligament to the third thoracic vertebra are ichthyomyine attributes that appear to be uniquely derived within the Sigmodontinae. Of these four character states, the attachment of the nuchal ligament to the third thoracic vertebra has not been described for any other muroids; the remaining three states (mystacial disposition, large masseteric tubercles, ovoid infraorbital foramen) are represented among other muroids only in a few ecologically similar genera from Africa, New Guinea, and Australia (see table 50 and accompanying text). Character states 1, 2, 3, 5, 6, 7, 8, 9, 10, 16, and 17 are additional attributes that seem likely to be derived based on considerations presented earlier (see Comparative Morphology).

Many of the attributes in which ichthyomyines resemble one another and differ from other New World muroid rodents are plausibly interpreted as locomotor, sensory, or masticatory specializations for semiaquatic carnivory (e.g., 1, 2, 4, 5, 8, 10, 11, 12, 16) and it is possible that two or more lineages may have evolved such similarities by convergent adaptation. Character variation within the tribe (to be discussed below) does not support a hypothesis of polyphyletic origin, however, and other diagnostic character states are not obviously related to semiaquatic carnivory (e.g., 3, 6, 7, 9, 13, 14, 15 and 17). In the absence of any substantial argument to the contrary, the entire ensemble of ichthyomyine synapomorphies identified above provides compelling evidence for tribal monophyly.

## RELATIONSHIPS WITH OTHER SIGMODONTINES

There is little consensus in the literature regarding any aspect of sigmodontine phylogeny. One of the earliest explicit hypotheses of relationships for these rodents was advanced by Hooper and Musser (1964) to reflect their interpretation of evolution in the muroid glans penis. They concluded that living sigmodontines comprise two lineages, one predominantly Nearctic with simple phalli and the other predominantly Neotropical with complex phalli, for which they proposed "North American cricetines" and "South American cricetines," respectively, as informal designations of affinity. This hypothesis of a phyletic dichotomy within the New World muroid fauna (first suggested by Rinker, 1954) provided the framework for much subsequent research in comparative morphology (Arata, 1964; Carleton, 1973), karyology (Gardner and Patton, 1976), and historical biogeography (Hershkovitz, 1966, 1972; Patterson and Pascual, 1972). Carleton (1980),

---

[5] Carleton (1980) and Carleton and Musser (1984) refer to the large sigmodontine pars flaccida as an accessory tympanum, but see Lay (1972) for a discussion of the homology of muroid auditory membranes.

however, pointed out that neither of the hypothesized lineages can be unambiguously diagnosed in terms of uniquely shared character states and warned that both might not be monophyletic. Most of the 73 recognized genera of the Sigmodontinae are presently sorted (following Carleton, op. cit., and Reig, 1980) into 11 suprageneric categories of implied or assigned tribal rank (akodontines, baiomyines, ichthyomyines, neotomines, oryzomyines, peromyscines, phyllotines, scapteromyines, sigmodonts, tylomyines, and wiedomyines). Some of these groups may well prove to be monophyletic but few have been diagnosed in more than one or two character complexes.

Most ichthyomyines resemble the majority of other Neotropical muroids in phallic morphology and, if Carleton (1980) is correct in hypothesizing that the component attributes of a complex penis are derived conditions, this resemblance would lend some support to the hypothesis that ichthyomyines are related to at least those "South American cricetines" whose complex phalli have been described (akodonts, oryzomyines, phyllotines, scapteromyines, sigmodonts; Hooper and Musser, 1964). Concordant evidence is provided by shared, apparently derived resemblances between ichthyomyines and some (perhaps all) "South American cricetines" in the absence of a stylohyal cartilage, the lack of an entoglossal process on the basihyal, the absence of an entepicondylar foramen on the humerus, and the articulation of the first rib with the transverse process of the seventh cervical vertebra. These data need to be interpreted with caution, however, because hyoid morphologies have been studied in only a few "South American cricetine" species (Carleton, 1980; Rinker, 1954; Sprague, 1941) and complex phalli are widespread in other muroid groups as well (Hooper and Hart, 1962; Lidicker, 1968, 1987). The other putative synapomorphies in which ichthyomyines resemble "South American cricetines" (absence of an entepicondylar foramen and the articulation of the first rib) are also exhibited by some North American muroids with simple phalli (Carleton, 1980).

If the cladistic evidence supporting a hypothesis of recent common ancestry between ichthyomyines and other Neotropical muroids with complex phalli appears tenuous, the data that support more specific suggestions of affinity are still less convincing. Hershkovitz (1962: fig. 2) clustered ichthyomyines together with phyllotines and sigmodonts because members of these three groups have tetralophodont molars (in which mesolophs and mesolophids are reduced or absent) and bony palates that are wide and long (see Comparative Morphology, above). Both of these character states are represented among other North and South American muroid groups, however, and therefore constitute an equivocal basis for hypothesizing propinquity of descent. I have not been able to discover any point of similarity among ichthyomyines, phyllotines, and sigmodonts that is not also widespread among other sigmodontines; none of the character states described in this report suggest close relationships among these animals.

Gardner and Patton (1976) did not explicitly defend their hypothesis that ichthyomyines are descended from the nominate subgenus of *Oryzomys* and, in the absence of criteria to establish chromosome segment homologies, it is difficult to evaluate the phylogenetic significance of the gross karyotypic comparisons that they provided. The single ichthyomyine whose karyotype has been published (Gardner, 1971) is a specimen of *Chibchanomys* with a diploid count of 92. This is the highest chromosome number known for any mammal and is reasonably interpreted as derived—but from what ancestral karyotype? Some populations of *Zygodontomys* (sensu stricto; see Voss and Linzey, 1981) have diploid numbers of 84 to 88, higher than any that have yet been reported in *Oryzomys,* and would seem by the simple-minded criterion of counting chromosomes to be at least as likely an ichthyomyine sister-group, but in view of the evident lability of karyotypes among Neotropical muroids, such speculations are pointless. No character states have been reported in the literature, nor have I discovered any, that are uniquely shared between ichthyomyines and any species of *Oryzomys.*

As an alternative to the hypotheses of relationships considered thus far, none of which appear adequately supported by characters, I suggest that the absence of many derived resemblances between ichthyomyines and other sigmodontine taxa be accepted at face value and propose that the Ichthyomyini may not be closely related to any other extant New World muroid taxon. The preceding discussions have assumed that ichthyomyines must be more closely related to some sigmodontine lineage than to members of other muroid subfamilies, but this expectation is not easily defended on any grounds other than zoogeographic plausibility. To be sure, ichthyomyines lack the conspicuous synapomorphies that define the subfamilies Arvicolinae, Gerbillinae, and Cricetinae, but the Sigmodontinae is devoid of diagnostic features by which ichthyomyine membership in it could be established or rejected. In effect, sigmodontines are better defined as a group by their exclusion from other, diagnosable muroid taxa than by any distinctive combination of character states, and the possibility that they represent a very early muroid radiation deserves serious attention (Carleton and Musser, 1984). Differing from other Sigmodontinae in so many aspects of their phenotype, the Ichthyomyini may be an ancient clade with no identifiable sister-group surviving among the descendants of that radiation.

## RELATIONSHIPS AMONG ICHTHYOMYINES

METHODS AND SAMPLES: In order to estimate the relative recency of common ancestry among ichthyomyine species and genera I employed methods of character compatibility analysis and numerical parsimony that operationalize the principles of phylogenetic inference first codified by Hennig (1966). Both methods analyze data in the form of qualitative characters that describe the evolutionary units (species or higher taxa) constituting a study collection of organisms whose relationships are of interest. Compatibility and parsimony methods are usefully employed together as complementary analytic perspectives.

Character compatibility analysis (reviewed by Meacham and Estabrook, 1985) is based on the concept of compatibility between cladistic characters (Estabrook, 1972; Meacham, 1980). Two cladistic characters (qualitative characters whose states have been ordered in primitive-to-derived sequence) are said to be compatible if there exists at least one hypothesis of phylogeny for the evolutionary units of the study collection that both can support. Therefore, if two cladistic characters are incompatible, both cannot support true estimates of evolutionary relationships; at least one of two incompatible characters must have undergone convergent or reversed state changes during their evolutionary history. All characters that support true phylogenetic relationships, however, must be mutually compatible. Given a study collection of evolutionary units and a set of cladistic characters that describe them, the compatibility of all character pairs can be analyzed and unique groups (cliques) of mutually compatible characters identified (Estabrook et al., 1977; Meacham, 1981a). For each clique of mutually compatible characters there exists at least one phylogenetic hypothesis that all member characters can support, and the tree supported by the largest clique is the preferred maximum-likelihood estimate of phylogeny under some models of character evolution (Felsenstein, 1981, 1982). It is also possible to calculate probabilities (under a reasonable random model) for observed pairs (or larger sets) of compatible characters as well as the number of random compatibilities that any given character may be expected to exhibit (Meacham, 1981b, 1984a). Comparisons of observed patterns of compatibility with random expectation provide the only statistical procedure currently available to demonstrate that morphological character data are potentially informative about phylogenetic relationships.

I used numerical parsimony methods (see Kluge and Farris, 1969, and Farris et al., 1970, for useful theoretical introductions) to calculate "most-parsimonious" hypotheses of phylogeny. A most-parsimonious phylogeny is defined to be that tree diagram requiring the least number of character state changes to generate the observed distribution of attributes among the evolutionary units of the study collection from the hypothesized phenotype of their most recent common ancestor. Although heuristic algorithms must generally be used to approximate most-parsimonious solutions due to the very large number of possible trees that exist for most study collections (Felsenstein, 1978b), the ichthyomyine taxa whose relationships are of interest here are few enough that I was able to employ exact branch-and-bound algorithms (Hendy and Penny, 1982).

Compatibility and parsimony methods provide maximum-likelihood estimates of phylogeny under different evolutionary circumstances (Felsenstein, 1981). Trees supported by the largest clique of compatible characters are the preferred maximum-likelihood estimates of phylogeny when rates of state transformation vary among independent characters such that some characters evolve very rapidly while others evolve slowly. This follows from the expectation that rapidly transforming, independent characters are often likely to undergo reversed or convergent state changes and will therefore seldom exhibit many compatibilities; such characters will belong to large cliques only by chance. Very slowly or infrequently transforming, independent characters will oftener exhibit unique, unreversed state changes and may therefore usually be compatible with one another and form large cliques. Most-parsimonious trees, on the other hand, are the preferred maximum-likelihood estimates of phylogeny when rates of state transformation are about equal across characters such that no large group of characters is likelier than others to exhibit unique and unreversed state transitions (see also Felsenstein, 1982).

In principle, differential character weighting provides an analytic continuum between (unweighted) parsimony and largest-clique criteria for estimating phylogeny (Farris, 1969; Felsenstein, 1981), but most character-weighting protocols either require prior knowledge of state transformation rates or bias the fit of data to the initial results of an unweighted analysis. If, by judicious choice (see below), most of the characters included in the study reflect conservative, independent phenotypic expressions, however, it seems reasonable to expect that both unweighted parsimony and largest-clique methods will yield similar results. In the absence of external information about the variance in rates of evolution across characters, preferred estimates of phylogenetic relationships may then be by that criterion offering the clearest discrimination among alternative hypotheses.

Applications of both largest-clique and numerical parsimony criteria require two basic assumptions: (1) that rates of state transformation in most characters are generally slow, and (2) that changes of state in different characters are independent (Felsenstein, 1983). If characters are evolutionarily labile and are not evolving independently then both largest-clique and parsimony methods may fail to converge on true estimates of phylogeny even as the number of characters analyzed increases without limit (Felsenstein, 1981). Clearly, inference may justifiably be based on a smaller number of plausibly conservative and independent characters than on a larger number of characters collected indiscriminately and without regard for their biological properties or relations.

I chose characters that exhibit minimal within-population variability and whose alternative expressions could readily be described as qualitative states. Character constancy within biological populations may be a reasonable predictor of evolutionary conservatism (see discussion by Farris, 1966) and choosing characters with easily described alternative expressions minimizes the possibility of errors in state assignments. Lacking detailed knowledge of functional or developmental relations that may violate assumptions of character independence, I selected characters from as diverse an array of tissues and organ systems as possible. Disproportionate attention to dental or integumental variation (for example) might otherwise result in most-parsimonious trees, or trees supported by large cliques, that reflect character convergence within functionally (or developmentally) integrated systems rather than recency of common ancestry.

In the absence of well-corroborated hypotheses of ichthyomyine outgroup relationships, I surveyed exemplar species of all sigmodontine genera represented by specimens in North American and European museums (67 of the 68 genera of non-ichthyomyine Sigmodontinae listed by Carleton and Musser, 1984; no specimens of *Juscelinomys* were examined) in order to estimate the polarity of ichthyomyine characters. In general, of two or more alternative character states exhibited among ichthyomyines, that state also observed among other sigmodontines is here hypothesized to be primitive. For some characters, however, I cite the research of previous investigators whose conclusions about polarities appear well founded.

Ichthyomyine species included in the following analyses are those represented by skins, skulls, postcranial skeletons, and fluid-preserved male specimens; of the 14 ichthyomyine species recognized as valid in this monograph, such complete materials are lacking only for *Ichthyomys stolzmanni, Neusticomys oyapocki,* and *N. peruviensis.* Two pairs of species, *Ichthyomys hydrobates/ I. tweedii* and *Rheomys raptor/R. thomasi* were treated each as single evolutionary units because members of each pair do not differ in the characters chosen for phylogenetic analysis. Population samples representing the 11 species (nine EU's) with complete anatomical preparations are listed below. The three-letter abbreviation (in parentheses) following the Latin name serves to identify the taxon in subsequent tables and tree diagrams.

*Anotomys leander* (Ale): Ecuador, Papallacta. Skins and skulls, 12; skeletons, 8; fluids, 12.

*Chibchanomys trichotis* (Ctr): Venezuela, Buena Vista. Skins and skulls, 5; skeletons, 4; fluids, 4.

*Ichthyomys hydrobates* (Ihy): Venezuela, La Mucuy and Mérida. Skins and skulls, 30; skeletons, 1; fluids, 1.

*Ichthyomys pittieri* (Ipi): Venezuela, Rancho Grande. Skins and skulls, 2; skeletons, 1; fluids, 1.

*Ichthyomys tweedii* (Itw): Ecuador, Mindo and Río Pachijal. Skins and skulls, 28; skeletons, 4; fluids, 8.

*Neusticomys monticolus* (Nmo): Ecuador, Guarumal. Skins and skulls, 8; skeletons, 4; fluids, 8.

*Neusticomys venezuelae* (Nve): Venezuela, Río Neverí. Skins and skulls, 2; skeletons, 2; fluids, 2.

*Rheomys mexicanus* (Rme): Mexico, San José Lachiguirí. Skins and skulls, 10; skeletons, 7; fluids, 2.

*Rheomys raptor* (Rha): Costa Rica, San Isidro. Skins and skulls, 6; skeletons, 4; fluids, 4.

*Rheomys thomasi* (Rtt): El Salvador, Mt. Cacaguatigue. Skins and skulls, 27; skeletons, 7; fluids, 2.

*Rheomys underwoodi* (Run): Costa Rica, Volcán Poás. Skins and skulls, 4; skeletons, 3; fluids, 3.

CHARACTERS: Eighteen qualitative morphological characters selected for phylogenetic analysis are described below and the distribution of their states among ichthyomyine species is recorded in table 45. The state labeled (a) is hypothesized to be primitive for each character. Hypothesized sequences of state transitions in multistate characters are described individually below.

Character 1. *Body pelage*:

(a) pelage glossy and grizzled-brownish, composed of wool hairs, buff-banded awns, and guard hairs;

(b) pelage dull and gray-black, composed of wool hairs and few, fine scattered guard hairs.

Most sigmodontine pelages are composed of three kinds of hairs and are usually grizzled-brownish in color resembling, but not identical, with state (a). Among non-ichthyomyines that I have examined, only *Chilomys instans* (an oryzomyine) has a wooly, gray-black pelt resembling state (b).

Character 2. *Ventral countershading*:

(a) pelage not countershaded, ventrum colored like dorsal fur;

(b) pelage countershaded, ventrum washed with pale gray or silvery.

My assignment of polarity for this character is not easily defended by straightforward outgroup comparisons. Venters that are colored like the dorsum and venters washed with contrasting pale gray or silvery are both represented among other sigmodontines. Dark venters, however, are more common among the small cursorial muroids (e.g., *Scotinomys, Melanomys, Microxus,* many small *Thomasomys*) that frequent the damp, leaf-littered floors of tropical lowland and montane rain forests, the likeliest habitats from which the rocky streams of the Andes and the Central American cordilleras might have been invaded by ancestral ichthyomyines.

Character 3. *Tail*:

(a) unicolored, dark above and below;

(b) bicolored, dark above, distinctly paler beneath.

TABLE 45
**Matrix of State Distributions for 18 Qualitative Characters Among 11 Ichthyomyine Species**

| | Characters[a] | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxa[b] | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
| *Ale* | b | b | a | b | b | a | b | b | b | a | a | b | a | b | b | b | a | b |
| *Ctr* | b | b | a | b | b | b | a | b | b | a | a | a | b | b | a | a | a | a |
| *Ihy* | a | b | a | a | a | b | a | b | a | b | b | c | a | b | a | b | b | a |
| *Ipi* | a | b | a | a | a | b | a | b | b | b | b | c | a | b | a | b | b | a |
| *Itw* | a | b | a | a | a | b | a | b | a | b | b | c | a | b | a | b | b | a |
| *Nmo* | b | a | a | a | a | b | a | a | b | a | a | a | a | a | a | a | a | a |
| *Nve* | a | a | a | a | a | b | a | a | b | a | a | a | b | a | a | a | a | a |
| *Rme* | a | b | b | b | b | b | c | b | b | a | a | c | a | b | b | b | a | c |
| *Rha* | a | b | a | a | a | b | b | b | a | a | a | c | a | b | a | b | a | c |
| *Rtt* | a | b | a | a | a | b | b | b | a | a | a | c | a | b | a | b | a | c |
| *Run* | a | b | b | b | b | b | c | b | a | a | a | c | a | b | a | b | a | c |

[a] Numbered and described in text.
[b] Abbreviated as described in text.

Unicolored and distinctly bicolored tails are both common among living sigmodontines. The polarity adopted here is conjectural but serves to minimize conflicts with other characters whose polarities are better supported by outgroup comparison.

Character 4. *Philtrum*:
(a) present;
(b) absent.

A naked philtrum is present in all living sigmodontines except for a few ichthyomyine species, and its absence is therefore almost certainly derived.

Character 5. *Pinnae*:
(a) present and large, visible above the fur of the head;
(b) present but small, concealed beneath the fur of the head, or absent.

Among other sigmodontines, only *Blarinomys breviceps* and *Notiomys edwardsii*, both fossorial species, have pinnae that are concealed in the fur of the head (state b); complete absence of pinnae is unique to *Anotomys leander* among living sigmodontines.

Character 6. *Superciliary vibrissae*:
(a) present;
(b) absent.

Superciliary vibrissae are absent only within the Ichthyomyini. All other sigmodontines possess well-developed vibrissae over the eyes, and the absence of these hairs is most plausibly interpreted as derived.

Character 7. *Plantar pads of manus*:
(a) hypothenar pad separate, not fused with the third interdigital;
(b) hypothenar and third interdigital pads fused;
(c) hypothenar and thenar pads fused with adjacent third and first interdigital pads, respectively (derived from state b).

Among sigmodontines, the fusion of carpal pads with interdigital pads is unique to the ichthyomyine species that exhibit this trait.

Character 8. *Fringing hairs on pes*:
(a) present but weakly developed;
(b) present and well developed.

Among other sigmodontines, only *Holochilus* and *Nectomys* possess fringes of stiffened hairs along the plantar surface of the pes, but these are only weakly developed. State (b) is unique, among living Sigmodontinae, to those ichthyomyine species that exhibit it.

Character 9. *Lower third molars*:
(a) m3 with two distinct enameled lobes, the entoconid-hypoconid cusp pair comprising a large posterior moiety of the tooth;
(b) m3 a simple peglike tooth, the entoconid-hypoconid cusp pair absent or reduced to a small conule.

Reduction of the posterior cusp pair of the third molar is a well-documented trend in muroid evolution (Carleton and Eshelman, 1979; Misonne, 1969; Hershkovitz, 1962); most other sigmodontines have S-shaped or

E-shaped lower third molars in which the entoconid and hypoconid are often subequal in size to the anterior cusps.

Character 10. *Nasal bones*:

(a) long, produced anteriorly beyond the premaxillae to conceal the incisors and nasal orifice in dorsal view;

(b) short, truncated behind the premaxillae to expose the incisors and nasal orifice in dorsal view.

Among sigmodontines, state (b) is exhibited only by species of *Ichthyomys*.

Character 11. *Supraorbital foramina*:

(a) on the lateral surface of the frontals within the orbital fossae;

(b) on the dorsal surface of the frontals between the orbital fossae.

The dorsal position of the supraorbital foramina is another state uniquely displayed by species of *Ichthyomys*.

Character 12. *Carotid arterial supply*:

(a) pattern 1;

(b) pattern 2;

(c) pattern 3 (derived from state b).

This sequence of successively derived carotid circulatory patterns follows Bugge's (1970) hypothesis that supraorbital and infraorbital branches of the stapedial artery primitively supplied the ophthalmic and internal maxillary circulations, respectively. All three character states are represented among other sigmodontines, however, and parallel (or reversed) changes in these patterns have evidently been a common occurrence in muroid phylogeny.

Character 13. *Orbicular apophysis of malleus*:

(a) present, a bony knob or spur;

(b) absent.

A distinct orbicular apophysis of the malleus is present in all sigmodontines except *Chibchanomys trichotis* and some species of *Neusticomys*.

Character 14. *Metatarsal configuration*:

(a) $III \geq IV > II \gg V > I$;

(b) $IV > III > II, V > I$.

The primitive ichthyomyine metatarsal configuration hypothesized here follows the discussion of this character advanced earlier (see Comparative Morphology); all subsequently derived morphologies (listed in table 11) have here been condensed to form a single state in order that metatarsal evolution not be disproportionately weighted in the phylogenetic reconstructions following.

Character 15. *Omohyoid muscle*:

(a) present;

(b) absent.

The omohyoid is present in all muroids that have been examined for this character (Parsons, 1896; Rinker, 1954). The muscle is known to be absent only in the two ichthyomyine species for which its loss is here reported.

Character 16. *Gastric glandular epithelium*:

(a) glandular epithelium present between the incisura angularis and the pyloric sphincter;

(b) glandular epithelium restricted to the greater curvature of the stomach.

Polarity for this character follows the conclusions of Carleton (1973) and Vorontsov (1979). The derived state (b), as represented in ichthyomyines, appears to be unique among the sigmodontines that have been surveyed for this character.

Character 17. *Gall bladder*:

(a) present;

(b) absent.

I interpret the absence of a gall bladder in *Ichthyomys* as the result of loss. Gall bladders are, however, present or absent in almost equal proportions among those muroids that have been surveyed for this character (Carleton, 1980; Vorontsov, 1979).

Character 18. *Bacular cartilage*:

(a) bacular cartilage tridigitate, the medial digit larger than the lateral two but not grossly swollen nor containing a calcified center;

(b) bacular cartilage with a single digit (derived from state a);

(c) bacular cartilage tridigitate, the medial digit grossly swollen with a well-defined calcified core (derived from state a).

The sequence of evolution of phallic character states within the Muroidea has been diversely interpreted. Hooper and Musser (1964) proposed that a "complex" penis with a tridigitate bacular cartilage is the primitive muroid condition, but Carleton (1980) pointed out that nonmuroid rodents have simple

TABLE 46
**Matrix of Pairwise Compatibilities[a] Among 18 Ichthyomyine Characters**

| | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **2** | 0 | | | | | | | | | | | | | | | | |
| **3** | 1 | 1 | | | | | | | | | | | | | | | |
| **4** | 0 | 1 | 1 | | | | | | | | | | | | | | |
| **5** | 0 | 1 | 1 | 1 | | | | | | | | | | | | | |
| **6** | 0 | 0 | 1 | 0 | 0 | | | | | | | | | | | | |
| **7** | 0 | 1 | 1 | 0 | 0 | 0 | | | | | | | | | | | |
| **8** | 0 | 1 | 1 | 1 | 1 | 0 | 1 | | | | | | | | | | |
| **9** | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | | | | | | |
| **10** | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | | | | | | | | |
| **11** | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | | | | | | | |
| **12** | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | | | | | | |
| **13** | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | | | | | |
| **14** | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | | | | |
| **15** | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | | | |
| **16** | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | | |
| **17** | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | |
| **18** | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** |

[a] Rows and columns in the matrix represent characters as numbered and described in the text. A matrix entry of (1) for any row and column intersection indicates that the corresponding pair of characters is compatible, an entry of (0) that the pair of characters is incompatible.

bacula and suggested that the most parsimonious hypothesis of bacular evolution would recognize the tridigitate condition as derived. The hypothesis of evolution in the ichthyomyine baculum proposed here is based on the observation that state (a) broadly resembles the tridigitate condition expressed among many other Neotropical muroid genera with grossly similar phalli (see Hooper and Musser, loc. cit.) while the unidigitate baculum of *Anotomys leander* (state b) is associated with unusual phallic attributes of that species (large, paired dorsolateral spines on the medial bacular mound; two dorsal papillae) that are not represented among other sigmodontines with simple bacular cartilages. State (c) is restricted to species of *Rheomys* and does not resemble bacular configurations of any other sigmodontines whose phalli have been described.

Results and Discussion: Pairwise compatibility relations (table 46) among the 18 characters described above reveal that not all ichthyomyine attributes are the result of unique and unreversed evolutionary events. Characters 5 and 9, for example, are incompatible [matrix entry of (0) in table 46] and it is therefore certain that either pinnae or

TABLE 47
**Expected Numbers of Compatibilities at Random and Observed Compatibilities for 18 Ichthyomyine Characters**

| Character | Expected compatibilities[a] | Observed compatibilities[b] | Standard deviations from expected |
|---|---|---|---|
| 1 | 6.3 ± 1.9 | 6 | −0.16 |
| 2 | 5.9 ± 1.7 | 13 | 4.18 |
| 3 | 9.2 ± 2.0 | 15 | 2.90 |
| 4 | 4.8 ± 1.7 | 9 | 2.47 |
| 5 | 4.8 ± 1.7 | 9 | 2.47 |
| 6 | 9.3 ± 1.8 | 6 | −1.83 |
| 7 | 4.0 ± 1.7 | 10 | 3.53 |
| 8 | 5.9 ± 1.7 | 13 | 4.18 |
| 9 | 4.5 ± 1.6 | 3 | −0.94 |
| 10 | 9.2 ± 2.0 | 16 | 3.40 |
| 11 | 9.2 ± 2.0 | 16 | 3.40 |
| 12 | 3.1 ± 1.5 | 10 | 4.60 |
| 13 | 9.2 ± 2.0 | 11 | 0.90 |
| 14 | 5.9 ± 1.7 | 13 | 4.18 |
| 15 | 9.2 ± 2.0 | 11 | 0.90 |
| 16 | 4.5 ± 1.6 | 12 | 4.69 |
| 17 | 9.2 ± 2.0 | 16 | 3.40 |
| 18 | 6.3 ± 1.9 | 13 | 3.53 |

[a] Calculated as described by Meacham (1981b, 1984a), plus or minus one standard deviation.
[b] From table 46.

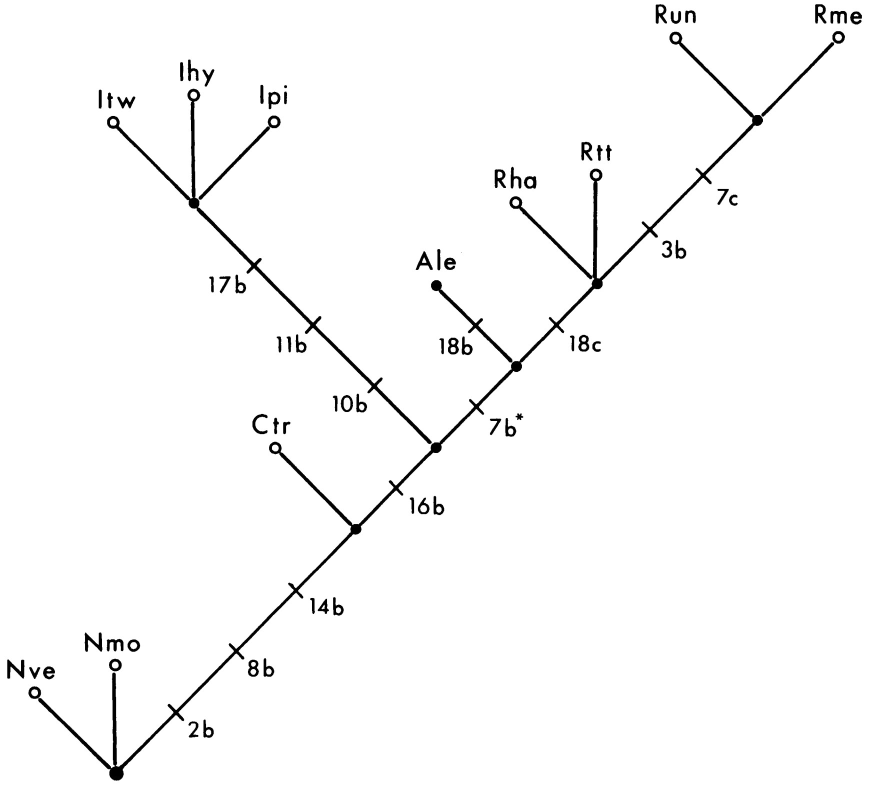


Fig. 86. Cladogram corresponding to clique I (table 48). Derived states of member characters are illustrated on the phyletic intervals where they are hypothesized to have evolved uniquely. The character state transformation marked by an asterisk provides evidence for relationships that conflict with the cladogram for clique II (fig. 87). Path lengths between solid nodes on the tree are drawn proportional to the number of intervening character transformations. Open terminal nodes represent taxa that do not differ from immediately ancestral nodes in any of the characters on which this cladogram is based (i.e., members of clique I); such terminal taxa have been removed by one arbitrary length unit from their ancestral nodes. Taxonomic abbreviations are defined in the accompanying text.

TABLE 48
**Memberships and Probabilities of All Cliques of Compatible Ichthyomyine Characters**

| Cliques | Membership[a] | Probability[b] |
|---|---|---|
| I | 2, 3, 7, 8, 10, 11, 14, 16, 17, 18 | $8.79 \times 10^{-12}$ |
| II | 2, 3, 8, 10, 11, 12, 14, 16, 17, 18 | $1.14 \times 10^{-11}$ |
| III | 2, 3, 4, 5, 8, 10, 11, 14, 17 | $1.75 \times 10^{-9}$ |
| IV | 2, 4, 5, 8, 10, 11, 14, 15, 17 | $1.75 \times 10^{-9}$ |
| V | 3, 7, 10, 11, 13, 16, 17, 18 | $9.18 \times 10^{-8}$ |
| VI | 3, 10, 11, 12, 13, 16, 17, 18 | $4.24 \times 10^{-8}$ |
| VII | 2, 8, 10, 11, 14, 15, 16, 17 | $1.29 \times 10^{-7}$ |
| VIII | 3, 6, 10, 11, 13, 17, 18 | $8.94 \times 10^{-5}$ |
| IX | 1, 3, 10, 11, 17, 18 | $2.48 \times 10^{-4}$ |
| X | 10, 11, 13, 15, 16, 17 | $5.96 \times 10^{-4}$ |
| XI | 9, 13, 15 | $1.53 \times 10^{-1}$ |
| XII | 1, 9 | $2.50 \times 10^{-1}$ |

[a] Characters belonging to each clique are numbered as in text and tables 45 and 46.

[b] Calculated as described by Meacham, 1981b.

lower third molars or both have undergone convergent or reversed changes of state in the course of ichthyomyine phylogeny. Conversely, characters 12 and 18 are compatible [matrix entry of (1) in table 46] because there exists one or more hypotheses of ichthyomyine phylogeny supported by derived states both of the carotid circulation and of the bacular cartilage. Although most pairs of ichthyomyine characters are compatible, the existence of incompatible character pairs guarantees that no hypothesis of ichthyomyine phylogeny will be consistent with all of the morphological data reported here.

Table 47 compares the observed number of compatibilities exhibited by each character (obtained by counting the 1's in corresponding rows and columns of the compatibility matrix) with the number of compatibilities

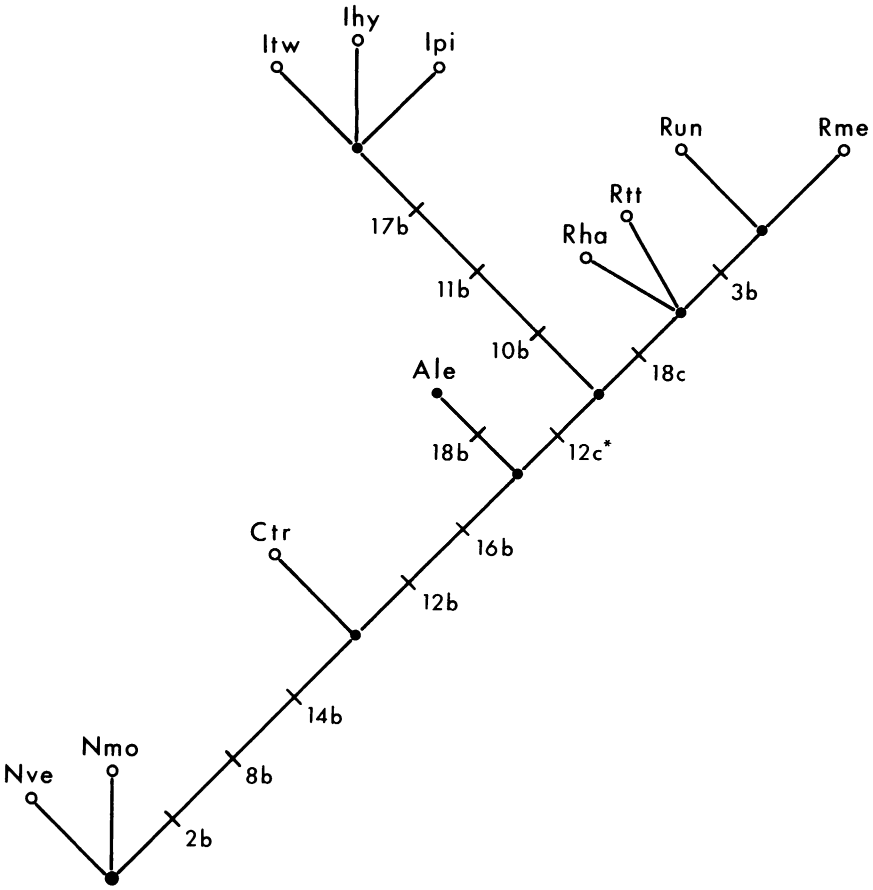


Fig. 87. Cladogram corresponding to clique II (table 48). The character state transformation marked by an asterisk provides evidence for relationships that conflict with the cladogram for clique I (fig. 86). Other conventions are explained in the caption to figure 86.

that would be expected (plus or minus one standard deviation) if character states were distributed randomly (sensu Meacham, 1981b, 1984a) among the nine ichthyomyine evolutionary units of this study collection. While some characters (1, 6, 9, 13, 15) do not exhibit many more (or fewer) compatibilities than random expectation, most others (2, 7, 8, 10, 11, 12, 14, 16, 17, 18) display highly nonrandom compatibility counts. Since characters that have undergone reversed or convergent changes of state are unlikely to be compatible with many other characters except by chance or because of developmental or functional dependence, the observation in these data of significantly more compatibilities than random expectation among characters representing a diversity of tissues and organ systems provides substantial evidence that at least some of the morphological variation among ichthyomyine taxa reflects recency of common ancestry.

Within the compatibility matrix (table 46) there are 12 cliques of mutually compatible characters each of which uniquely supports one or more hypotheses of ichthyomyine phylogeny. The member characters for each clique together with their estimated probability of groupwise compatibility are listed in table 48. Cliques I and II, with 10 member characters apiece, represent the largest patterns of cladistic character agreement in the data and merit special attention also because their estimated probabilities are two orders of magnitude further removed from random expectation than any probability estimates for smaller cliques.

Cliques I and II share nine characters (2,

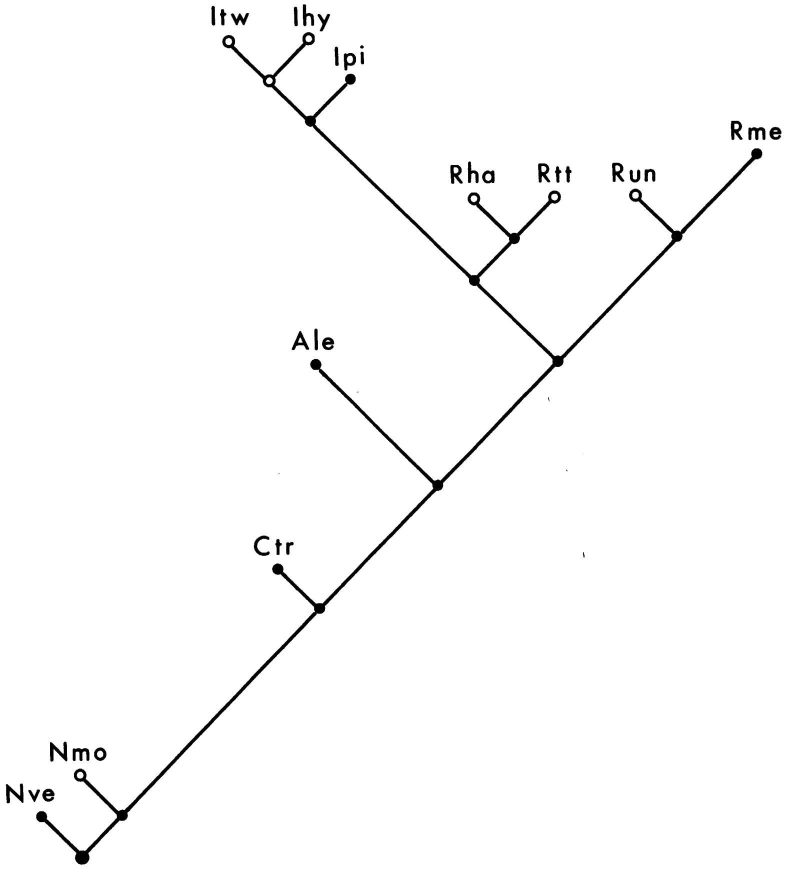


Fig. 88. The most parsimonious hypothesis of ichthyomyine relationships. This topology requires 32 transformations in the 18 characters analyzed (table 45); the consistency index (defined by Kluge and Farris, 1969) for this tree is therefore 21/32 = .66. Branch lengths are drawn proportional to the number of character transformations between nodes. Other conventions follow figure 86.

3, 8, 10, 11, 14, 16, 17, 18) that support patterns of hypothesized relationships common to both of their corresponding cladograms (figs. 86, 87): (1) Species of the genus *Neusticomys* exhibit the primitive states for characters 2 (pelage countershading), 8 (fringing hairs of pes), and 14 (metatarsal proportions), while all remaining ichthyomyine taxa, apomorphic for these characters, are hypothesized to form a monophyletic group. (2) A shared, derived transformation of the stomach (character 16) unites species of *Anotomys, Rheomys,* and *Ichthyomys* as a monophyletic group that does not include *Chibchanomys trichotis.* (3) Characters 10 (length of nasals), 11 (position of supraorbital foramina), and 17 (presence/absence of a gall bladder) support the monophyly of *Ichthyomys.* (4) The genus *Rheomys* is characterized by a uniquely derived bacular morphology (character 18). (5) *Rheomys underwoodi* and *R. mexicanus* are sister taxa united by their shared, derived similarity in tail coloration (character 3).

Cliques I and II differ by including either characters 7 or 12, respectively. Shared, derived fusions of the plantar pads of the manus (character 7) support a hypothesized sister-group relationship of *Anotomys* with *Rheomys* and provide additional evidence for recent common ancestry between *Rheomys underwoodi* and *R. mexicanus* (fig. 86). Derived resemblances in patterns of carotid arterial supply (character 12), on the other hand, lend additional support to monophyly of the *Anotomys/Ichthyomys/Rheomys* cluster but also support a sister-group relationship between *Ichthyomys* and *Rheomys* (fig. 87). Either fusions of the plantar pads of the manus or patterns of carotid supply (or both) have undergone homoplasy in the course of ichthyomyine phylogeny and there is no preponderant evidence from the relatively small difference in the probabilities of cliques I and II to resolve the conflicting testimony of relationships that these characters provide.

Numerical parsimony analysis of the character data in table 45 using exact branch-and-bound algorithms reveals one most-parsimonious topology requiring 32 character state transformations (fig. 88), but there are 10 other trees that each require only 33 character state transformations and such a small difference in parsimony does not permit confident probabilistic discrimination among alternative hypotheses (Cavender, 1978, 1981). The strict consensus diagram (Rohlf, 1982), illustrating just those monophyletic groups common to all of the trees with lengths of 32 or 33 (fig. 89), is largely unresolved and recognizes just the monophyly of *Ichthyomys* and of the larger group that includes *Chibchanomys, Anotomys, Ichthyomys,* and *Rheomys.*

While no tree topology seems supported by a uniquely largest clique or requires a significantly least number of character state transformations, the phylogeny illustrated in figure 90 provides the most biologically compelling hypothesis of ichthyomyine relationships and is nearly optimal by both compatibility and numerical parsimony criteria. This tree is a resolution of the cladogram corresponding to clique II (fig. 87) and is therefore supported by unique and unreversed transitions of state in all characters that are members of that clique. Overall, the topology requires one more character state transition (33 total) than the most-parsimonious alternative (fig. 88) with which closer comparison merits discussion.

The tree illustrated in figure 90 depicts members of the genus *Rheomys* as a monophyletic group, an arrangement that is supported by their common possession of a bulbous medial bacular digit with a calcified core (character state 18c, see fig. 91, right); this morphological condition appears uniquely derived among Sigmodontines. By contrast, the most-parsimonious hypothesis (fig. 88), that *Rheomys raptor* and *R. thomasi* are more closely related to species of *Ichthyomys* than to *R. mexicanus* and *R. underwoodi,* is not supported by any uniquely shared, derived character state but instead reflects the most economical interpretation of homoplasies (fig. 91, left) in characters 4 (presence/absence of philtrum) and 5 (size of pinnae). Among the many other phenotypic attributes that I surveyed but did not code as characters (see Comparative Morphology), there are none for which *Rheomys raptor, R. thomasi,* and *Ichthyomys* exhibit unique resemblances. Neither *R. raptor* nor *R. thomasi* display supraorbital foramina on the dorsal surface of the frontals, possess truncated nasal bones, or lack a gall bladder, derived attributes that might confirm a sister-group relationship with *Ichthyomys* and compromise the monophyly of *Rheomys.* Since the most-parsimonious arrangement clusters *R. raptor* and *R. thomasi* with *Ichthyomys* on the basis of homoplasious similarities and because that cluster lacks other evidence of recent common ancestry, monophyly of *Rheomys* seems the better-supported alternative.

Another distinctive feature of the phylo-

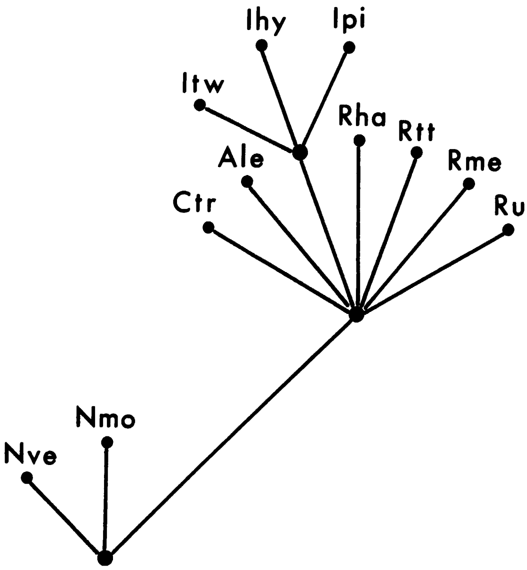


Fig. 89. The diagram of strict consensus among all hypotheses of ichthyomyine relationships that require 33 or fewer state transformations in the character data of table 45.

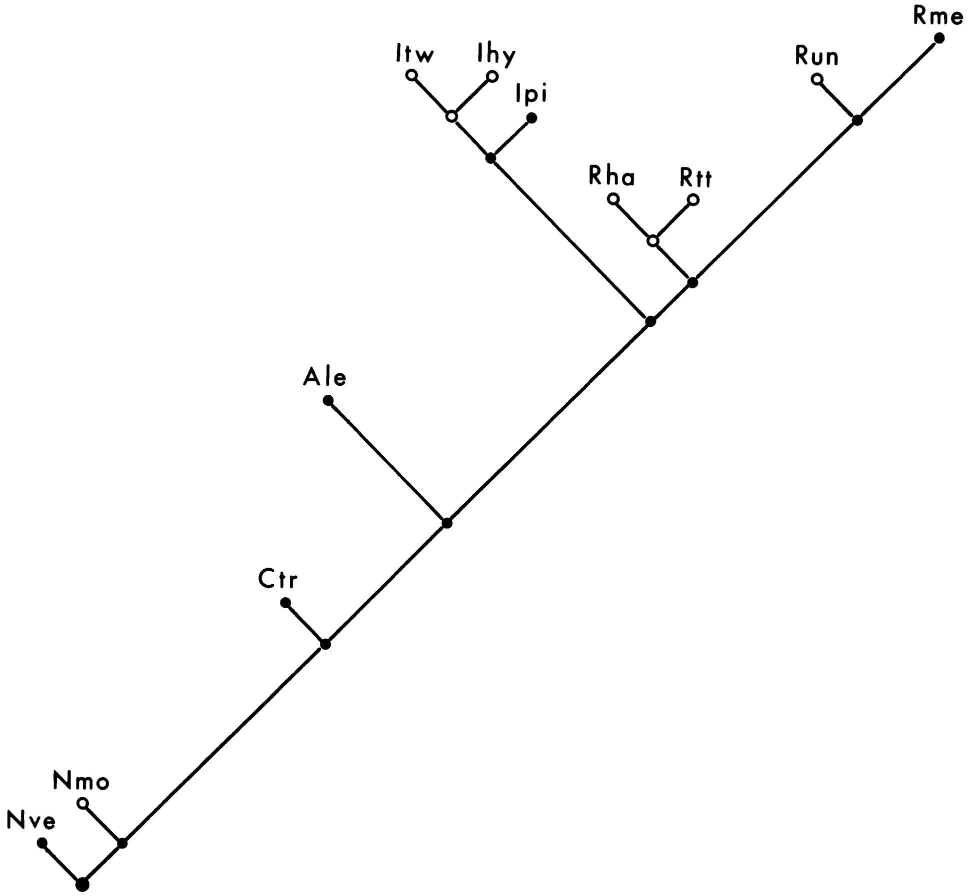


Fig. 90. Hypothesis of ichthyomyine relationships favored here. This topology is a resolution of the cladogram for clique II (fig. 87) and requires 33 state transformations in the 18 characters analyzed. Branch lengths are drawn proportional to the number of character transformations between nodes. Other conventions follow figure 86.

genetic hypothesis illustrated in figure 90 is the sister-group relationship of *Rheomys* and *Ichthyomys*. That these two monophyletic genera are each other's closest relatives is supported by their uniquely shared, derived carotid circulation (character state 12c), and is further suggested by a close similarity in pelage (character state 1a). Although a grizzled-brown pelage like that of *Ichthyomys* and *Rheomys* is also observed among some species of *Neusticomys*, the most-parsimonious interpretation of pelage evolution given the topology of figure 90 suggests that this similarity resulted from a reversal in the lineage immediately ancestral to the former two genera (fig. 92, right). An alternative arrangement, in which *Anotomys* is the sister taxon of *Rheomys* (fig. 92, left; this is a resolution of the cladogram for clique I, fig. 86) is supported by the derived fusion of the hypothenar and 3rd interdigital pads of the manus (character state 7b) that members of these genera uniquely share. This hypothesis necessarily implies convergent or reversed evolution in the carotid circulation (character 12), however, as well as additional homoplasies in the pelage (character 1; see fig. 92, left). Since uniquely shared, derived similarities other than those cited above are not presently available to determine which of the two alternative phyletic arrangements of *Anotomys*, *Rheomys*, and *Ichthyomys* is better supported, the hypothesis that *Rheomys* and *Ichthyomys* are sister-groups can be argued

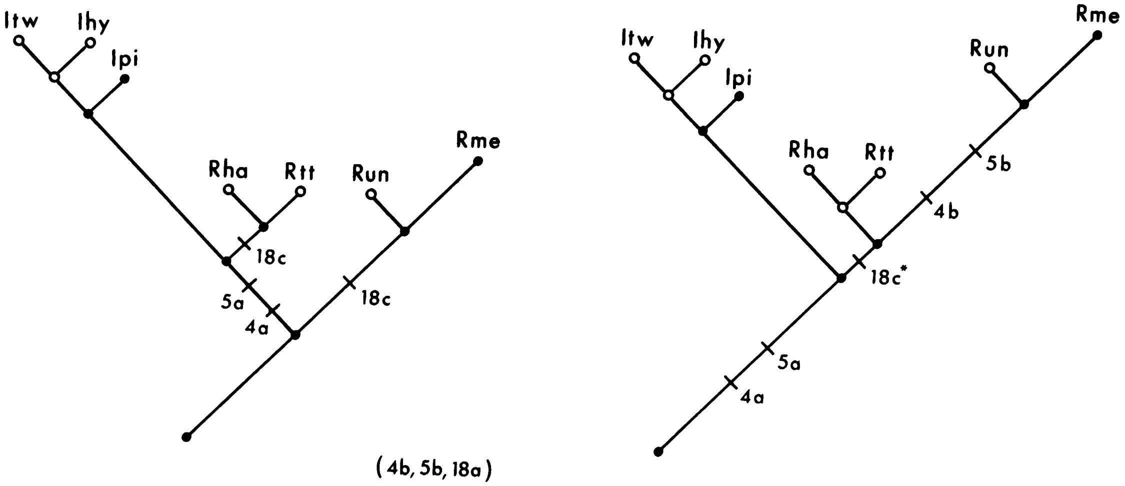


Fig. 91. Two hypotheses of relationships among the species of *Ichthyomys* and *Rheomys*. The diagram on the left is a detail of the most-parsimonious phylogeny (from fig. 88). The diagram on the right is a detail from figure 90. Only the three characters in which the two hypotheses differ are shown. The basal nodes in both subtrees have the same character state assignments (given in parentheses). An asterisk marks the only uniquely derived and unreversed state transformation hypothesized by either subtree for these characters. Branch lengths are drawn as reconstructed from the total character data (table 45). Other conventions follow figure 86.

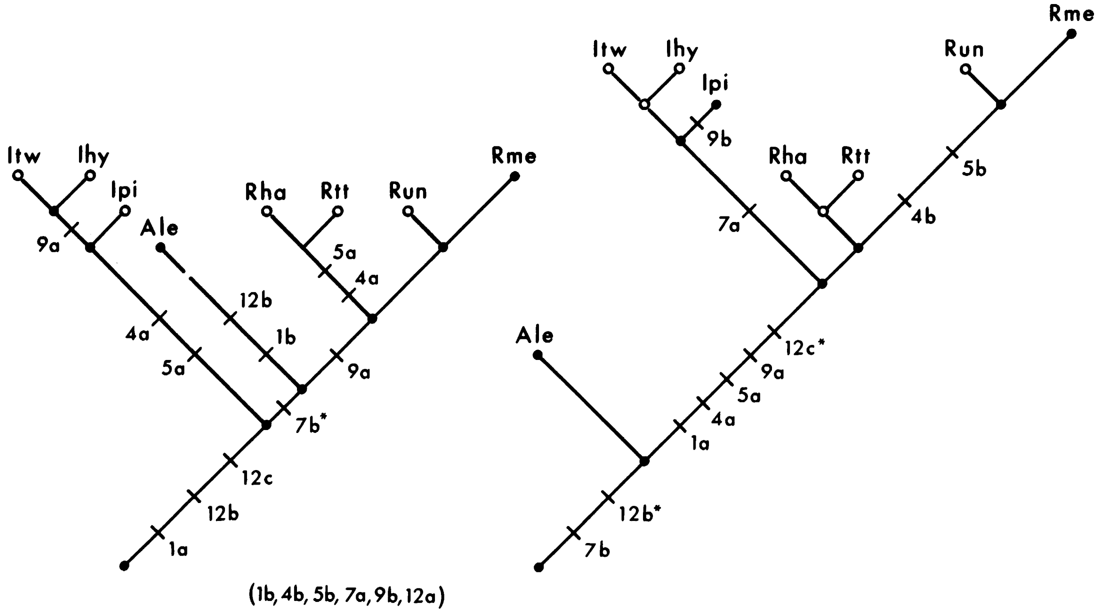


Fig. 92. Two hypotheses of relationships among the species of *Anotomys, Ichthyomys,* and *Rheomys.* The left-hand diagram is a resolution of the cladogram for clique I (fig. 86). The right-hand diagram is a detail from figure 90. Only the six characters in which the two hypotheses differ are shown. Both subtrees have the same character state assignments (given in parentheses) at their basal nodes. Asterisks mark character states hypothesized to be uniquely derived and unreversed. Branch lengths are drawn as reconstructed from the total character data (table 45). Other conventions follow figure 86.

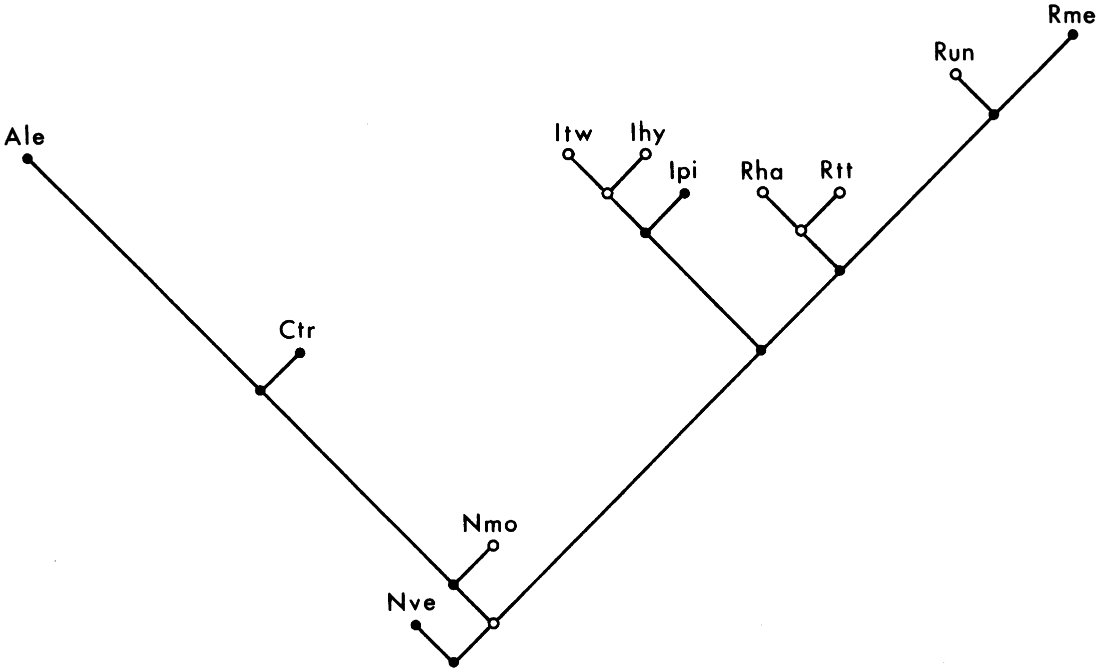


Fig. 93. Hypothesis of ichthyomyine phylogeny with character 1 heavily weighted. *Anotomys leander* (**Ale**), *Chibchanomys trichotis* (**Ctr**), and *Neusticomys monticolus* (**Nmo**) uniquely exhibit the derived state for this character and form a monophyletic group. This topology requires 35 state transformations in the total character data (table 45) from which the branch lengths are reconstructed.

only on the basis of minimizing homoplasy in characters that are inconsistent with both hypotheses.

I regard the monophyly of the *Rheomys underwoodi/R. mexicanus* species pair, the monophyly of *Rheomys,* the monophyly of *Ichthyomys,* and the sister-group relationship between *Ichthyomys* and *Rheomys* to be reasonably well-corroborated aspects of ichthyomyine phylogeny insofar as most characters that support these relationships have well-defined states and plausible polarities and because alternative hypotheses are either less parsimonious or lack unequivocal character support. Other aspects of ichthyomyine phylogeny are less intuitively satisfying and could be variously interpreted. The monophyly of the group composed of *Rheomys, Ichthyomys, Anotomys,* and *Chibchanomys,* for example, is common to all compatibility and numerical parsimony results discussed above, but the derived states of two of the three characters that support this hypothesis (8, fringing hairs of pes, and 14, metatarsal proportions) are also observed in many other small, semiaquatic-carnivorous mammals (see Convergence and Adaptive Radiation, below) and might therefore have evolved together in two or more independent lineages as adaptations to rheophilic habits. Also, conspicuously countershaded pelages (character 2) cannot be determined as unequivocally derived by outgroup comparison, and thus lend but weak support to the same hypothesis of monophyly. Some species of *Neusticomys,* as that genus is here constituted, might therefore be more closely related to *Chibchanomys* or to *Anotomys* than straightforward interpretations of the available character data suggest. If the uniquely shared, derived plumbeous pelage (1b) of *Neusticomys monticolus, Chibchanomys,* and *Anotomys* is given greater weight, for example, the hypothesis depicted in figure 93 gains some credence. This tree topology is less parsimonious than any alternatives hitherto considered (35 steps total) and is supported by only a small clique of mutually

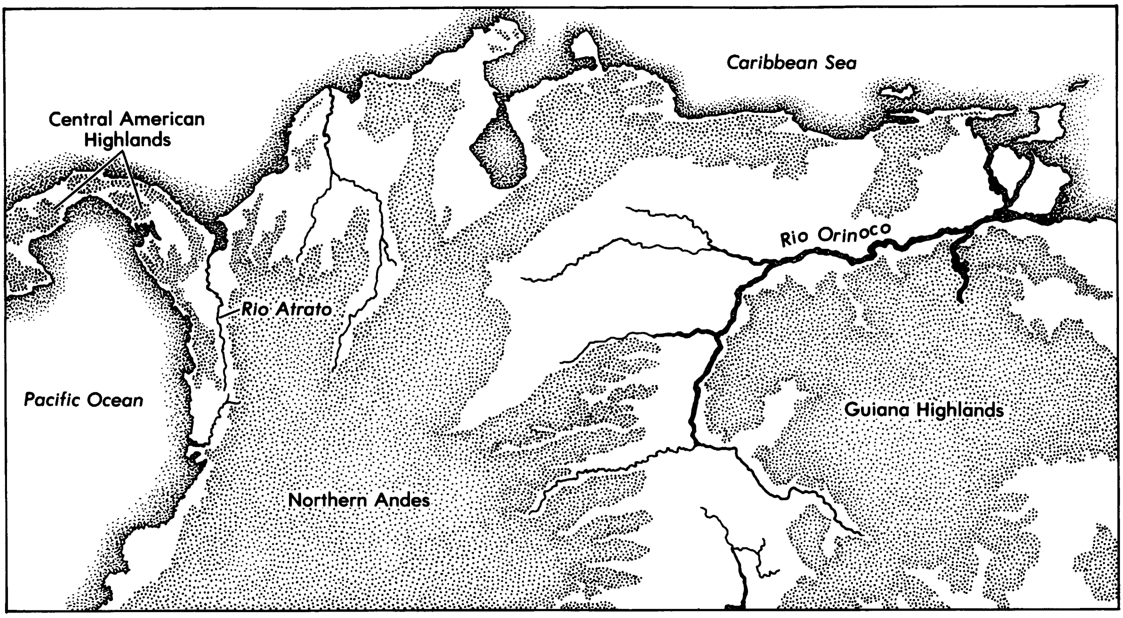


Fig. 94. Major highland regions in the northern Neotropics. Shaded areas represent elevations in excess of 100 m above sea level.

compatible characters (clique IX, table 48); however, I propose it as a conjecture that may reward attention by future investigators.

## ZOOGEOGRAPHY

The Río Atrato in northwestern Colombia and the Río Orinoco in central Venezuela divide the highlands of the northern Neotropics into three regions, each with a distinctive ichthyomyine fauna (fig. 94, table 49).

(1) The northern Andes, including the mountains southeast of Lago Maracaibo together with the coastal cordilleras of Venezuela, is the center of ichthyomyine diversity (as Reig, 1984, previously recognized). Of the five genera and 14 species recognized in this monograph, four genera and nine species occur in the northern Andes and their skirting piedmont landscapes. Two monotypic genera (*Anotomys* and *Chibchanomys*) are endemic to the northern Andes as are five species (*Ichthyomys hydrobates, I. pittieri, I. stolzmanni, Neusticomys monticolus, N. peruviensis*) in genera that also have extralimital representatives.

(2) The Guiana highlands south and east of the Río Orinoco, comprising the eroded sandstone landscapes of southern Venezuela and the low mountains of Guyana, Suriname, and French Guiana, appear to have a depauperate ichthyomyine fauna. Only two species

TABLE 49
**Geographical Distribution of Ichthyomyine Species**

| Species | Major regions[a]<br>Northern Andes | <br>Guiana Highlands | <br>Central America |
|---|---|---|---|
| *Anotomys leander* | X | | |
| *Chibchanomys trichotis* | X | | |
| *Ichthyomys hydrobates* | X | | |
| *Ichthyomys pittieri* | X | | |
| *Ichthyomys stolzmanni* | X | | |
| *Ichthyomys tweedii* | X | | X |
| *Neusticomys monticolus* | X | | |
| *Neusticomys oyapocki* | | X | |
| *Neusticomys peruviensis* | X | | |
| *Neusticomys venezuelae* | X | X | |
| *Rheomys mexicanus* | | | X |
| *Rheomys raptor* | | | X |
| *Rheomys thomasi* | | | X |
| *Rheomys underwoodi* | | | X |

[a] As defined in accompanying text.

of *Neusticomys* are known from this region; one (*N. oyapocki*) is endemic, while the other (*N. venezuelae*) occurs also in the easternmost coast range of Venezuela north of the Orinoco.

(3) The Central American highlands from Oaxaca, Mexico, south and east to the Río Atrato, harbor one endemic ichthyomyine genus, *Rheomys,* with four included species. In addition, *Ichthyomys tweedii* is known from the lowlands of central Panama.

While numerous physiographic features account for coincident range discontinuities and delimit significant faunal assemblages for other organisms within each of these large regions, ichthyomyines are sufficiently difficult to collect that finer zoogeographic discrimination is not presently warranted. For example, the absence of specimens of *Chibchanomys trichotis* from the Sierra Nevada in western Venezuela could either be attributed to the lack of adequate collecting there or it could reflect the effectiveness of the Táchira depression (Vuilleumier and Ewert, 1978) as a barrier to dispersal of highland taxa between those mountains and the Cordillera Oriental of Colombia where *C. trichotis* is known to occur. Observed differences in ichthyomyine faunal composition among the three zoogeographic regions distinguished here, however, are less likely due to sampling artifacts. The Guiana region has been the focus of several mammalian faunal survey efforts (reported by Tate, 1939; Handley, 1976; Husson, 1978; Genoways et al., 1981) which might reasonably have been expected to collect additional ichthyomyine taxa if a fauna as diverse as that of the northern Andes exists there. Similarly, the absence, in Central America, of any endemic ichthyomyine taxa other than species of the genus *Rheomys* would seem reasonably well established given the considerable collections from that region accumulated by many North American and European workers over the last century. Nevertheless, the recent (1970) discovery of *Ichthyomys tweedii* in central Panama, a country whose mammalian fauna has received the attention of two intensive episodes of field inventory (summarized by Goldman, 1920, and Handley, 1966) underscores the cryptic habits of these animals and suggests cautious evaluation of zoogeographic scenarios predicated on the absence of taxa from specific areas.

The fact that two lowland river valleys correspond with significant geographic discontinuities in the distribution of semiaquatic mammals known to occur elsewhere at elevations near sea level is an apparent anomaly that may relate to aspects of ichthyomyine ecology discussed earlier. Ichthyomyines have usually been collected from small, clear, rocky-bottomed forest streams, a common freshwater habitat in mountains, foothills, and piedmont landscapes or, indeed, wherever rocks are sufficiently close to the surface to be exposed by running water. Significantly, such watercourses support taxonomically diverse and productive communities of benthic macroinvertebrates (see Hynes, 1970, and the preceding discussion of ichthyomyine ecology). By contrast, forest streams in tropical lowland river valleys are often spring- or swamp-fed, with oxygen-depleted, acid-stained waters flowing over deep deposits of nutrient-poor alluvial sands or clays. Such streams typically do not support equivalently diverse or productive macroinvertebrate faunas (Fittkau, 1967). Sediment-laden whitewater rivers, usually subject to seasonal fluctuations in discharge that may overflow most of their minor tributaries, constitute another class of lowland aquatic habitat from which ichthyomyines are unknown, perhaps due to the effect of periodic silt deposition on benthic arthropod communities (see Hynes, 1970, and Minshall, 1984, for ecological discussions of silt in streams). The apparent effectiveness of the valleys of the Ríos Atrato and Orinoco as barriers to ichthyomyine distribution may therefore be related as much to limnological considerations as to elevational discontinuities, but the credibility of this conjecture can only be evaluated with information that is not presently available. To the best of my knowledge, no relevant ecological studies of streams in either the Atrato or Orinoco basins have been published.

The valley of the Río Atrato traces the course of the Bolivar Geosyncline (Nygren, 1950) and marks the position of the last marine barrier between Central and South America in the Late Tertiary (Haffer, 1970). Presently a trough of swampy lowlands, the Atrato valley separates distinctive montane

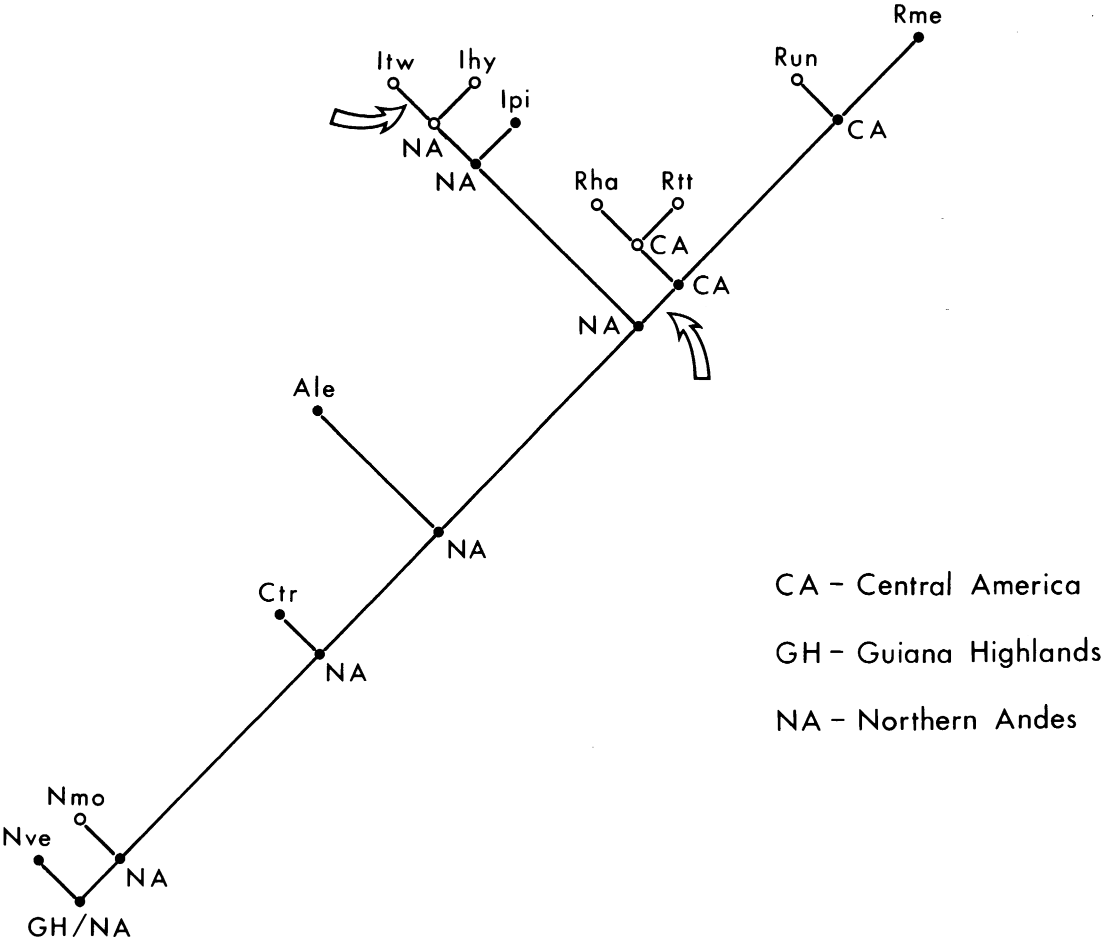


Fig. 95. Parsimonious assignments of geography to internal nodes of the best-supported hypothesis of ichthyomyine phylogeny. The geographical distribution of the terminal taxa is given in table 49 and the areas in question are illustrated in figure 94. Arrows indicate the phyletic lineages that are hypothesized to have dispersed from the northern Andean region to Central America.

faunas in the serranías of eastern Panama and in the Cordillera Occidental of the Colombian Andes. While this barrier has evidently been crossed by several mammalian taxa with disjunct populations in both highland areas (e.g., *Monodelphis adusta, Cryptotis, Oryzomys albigularis, Reithrodontomys mexicanus*; see Hooper, 1952; Handley, 1972; Choate, 1970), other mammalian distributions provide evidence of faunal isolation. Members of the Central American muroid genera *Isthmomys* and *Nyctomys,* for example, co-occur with *Rheomys* in the Serranía de Pirre immediately west of the Río Atrato but are unknown from the Andes. Similarly, *Akodon, Microryzomys,* and *Thomasomys* co-occur with *Neusticomys* in the Cordillera Occidental just east of the Río Atrato but are unknown from any Central American mountains. Such zoogeographic discontinuities, in conjunction with the ecological considerations discussed earlier, suggest that dispersals across the Atrato lowlands are events that should be minimized by credible reconstructions of ichthyomyine historical geography.

Figure 95 illustrates the best-supported hypothesis of ichthyomyine phylogeny analyzed previously on which both the observed geographic distribution of extant species and the inferred distribution of hypothetical ancestors are indicated. The most plesiomorphic ichthyomyines, members of the genus *Neusticomys* (including *N. oyapocki* and *N. peruviensis,* not diagrammed in fig. 95) are South American endemics distributed either in the northern Andean region (NA) or the Guiana highlands (GH). Most subsequent speciation events have given rise to lineages endemic to the northern Andes (*Chibchanomys, Anotomys,* most *Ichthyomys* species). Parsimonious assignments of geography to internal nodes therefore suggest that the most recent common ancestor of extant ichthyomyines was South American and that *Rheomys* is descended from a single invasion (arrow in fig. 95) from South America eastward across the Río Atrato valley into Central America. Hypotheses of ichthyomyine relationships in which *Rheomys* is not monophyletic (e.g., fig. 88) would require multiple dispersals across the Río Atrato, but it seems unnecessary to entertain such complex scenarios when phylogenies that are better supported by characters are also consistent with simpler zoogeographic inferences.

# CONVERGENCE AND ADAPTIVE RADIATION

The patterns of qualitative and quantitative character variation documented above together with information about habitats and diets provide the materials for analysis of ichthyomyine morphological evolution in relation to ecology. Since ichthyomyines are of particular evolutionary interest as examples of adaptive convergence with other ecologically similar but unrelated mammals, and of adaptive divergence from related but ecologically dissimilar Neotropical muroids, the following discussions necessarily adopt a broader phylogenetic perspective than earlier parts of this monograph. Consideration of other ecologically similar mammals serves as a useful introduction to analysis of the ichthyomyine data.

## SEMIAQUATIC CARNIVORY IN SMALL MAMMALS

Although many mammals prey on freshwater organisms, few exhibit close ecological resemblances to ichthyomyines. Platypuses (*Ornithorhynchus*), water opossums (*Chironectes*), star-nosed moles (*Condylura*), Russian desmans (*Desmana*), giant African water shrews (Potamogale), water civets (*Cynogale* and *Osbornictis*), otters (*Lutra, Pteronura* and *Aonyx*), minks (*Mustela vison*), raccoons (*Procyon*), muskrats (*Ondatra*), Australian water rats (*Hydromys chrysogaster*), and most other semiaquatic rodents are either substantially larger than ichthyomyines, regularly include vertebrates or plant material in their diets, rely also on terrestrial food sources to a significant extent, or often utilize palustrine or lacustrine habitats.

By contrast, ecobehavioral similarities to ichthyomyines are striking among seven genera of soricid, talpid, and tenrecid lipotyphlans and four species of Old World muroid rodents (table 50). Ranging from 14 to 202 g mean adult body weight, these phyletically and geographically diverse mammals nevertheless exhibit considerable uniformity in habitats and diets (table 51): all of them typically forage in clear running waters, usually small mountain streams or rivers, where they prey predominantly on aquatic arthropods.

METHODS: Morphological adaptations to semiaquatic carnivory can be inferred from comparisons of these animals with closely related terrestrial species. Table 52 lists the terrestrial taxa appropriate for comparison with selected semiaquatic-carnivorous lipotyphlans and Old World muroids. In the absence of relevant phylogenetic hypotheses, I chose comparisons within the most restricted taxonomic unit (genus, tribe, or subfamily) that includes both semiaquatic and terrestrial species. Where possible, like-size terrestrial species without conspicuous specialization for other habits (e.g., subterranean burrowing) were chosen. I made all of the morphological comparisons reported here with specimens of both semiaquatic and terrestrial taxa in hand; since specimens of *Micropotamogale* are presently unavailable in North American museums, that genus is excluded from table 52 and from the results reported below. Time and materials limited the survey of characters to those that could be determined from skin-and-skull preparations supplemented, where possible, by external examination of fluid-preserved material.

RESULTS: The small semiaquatic-carnivorous lipotyphlans and Old World muroid rodents listed in table 52 resemble one another and differ from closely related terrestrial species in numerous external and cranial attributes.

(1) The mystacial vibrissae are stiffer, more abundantly distributed between the rhinarium and superior oral margins, and supported by conspicuously thicker mystacial pads in semiaquatic taxa than in related terrestrial species.

(2) The philtrum is reduced in width, incomplete or absent in most semiaquatic species, but well-developed and distinct in terrestrial counterparts. *Sorex palustris* and *Limnogale mergulus*, however, have philtra that appear similar to those of related terrestrial taxa. Also, in *Galemys* and *Uropsilus* the presence of a fleshy proboscis obscures homologies in the vicinity of the rhinarium and precludes meaningful comparisons for this character.

(3) Pinnae are conspicuously reduced and more densely furred in most semiaquatic species than in terrestrial relatives. *Nectogale, Galemys,* and *Crossomys* lack definitive pinnae entirely. The pinnae of *Colomys* are less reduced from their relative size in *Malacomys* than the average difference in other semiaquatic-terrestrial comparisons.

(4) The plantar margins of the hindfoot are provided with dense fringes of stiff, silvery hairs in all semiaquatic lipotyphlans; such fringing hairs are absent in terrestrial lipotyphlan exemplars. In semiaquatic soricids, fringing hairs are present along both lateral and medial plantar margins and between the digits. In *Limnogale* the lateral and medial plantar edges but not the interdigital margins are fringed. In *Galemys* only the lateral margin of the pes is fringed. *Colomys* and *Hydromys* lack fringing hairs on their hindfeet. In *Crossomys* fringing hairs occur for a short interval along the lateral plantar margin just distal to the calcaneum.

TABLE 50
**Taxonomy and Distribution of Small, Semiaquatic, Carnivorous Mammals**

| Taxa[a] | Distribution |
|---|---|
| LIPOTYPHLA | |
| Soricidae | |
| *Chimarrogale* (3 sp.) | E. and S.E. Asia, Japan, Taiwan, Borneo, and Sumatra |
| *Nectogale elegans* | mountainous southern Asia |
| *Neomys* (3 sp.) | Europe and northern Asia |
| *Sorex palustris* | boreal/montane North America |
| Talpidae | |
| *Galemys pyrenaicus* | Pyrennes and northern Iberia |
| Tenrecidae | |
| *Limnogale mergulus* | Madagascar |
| *Micropotamogale* (2 sp.) | equatorial Africa |
| RODENTIA | |
| Muridae | |
| *Colomys goslingi* | central and eastern Africa |
| *Crossomys moncktoni* | New Guinea |
| *Hydromys habbema* | New Guinea |
| *Hydromys hussoni* | New Guinea |

[a] Species taxonomy after Honacki et al. (1982).

(5) The digits of the hindfoot are wholly or partly webbed in all semiaquatic species except *Colomys*; webbing is absent from all terrestrial counterparts. Webbing is best developed (extending to the last phalange) in *Galemys, Limnogale,* and *Crossomys,* least developed (not extending beyond the first phalange) in *Chimarrogale, Neomys,* and *Sorex palustris.* Other semiaquatic taxa exhibit intermediate morphologies.

(6) The tails of all semiaquatic species are round in cross-section but the ventral caudal hairs are conspicuously longer and denser than the hairs of the caudal dorsum. In all terrestrial exemplars, by contrast, ventral and dorsal caudal hairs are of equal length and density. In *Chimarrogale, Nectogale, Limnogale,* and *Crossomys* the ventral caudal hairs, long, stiff and very densely set, form one (*Chimarrogale, Limnogale, Crossomys*) or more (*Nectogale*) distinct keels that extend from the base of the tail to its tip. In *Neomys, Sorex*

## TABLE 51
## Body Size, Habitats, and Diets of Small, Semiaquatic, Carnivorous Mammals

| Species | Body size[a] HBL (mm) | Body size[a] Weight (g) | Habitat | Diet[b] | Sources |
|---|---|---|---|---|---|
| *Chimarrogale himalayica* | 111 | 32 | clear forest streams | no primary data available | Arai et al. (1985) |
| *Nectogale elegans* | 116 | — | torrential mountain streams | aquatic insect nymphs and larvae (Ephemeroptera, Trichoptera, Diptera) exclusively in five stomachs examined | Anthony (1941), this study[c] |
| *Neomys fodiens* | — | — | most freshwater habitats | predominantly aquatic insects but also gastropods, oligochaetes, fishes, and frogs (review of many studies) | Churchfield (1985) |
| *Sorex palustris* | 79 | 14 | fast, cold mountain streams bordered by forest vegetation | mostly aquatic insects but also oligochaetes, arachnids, fish, and vegetable matter (87 stomachs) | Conaway (1952) |
| *Galemys pyrenaica* | 120 | 68 | clear, cold streams | Amphipods and aquatic insects (no sample sizes available) | Peyre (1956)<br>Niethammer (1970) |
| *Limnogale mergulus* | 141 | 80 | streams in mountains and lowlands, perhaps other freshwater habitats | frogs, aquatic crustaceans and aquatic insects (no sample sizes available) | Malzay (1965)<br>Gould and Eisenberg (1966) |
| *Micropotamogale ruwenzorii* | 188 | 135 | small rivers and streams | worms, aquatic insects, crabs, small vertebrates (anecdotes) | Kingdon (1974) |
| *Colomys goslingi* | 126 | 56 | small streams bordered by lowland or montane rain forest | predominantly aquatic insects but some terrestrial arthropods and gastropods (15 stomachs) | Dieterlen and Statzner (1981)<br>Dieterlen (1983) |
| *Crossomys moncktoni* | 175 | 202 | mountain streams bordered by rain forest or grass | insects exclusively in 8 stomachs, mostly aquatic nymphs and larvae (Ephemeroptera, Trichoptera, Diptera, Lepidoptera) but some alate adults | Van Deusen (n.d.), this study[d] |
| *Hydromys habbema* | 137 | 79 | mountain streams | insects, predominantly aquatic nymphs and larvae (Ephemeroptera, Trichoptera, Diptera, Lepidoptera) but also leeches and small vertebrates (6 stomachs) | Menzies and Dennis (1979), this study[e] |

[a] Adult mean values (males and females combined) from representative populations.

[b] Only primary data (analyses of digestive tract contents or feces) are reported.

[c] Stomachs of AMNH 114831–114833, 115571, 115573.

[d] Stomachs of AMNH 156701, 191449, 194924–194928, 195174.

[e] Stomachs and intestines of AMNH 152827, 191440–191444.

*palustris, Galemys,* and *Hydromys habbema* a hairy ventral keel is developed distally but does not extend all the way to the base of the tail. The caudal pelage is least specialized in *Colomys* where distinctively longer ventral hairs are only evident near the tail tip.

(7) The metatarsal configurations of most semiaquatic species differ consistently from the strongly mesaxonic morphology of their terrestrial relatives by disproportionate elongation of the lateralmost elements. Thus, while terrestrial soricids, *Microgale,* and most terrestrial muroids have metatarsals ordered by relative lengths III > II = IV ≫ V ≥ I, semiaquatic soricids, *Limnogale, Crossomys,* and *Hydromys* exhibit IV > III > II ≥ V > I. The Chinese shrew-mole *Uropsilus soricipes* has less mesaxonic proportions than other terrestrial exemplars (III = IV > V = II > I), but *Galemys* differs by an even greater hypertrophy of the lateralmost bones (IV > V > III > II > I). Of the semiaquatic/terrestrial comparisons tabulated, *Colomys* and *Malacomys* exhibit the least difference in metatarsal proportions.

(8) The infraorbital foramen is conspicuously larger in all semiaquatic species by comparison with terrestrial relatives. Where the foramen transmits only sensory fibers of the trigeminal nerve (lipotyphlans), the enlargement in semiaquatic species is overall; where the foramen transmits muscle and nerve (muroid rodents), the ventral, nerve-bearing moiety is disproportionately enlarged in the semiaquatic taxa.

(9) In most semiaquatic species, the foramen magnum is proportionately larger than in related terrestrial species. (Hutterer, 1985, illustrates the larger foramen magnum of neomyine water shrews, *Neomys, Chimarrogale,* and *Nectogale,* by comparison with terrestrial *Sorex.*) The foramen is particularly large in *Limnogale* and *Crossomys* in contrast with related terrestrial morphologies. In *Galemys, Colomys,* and *Hydromys habbema,* however, the foramen magnum appears roughly the same relative size as in terrestrial exemplars.

DISCUSSION: While examination of additional organ systems, particularly the postcranial skeleton, may reveal other special anatomical resemblances among these small, semiaquatic-carnivorous mammals, this brief survey of external and cranial morphology serves adequately to illustrate several points.

TABLE 52
**Semiaquatic-Terrestrial Comparisons**
(See text for explanation)

| Semiaquatic taxa | Comparison |
|---|---|
| *Chimarrogale*<br>*Nectogale*<br>*Neomys* | terrestrial Neomyini[a] (e.g., *Soriculus*) |
| *Sorex palustris* | terrestrial *Sorex* (e.g., *S. araneus*) |
| *Galemys pyrenaicus* | *Uropsilus soricipes* |
| *Limnogale mergulus* | terrestrial Oryzorictinae (e.g., *Microgale talazaci*) |
| *Colomys goslingi* | *Malacomys longipes* |
| *Crossomys moncktoni*<br>*Hydromys* species | terrestrial hydromyines (e.g., *Leptomys*) |

[a] After Repenning (1967).

Firstly, all of the traits enumerated above are exhibited to a greater or lesser degree by ichthyomyines but are seldom encountered together among larger semiaquatic mammals or among like-size mammals that differ substantially in ecobehavioral traits; instead, the latter frequently exhibit other specializations. Muskrats (*Ondatra*) and Russian desmans (*Desmana*), for example, both much larger than ichthyomyines and more palustrine in habits, possess fringing hairs on their hindfeet but have laterally compressed tails that lack a hairy midventral keel. Giant African water shrews (*Potamogale*), also much larger than ichthyomyines though similar (apparently) in some aspects of diet and habitat, exhibit similar vibrissal and trigeminal specializations but have typically terrestrial hindfeet (a laterally flattened tail is the main propulsive organ). Neither ichthyomyines nor any of the other ecobehaviorally similar small lipotyphlans and muroids described above exhibit the tactile specialization of the manus whereby *Chironectes, Procyon,* and *Aonyx* forage for aquatic invertebrates, and many more such differences could be cited. In short, most of the anatomical features listed above, in combination, are peculiar to ichthyomyines together with a small number of like-size, ecologically similar taxa. Prima facie, the details of this special resemblance among representatives of disparate phyletic lineages from North and South America, Europe, Asia, Africa, Madagascar, and New Guinea suggest a consistent pattern of adaptations by small mammals evolving to prey on arthropods in streams.

Secondly, morphological specializations of small semiaquatic-carnivorous mammals are for the most part readily grouped in functional complexes. Among the traits listed above, for example, fringing hairs along the plantar margins of the hindfeet, webbing between the digits of the hindfoot, metatarsal proportions, and the development of a midventral concentration of long, stiff caudal hairs all plausibly reflect locomotor modification for aquatic propulsion (see preceding discussions of ichthyomyine anatomy and Howell, 1930). Similarly, stiff and abundant vibrissae on the upper lip and muzzle, an enlarged infraorbital foramen, and a spacious foramen magnum all appear related to the predominant sensory role of trigeminal innervation in predatory, aquatic small mammals (see fig. 72 and accompanying text). Some attributes of semiaquatic forms, however, may reflect two or more coincident functional demands: reduced pinnae may contribute to a more streamlined body form (locomotion) and also reflect the diminution of sensory systems other than trigeminal mechanoreception. The functional significance of the philtrum is obscure.

Thirdly, character expressions appear correlated across taxa within functional complexes but such correlations are not necessarily simple and many difficulties arise in attempting a rigorous demonstration with the few qualitative comparisons available. Inspection of table 53 wherein nine semiaquatic lipotyphlans and Old World muroids are ranked by degree of specialization in four characters plausibly related to aquatic locomotion serves to illustrate both interpretive problems and possible patterns. Under each character, taxa are ranked from least (1) to most specialized (4 or 5) with morphologies judged equivalent assigned the same rank. A comparison of ranks in the first and second columns, for fringing hairs and interdigital webbing on the hind feet, respectively, reveals an almost complete lack of concordance. Fringing hairs and webbing may both serve to increase the effective surface area of the foot, however, so that when one is highly developed the other is perhaps superfluous. Further, when interdigital webbing is complete (rank of 5), fringing hairs cannot be maximally developed (between the toes) since the interdigital plantar margins are obliterated. An inverse correlation might consequently be predicted save for the fact that species little adapted for aquatic locomotion have neither well-developed fringes nor webs. It seems more meaningful, therefore, to sum the ranks for these two characters and then to rank the sums as a joint index of integumental specialization of the hindfoot (table 53, third column). Regarding the last four columns of the table then, it can be seen that those taxa least specialized in either the integument or the osteology of the hindfoot or in tail pelage or the ear are least specialized in the other characters as well, and that taxa most specialized in one character tend to be specialized in others too. While degree of vibrissal development and relative foraminal capacity are difficult to rank meaningfully due to allometric relationships that cannot be estimated with so few available samples, and to other confounding factors, visual comparisons of taxa for characters in the trigeminal sensory complex also suggest coordinate specialization of functionally related attributes.

Finally, there is some suggestion of correlated specialization among characters in different functional complexes. *Nectogale, Limnogale,* and *Crossomys,* for example, exhibit the (subjectively evaluated) best developed vibrissal arrays, most hypertrophied infraorbital foramina, and largest foramina magna, and are also among the most locomotor-specialized of the species considered here. Correspondingly, *Sorex palustris, Colomys goslingi,* and *Hydromys habbema* appear (subjectively) least specialized in trigeminal sensory structures and are (demonstrably) least modified in most aspects of locomotor morphology as well.

In summary, distantly related small mammals that prey on rheophilic arthropods in every major zoogeographic region of the world exhibit a consistent pattern of derived morphological resemblances, and those resemblances can reasonably be grouped into functional complexes within (and possibly

TABLE 53
**Nine Semiaquatic, Carnivorous Small Mammals Ranked by Degree of Specialization in Five Morphological Characters**

| | Integument of hindfoot | | | | | |
|---|---|---|---|---|---|---|
| Species | Fringing hairs on hindfoot[a] | Interdigital webbing on hindfoot[b] | Ranked sum of ranks[c] | Metatarsal proportions[d] | Midventral caudal hairs[e] | Ear[f] |
| *Chimarrogale himalayica* | 5 | 2 | 3 | 3 | 4 | 3 |
| *Nectogale elegans* | 5 | 4 | 5 | 4 | 5 | 4 |
| *Neomys fodiens* | 5 | 2 | 3 | 3 | 3 | 3 |
| *Sorex palustris* | 5 | 2 | 3 | 3 | 2 | 3 |
| *Galemys pyrenaica* | 3 | 5 | 4 | 4 | 2 | 4 |
| *Limnogale mergulus* | 4 | 5 | 5 | 3 | 4 | 3 |
| *Colomys goslingi* | 1 | 1 | 1 | 1 | 1 | 1 |
| *Crossomys moncktoni* | 2 | 5 | 3 | 3 | 4 | 4 |
| *Hydromys habbema* | 1 | 3 | 2 | 2 | 2 | 2 |

[a] Explanation of ranks: 1, no fringing hairs; 2, hairs on proximal part of lateral metatarsal margin; 3, hairs along whole lateral metatarsal margin; 4, hairs along lateral and medial plantar margins; 5, hairs along all plantar margins (between digits).

[b] Explanation of ranks: 1, no webbing; 2, webbing does not extend to first interphalangeal joints; 3, webbing extends to first interphalangeal joints of digits I–IV, but digit V free; 4, webbing to first interphalangeal joint of all digits; 5, webbing complete to base of claws of all digits.

[c] See text for explanation.

[d] Explanation of ranks: 1, metatarsals IV = III > II ≫ V > I; 2, metatarsals IV > III > II ≫ V > 1; 3, metatarsals IV > III > II > V > I; 4, metatarsals IV > III > V = II > I or IV > V > III > II > I.

[e] Explanation of ranks: 1, hairs longer and denser than dorsal caudal pelage but no distinct keel; 2, hairs form distinct keel along distal ⅓ or less of tail; 3, hairs form distinct keel along distal ⅔ of tail; 4, hairs form keel from base to tip of tail; 5, complete midventral keel plus lateral and dorsal keels.

[f] Explanation of ranks: 1, pinnae large, sparsely haired, and clearly visible above head pelage; 2, pinnae smaller and well furred but visible above head pelage; 3, pinnae very small, buried in fur of head; 4, pinnae absent.

between) which character expressions appear grossly correlated. Such independently evolved and geographically widespread ecomorphological correspondences imply a uniformity of adaptive response that may reflect the functional constraints of size (since larger semiaquatic-carnivorous mammals exhibit other characters) and of a common mammalian heritage. Additional inferences about patterns of morphological character covariation with ecology among these semiaquatic lipotyphlans and Old World muroids, however, are limited by the nature of available information: the characters in question cannot defensibly be quantified on a continuous scale nor is meaningful morphometric analysis possible with such a small and phylogenetically heterogeneous sample. Further, what knowledge exists of the diets and habitats of these animals is insufficient for satisfactory ecological comparisons among them. Inference based on analyses of more extensive data, however, is possible for ichthyomyines.

## ICHTHYOMYINE ADAPTIVE RADIATION

Morphological comparisons among ichthyomyines in qualitative and quantitative characters have hitherto been treated separately in this monograph because of the different analytic methods appropriate to each. It will therefore be useful to briefly review the results of quantitative and qualitative analyses and to consider what interpretation each can sustain in the course of evolutionary hypothesis testing.

REVIEW OF METHODS: Quantitative characters that measure anatomical dimensions are almost always highly correlated within species due to their joint dependence on growth and among species due to their joint dependence on general size. Biological interpretation of metric character data is therefore facilitated by decomposing observed correlations (or covariances) into a fraction attributable to growth and/or general size (depending on the comparative context) and a residual fraction that is growth (or size) independent. The latter, residual correlations may then be scrutinized for evidence of morphological integration, phyletic divergence, or other hypothesized sources of character dependence. Multivariate correlation structures are usually partitioned and described by linear statistical models whose factor coefficients together with external information may then suggest underlying causal phenomena. Two sets of metric character data, one representing external and postcranial skeletal measurements, the other representing craniodental measurements, have been so analyzed in this monograph. The resulting factors and their presumed biological significance have been described earlier but merit summary repetition here.

Analysis of external and postcranial measurement data by principal components (tables 2–9) suggests that nearly all of the interspecific variation in ichthyomyine body proportions can be accounted for by just two factors. The uniformly large and positive coefficients of the first principal component reflect static adult size (and allometry), while large negative and positive coefficients on the second principal component reflect size-independent associations of external and postcranial skeletal dimensions consistent with previously calculated ratio correlations. Parallel analyses of measurement data from nonaquatic sigmodontines document the generality of static size covariance patterns but indicate that the pattern of morphological integration described by variable loadings on the ichthyomyine second principal component may not be common to terrestrial muroids. Instead, information from published descriptions and analyses of limb proportions in other mammals suggest that the correlated, size-independent proportions of limb bones, hind foot, and tail described by the latter factor represent skeletal adaptations for aquatic locomotion. Projection of terrestrial sigmodontine species onto the ichthyomyine second principal component (fig. 21) corroborates this hypothesis and suggests the utility of species scores as a quantitative index of locomotor specialization.

Analysis of craniodental measurement data (tables 29–37, figs. 49–55) differs methodologically from the preceding treatment of postcranial data because an a priori estimate of multivariate growth obtained from mixed cross-sectional population samples is available to model size as a biologically explicit source of measurement covariance. Eigenanalysis of the residual covariance matrix then yields a large size-independent shape factor with substantial positive and negative coefficients for molar and incisor measurements, measurements of interdental spaces, and for two measurements of the neurocranium. Microscopic examination of worn dental surfaces, dissections of masticatory muscles, and knowledge of diets of ichthyomyine species with divergent scores on the shape factor suggest that the underlying covariance structure reflects functional modifications of teeth and the facial skeleton for diets of varying prey size. The apparently incongruent participation of two neurocranial dimensions in this pattern of morphological integration is in fact consistent with the hypothesized adaptive interpretation given reasonable assumptions about requisite tactile discrimination in relation to prey size and knowledge of the neural pathways of trigeminal sensory projection.

In contrast to the quantitative characters thus analyzed, most of which measure skeletal structures whose dimensions change with growth, the qualitative characters employed in phylogenetic analyses represent a diversity of organ systems and describe species comparisons that appear ontogenetically static or that can meaningfully be standardized among adult morphologies. Statistically significant patterns of association among qualitative characters are demonstrable in their compatibility relations, but unlike metric character correlations and covariance structures, observed cliques of mutually compatible qualitative characters have no evident functional interpretation. Instead, nonrandom patterns of character compatibility may represent the distribution of uniquely derived and unreversed morphological attributes and provide evidence of recency of common ancestry among ichthyomyine species. Reso-

TABLE 54
**Factor Scores and Elevation for 14 Ichthyomyine Species Samples**

| | Factor scores[a] | | | | |
|---|---|---|---|---|---|
| Species[c] | Cranial size (*S*) | Cranial shape (*H*) | Postcranial size (*PC*1) | Postcranial proportions (*PC*2) | Elevation[b] (meters) |
| *Ale* | 4.90 | 3.24 | 9.54 | −0.40 | 3678 |
| *Ctr* | 4.95 | 3.06 | 9.39 | −0.50 | 2538 |
| *Ihy* | 5.53 | 2.65 | 9.67 | −0.71 | 1871 |
| *Iso* | 5.61 | 2.73 | — | −0.59[d] | 2730 |
| *Ipi* | 5.68 | 2.43 | — | −0.93[d] | 950 |
| *Itw* | 6.00 | 2.64 | 9.89 | −0.83 | 962 |
| *Nmo* | 4.92 | 2.80 | 9.14 | −0.68 | 2268 |
| *Npe* | 5.54 | 2.49 | — | −0.80[d] | 300 |
| *Nve* | 5.21 | 2.60 | — | −0.79[d] | 738 |
| *Rme* | 5.62 | 3.13 | 9.80 | −0.54 | 1385 |
| *Rha* | 5.23 | 2.69 | 9.21 | −0.75 | 1538 |
| *Rts* | 5.43 | 2.80 | 9.51 | −0.67 | 2462 |
| *Rtt* | 5.30 | 2.78 | 9.35 | −0.63 | 1262 |
| *Run* | 5.36 | 3.19 | 9.75 | −0.54 | 2000 |

[a] From analyses of population samples described in Comparative Morphology and Cranial Morphometrics sections.

[b] See Gazetteer entries for population samples as per footnote [a]; recorded values are midpoints of sample locality elevations.

[c] Abbreviated as in Cranial Morphometrics section.

[d] Regression estimates calculated as described in accompanying text.

TABLE 55
**Correlations of Species Factor Scores[a]**

| | N | Cranial size (*S*) | Cranial shape (*H*) |
|---|---|---|---|
| Postcranial size (*PC*1) | 10 | .75 | .20 |
| Postcranial proportions (*PC*2)[b] | 10 | −.59 | .93 |
| Postcranial proportions (*PC*2)[c] | 14 | −.54 | .92 |

[a] Tabulated values are coefficients of product-moment correlation among columns 1–4 of table 54.

[b] Regression-estimated scores not included.

[c] Regression-estimated scores included.

lution of one of the two largest cliques of compatible ichthyomyine characters is maximally parsimonious of state transformations in most other characters and also provides the simplest historical interpretation of contemporary ichthyomyine geography.

Multivariate factors and cladograms, despite their derivation from very different analytic paradigms, both serve as effective summaries of morphological character variation and together provide a more substantial basis for evolutionary inference than either considered separately. In their present application, multivariate factors yield quantitative representations of ichthyomyine specialization within functionally related character complexes analogous to, but considerably more concise (and operational) than the crude (and subjective) rank correlation of qualitative character expressions among ecologically similar lipotyphlans and Old World muroids (above, table 53). Cladograms based on analyses of qualitative characters, on the other hand, provide the necessary framework for evaluating those patterns of functional specialization as they may relate to higher levels of morphological integration, genealogical relationships, and ecological adaptation.

RESULTS: The first four columns of table 54 record the scores of 14 ichthyomyine species or subspecies on the multivariate factors described above. Because fewer populations are represented by postcranial skeletons than by cranial material, some values for scores on postcranial factors are missing. Four species scores on the postcranial shape factor (fourth column, table 54) are regression estimates. Least-squares linear regressions of second principal component scores on the ratio of hindfoot to head-and-body (HF/HBL; table 4) and on the ratio of tail to head-and-body (LT/HBL; table 4) were calculated for the ten ichthyomyine samples with complete postcranial measurement data (coefficients of determination are .87 and .80, respectively). Known mean values of HF/HBL and LT/HBL for *Ichthyomys hydrobates soderstromi, I. pittieri, Neusticomys peruviensis,* and *N. venezuelae* were then substituted in the corresponding equations to obtain predicted factor scores, recorded in table 54 as the average of both estimates.

While the factors themselves, together with relevant external information, provide compelling evidence of functional relations within locally articulated or co-ossified skeletal systems, correlations between craniodental and postcranial factors (table 55) suggest the existence of yet higher levels of morpholog-

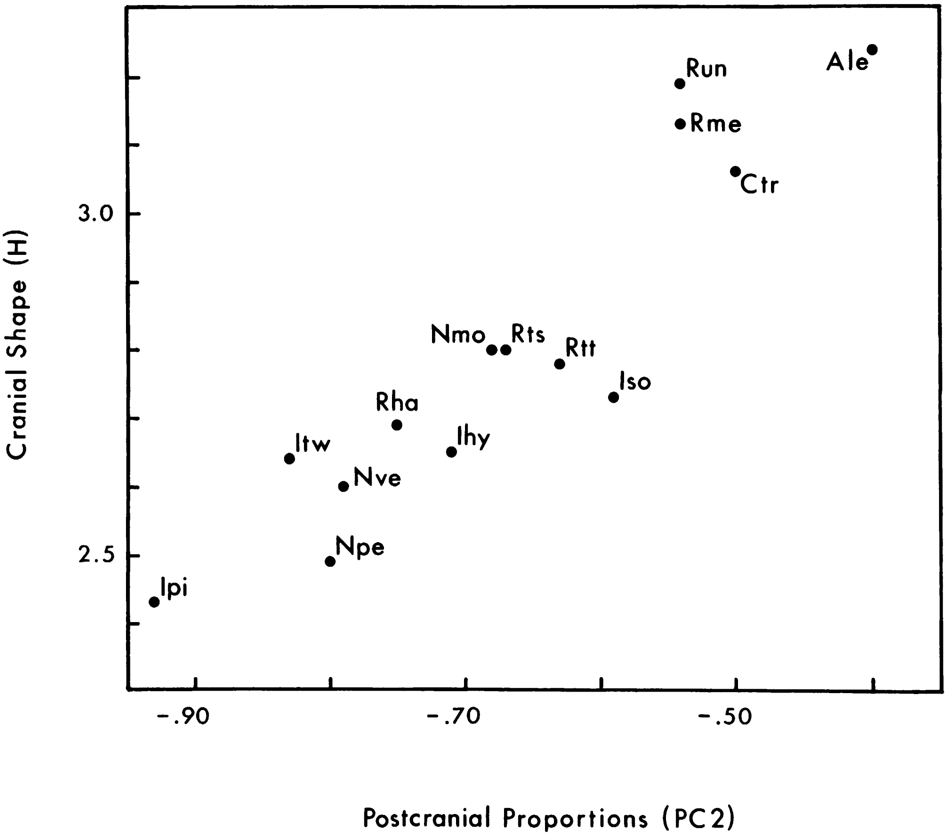


Fig. 96. Scatterplot of ichthyomyine population scores on cranial and postcranial shape factors. Taxonomic abbreviations are defined in the text of Cranial Morphometrics.

ical integration in the ichthyomyine phenotype. A reasonably high correlation between species scores on *S* (cranial size) and *PC*1 (postcranial size) is expected insofar as phyletic increase in size of organisms is generally accompanied by increase in size of all their constituent parts. That indices of size-independent shape variation (*H* and *PC*2), each reflecting a complex pattern of anatomical adjustments within separate skeletal regions, should be strongly correlated, however, is sufficiently surprising that two biologically null hypotheses merit consideration.

TABLE 56
**Ten Independent Contrasts in Ichthyomyine Phylogeny**
(See text for explanation)

| Independent contrasts | Cranial shape (*H*) | Postcranial proportions (*PC*2) |
|---|---|---|
| Rme-Run | – | 0 |
| Rtt-Rha | + | + |
| I-J | – | – |
| Ihy-Itw | + | + |
| Ipi-G | – | – |
| F-H | – | – |
| Ale-E | + | + |
| Ctr-D | 0 | 0 |
| Nmo-C | – | – |
| Nve-B | – | – |

Null Hypothesis 1: *The correlation is a statistical artifact.* This is impossible. The measurement sets from which *PC*2 and *H* are separately calculated share no anatomical dimensions in common. To be sure, length of head-and-body (HBL) loads significantly on *PC*2 (table 7) and includes the skull within its endpoints, but cranial length (CIL) loads negligibly on *H* (table 34) and cannot account for the observed correlation. If cranial and postcranial size were very highly correlated measured variables, it is conceivable that cranial and postcranial regression residuals might be correlated in consequence, but size is not a measured variable in the factor models employed here and the correlation between cranial and postcranial size is in fact substantially less than the correlation between shape scores.

Null Hypothesis 2: *The correlation is a phylogenetic artifact.* Apparent correlations of two or more variables across species cannot properly be evaluated without taking phylogenetic relationships into account. This difficulty arises from the necessary statistical assumption that the observations recorded for each of $n$ species are drawn independently from the same distribution. To the extent that recency of common ancestry may contribute to phenotypic similarity, such independence can obviously not be assumed. In the worst case, a correlation observed between two characters measured across $n$ taxa might seem highly significant (with $n - 2$ degrees of freedom) but reflect only the acquisition of extreme values for both variables in one phyletic lineage; the appropriate degrees of freedom are then more nearly zero with no significance attributable to the observed pattern (see Felsenstein, 1985, for examples and discussion).

Examination of the scatter plot of species scores on postcranial and cranial shape factors (fig. 96) and reference to the best-supported hypothesis of ichthyomyine phylogeny (fig. 97) reveal that neither the species with highest values for both variables (*Anotomys leander, Chibchanomys trichotis, Rheomys mexicanus, R. underwoodi*) nor those with lowest values (*Ichthyomys pittieri, I. tweedii, Neusticomys venezuelae, Rheomys raptor hartmanni*) constitute monophyletic groups, so it is unlikely that the observed correlation is entirely attributable to phylogenetic artifacts in the sense just explained. Nevertheless, *Rheomys mexicanus* and *R. underwoodi* are sister species, and most members of the genus *Ichthyomys* exhibit low values for both variables, so some phylogenetic contribution to the correlation seems likely and it is useful to attempt to correct for this in a test for statistical significance.

A nonparametric test for correlation between cranial shape and postcranial proportions can be derived from independent contrasts in ichthyomyine phylogeny obtained as follows: take any pair of sister taxa, subtract from the factor scores of one the respective values of the other, and record the sign of the resulting difference for each factor. Thus, subtracting the scores on *H* and *PC*2 (table 54) of *Rheomys underwoodi* from those of *R. mexicanus* yields differences that are negative for *H* and zero for *PC*2 (table 56, first row); for the pair *R. thomasi* and *R. raptor hartmanni,* the corresponding differences are either both positive or both negative (table 56, second row). Since differences between *R. mexicanus* and *R. underwoodi* evolved after their divergence from ancestor J (fig. 97) while those between *R. thomasi* and *R. raptor hartmanni* evolved after their divergence from ancestor I, the two contrasts are independent. Since independent contrasts in two uncorrelated variables are expected as often to be of the same as of different sign, a significant departure in the count of same- or different-signed contrasts from binomial expectation effectively tests for positive or negative correlation, respectively, between the variables. Table 56 lists all of the independent contrasts, including ancestors, that can be extracted from figure 97. Ancestral phenotypes, calculated using Farris' (1970) HTU-optimizing algorithm, are listed in table 57. While the estimated factor scores of (say) ancestor J are clearly not independent of scores for

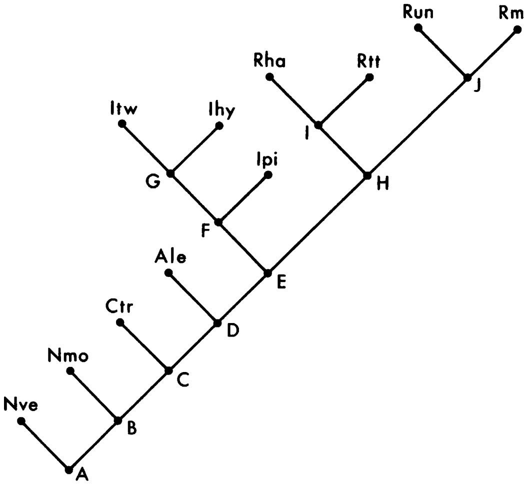


Fig. 97. Hypothesis of ichthyomyine relationships with labeled interior nodes.

TABLE 57
**Reconstructed Ancestral Factor Scores**
(See text for explanation)

| Ancestors[a] | Cranial shape ($H$) | Postcranial proportions ($PC2$) |
|---|---|---|
| A | 2.70 | −0.74 |
| B | 2.80 | −0.68 |
| C | 3.06 | −0.50 |
| D | 3.06 | −0.50 |
| E | 2.79 | −0.63 |
| F | 2.64 | −0.83 |
| G | 2.64 | −0.83 |
| H | 2.79 | −0.63 |
| I | 2.79 | −0.63 |
| J | 3.13 | −0.54 |

[a] As represented by labeled interior nodes on the tree illustrated in figure 97.

observed descendant species, nor those of I from its descendants, the contrast between I and J (table 56, third row) is independent of preceding or subsequent contrasts between other sister elements in the tree. Ten contrasts are therefore available, of which two are discarded because of ties (zero difference); of the eight remaining, all are of the same sign in both variables, which is of course significantly different from binomial expectation.

The simple interpretation therefore seems justified, that size-independent cranial shape and postcranial proportions are correlated across ichthyomyine species, and that this correlation is neither a computational nor a phylogenetic artifact. Fortunately, the anatomical relations suggested by these analyses of highly derived statistics are plainly visible with specimens in hand: Ichthyomyine species with narrow, delicate incisors, large molars, broad palates, and inflated braincases (e.g., *Anotomys leander, Chibchanomys trichotis, Rheomys mexicanus,* and *R. underwoodi*) also have long tails, large hindfeet, and long distal limb bones while species with robust incisors, small molars, narrow palates, and uninflated braincases (e.g., *Ichthyomys pittieri, I. tweedii, Neusticomys venezuelae*) have short tails, small hindfeet, and short distal limb bones. The empirical significance of this correlation is best appreciated graphically.

Superimposing phylogenetic relationships on the scatterplot of cranial and postcranial shape factor scores for extant ichthyomyine species and their hypothetical ancestors (fig. 98) makes it apparent that ichthyomyine evolution has occupied only a narrow diagonal in the rectangular morphological space that encloses extreme values of scores on both factors. Since unobserved phenotypes are easily imagined (a species with narrow incisors, large molars, and inflated braincase but a short tail, small hindfeet, and short distal limb elements, for example, would occupy the empty upper left corner of fig. 98) it is reasonable to ask why ichthyomyine skeletal evolution has been so constrained.

Strong genetic correlations (pleiotropy) might sometimes account for interspecific metric character covariance patterns but are unlikely to be responsible for the pattern of interest here. Hormone-mediated growth of the whole body, for example, is surely under partial genetic control and is likely responsible for much of the high positive covariance among most skeletal measurements. This joint dependence on growth (or general size) is represented by cranial $S$ and postcranial $PC1$ whose coefficients also describe accompanying ontogenetic or static allometries. The correlation between species scores on $S$ and $PC1$ as well as the covariance structures that each of those factors represents might therefore be attributed, at least in part, to the pleiotropic effects of genes that influence the onset, rate, or duration of overall growth. Significantly, the growth and static allometries described among ichthyomyines by $S$ and $PC1$, respectively, resemble those of other muroid rodents.

Independent of the systemic influence of overall growth, however, the size and proportions of vertebrate skeletal structures usually appear regulated among adjacent elements constituting discrete organs or local functional matrices (Moss, 1972; Bryant and Simpson, 1984). To the extent that pleiotropy might be partially responsible for size-independent character correlations observed across species, such correlations are then to be expected locally in the phenotype and not among the anatomically distant elements represented in the shape factors considered here. The constraints on ichthyomyine skeletal evolution evident from examination of

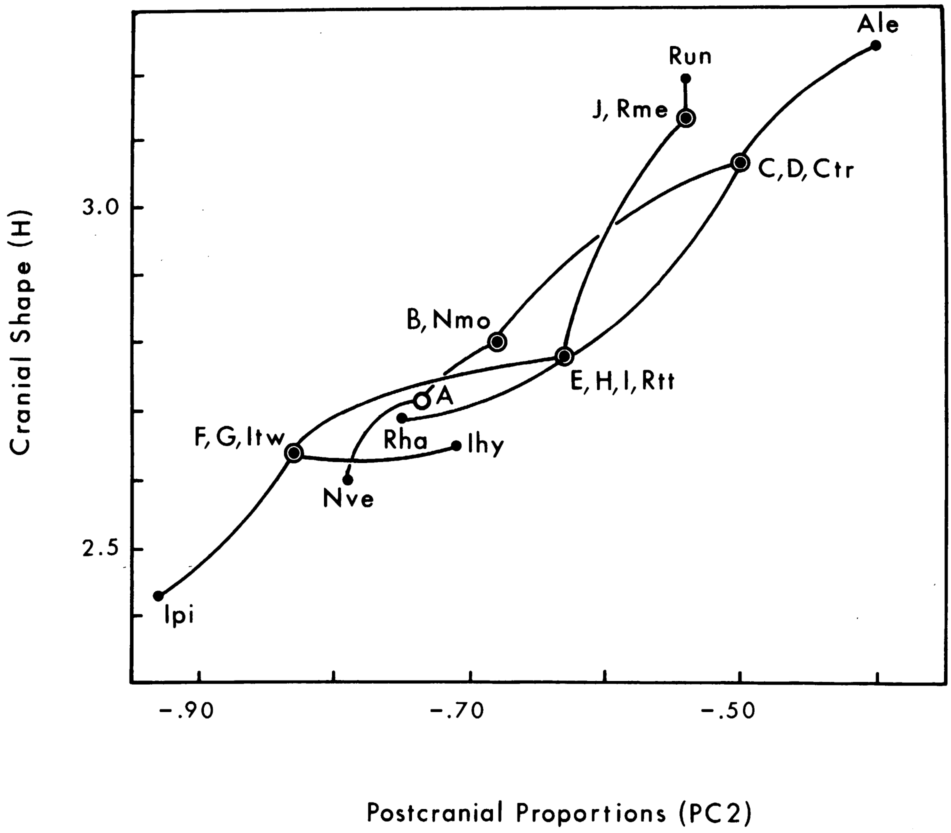


Fig. 98. Scatterplot of ichthyomyine population scores on cranial and postcranial shape factors with phylogenetic relationships superimposed. Points labeled with capital letters correspond to interior nodes in the phylogeny of figure 97. Most-parsimonious estimates of ancestral factor scores are provided in table 57.

figure 98 therefore require adequate explanation in other terms.

The comparative and functional arguments summarized earlier in this monograph suggest that size-independent differences among ichthyomyine species in cranial shape and postcranial proportions chiefly represent morphological adaptations to prey size and for aquatic locomotion, respectively. Since the size distribution of aquatic arthropod faunas and the mean current speed in streams both change with elevation, the diagonal distribution of species in the morphological space determined by *H* and *PC*2 could reflect the constraining influence of correlated ecological circumstances encountered by evolving ichthyomyine populations that vary in altitudinal distribution. Streams at high elevations in forested Neotropical mountains appear to lack many large arthropods and are usually fast-flowing on steep gradients. Presumably, selection for functional competence with small prey in a physically demanding aquatic environment would therefore obtain for montane ichthyomyine species. Streams of the forested tropical lowlands, by contrast, harbor more large aquatic arthropods and descend gentler gradients; increased prey size and relaxed selection for aquatic propulsion likely obtain there. Within this explanatory framework, ichthyomyine phenotypes that do not fall along the diagonal distribution of factor scores in figure 98 are unobserved because they are poorly adapted to conditions averaged at any point along the gradients of arthropod prey size and current speed jointly influenced by elevation.

Significant positive correlations of eleva-

TABLE 58
**Correlations of Species Factor Scores With Elevation**

| Factors | N | Correlation with elevation[a] |
|---|---|---|
| Cranial size (*S*) | 14 | −.53* |
| Cranial shape (*H*) | 14 | .67** |
| Postcranial size (*PC*1) | 10 | −.25 |
| Postcranial proportions (*PC*2)[b] | 10 | .70* |
| Postcranial proportions (*PC*2)[c] | 14 | .78** |

[a] Tabulated values are coefficients of product-moment correlation between columns 1–4 and 5 of table 54; one asterisk indicates significant values ($p \leq .05$), two asterisks indicate highly significant values ($p \leq .01$).

[b] Regression-estimated scores not included.

[c] Regression-estimated scores included.

tion with species scores on *H* and *PC*2 (table 58) lend credence to this ecological interpretation of observed morphological constraints. Not all ichthyomyine species with high scores on *H* and *PC*2 are restricted to high elevations, nor are all species with low factor scores exclusively encountered in lowland habitats. The average tendency is significant, however, whether correlations are calculated over just these population samples or over species' means. Because altitude is only an approximate predictor of prey size and current speed, and because current speed may influence aquatic arthropod communities directly, the fact that *H* and *PC*2 are more highly correlated with each other than either is with elevation is not inconsistent with the hypothesis that ecological factors are the cause of their joint distribution.

An adaptive interpretation of head-to-tail morphological integration of the ichthyomyine skeleton is therefore supported both by the consistency of inferred causal relations with the results of prior data analyses and by the empirical correlation of factor scores with altitude. Nevertheless, some independent test of this involved hypothesis would be valuable. If it could be assumed, for example, that the limnological correlates of elevation in other forested equatorial regions are similar to those demonstrated in the Neotropics, then highland and lowland populations of Old World muroids that are ecologically comparable to ichthyomyines should exhibit morphological differences consistent with the correlations reported in table 58. While I have encountered no information about stream arthropod size distributions or current speed in relation to altitude for other equatorial regions, the presumed underlying causal factors (the atmospheric lapse rate of temperature and mountain slope profiles, respectively) are likely similar throughout the humid tropics worldwide. If this is so, then two species among those listed in table 50 provide a suitable comparison.

*Hydromys habbema* and *H. hussoni* are small muroid rodents from New Guinea; *H. habbema* is known to be semiaquatic and carnivorous (table 51) and *H. hussoni* may be presumed so because it shares all of the qualitative adaptations described earlier for *H. habbema*. Little else is known of either species except for the morphological and geographic data summarized by Musser and Piik (1982). *H. habbema* is known from scattered localities in Papua and Irian Jaya between 1500 and 3600 m; the mean elevation of seven collection localities from which data are available is 2590 m. *H. hussoni* is known only from the vicinity of Paniai Meer, one of the Wissel Lakes in Irian Jaya; the elevation of Enarotali, the type locality on the east shore of Paniai Meer, is 1765 m. While little can be said of the elevational distribution of *H. hussoni* based on one locality, the contrast between the short, hard, glossy pelage of that species with the longer, softer and denser, dull pelage of *H. habbema* is consistent with lowland-highland comparisons in many other tropical muroid genera.

Sample statistics (table 59) for the type series of *H. hussoni* (Enarotali, 1765 m) and of *H. habbema* (Lake Habbema, 3225 m) provide comparisons in the same external and craniodental dimensions measured for ichthyomyines; scores on the ichthyomyine cranial shape factor (plotted in fig. 99) were calculated as the usual sum-of-products for every specimen with complete measurement data in these series. Reference to table 59, figure 99, and the verbal descriptions of Musser and Piik (1982) confirms that the morphological differences between *H. hussoni* and *H. habbema* are strikingly similar to those distinguishing lowland from highland ichthyomyines: Approximately the same overall size

TABLE 59
**Sample Statistics for External and Craniodental Measurements (in millimeters) of Adult Specimens of *Hydromys hussoni* and *H. habbema***
(The mean plus or minus one standard deviation, and the range in parentheses are provided for each measurement)

| | *Hydromys hussoni*[a] | *Hydromys habbema*[b] |
|---|---|---|
| Sex | 12 males, 8 females | 7 males, 7 females |
| HBL | 147.9 ± 15.4 (122–171) | 148.6 ± 8.1 (134–160) |
| LT | 126.4 ± 13.8 (103–152) | 172.3 ± 12.5 (154–187) |
| HF | 29.8 ± 2.0 (27–33) | 37.0 ± 1.2 (35–39) |
| Ear | 12.1 ± 0.8 (11–14) | 8.6 ± 0.6 (7–9) |
| CIL | 30.5 ± 1.41 (27.9–32.9) | 32.7 ± 0.76 (31.6–34.0) |
| LD | 8.5 ± 0.54 (7.6–9.3) | 8.7 ± 0.30 (8.1–9.3) |
| LM | 4.6 ± 0.12 (4.4–4.8) | 5.1 ± 0.14 (4.8–5.3) |
| LIF | 3.0 ± 0.33 (2.0–3.3) | 4.0 ± 0.17 (3.7–4.2) |
| BIT | 1.6 ± 0.15 (1.4–1.9) | 1.5 ± 0.08 (1.3–1.6) |
| BIF | 2.0 ± 0.17 (1.7–2.2) | 2.1 ± 0.09 (2.0–2.3) |
| BPB | 3.2 ± 0.31 (2.7–3.8) | 3.8 ± 0.29 (3.4–4.5) |
| LN | 9.8 ± 0.68 (8.6–11.2) | 11.2 ± 0.40 (10.1–11.6) |
| BN | 3.1 ± 0.18 (2.8–3.4) | 3.3 ± 0.19 (3.0–3.6) |
| LIB | 5.3 ± 0.14 (5.0–5.6) | 5.3 ± 0.16 (5.0–5.6) |
| ZB | 15.5 ± 0.87 (14.0–17.3) | 17.2 ± 0.44 (16.5–18.1) |
| BB | 13.7 ± 0.36 (13.0–14.4) | 15.6 ± 0.26 (15.2–16.1) |
| BZP | 1.7 ± 0.13 (1.5–2.0) | 1.5 ± 0.16 (1.2–1.8) |
| BM1 | 1.6 ± 0.06 (1.5–1.7) | 1.8 ± 0.06 (1.7–1.9) |
| HI | 5.2 ± 0.45 (4.5–6.0) | 5.9 ± 0.36 (5.2–6.4) |
| DI | 1.5 ± 0.12 (1.3–1.7) | 1.6 ± 0.07 (1.5–1.7) |
| BOC | 8.4 ± 0.26 (7.9–9.0) | 9.3 ± 0.35 (8.6–9.7) |

[a] RMNH 12585, 29140, 29141, 29144–29147, 29152, 29159, 29161, 29162, 29164–29167, 29169, 29170, 29172, 29177, 29179.

[b] AMNH 110049, 110050, 110052, 110053, 110055, 110056, 110059, 110060, 110064, 110067, 110072, 110074, 110076, 110077.

as *H. habbema, H. hussoni* differs by its relatively shorter tail and hindfoot, smaller molars, broader incisors, narrower palate, broader zygomatic plate, less inflated braincase, and narrower occiput.

While the simple observation of this familiar distribution of external and skeletal shape differences with altitude among hydromyines is insufficient to corroborate the detailed causal relations postulated above, the predicted ecomorphological correlation is clearly not restricted just to ichthyomyines evolving in Neotropical habitats. Whether such a pattern could have been expected otherwise or admits of other plausible adaptive explanations, the existence of direct or indirect paths of cause-and-effect between elevation on the one hand and size-independent covariance of craniodental and postcranial proportions on the other seems likely.

Since size is correlated with size and shape with shape between cranial and postcranial skeletal data sets, phyletic divergence in ichthyomyine skeletal morphology can be represented with little loss of information in the size-shape plane of cranial variation alone (fig. 100). Drawn in that plane, the position of the most recent common ancestor (ANC) is approximately as reconstructed using Farris' (1970) algorithm, but other interior nodes (hypothetical ancestors) have been displaced from their most-parsimonious loci in order to better depict cladistic relations. Therefore, only the spatial distribution of terminal taxa is strictly informative.

South American ichthyomyines exhibit an orderly phyletic dispersion in this bivariate morphospace. The sequential cladogenesis of *Neusticomys venezuelae, N. monticolus, Chibchanomys trichotis,* and *Anotomys lean-*

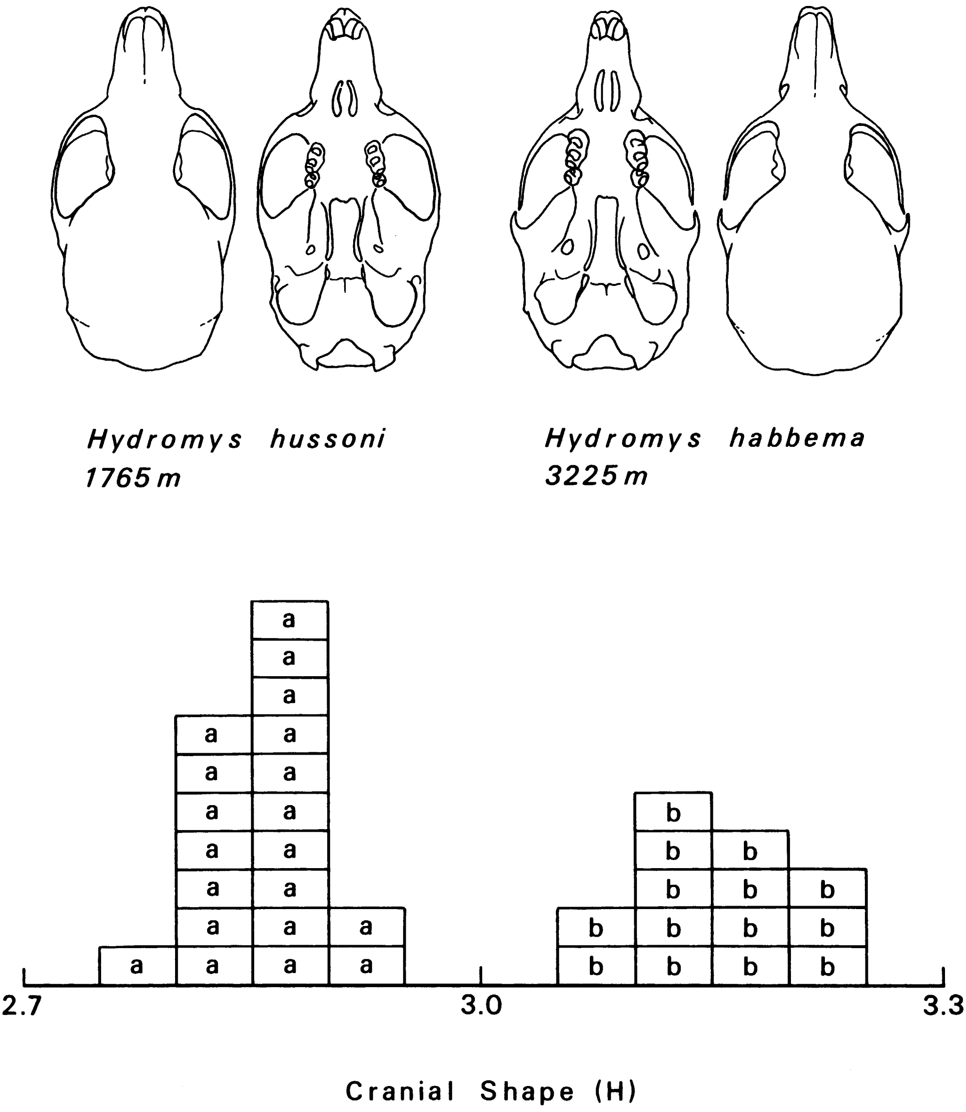


Fig. 99. Specimen scores of *Hydromys hussoni* (**a**'s) and *Hydromys habbema* (**b**'s) on the ichthyomyine cranial shape factor. See text for explanation and discussion.

*der* traces a monotonic morphocline of predominantly small species along the principal axis of shape variation from forms with robust incisors, diminutive molars, narrow palates, and uninflated braincases (and correlated postcranial proportions) to those with narrow incisors, large molars, broad palates, and inflated braincases. Members of the genus *Ichthyomys,* well removed from other South American lineages, form a discrete cluster of large species with incisor-emphasized dentitions.

Central American endemic taxa, comprising just the *Rheomys* clade (arrow in fig. 100) are narrowly distributed along the size axis between *Ichthyomys* and other South American ichthyomyines, but are widely dispersed along the axis of cranial shape. Small species of *Rheomys* (Rha and Rtt in fig. 100 plus Rts in table 54) overlap South American *Neusticomys* and *Ichthyomys* species in size-independent skeletal proportions while large species of *Rheomys* (Rme, Run) resemble South American *Anotomys* and *Chibchano-*

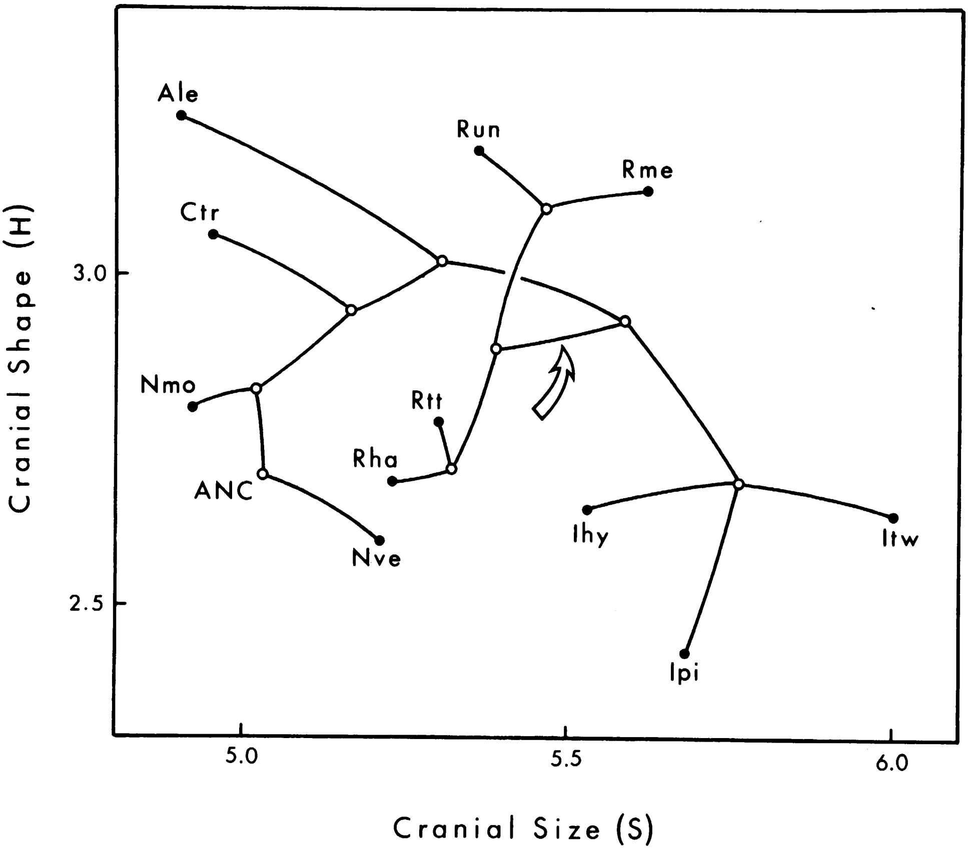


Fig. 100. Distribution of 11 ichthyomyine species in the plane of cranial size and shape with phylogenetic relations superimposed. The arrow marks the endemic Central American lineage of *Rheomys.*

*mys* in the same respects. This single Central American clade therefore spans a substantial fraction of the total range in shape variation encompassed by the South American ichthyomyine radiation.

The biological significance of size differences among ichthyomyines is obscure. Cranial size is negatively correlated with altitude at a marginal level of significance, but postcranial size is not (table 58). Neither size index appears correlated with other ecological variables for which data are presently available and little can be said, in consequence, about the evolutionary dispersion of species along the horizontal of figure 100.

While phyletic patterns of size variation must be left unexplained for want of external information, reasonable inference is possible concerning the ecology and historical biogeography of ichthyomyine evolution with respect to skeletal shape. Parsimony reconstruction of ancestral cranial and postcranial proportions (fig. 98, table 57) is consistent with outgroup comparisons (figs. 21, 55) in suggesting that primitive ichthyomyines were short-tailed with short distal limb elements, small hindfeet, incisor-emphasized dentitions, and uninflated braincases. If the adaptive interpretation of shape variation elaborated here is correct, then associated primitive habitats were probably lowland or foothill situations. *Neusticomys venezuelae,* an extant lowland species, exhibits such size-independent proportions, is primitive in nearly all qualitative characters as well (table 45), and provides a credible living model of the ancestral phenotype.

Convergence in ichthyomyine skeletal evolution is chiefly evident in shape comparisons of Central American with South American taxa, while phyletic divergence in skeletal size and shape is apparent within each of these regions. Since parsimonious zoogeographic reconstructions (fig. 95) suggest a tribal origin in South America, and because the Panamanian landbridge is a lowland isthmus, the likeliest scenario consistent with observed patterns of homoplasy is the independent acquisition of derived craniodental and postcranial proportions as adaptations to separate ecological invasions of highland streams in the Andes (by *Anotomys* and *Chibchanomys*) and in the Central American cordilleras (by *Rheomys mexicanus* and *R. underwoodi*). A hypothesis of ecological displacement among sympatrically evolving lineages would be consistent with predominantly divergent shape trends among geographically co-occurring taxa north and south of the isthmus, but evaluating that scenario would require far more detailed information about diets and habitats than is currently available.

## THE NEOTROPICAL MUROID FAUNA

In all of Eurasia there are only eight species of small mammals that prey on rheophilic arthropods; there are three such species in Africa, three in New Guinea, and one in Madagascar (table 50). By contrast, 14 species of ichthyomyines, numbering almost as many as all their ecological counterparts throughout the rest of the world, are distributed from southern Mexico to central Peru. Yet ichthyomyines represent just one lineage in a Neotropical muroid fauna that also includes species feeding on fungi, leaves, roots, fruit, seeds, worms, termites, other insects, and molluscs, and whose habitats range from alpine meadows to lowland savannas, rain forests, thornscrub, deserts, and swamps (see Hershkovitz, 1962 and 1972, for general accounts). Muroids are represented by more species than any other monophyletic group of comparable taxonomic rank in communities of nonvolant small mammals throughout Central and South America, and achieve their highest sympatric diversity in the tropical rain forest faunas to which ichthyomyines belong (table 43).

In their phyletic diversity, their broad ecological range, and their faunal dominance, Neotropical muroids resemble other tropical American vertebrate taxa such as characoid and siluroid fishes (Roberts, 1972; Fink and Fink, 1979), leptodactylid and hylid frogs (Lynch, 1979), tyrannoid birds (Dorst, 1976; Haffer, 1985), and phyllostomid bats (Koopman, 1982; Humphrey and Bonaccorso, 1979). The remarkable evolutionary diversification of these other groups, particularly in South America, may possibly be attributable to common historical and ecological circumstances. The causal hypothesis most often advanced by the authors cited above postulates extensive cladogenesis of a few original or immigrant ancestral lineages in South America during the long Cenozoic isolation of that continent from neighboring land masses. In the absence of many other groups of fishes, frogs, birds, or bats, these clades are conjectured to have experienced few of the restraints that ecological interactions among higher taxa might impose on the adaptive radiation of single lineages in less insular faunas.

Fossils or biochemical comparisons are available to suggest that most of these vertebrate taxa have evolved for a long time in South America. Characoid and siluroid fishes, leptodactylid and hylid frogs, and suboscine passerine birds are all believed to have been present in South America since the Cretaceous and to have radiated there throughout the Cenozoic (Roberts, 1972; Baez and de Gasparini, 1979; Sibley and Ahlquist, 1985). Phyllostomid bats are known from at least the middle Miocene of South America (Savage, 1951), but given the general scarcity of chiropteran fossils, phyllostomids may well have been present on the continent from a considerably earlier date and yet remain undiscovered as fossils in older strata.

In striking contrast to the reasonably certain antiquity of most other dominant South American vertebrate radiations, however, muroid rodents make an abrupt appearance in the very late South American Cenozoic fossil record, in Montehermosan faunas from Argentina presently dated at about 3.5 million years B.P. (Marshall et al., 1979), or about contemporaneous with the emergence of a Panamanian landbridge. Hershkovitz (1966) pointed out that these Argentine fossils resemble extant taxa that inhabit temperate grassland habitats in the same region today and subsequent studies of Argentine fossil muroids have supported similar conclusions (Reig, 1978). Because these middle Pliocene specimens represent endemic South American genera of modern aspect and do not correspond with expected ancestral morphologies, Hershkovitz (1966, 1972) and Reig (1980, 1984) suggested that muroids invaded South America by overwater dispersal at a much earlier date, in the Miocene or even late Oligocene. Reig (1978) and Marshall (1979) speculated that the muroid taxa appearing abruptly in the Pliocene savanna faunas of Argentina evolved elsewhere on the continent, perhaps in the nonforest vegetation formations of the central Andes or in northern, tropical grasslands, prior to invading more southerly latitudes. While these conjectures, together with the hypothesis that South American muroids were primitively forest-adapted (Hershkovitz, 1962) might account for some delay in geologic time between the arrival of immigrant muroid ancestors (from Central America) in the tropical, presumably forested, northwestern part of the continent and the subsequent appearance of their descendants in temperate Patagonian savannas, the absence of muroids from Friasian (middle Miocene) faunas in Colombia that include other forest-adapted small mammals (Stirton, 1953) would appear to argue against a very much older invasion.

By contrast, Patterson and Pascual (1972) and Baskin (1978) suggested a literal interpretation of the Argentine fossils as recording the earliest immigrant muroids in South America, contemporaneous with uplift of the Panamanian landbridge. They explain the extant diversity of South American muroids, as well as the unancestral appearance of mid-Pliocene and Pleistocene Argentine fossils, by postulating that the southern continent was invaded by a muroid fauna that had already undergone considerable cladogenesis and morphological differentiation in North or Central America. Baskin (1978) and Jacobs and Lindsay (1984) hypothesized that several North American early or middle Pliocene muroid taxa, *Bensonomys, Symmetrodontomys,* and *Prosigmodon,* represent lineages ancestral to several different muroid tribes, now predominantly or exclusively South American, that may have evolved in North America prior to emergence of the landbridge. Reig (1980), however, argued that resemblances between North American fossil *Bensonomys* and extant South American genera do not provide convincing evidence of close relationship and neither he nor Hershkovitz (1966, 1972) believed that any of the major suprageneric groups of extant South American muroids evolved north of the Panamanian landbridge.

The geological record is therefore subject to widely divergent interpretations, but critical attention has focused almost exclusively on the time of arrival of muroids in South America and on the time and place of origin of Neotropical muroid tribes as independent phyletic lineages. While these chronological and geographical issues are of considerable interest and might eventually be reconstructed from fossil evidence, much of the biological detail of muroid evolution in the New World tropics must derive from studies of the neglected living fauna. The data, analyses, and conclusions reported here provide such detail for one extant Neotropical muroid lineage and also address some of the issues disputed in the literature cited above.

To the extent that the distribution of living species is not completely misleading, parsimonious phylogenetic reconstructions of ichthyomyine geography support a South American origin for the tribe. While it is obviously impossible to conclude with certainty whether or not the subsequent cladogenesis and differentiation of descendant ichthyomyine lineages could have transpired since the emergence of a Panamanian landbridge, the evidence favors Hershkovitz's (1966, 1972) and Reig's (1980, 1984) conceptions of an indigenous South American muroid radiation rather than Patterson and Pascual's (1972) hypothesis that South American muroid diversity is largely attributable to prior cladogenesis and phyletic divergence in Central America. Clearly, the Recent occurrence in Central America of members of predominantly South American muroid lineages conveys no information of historical-biogeographic significance in the absence of relevant hypotheses of phylogenetic relationships; the endemic Central American genus *Rheomys* is a highly derived terminal taxon and not the sister-group to South American ichthyomyines that Patterson and Pascual's hypothesis would predict.

This monograph documents ecomorphological correlations among ichthyomyines and other small mammals that, together with functional analyses and phylogenetic reconstructions, provide evidence for evolved adaptations to diet and habitat. Adaptive "explanations" have often been appended to descriptions of morphological character differences among South American muroid lineages and to descriptions of convergent similarities between South American muroids and distantly related taxa from other continents. Such explanations may not be inappropriate. But credible hypotheses of adaptive divergence or convergence require adequate functional-morphological and ecological documentation as well as a phylogenetic framework for comparisons. As this information becomes available for other lineages, it seems probable that the evolutionary processes responsible for Neotropical muroid diversity will prove to be far more complex than the dichotomous adaptation to "sylvan" or "pastoral" habitats invoked by most current biogeographic scenarios.

Unlike many groups of larger Neotropical mammals that were extinguished or dwindled in phyletic diversity during late Tertiary faunal exchanges, Quaternary climatic fluctuations, or by human exploitation, living South American muroids may represent a substantially intact continental fauna that can provide useful comparisons with other Neotropical vertebrate taxa. Congruent phylogenetic patterns of ecological or geographical distributions observed among characoid fishes, hylid frogs, tyrannoid birds, phyllostomid bats, and muroids, for example, would provide compelling evidence for common causal factors in the evolution of the Neotropical biota. Alternatively, the lack of such congruence may suggest important differences in the historical and geographical circumstances or ecological relations that have influenced the Neotropical diversification of major vertebrate clades. Effective comparisons with these objectives, however, require a sound systematic basis as well as natural history data that are presently unavailable for muroids. Most South American muroid tribes have not been diagnosed in more than a few characters of the skin and skull, most genera remain unrevised and inadequately defined, hypotheses of phylogenetic relationships are seldom supported by substantive analyses of characters, and published information about ecology consists almost entirely of undocumented generalizations. This absence of elementary biological information about most South American rats and mice provides abundant opportunity for significant future research.

## APPENDIX: GAZETTEER

This gazetteer summarizes geographical and ecological information about ichthyomyine collection localities and habitats. Since many localities do not appear on published maps and are not included in standard references, some entries require evaluation and discussion of information from fieldnotes and other original sources.[6] Latitude and longitude are usually those provided in gazetteers approved by the United States Board on Geographic Names. Altitudes are reported verbatim from specimen tags, collector's field-notes, or other cited documents. Administrative units within countries are usually abbreviated: Depto. (Departamento), Edo. (Estado), Prov. (Provincia). Numbered localities appear on the accompanying maps.

### COLOMBIA (Map 1)

1. **Cerro Munchiquito** (presumed synonymous with Cerro Munchique, see below; mountain in Cordillera Occidental; 2°32′N, 76°57′W), Depto. Cauca. One specimen of *Ichthyomys hydrobates* collected in a small forest stream at 8500 ft

---

[6] My efforts to retrace the peregrinations of G. H. H. Tate and H. E. Anthony, and to retrieve ecological information from their fieldnotes, were materially assisted by Bill Glover and his indefatigable colleagues. Mr. Glover and his volunteer staff have meticulously organized the AMNH Department of Mammalogy archives and made the manuscript notes and correspondence of hundreds of field collectors accessible to present and future researchers. This valuable contribution of time and energy requires special acknowledgment here.

elevation by M. A. Carriker, Jr., 8 August 1952. Paynter and Traylor (1981) record Carriker's activity at Cerro Munchique in August 1952; the diminutive may refer to a minor peak.

2. **Chisquío** (village on E slope of Cordillera Occidental; 2°29′N, 76°52′W), Depto. Cauca. One specimen of *Ichthyomys hydrobates* collected at 1800 m elevation by K. von Sneidern, 15 July 1958.

   **Cundinamarca** (Departamento, administrative unit with capital at Bogotá; 4°36′N, 74°05′W). Holotype of *Chibchanomys trichotis* collected by G. D. Child labeled "W[est]. Cundinamarca," date unknown. See discussion of this locality in taxonomic account for *C. trichotis.*
3. **Paime** (village in western foothills of Cordillera Oriental; 5°22′N, 74°10′W), Depto. Cundinamarca. Holotype of *Ichthyomys hydrobates nicefori* collected by Hno. Nicéforo M., August 1923. Paynter and Traylor (1981) give the elevation of Paime as 1038 m.
4. **Pichindé** (village on E slope of Cordillera Occidental; 3°26′N, 76°37′W), Depto. Valle. Four specimens of *Neusticomys monticolus* collected at 1800–1900 m elevation by L. Velasquez, January–October 1969.
5. **San Antonio** (locality on E slope of Cordillera Central; ca. 1°58′N, 76°35′W), Depto. Huila. Two specimens of *Neusticomys monticolus* collected at 2200–2350 m elevation by P. Hershkovitz, 2–16 September 1951. Local habitat formerly temperate rain forest [cloud forest] but with mixed pasture and scrub at the time of this collection (Hershkovitz, in litt.); Hershkovitz wrote me that his ichthyomyine specimens (these and others from Santa Bárbara and San Cristobal, see below) were taken "alongside fast flowing but not cascading narrow rocky streams."
6. **San Cristobal** (valley in Cordillera Oriental SE of Bogotá; 4°35′N, 74°05′W), Depto. Cundinamarca. One specimen of *Chibchanomys trichotis* collected alongside a narrow, scrub-bordered stream at 2900 m elevation by P. Hershkovitz, 29 June 1952.
7. **Santa Bárbara** (locality in Cordillera Occidental; ca. 6°25′N, 76°00′W), Depto. Antioquia. Six specimens of *Neusticomys monticolus* collected at 2700–2800 m elevation by P. Hershkovitz, 15–27 April 1951. Santa Bárbara is the site of an abandoned homestead on the upper Río Urrao (= Río Herradura) at the southeast base of the Páramo de Frontino; local habitat formerly cloud forest, lumbered and burned at the time of this collection, the area still wooded but mixed with scrub. Specimens were collected along a narrow, deeply channeled stream (Hershkovitz, in litt.).

COSTA RICA (Map 2)

8. **Monte Verde** (settlement on Pacific versant of Cordillera de Tilarán; 10°20′N, 84°50′W), Prov. Puntarenas. One specimen of *Rheomys raptor* collected in the Río Guácimal by E. T. Hooper, 5 May 1969. The Río Guácimal at Monte Verde (ca. 1300 m elevation) is a clear, rocky-bottomed stream bordered by dense cloud forest growing on steep valley slopes (Hooper, 1968; personal obs.).
9. **San Isidro** (town in Pacific foothills of Cordillera de Talamanca; 9°22′N, 83°42′W), Prov. San José. Six specimens of *Rheomys raptor* collected at 4800–5200 ft elevation by E. T. Hooper, G. G. Musser, and D. J. Klingener (20–21 July 1962) and by A. Starrett (14 July 1963), 9–11 mi (by road) N of San Isidro. Specimens were collected in or along small, clear, rocky-bottomed tributaries of the Río Buena Vista; descriptions of bordering cloud forest vegetation and the circumstances of capture are provided in Musser's fieldnotes (UMMZ, Division of Mammals archives; abstracted by Hooper, 1968).
10. **Tres Ríos** (city in central valley of Cordillera Central; 9°54′N, 83°58′W), Prov. Cartago. The holotype of *Rheomys underwoodi* collected by C. F. Underwood, 5 May 1905. Elevation, habitat, and exact collection locality unknown.
11. **Volcán Poás** (mountain in Cordillera Central; 10°11′N, 84°13′W), Prov. Alajuela. Four specimens of *Rheomys un-*

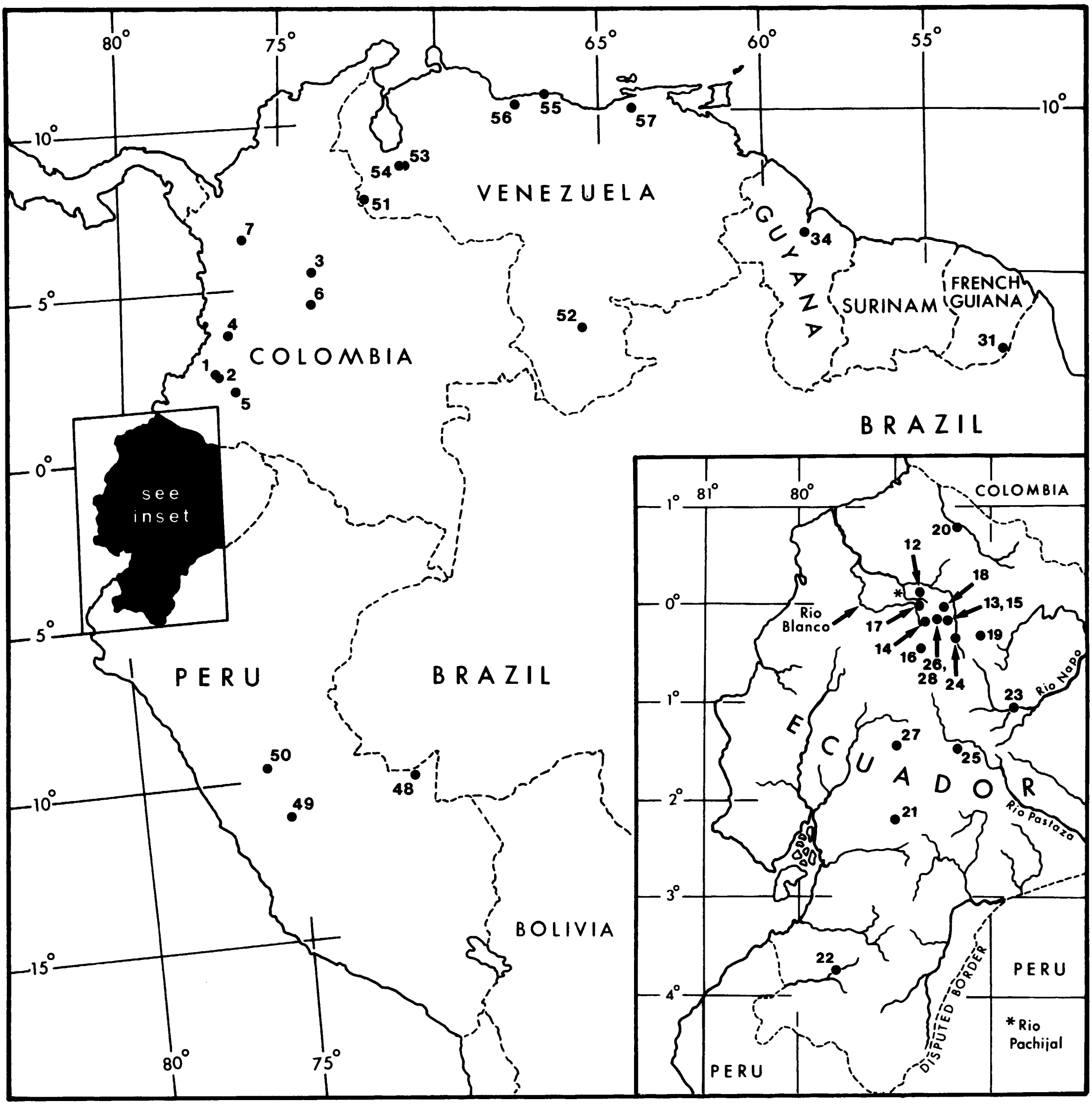
*derwoodi* collected at 2000 m elevation by J. H. Brown and E. T. Hooper (6–7 April 1966) and G. F. Fisler (10 April 1966). Specimens were collected in or along the Río Poasito, a clear, rocky-bottomed stream bordered by cloud forest vegetation near the Volcán Poás highway (Hooper, 1968; Starrett and Fisler, 1970).

ECUADOR (Map 1, inset)

**Cacao Cocha** (locality on Río Blanco; coordinates unknown), Prov. Pichincha or Esmeraldas. Five specimens of *Ichthyomys tweedii* collected by "Olalla e hijos," 5–10 July 1931. See entry for Río Blanco.

**Chinchin Cocha.** No locality information available. One specimen of *Anotomys leander* collected at 4000 m elevation by C. Olalla, 12 April 1939.

12. **Gualea** (town in western foothills of Cordillera Occidental; 0°07′N, 78°50′W), Prov. Pichincha. The holotype of *Ichthyomys caurinus* (= *I. tweedii*) is labeled "near Pechahal below Gualea 2–3000 feet," and dated August 1923. This is one of the many ichthyomyine specimens sent by Ludovic Söderström, the Swedish Consul-General, to American and European museums. Söderström bought his specimens from local collectors who often used the names of towns in a vague, regional sense that is sometimes very misleading (Chapman, 1926: 10–11). Pechahal (spelled Pachijal on recent maps) is a watercourse that passes near Gualea (at about 1500 m; Paynter and Traylor, 1977) in the upper Río Esmeraldas drainage (see entry for Río Pachijal, below).
13. **Guápulo** (town near Quito on western edge of central valley; 0°12′S, 78°29′W), Prov. Pichincha. Twenty-two specimens (including the holotype) of *Ichthyomys hydrobates soderstromi* collected along the Río Machángara at Guápulo between 8750 and 9000 ft elevation by collectors in the employ of L. Söderström (1895 to 1916) and by G. H. H. Tate (14 September 1923). Handwritten notes on Söderström's original specimen tags describe captures by hand in springs or among rocks at streamside; Tate's (1931) account differs.
14. **Guarumal** (populated place on SE slope of Volcán Pichincha in Cordillera Occidental; 0°17′S, 78°43′W), Prov. Pichincha. Eight specimens of *Neusticomys monticolus* collected from tiny streams in dense secondary growth 1–2 km (by road) E of Guarumal at 2245–2290 m elevation by R. S. Voss, 4–5 June 1978 and 31 May–1 June 1980. One specimen of *Ichthyomys hydrobates* was also collected about 100 m downslope at the same locality in a small stream near the Río Saloya by R. S. Voss, 5 June 1978. Habitats near Guarumal are described in the Ecology section of this monograph.
15. **La Carolina** (locality; exact coordinates uncertain), Prov. Pichincha. One specimen of *Anotomys leander* labeled "La Carolina North of Quito Alt 9,400 ft, caught in a pool of fresh water"; collected or purchased by L. Söderström, 17 March 1918. La Carolina was a large tract of low-lying land at the northern border of Quito (0°13′S, 78°30′W) according to Chapman (1926); it is now part of suburban Quito.
16. **Las Machinas** (locality in Cordillera Occidental; exact coordinates unknown), Prov. Pichincha. Six specimens of *Neusticomys monticolus* collected at 6800–7000 ft elevation by G. H. H. Tate and H. E. Anthony, 21–23 September 1923. Las Machinas was the site of an abandoned sawmill near the confluence of the Río Silanti and the Río San Lorenzo (= Río Naranjal) on the western slopes of Corazón (0°32′S, 78°39′W) and on the trail from Alóag (0°28′S, 78°35′W) to Santo Domingo (0°15′S, 79°09′W). Tate's fieldnotes (AMNH, Department of Mammalogy archives) describe cloud forest vegetation at Las Machinas similar to that at Guarumal (see the Ecology account for *N. monticolus* in this monograph). The specimens were collected "along the bases of moist bluffs often 30 feet from water where they might swim" (Tate's fieldnotes for 23 September 1923).
17. **Mindo** (village in western foothills of Cordillera Occidental; 0°03′S, 78°46′W), Prov. Pichincha. Eight specimens of



Map 1. Ichthyomyine collection localities in South America.

*Ichthyomys tweedii* collected from rainforest streams in the vicinity of Mindo at 1290–1330 m elevation by R. S. Voss, 23 May 1978 and 1–21 June 1980. See the account for *I. tweedii* in the Ecology section of this monograph for descriptions and illustrations of habitats near Mindo. Many Söderström specimens of *I. tweedii* are labeled "Pechehal, below Mindo." For these, I assume that Mindo is used in the regional sense (see entry for Gualea, above) and that Pechehal (a river, see entry for Río Pachijal, below) is the more definite locality. One Söderström specimen dated June 1925 is labeled "below Río Blanco, Mindo."

18. **Nono Farm "San Francisco"** (locality in Cordillera Occidental; coordinates uncertain, see below), Prov. Pichincha. The holotype of *Neusticomys monticolus* collected at 10,500 ft elevation, 16 February 1916. This is another Söderström specimen (see entry for Gualea, above) that was probably purchased from a local col-

lector. Nono (0°04'S, 78°35'W) is a small town situated about 13 km NW of Quito on the road to San Miguel de los Bancos. Hacienda San Francisco, about 4.5 km N of Nono, is the only landholding by that name in the vicinity that I am able to locate on any map, but lies at only 2640 m (8580 ft). Although this is the locality labeled on map 2, the discrepancy in elevation should be noted.

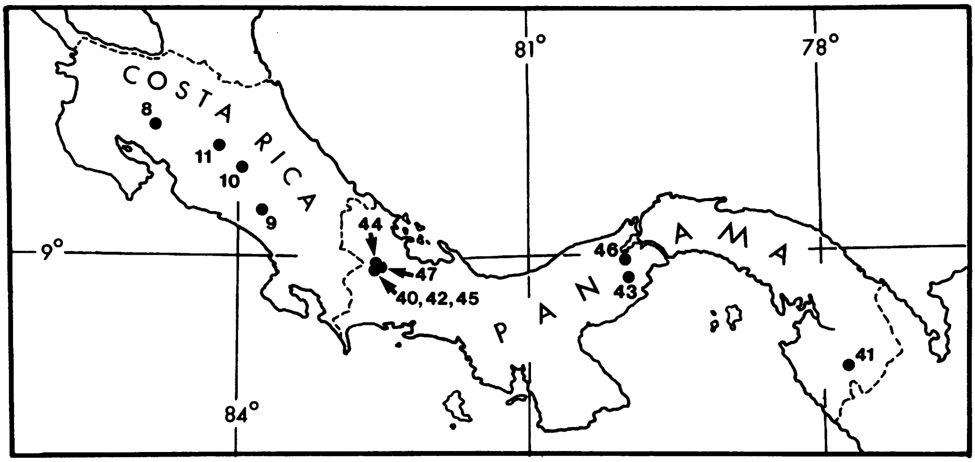
19. **Papallacta** (village in Cordillera Oriental; 0°22'S, 78°08'W), Prov. Napo. Twelve specimens of *Anotomys leander* and six specimens of *Neusticomys monticolus* collected from streams in the vicinity of Papallacta by R. S. Voss, 8 May–11 June 1978 and 4–22 March 1980. Stream habitats of *A. leander* near Papallacta are described in the Ecology section of this monograph. Three specimens of *N. monticolus* were collected from rivulets less than 0.5 m in width and a few centimeters in depth descending narrow ravines choked with dense, wet, secondary growth at 3070 m elevation, 1.4 km (by road) E Papallacta. Three other specimens of *N. monticolus* were collected in the larger streams from which *A. leander* were taken (6.2–8.2 km W Papallacta at 3600–3754 m), but while *A. leander* was often trapped on rocks or logs surrounded on all sides by swift current, the three specimens of *N. monticolus* from these streams were all trapped in sheltered situations along the water's edge.
20. **Paramba** (hacienda on left bank of Río Mira in foothills of Cordillera Occidental; 0°49'N, 78°21'W), Prov. Imbabura. One specimen of *Ichthyomys tweedii* caught in the river by R. Miketa, 1 July 1898. Chapman (1926) gives the elevation of Paramba as 3500 ft and the local habitat as tropical forest.
21. **Pauchi** (locality in Cordillera Occidental; exact coordinates unknown), Prov. Chimborazo. One specimen of *Neusticomys monticolus* trapped beside a small, rocky stream in a forested ravine by H. E. Wickenheiser, 13 November 1922. According to a typewritten document describing the collecting activities of Wickenheiser and G. H. H. Tate in 1922 (AMNH Department of Mammalogy archives), Pauchi is a four-hour ride from Huigra (2°17'S, 78°59'W) and lies between 6000 and 7000 ft elevation.
22. **Portovelo** (mining camp on Río Amarillo in western lowlands; 3°43'S, 79°39'W), Prov. El Oro. The holotype of *Ichthyomys tweedii* was obtained by H. E. Anthony from a boy who caught it near the banks of the Río Amarillo at 2000 ft elevation, 16 July 1920. The region of Portovelo is humid (Chapman, 1926) but was largely deforested at the time of this collection. Anthony's photographs of the area (AMNH Department of Mammalogy archives) show grazed, scrubby hillsides with patches of forest remaining on some upper slopes and in ravines along the Río Amarillo.

    **Río Blanco** (river in western lowlands; see account below for coordinates), Prov. Pichincha and Esmeraldas. The Río Blanco drains the western slopes and foothills of the Cordillera Occidental due W of Quito. The name applies to some 100 km or more of waterway from Rosa Zárate (also called Quinindé; 0°20'N, 79°28'W) upstream to the confluence of the Río Saloya and the Río Mindo near Mindo (q.v., 0°02'S, 78°48'W). One specimen of *Ichthyomys tweedii* labeled "near Río Blanco, 4000 ft about" collected or purchased by L. Söderström in June 1926 is probably from the vicinity of Mindo. Three specimens of *I. tweedii* collected by Spillmann between 7 and 15 September 1931 and labeled simply "Río Blanco" could be from anywhere along this river. The natural vegetation throughout the Río Blanco valley is Lowland Rain Forest.
23. **Río Napo** (river in eastern lowlands; see account below for coordinates), Prov. Napo. The holotype and five other specimens of *Ichthyomys stolzmanni orientalis* labeled "near the river Napo" with recorded elevations of "about" 2000 to 3000 ft were purchased or collected by L. Söderström in June and September of 1921. The Río Napo drains the eastern slopes of the Cordillera Oriental from the latitude of Baños (2°14'S) N to the Co-

lombian border. The name applies to about 1000 km of waterway from Tena (0°59′S, 77°49′W) at 518 m elevation to the Amazon just below Iquitos (3°46′S, 73°15′W) at 106 m, all of which is claimed by Ecuador. From the elevations provided, it seems probable that these specimens were collected near Tena (where they are located on map 1), but Chapman (1926) emphasizes the inexact sense in which "Napo" and "Río Napo" were used by indigenous collectors, and there is no way to be certain of this inference.

**Río Pachijal** (river in western lowlands; see account below for coordinates), Prov. Pichincha. The Río Pachijal is a tributary of the Río Guayllabamba with its headwaters in the Cordillera Occidental near Tandayapa (0°01′S, 78°46′W) at about 2000 m elevation. The confluence of the Río Pachijal and the Río Guayllabamba is shown at about 0°11′N, 78°55′W on recent maps. Twenty specimens of *Ichthyomys tweedii* purchased from local collectors by L. Söderström in 1924 and 1925 are labeled "Pechehal, below Mindo" with recorded elevations of 2000 or 2500 ft. These labels are misleading because Mindo (q.v.) is in the drainage of the Río Blanco which only joins the Guayllabamba several hundred km to the NW. Mindo lies only a few km from the upper course of the Río Pachijal, but town and river are separated by a steep-sided spur of the Cordillera Occidental. Söderström's "Pechehal" specimens of *I. tweedii* can therefore only be assigned to the general vicinity of Mindo, but might be as much as 20 airline km distant and in a different watershed. Four specimens of *I. tweedii* collected by M. Olalla on 24 October 1962 are simply labeled "Loc. Pachijal Occidente."

24. **Río Pita** (stream in central valley E of Quito; exact coordinates uncertain), Prov. Pichincha. Nine specimens of *Neusticomys monticolus* assigned to this locality and labeled "Cañon of Río Pita," "Santa Rosa above Río Pita, 9600 ft," and "Río San Rafael, 9000 ft" were collected by H. E. Anthony and G. H. H. Tate between 28 August and 6 September 1923. Anthony and Tate camped from 26 August to 2 September at Santa Rosa, a power-generating station on a ridge between the Río Pita and the Río San Rafael a few km SE of Sangolquí (0°19′S, 78°27′W) on the road from Quito; the Río San Rafael site was only 20 minutes ride from Santa Rosa (this and following information from Anthony and Tate's fieldnotes in AMNH Department of Mammalogy archives). The area around Santa Rosa was largely cleared for cultivation; four specimens of *N. monticolus* were collected there in asequias (narrow irrigation canals) bordered by mossy brush. One specimen was collected along the Río San Rafael. Tate and Anthony left Santa Rosa at 0730 hrs on 2 September and established a new camp in the canyon of the Río Pita at 9700 ft elevation by 1030 hrs on the same day. At the "Cañon of Río Pita" camp, three specimens of *N. monticolus* were collected in forest traplines, but the circumstances of capture were not recorded.
25. **San Antonio** (hacienda on Río Ulva in Cordillera Oriental near Baños; exact coordinates uncertain), Prov. Tunguragua. One specimen of *Neusticomys monticolus* collected at 6727 ft by G. H. H. Tate, 24 January 1924. San Antonio is on the left bank of the Río Ulva (a tributary of the upper Río Pastaza) and four hours' ride with pack animals E and then S from Baños (2°14′S, 78°25′W). The local habitat was dense, wet cloud forest (Tate's fieldnotes, AMNH Department of Mammalogy archives).
26. **San Ignacio** (hacienda near Quito on S slope of Volcán Pichincha in Cordillera Occidental; 0°12′S, 78°33′W), Prov. Pichincha. Two specimens of *Neucticomys monticolus* collected at 11,150 ft elevation by H. E. Anthony and G. H. H. Tate, 17–18 August 1923. Anthony and Tate camped about .5 mi N of Hacienda San Ignacio, a three-hour ride with pack animals from Quito, in a shrubby ecotone between the dwarfed cloud forests of the lower slopes and the grassy páramo of the upper slopes. One specimen of *N.*



Map 2. Ichthyomyine collection localities in eastern Central America.

*monticolus* was trapped at the edge of a shallow pool in a small stream near the base of a waterfall; no information was recorded about the habitat of the second specimen.

27. **Sinche** (hacienda on W slope of Chimborazo in Cordillera Occidental; 1°32'S, 78°59'W), Prov. Bolívar. One specimen of *Neusticomys monticolus* collected at 11,100 ft elevation by G. H. H. Tate, 25 November 1923. Sinche (also spelled "Sinchig" and "Sinchic") is on the Río Salinas in the upper Río Chimbo drainage. Tate collected about 1000 ft above the hacienda where patches of low forest, drained by many small streams, were interspersed with grassy páramo vegetation and marshes.
28. **Volcán Pichincha** (mountain in Cordillera Occidental; highest peak at 0°10'S, 78°36'W), Prov. Pichincha. Pichincha is the extinct volcano against whose southeastern flanks the city of Quito is built. Habitats on the E slopes above the city include cultivated fields, wet pastures, groves of eucalyptus, patches of Subalpine Rain Forest, and páramo. On the W slopes there is an undisturbed altitudinal succession from alpine grasslands to Lower Montane Rain Forest. Because of its long accessibility to collectors and this extraordinary ecological diversity, Pichincha is an important collection locality for hundreds of vertebrate species, but "Pichincha" specimens unaccompanied by other geographical information may have been collected in almost any montane habitat. Two specimens of *Anotomys leander* labeled "Mt. Pichincha" with recorded elevations of 11,500 ft (the holotype, collected or purchased by L. Söderström, 5 August 1905) and 12,000 ft (collected by C. S. Webb, 4/3/38) were probably taken near treeline and in the lower páramo zone, respectively. Two other specimens of *A. leander* labeled only "Mt. Pichincha" (L. Söderström, 1923) and one labeled "Rinconada faldas Pichincha" (Carlos Olalla and sons, 13 April 1936) provide no basis for ecological inference.

EL SALVADOR (Map 3)

29. **Cerro Cacaguatique** (mountain; 13°46'N, 88°13'W), Deptos. San Miguel and Morazan. Twenty-eight *Rheomys thomasi* collected from small streams bordered by coffee and other crops between 3500 and 4700 ft elevation by R. A. Stirton (24 November–21 December 1925; 26 December 1941–2 January 1942) and M. Hildebrand (2–3 January 1942). See Stirton (1944) for descriptions of local habitats and illustrations of collection methods.
30. **Los Esesmiles** (mountain range adjacent to Honduran highlands; 14°17'N,

89°07′W), Depto. Chalatenango. Nine specimens of *Rheomys thomasi* collected from a stream in cloud forest at 8000 ft elevation by R. A. Stirton (20–24 February 1927; 27–28 March 1942) and M. Hildebrand (28 March 1942). Descriptions and a photograph of local habitats are provided by Stirton (1944).

FRENCH GUIANA (Map 1)

31. **Trois Sauts** (locality on Oyapock river; 2°10′N, 53°11′W). One specimen of *Neusticomys oyapocki* collected "non loin des rives de l'Oyapock" (Dubost and Petter, 1978) by G. Dubost, 3 April 1976.

GUATEMALA (Map 3)

32. **El Injerto** (hacienda near Mexican border in Sierra Madre; ca. 15°34′N, 92°02′W), Depto. Huehuetenango. Four specimens of *Rheomys thomasi* collected from small streams in the vicinity of El Injerto at 4000 ft elevation by T. Betz (3 June 1965) and at 1600 m by M. D. Carleton (14–15 May 1970). Hooper (1968) provides additional geographic details.
33. **Quezaltenango** (city in Sierra Madre; 14°50′N, 91°31′W), Depto. Quezaltenango. One specimen of *Rheomys thomasi* collected 6 mi NNE Quezaltenango at 8800 ft elevation by D. C. Gall, 12 February 1963.

GUYANA (Map 1)

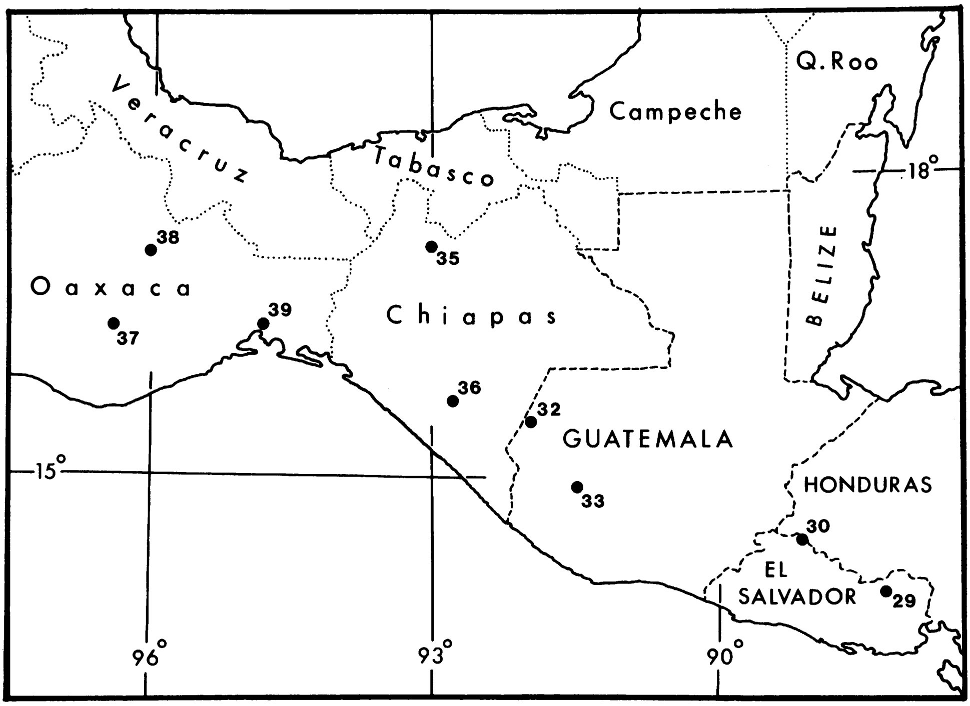
34. **Kartabo** (research station at confluence of Mazaruni and Cuyuni rivers; 6°23′N, 58°42′W), Mazaruni-Potaro District. One specimen of *Neusticomys venezuelae* collected by W. Beebe, 1920. Lowland Rain Forest habitats at Kartabo are described by Beebe (1925); local elevations range from 30 to 50 ft.

MEXICO (Map 3)

35. **Ixhuatán** (town in Caribbean foothills of Sierra Madre de San Cristobal; 17°17′N, 93°02′W), Edo. Chiapas. One specimen of *Rheomys thomasi* collected near a stream in forest 1.8 mi W Ixhuatán at 1200 ft elevation by M. D. Tuttle, 28 June 1962.
36. **Prusia** (finca in Sierra Madre de Chiapas; 15°45′N, 92°43′W), Edo. Chiapas. One specimen of *Rheomys thomasi* collected from a concrete canal by H. O. Wagner, 14 March 1942. Montane forest habitats near Prusia, where Wagner collected between 1000 and 1100 m elevation (Hooper, 1947), are described by Wagner (1961).
37. **San José Lachiguirí** (town; 16°23′N, 96°20′W), Edo. Oaxaca. Eleven specimens of *Rheomys mexicanus* collected by local fisherman and sold to T. MacDougall from 1958 to 1964. Elevation of San José Lachiguirí is given by Goodwin (1969) as either 4000 or 5000 ft; Goodwin (1959) gave elevation as 4000 ft and said that specimens of *R. mexicanus* were taken "in a rather slow, rocky stream passing through dry cactus country with some stands of oak and pine."
38. **Totontepec** (town in Sierra Mixes; 17°13′N, 96°03′W), Edo. Oaxaca. Two specimens of *Rheomys mexicanus* collected from a small stream on a steep slope in cloud forest 3.6 mi W Totontepec at 6800 ft elevation by J. A. Campbell, 8 April 1978.
39. **Unión Hidalgo** (town near Pacific coast; 16°28′N, 94°50′W), Edo. Oaxaca. Fourteen specimens of *Rheomys mexicanus* collected in the Río Chiapa below the town by local fisherman and sold to T. MacDougall from 1960 to 1964. According to Goodwin (1969), the Río Chiapa below Unión Hidalgo (which is near sea level) "flows rapidly from the mountains and is still cold."

PANAMA (Map 2)

40. **Candela** (locality in western highlands; ca. 8°54′N, 82°43′W), Prov. Chiriquí. Two specimens of *Rheomys underwoodi* labeled "Candela" and collected by R. K. Enders on 19 and 21 March 1974 are from "El Volcán, 17 km NNW head of Río Candela, 2000 m elevation" according to C. O. Handley, Jr. (personal commun.).



Map 3. Ichthyomyine collection localities in western Central America.

41. **Cerro Pirre** (highest peak in Serranía de Pirre near Colombian frontier; 7°51′N, 77°44′W), Prov. Darién. Three specimens (including the holotype) of *Rheomys raptor* collected from a small stream in the headwaters of the Río Limón at 4500–5200 ft elevation by E. A. Goldman, 24–28 April 1912. See Goldman (1920) for details of trapping and other observations. Myers (1969) described cloud forest habitats in the Serranía de Pirre.
42. **Cotito Hot Springs** (locality on Pacific slope of western highlands; ca. 8°52′N, 82°44′W), Prov. Chiriquí. Four specimens (including the holotype) of *Rheomys raptor hartmanni* collected in streams near hot springs of the Río Cotito at 4900 ft elevation by R. K. Enders (17 March 1937; 25–26 March 1971) and Bishop (20 March 1937).
43. **El Aguacate** (town in central lowlands; ca. 8°45′N, 79°58′W), Prov. Panamá. Three specimens of *Ichthyomys tweedii* collected by R. B. Tesh in 1970, 1971, and 1972. Tesh (1970) gives the elevation of El Aguacate as about 1000 ft and describes local habitats.
44. **First Water** (camp on Atlantic slope of western highlands; ca. 8°56′N, 82°42′W), Prov. Bocas del Toro. One specimen of *Rheomys raptor* collected between 6250 and 6800 ft elevation by R. K. Enders, 30 March 1976.
45. **Río Chiriquí Viejo** (stream in western highlands; mouth at 8°20′N, 82°41′W), Prov. Chiriquí. One specimen of *Rheomys underwoodi* trapped on a log in the rapids of the upper Río Chiriquí Viejo near Cerro Punta (8°52′N, 82°35′W) at 1700 m elevation by M. D. Carleton, 12 May 1969. The natural vegetation of the upper Río Chiriquí valley is cloud forest, remnants of which persisted on slopes above the river at the time of this collection.
46. **Río Trinidad** (stream in central lowlands; mouth at 9°01′N, 79°58′W), Prov. Panamá. One specimen of *Ichthyomys tweedii* collected 7 mi S of mouth of Río Trinidad. Unaccompanied by other data, this specimen was sent to LACM in 1973

by N. Smythe of the Smithsonian Tropical Research Institute.

47. **Velo** (locality on Pacific slope of western highlands; ca. 8°47'N, 82°26'W), Prov. Chiriquí. One specimen of *Rheomys underwoodi* collected at 5000 ft elevation by R. K. Enders, 1937.

PERU (Map 1)

48. **Balta** (Indian village on Río Curanja in Amazonian lowlands; ca. 10°08'S, 71°13'W), Depto. Loreto (now Ucayali). One specimen of *Neusticomys peruviensis* trapped in a shallow forest stream at 300 m elevation by A. L. Gardner, 28 July 1968. Musser and Gardner (1974) provide additional habitat information.
49. **Chanchamayo** (valley of Río Chanchamayo; ca. 11°03'S, 75°19'W), Depto. Junín. The holotype of *Ichthyomys stolzmanni* collected at about 3000 ft elevation by J. Kalinowski (Thomas, 1893). Coordinates for this locality follow Stephens and Traylor (1983).
50. **Cordillera Carpish** (mountain range; ca. 9°40'S, 76°09'W), Depto. Huánuco. One specimen of *Chibchanomys trichotis* trapped beside running water in a roadside ditch along the Carretera Central on the cloud-forested E slope of the Cordillera Carpish at 2400 m elevation by A. L. Gardner, 15 August 1968. Coordinates for this locality follow Stephens and Traylor (1983).

VENEZUELA (Map 1)

51. **Buena Vista** (locality in Táchira Andes; ca. 7°26'N, 72°26'W), Edo. Táchira. Five specimens of *Chibchanomys trichotis* collected from a stream in cloud forest at 2400–2584 m elevation by F. P. Brown (24 March 1968) and R. S. Voss (8–12 January 1980). See Ecology account of *C. trichotis* for detailed description and illustrations of local habitats.
52. **Cerro Duida** (table mountain in southern highlands; 3°37'N, 65°41'W), Territorio Federal Amazonas. One specimen of *Neusticomys venezuelae* collected beside a stream at 1400 m elevation by M. D. Tuttle and F. L. Harder, 15 February 1967. Local habitat is described by Handley (1976) under locality name "Cabecera del Caño Culebra"; additional details are provided by Musser and Gardner (1974).
53. **La Mucuy** (locality in Sierra Nevada; 8°38'N, 71°02'W), Edo. Mérida. One specimen of *Ichthyomys hydrobates* collected in a small, clear, rocky-bottomed stream bordered by wet secondary growth at 6960 ft elevation by R. S. Voss, 28 December 1979. The natural vegetation of the valley of the Quebrada La Mucuy is Lower Montane Rain Forest, remnants of which persist on steeper slopes.
54. **Mérida** (city above right bank of Río Chama, between Sierra de la Culata and Sierra Nevada; 8°36'N, 71°08'W), Edo. Mérida. Twenty-seven specimens of *Ichthyomys hydrobates* collected by S. Briceño in the vicinity of Mérida from 1895 to 1909. Eleven of these are labeled "Mérida, asequias" or "asequias de Mérida"; six are labeled "Río Albarregas, Mérida" or "Río Albarregas," and ten are simply labeled "Mérida." Asequias are narrow irrigation canals on the outskirts of the city that distribute water from the nearby Río Albarregas (a tributary of the Río Chama). Recorded elevations of Briceño specimens range from 1600 to 1700 m.
55. **Naiguatá** (village on Caribbean littoral; 10°37'N, 66°44'W), Distrito Federal. Four specimens of *Ichthyomys pittieri* (one examined in this study) collected from concrete canals and water tanks on the forested N slope of the Cordillera de la Costa above Naiguatá at 700 m elevation by J. L. Silva L. and J. A. Valdés L., in 1979 and 1980. Local habitats are described by Voss et al. (1982).
56. **Rancho Grande** (research station in Cordillera de la Costa; 10°22'N, 67°41'W), Edo. Aragua. Three specimens of *Ichthyomys pittieri* collected from a small rainforest stream at 900–1000 m elevation by G. Medina (20 April 1958), R. S. Voss (22 November 1979) and J. Pefaur (November 1980). See Ecology account of *I. pittieri* for descriptions and illustrations of local habitats.
57. **Río Neverí** (stream in eastern highlands; exact coordinates uncertain), Edo. Sucre.

Two specimens (including the holotype) of *Neusticomys venezuelae* trapped beside a rocky-bottomed stream in forested headwaters of Río Neverí about 24 km W of Cumanacoa (10°15'N, 63°55'W) at 2400 ft elevation by G. H. H. Tate, 8–14 March 1925. See Musser and Gardner (1974) for additional information.

## REFERENCES

Allen, J. A.
1894. Cranial variation in *Neotoma micropus* due to growth and individual differentiation. Bull. Am. Mus. Nat. Hist. 6: 233–246.

Ambühl, H.
1959. Die Bedeutung der Strömung als ökologischer Faktor. Schweiz. Z. Hydrol. 21: 133–264.

Anderson, N. H., and J. R. Sedell
1979. Detritus processing by macroinvertebrates in stream ecosystems. Annu. Rev. Entomol. 24: 351–377.

Anthony, H. E.
1921. Preliminary report on Ecuadorean mammals No. 1. Am. Mus. Novitates 20: 6 pp.
1923. Preliminary report on Ecuadorean mammals No. 3. Am. Mus. Novitates 55: 14 pp.
1929. Two genera of rodents from South America. Am. Mus. Novitates 383: 6 pp.
1941. Mammals collected by the Vernay-Cutting Burma expedition. Zool. Ser. Field Mus. Nat. Hist. 27: 37–123.

Arai, S., T. Mori, H. Yoshida, and S. Shiraishi
1985. A note on the Japanese water shrew, *Chimarrogale himalayica platycephala*, from Kyushu. J. Mammal. Soc. Japan 10:193–203.

Arata, A. N.
1964. The anatomy and taxonomic significance of the male accessory reproductive glands of muroid rodents. Bull. Florida State Mus. Biol. Sci. 9: 42 pp.

Arvy, L.
1974. Contribution a la connaissance de l'appariel mammaire chez les rongeurs. Mammalia 38: 108–138.

Atchley, W. R., and D. Anderson
1978. Ratios and the statistical analysis of biological data. Syst. Zool. 27: 71–78.

Atchley, W. R., C. T. Gaskins, and D. Anderson
1976. Statistical properties of ratios. I. Empirical results. Syst. Zool. 25: 137–148.

Bader, R. S.
1965. Heritability of dental characters in the house mouse. Evolution 19: 378–384.

Báez, A. M., and Z. B. de Gasparini
1979. The South American herpetofauna: an evaluation of the fossil record. *In* W. E. Duellman (ed.), The South American herpetofauna: its origin, evolution and dispersal. Monogr. Mus. Nat. Hist. Univ. Kansas 7: 29–54.

Baker, R. H.
1969. Cotton rats of the *Sigmodon fulviventer* group. Misc. Publ. Mus. Nat. Hist. Univ. Kansas 51: 177–232.

Barry, R. E.
1977. Length and absorptive surface area apportionment of segments of the hindgut for eight species of mammals. J. Mammal. 58: 419–420.

Baskin, J. A.
1978. *Bensonomys, Calomys,* and the origin of the phyllotine group of Neotropical cricetines. J. Mammal. 59: 125–135.

Bauchot, R., and H. Stephan
1968. Etude des modifications encéphaliques observées chèz les insectivores adaptés à la recherche de nourriture en milieu aquatique. Mammalia 32: 228–275.

Becht, G.
1953. Comparative biologic-anatomical researches on mastication in some mammals. Proc. Kon. Nederl. Akad. Wetensch.(C), 56: 508–527.

Beddard, F. E.
1902. Observations upon the carpal vibrissae in mammals. Proc. Zool. Soc. London 1902: 127–136.

Beebe, W.
1925. Studies of a tropical jungle. One quarter of a square mile of jungle at Kartabo, British Guiana. Zoologica 6: 1–193.

Bigelow, R. S.
1958. Classification and phylogeny. Syst. Zool. 7: 49–59.

Birney, E. C.
1973. Systematics of three species of woodrats

(genus *Neotoma*) in central North America. Misc. Publ. Mus. Nat. Hist. Univ. Kansas 58: 173 pp.

Bishop, J. E.
1973. Limnology of a small Malayan river, Sungai Gombak (Monographiae Biologicae 22). The Hague: Dr. W. Junk.

Bock, W. J., and C. R. Shear
1972. A staining method for gross dissection of vertebrate muscles. Anat. Anz. 130: 222–227.

Bookstein, F. L.
1978. The measurement of biological shape and shape change (Lecture Notes in Biomathematics 24). New York: Springer-Verlag.

Böttger, K.
1975. Produktionsbiologische Studien an dem zentralafrikanischen Bergbach Kalengo. Arch. Hydrobiol. 75: 1–31.

Bou, J., A. Casinos, and J. Ocaña.
1987. Allometry of the limb long bones of insectivores and rodents. J. Morphol. 192: 113–123.

Brown, J. C.
1971. The description of mammals 1. The external characters of the head. Mammal Rev. 1: 151–168.

Brown, J. C., and D. W. Yalden
1973. The description of mammals 2. Limbs and locomotion of domestic mammals. Mammal Rev. 3: 107–134.

Bryant, P. J., and P. Simpson
1984. Intrinsic and extrinsic control of growth in developing organs. Q. Rev. Biol. 59: 387–415.

Bugge, J.
1970. The contribution of the stapedial artery to the cephalic arterial supply in muroid rodents. Acta Anat. 76: 313–336.

Burnaby, T. P.
1966. Growth-invariant discriminant functions and generalized distances. Biometrics 22: 96–110.

Bursell, E.
1974. Environmental aspects—temperature. *In* M. Rockstein (ed.), The physiology of insects, vol. 2. New York: Academic Press, pp. 1–41.

Burt, W. H., and R. A. Stirton
1961. The mammals of El Salvador. Misc. Publ. Mus. Zool. Univ. Michigan 117: 69 pp.

Cabrera, A.
1961. Catálogo de los mamíferos de América del Sur. Rev. Mus. Argentina Cienc. Nat. "Bernardino Rivadavia" 4(2): 309–732.

Carleton, M. D.
1973. A survey of gross stomach morphology in New World Cricetinae (Rodentia, Muroidea), with comments on functional interpretations. Misc. Publ. Mus. Zool. Univ. Michigan 146: 43 pp.
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.

Carleton, M. D., and R. E. Eshelman
1979. A synopsis of fossil grasshopper mice, genus *Onychomys,* and their relationships 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.

Carter, G. S.
1934. Results of the Cambridge Expedition to British Guiana, 1933. The fresh waters of the rain-forest areas of British Guiana. J. Linnean Soc. London Zool. 39: 147–193.

Cavender, J. A.
1978. Taxonomy with confidence. Math. Biosci. 40: 271–280 [erratum, 44: 308 (1979)].
1981. Tests of phylogenetic hypotheses under generalized models. Math. Biosci. 54: 217–229.

Chapman, F. M.
1926. The distribution of bird-life in Ecuador. Bull. Am. Mus. Nat. Hist. 55: i–xiv, 1–784, folding map.

Choate, J. R.
1970. Systematics and zoogeography of Middle American shrews of the genus *Cryptotis.* Univ. Kansas Publ. Mus. Nat. Hist. 19: 195–317.

Churchfield, S.
1985. The feeding ecology of the European water shrew. Mammal Rev. 15: 13–21.

Clark, F. H.
1941. Correlation and body proportions in mature mice of the genus *Peromyscus.* Genetics 26: 283–300.

Cleall, J. F., G. N. Wilson, and D. S. Garnett
1968. Normal craniofacial skeletal growth of the rat. Am. J. Phys. Anthrop. 29: 225–242.

Cock, A. G.
1966. Genetical aspects of metrical growth and

form in animals. Q. Rev. Biol. 41: 131–190.

Cockerell, T. D. A., L. I. Miller, and M. Printz
1914. The auditory ossicles of American rodents. Bull. Am. Mus. Nat. Hist. 33: 347–380.

Colless, D. M.
1970. The phenogram as an estimate of phylogeny. Syst. Zool. 19: 352–362.

Conaway, C. H.
1952. Life history of the water shrew (*Sorex palustris navigator*). Am. Midl. Nat. 48: 219–248.

Conover, W. J.
1980. Practical nonparametric statistics, 2nd ed. New York: Wiley.

Corbet, P. S.
1964. Temporal patterns of emergence in aquatic insects. Can. Entomol. 96: 264–279.

Costa, R. L., Jr., and W. S. Greaves
1981. Experimentally produced tooth wear facets and the direction of jaw motion. J. Paleontol. 3: 635–638.

Cummins, K. W.
1966. A review of stream ecology with special emphasis on organism-substrate relationships. Spec. Publ. Pymatuning Lab. Field Biol. 4: 2–51.

Cummins, K. W., and M. J. Klug
1979. Feeding ecology of stream invertebrates. Annu. Rev. Ecol. Syst. 10: 147–172.

de Winton, W. E.
1896. On some mammals from Ecuador. Proc. Zool. Soc. London 1906: 507–513.

Dickey, D. R.
1928. Five new mammals of the rodent genera *Sciurus, Orthogeomys, Heteromys,* and *Rheomys* from El Salvador. Proc. Biol. Soc. Washington 41: 7–14.

Dickey, D. R., and A. J. van Rossem
1938. The birds of El Salvador. Field Mus. Nat. Hist. Zool. Ser. 23: 609 pp.

Dieterlen, F.
1983. Zur Systematik, Verbreitung und Ökologie von *Colomys goslingi* Thomas and Wroughton, 1907 (Muridae; Rodentia). Bonn. zool. Beitr. 34: 73–106.

Dieterlen, F., and B. Statzner
1981. The African rodent *Colomys goslingi* Thomas and Wroughton, 1907 (Rodentia: Muridae)—a predator in limnetic ecosystems. Z. Säugetierkd. 46: 369–383.

Dixon, W. J., and F. J. Massey
1969. Introduction to statistical analysis. New York: McGraw-Hill.

Dobson, G. E.
1883. A monograph of the Insectivora, systematic and anatomical. London: John van Voorst.

Dodds, G. S., and F. L. Hisaw
1925. Ecological studies of aquatic insects. IV. Altitudinal range and zonation of mayflies, stoneflies and caddisflies in the Colorado Rockies. Ecology 6: 380–390.

Dorst, J.
1976. Historical factors influencing the richness and diversity of the South American avifauna. Proc. 16th Int. Ornithol. Congr., pp. 17–35.

Dubost, G., and F. Petter
1978. Une espèce nouvelle de "rat-pêcheur" de Guyane française: *Daptomys oyapocki* sp. nov. (Rongeurs, Cricetidae). Mammalia 42: 435–439.

Dukelski, N. M.
1927. External characters in the structure of the feet and their value for classification of voles. J. Mammal. 8: 133–140.

Dunn, R. B.
1958. Growth of the mouse coat, VI. Distribution and number of vibrissae in the house mouse. Australian J. Biol. Sci. 11: 95–105.

Edmunds, G. F., Jr., S. L. Jensen, and L. Berner
1976. Mayflies of North and Central America. Minneapolis: Univ. Minnesota Press.

Eisentraut, M.
1976. Das Gaumenfaltenmuster der Säugetiere und seine Bedeutung für stammesgeschichtliche und taxonomische Untersuchungen. Bonn. zool. Monogr. 8: 214 pp.

Ellerman, J. R.
1941. The families and genera of living rodents, vol. 2. Muridae. London: British Museum (Natural History).

Enders, R. K.
1939. A new rodent of the genus *Rheomys* from Chiriqui. Proc. Acad. Nat. Sci. Philadelphia 90: 295–296.

Engels, H.
1979. Das postnatale Schädelwachstum bei der Hausmaus *Mus musculus* Linné, 1758, und bei zwei verschieden grossen Unterarten der Feldmaus *Microtus arvalis* Pallas, 1779. Gegenbaurs morph. Jahrb., Leipzig 125: 550–571.

Ernest, K. A., and M. A. Mares
1986. Ecology of *Nectomys squamipes,* the Neotropical water rat, in central Brazil: home range, habitat selection, reproduction and behavior. J. Zool. London (A), 210: 599–612.

Estabrook, G. F.
1972. Cladistic methodology: a discussion of the theoretical basis for the induction of evolutionary history. Annu. Rev. Ecol. Syst. 3: 427–456.
1978. Some concepts for the estimation of evolutionary relationships in systematic botany. Syst. Botany 3: 146–158.

Estabrook, G. F., J. G. Strauch, and K. L. Fiala
1977. An application of compatibility analysis to the Blackliths' data on orthopteroid insects. Syst. Zool. 26: 269–276.

Farris, J. S.
1966. Estimation of conservatism of characters by constancy within biological populations. Evolution 20: 587–591.
1969. A successive approximations approach to character weighting. Syst. Zool. 18: 374–385.
1970. Methods for computing Wagner Trees. Syst. Zool. 19: 83–92.

Farris, J. S., A. G. Kluge, and M. J. Eckardt
1970. A numerical approach to phylogenetic systematics. Syst. Zool. 19: 172–191.

Felsenstein, J.
1978a. Cases in which parsimony or compatibility methods will be positively misleading. Syst. Zool. 27: 401–410.
1978b. The number of evolutionary trees. Syst. Zool. 27: 27–33.
1981. A likelihood approach to character weighting and what it tells us about parsimony and compatibility. Biol. J. Linnean Soc. 16: 183–196.
1982. Numerical methods for inferring evolutionary trees. Q. Rev. Biol. 57: 379–404.
1983. Parsimony in systematics: biological and statistical issues. Annu. Rev. Ecol. Syst. 14: 313–333.
1985. Phylogenies and the comparative method. Am. Nat. 125: 1–15.

Fink, W. L., and S. V. Fink
1979. Central Amazonia and its fishes. Comp. Biochem. Physiol. 62A: 13–29.

Fish, F. E.
1982. Function of the compressed tail of surface swimming muskrats (*Ondatra zibethicus*). J. Mammal. 63: 591–597.

Fish, H. S., P. D. Malone, and C. P. Richter
1944. The anatomy of the tongue of the domestic Norway rat, I. The skin of the tongue; the various papillae; their number and distribution. Anat. Rec. 89: 429–440.

Fittkau, E. J.
1964. Remarks on limnology of central Amazon rain-forest streams. Verh. int. Verein. Limnol. 15: 1092–1096.
1967. On the ecology of Amazonian rain-forest streams. Atas do Simpósio sôbre a Biota Amazônica. 3: 97–108.

Gardner, A. L.
1971. Karyotypes of two rodents from Peru, with a description of the highest diploid number recorded for a mammal. Experientia 26: 1088–1089.

Gardner, A. L., and J. L. Patton
1976. Karyotypic variation in oryzomyine rodents (Cricetinae) with comments on chromosomal evolution in the Neotropical cricetine complex. Occas. Pap. Mus. Zool. Louisiana State Univ. 49: 48 pp.

Genoways, H. H., and J. K. Jones, Jr.
1972. Variation and ecology in a local population of the vesper mouse (*Nyctomys sumichrasti*). Occas. Pap. Mus. Texas Tech. Univ. 3: 22 pp.

Genoways, H. H., S. L. Williams, and J. A. Groen
1981. Results of the Alcoa Foundation-Suriname expeditions. V. Noteworthy records of Surinamese mammals. Ann. Carnegie Mus. 450: 319–332.

Goldman, E. A.
1912. New mammals from eastern Panama. Smith. Misc. Collect. 60(2): 18 pp.
1920. Mammals of Panama. Smith. Misc. Collect. 69(5): 309 pp.

Goodwin, G. G.
1959. Descriptions of some new mammals. Am. Mus. Novitates 1967: 8 pp.
1969. Mammals from the state of Oaxaca, Mexico, in the American Museum of Natural History. Bull. Am. Mus. Nat. Hist. 141: 1–270, 40 pl.

Gorniak, G.
1977. Feeding in golden hamsters, *Mesocricetus auratus*. J. Morphol. 154: 427–458.

Gould, E., and J. F. Eisenberg
1966. Notes on the biology of the Tenrecidae. J. Mammal. 47: 660–686.

Gould, S. J., and R. H. Garwood
1969. Levels of integration in mammalian dentitions: an analysis of correlations in *Nesophontes micrus* (Insectivora) and *Oryzomys couesi* (Rodentia). Evolution 23: 276–300.

Greene, E. C.
1935. Anatomy of the rat. Trans. Am. Philos. Soc. new ser. 27: 370 pp.

Grubb, P. J.
1977. Control of forest growth and distribution on wet tropical mountains. Annu. Rev. Ecol. Syst. 8: 83–107.

Gyldenstolpe, N. C. G.
1932. A manual of Neotropical sigmodont rodents. Kungl. Svenska Vetenskapsakad. Handl. ser. 3, 11(3): 164 pp., 18 pls.

Haffer, J.
1970. Geological history and zoogeographic significance of the Urubá region of northwestern Colombia. Caldasia 10: 603–636.
1985. Avian zoogeography of the Neotropical lowlands. *In* P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley (eds.), Neotropical ornithology (Ornithological Monograph 36, American Ornithological Union), pp. 113–145. Lawrence: Allen Press.

Hall, E. R.
1981. The mammals of North America, 2nd ed., 2 vols. New York: Wiley.

Handley, C. O., Jr.
1966. Checklist of the mammals of Panama. *In* R. L. Wenzel and V. J. Tipton (eds.), Ectoparasites of Panama, pp. 753–795. Chicago: Field Museum of Natural History.
1972. Mammalogy in Panama. Bull. Biol. Soc. Washington 2: 217–227.
1976. Mammals of the Smithsonian Venezuelan Project. Brigham Young Univ. Sci. Bull. Biol. Ser. 20(5): 89 pp., fig. 1.

Handley, C. O., Jr., and E. Mondolfi
1963. A new species of fish-eating rat, *Ichthyomys,* from Venezuela (Rodentia, Cricetidae). Acta Biol. Venezuelica 3: 417–419.

Hendy, M. D., and D. Penny
1982. Branch and bound algorithms to determine minimal evolutionary trees. Math. Biosci. 59: 277–290.

Hennig. W.
1966. Phylogenetic systematics. Urbana: Univ. Illinois Press.

Hershkovitz, P.
1944. A systematic review of the Neotropical water rats of the genus *Nectomys* (Cricetinae). Misc. Publ. Mus. Zool. Univ. Michigan 58: 101 pp., folding map.
1962. Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Fieldiana Zool. 46: 524 pp.
1966. Mice, land bridges and Latin American faunal interchange. *In* R. L. Wenzel and V. J. Tipton (eds.), Ectoparasites of Panama, pp. 725–751. Chicago: Field Museum of Natural History.
1972. The Recent mammals of the Neotropical Region: a zoogeographic and ecological review. *In* A. Keast, F. C. Erk and B. Glass (eds.). Evolution, mammals and southern continents, pp. 311–431. Albany: SUNY Press.

Hiiemae, K.
1971. The structure and function of the jaw muscles in the rat (*Rattus norvegicus* L.) III. The mechanics of the muscles. Zool. J. Linnean Soc. 50: 111–132.

Hiiemae, K. M., and G. M. Ardran
1968. A cinefluorographic study of mandibular movement during feeding in the rat (*Rattus norvegicus*). J. Zool. London 154: 139–154.

Hiiemae, K., and W. J. B. Houston
1971. The structure and function of the jaw muscles in the rat (*Rattus norvegicus* L.). I. Their anatomy and internal architecture. Zool. J. Linnean Soc. 50: 75–99.

Hildebrand, M.
1961. Body proportions of didelphid (and some other) marsupials with emphasis on variability. Am. J. Anatomy 109: 239–249.
1978. Insertions and functions of certain flexor muscles in the hindleg of rodents. J. Morphol. 155: 111–122.

Hill, J. E.
1935. The cranial foramina in rodents. J. Mammal. 16: 121–129.

Hoffmeister, D. F.
1951. A taxonomic and evolutionary study of the piñon mouse, *Peromyscus truei.* Illinois Biol. Monogr. 21: i–x, 1–104.

Holdridge, L. R.
1967. Life zone ecology. San José, Costa Rica: Tropical Science Center.

Honacki, J. H., K. E. Kinman, and J. W. Koeppl
1982. Mammal species of the world. Lawrence: Allen Press.

Hooper, E. T.
1947. Notes on Mexican mammals. J. Mammal. 28: 40–57.
1952. A systematic review of the harvest mice (genus *Reithrodontomys*) of Latin America. Misc. Publ. Mus. Zool. Univ. Michigan 77: 255 pp., 9 pls.
1958. The male phallus in mice of the genus *Peromyscus.* Misc. Publ. Mus. Zool. Univ. Michigan 105: 24 pp., 14 pls.
1962. The glans penis in *Sigmodon, Sigmomys,* and *Reithrodon* (Rodentia, Cricetinae). Occas. Pap. Mus. Zool. Univ. Michigan 625: 11 pp.
1968. Habitats and food of amphibious mice of the genus *Rheomys.* J. Mammal. 49: 550–553.
1972. A synopsis of the rodent genus *Sco-*

*tinomys*. Occas. Pap. Mus. Zool. Univ. Michigan 665: 32 pp.

Hooper, E. T., and M. D. Carleton
1976. Reproduction, growth and development in two contiguously allopatric rodent species, genus *Scotinomys*. Misc. Publ. Mus. Zool. Univ. Michigan 151: 52 pp.

Hooper, E. T., and B. S. Hart
1962. A synopsis of Recent North American microtine rodents. Misc. Publ. Mus. Zool. Univ. Michigan 120: 68 pp.

Hooper, E. T., and G. G. Musser
1964. The glans penis in Neotropical cricetines (Muridae) with comments on classification of muroid rodents. Misc. Publ. Mus. Zool. Univ. Michigan 123: 57 pp.

Hora, S. L.
1930. Ecology, bionomics and evolution of the torrential fauna, with special reference to the organs of attachment. Philos. Trans. R. Soc. B218: 171–282.

Horner, B. E., J. M. Taylor, and H. A. Padykula
1965. Food habits and gastric morphology of the grasshopper mouse. J. Mammal. 45: 513–535.

Howell, A. B.
1926. Anatomy of the woodrat (Monogr. Am. Soc. Mammal. No. 1). Baltimore: Williams and Wilkins.
1930. Aquatic Mammals. Baltimore: Charles C Thomas.

Humphrey, S. R., and F. J. Bonaccorso
1979. Population and community ecology. *In* R. J. Baker, J. K. Jones, and D. C. Carter (eds.), Biology of bats of the New World family Phyllostomatidae, pt. III. Spec. Publ. Mus. Texas Tech. Univ. 16: 409–441.

Humphries, J. M., F. L. Bookstein, B. Chernoff, G. R. Smith, R. L. Elder, and S. G. Poss
1981. Multivariate discrimination by shape in relation to size. Syst. Zool. 30: 291–308.

Husson, A. M.
1978. The mammals of Suriname. Leiden: E. J. Brill.

Hutterer, R.
1985. Anatomical adaptations of shrews. Mammal Rev. 15: 43–55.

Hutterer, R., and T. Hürter
1981. Adaptive Haarstrukturen bei Wasserspitzmäusen. Z. Säugetierkd. 46: 1–11.

Hynes, H. B. N.
1961. The invertebrate fauna of a Welsh mountain stream. Arch. Hydrobiol. 57: 344–388.
1970. The ecology of running waters. Toronto: University of Toronto Press.

Illies, J.
1964. The invertebrate fauna of the Huallaga, a Peruvian tributary of the Amazon River, from the sources down to Tingo Maria. Verh. int. Verein. Limnol. 15: 1077–1083.

Jacobs, L. L., and E. H. Lindsay
1984. Holarctic radiation of Neogene muroid rodents and the origin of South American cricetids. J. Vertebr. Paleontol. 4: 265–272.

Jameson, E. W., Jr.
1952. Food of deermice, *Peromyscus maniculatus* and *P. boylei*, in the northern Sierra Nevada, California. J. Mammal. 33: 50–60.

Janzen, D. H.
1967. Why mountain passes are higher in the tropics. Am. Nat. 101: 233–249.

Janzen, D. H., M. Ataroff, M. Fariñas, S. Reyes, N. Rincon, A. Soler, P. Soriano, and M. Vera
1976. Changes in the arthropod community along an elevational transect in the Venezuelan Andes. Biotropica 8: 193–203.

Johnson, A. M.
1976. The climate of Peru, Bolivia and Ecuador. *In* W. Schwerdtfeger (ed.), World survey of climatology, vol. 12, pp. 147–218. New York: Elsevier.

Jolicoeur, P.
1963. The multivariate generalization of the allometry equation. Biometrics 19: 497–499.

Kamler, E.
1967. Distribution of Plecoptera and Ephemeroptera in relation to altitude above mean sea level and current speed in mountain waters. Polskie Arch. Hydrobiol. 14(2): 29–42.

Kay, R. F., and K. M. Hiiemae
1974. Jaw movement and tooth use in Recent and fossil primates. Am. J. Phys. Anthrop. 40: 227–256.

Kesner, M. H.
1980. Functional morphology of the masticatory musculature of the rodent subfamily Microtinae. J. Morphol. 165: 205–222.

King, J. A., and B. E. Eleftheriou
1960. Differential growth in the skulls of two subspecies of deermice. Growth 24: 179–192.

Kingdon, J.
1974. East African mammals, vol. 2, part A (insectivores and bats). London: Academic Press.

Klingener, D.
1964. The comparative myology of four dipo-

doid rodents (genera *Zapus, Napeozapus, Sicista,* and *Jaculus*). Misc. Publ. Mus. Zool. Univ. Michigan 124: 100 pp.

1968. Anatomy. *In* J. A. King (ed.), Biology of *Peromyscus* (Rodentia). Spec. Publ. No. 2, Am. Soc. Mammal., pp. 127–147.

Kluge, A. G., and J. S. Farris

1969. Quantitative phyletics and the evolution of anurans. Syst. Zool. 18: 1–32.

Koopman, K. F.

1982. Biogeography of the bats of South America. *In* M. A. Mares and H. H. Genoways (eds.), Mammalian biology in South America. Spec. Publ. Ser. Pymatuning Lab. Ecol. Univ. Pittsburgh 6, pp. 273–302.

Krause, D. W.

1982. Jaw movement, dental function, and diet in the Paleocene multituberculate *Ptilodus.* Paleobiology 8: 265–281.

Kuhn, H. J.

1964. Zur Kenntnis von *Micropotamogale lamottei* Heim de Balsac, 1954. Z. Säugetierkd. 29: 152–173.

Kutuzov, H., and H. Sicher

1952. Anatomy and function of the palate in the white rat. Anat. Rec. 114: 67–84.

Landry, S. O.

1958. The function of the entepicondylar foramen in mammals. Am. Midl. Nat. 60: 100–112.

1970. The Rodentia as omnivores. Q. Rev. Biol. 45: 351–372.

Latimer, H. B., and R. B. Riley

1934. Measurements of the skull and of some of the long bones of the muskrat *Ondatra zibethica cinnamominus.* J. Morphol. 56: 203–212.

Lay, D. M.

1972. The anatomy, physiology, functional significance and evolution of specialized hearing organs of gerbilline rodents. J. Morphol. 138: 41–120.

Layne, J. N.

1968. Ontogeny. *In* J. A. King (ed.), Biology of *Peromyscus* (Rodentia). Spec. Publ. No. 2, Am. Soc. Mammal., pp. 148–253.

Lemire, M.

1966. Particularites de l'appareil masticateur d'un rongeur insectivore *Deomys ferrugineus* (Cricetidae, Dendromurinae). Mammalia 30: 454–494.

Leopold, L. B., M. G. Wolman, and J. P. Miller

1964. Fluvial processes in geomorphology. San Francisco: Freeman.

Lidicker, W. Z., Jr.

1968. A phylogeny of New Guinea rodents based on phallic morphology. J. Mammal. 49: 609–643.

1987. The conilurine rodent radiation of Australia, analyzed on the basis of phallic morphology. J. Mammal. 68: 617–641.

Ling, J. K.

1977. Vibrissae of marine mammals. *In* R. J. Harrison (ed.), Functional anatomy of marine mammals, vol. 3. New York: Academic Press, pp. 387–415.

Linzey, A. V., and J. N. Layne

1974. Comparative morphology of spermatozoa of the rodent genus *Peromyscus* (Muridae). Am. Mus. Novitates 2532: 20 pp.

Lynch, J. D.

1979. The amphibians of the lowland tropical forests. *In* W. E. Duellman (ed.), The South American herpetofauna: its origin, evolution, and dispersal. Monogr. Mus. Nat. Hist. Univ. Kansas 7: pp. 189–216.

Macan, T. T.

1958. The temperature of a small stony stream. Hydrobiologia 12: 89–106.

1962. Biotic factors in running water. Schweiz. Z. Hydrol. 24: 386–407.

Malzay, P.

1965. Un mammifere aquatique de Madagascar: le limnogale. Mammalia 29: 400–411.

Mani, M. S.

1962. Introduction to high altitude entomology. London: Methuen.

1968. Ecology and biogeography of high altitude insects (Series Entomologica 4). The Hague: Dr. W. Junk.

Marshall, L. G.

1978. *Chironectes minimus.* Mammalian Species 109: 6 pp.

1979. A model for paleobiogeography of South American cricetine rodents. Paleobiology 5: 126–132.

Marshall, L. G., R. F. Butler, R. E. Drake, G. H. Curtis, and R. H. Tedford

1979. Calibration of the great American interchange. Science 204: 272–279.

Meacham, C. A.

1980. Phylogeny of the Berberidaceae with an evaluation of classifications. Syst. Botany 5: 149–172.

1981a. A manual method for character compatibility analysis. Taxon 30: 591–600.

1981b. A probability measure for character compatibility. Math. Biosci. 57: 1–18.

1984a. Evaluating characters by character compatibility analysis. *In* T. Duncan and T. F. Stuessy (eds.), Cladistics: perspectives on the reconstruction of evolutionary history, pp. 152–165. New York: Columbia University Press.

1984b. The role of hypothesized direction of characters in the estimation of evolutionary history. Taxon 33: 26–38.

Meacham, C. A., and G. F. Estabrook
1985. Compatibility methods in systematics. Annu. Rev. Ecol. Syst. 16: 431–446.

Menzies, J. I., and E. Dennis
1979. Handbook of New Guinea rodents. Wau Ecology Institute Handbook No. 6: 68 pp.

Merriam, C. H.
1895. Monographic revision of the pocket gophers, family Geomyidae. N. Am. Fauna 8: 258 pp., 4 maps.

Merritt, R. W., K. W. Cummins, and T. M. Burton
1984. The role of aquatic insects in the processing and cycling of nutrients. *In* V. H. Resh and D. M. Rosenberg (eds.), The ecology of aquatic insects, pp. 134–163. New York: Praeger.

Miller, L. M., and S. Anderson
1977. Bodily proportions of Uruguayan myomorph rodents. Am. Mus. Novitates 2615: 10 pp.

Minshall, G. W.
1984. Aquatic insect-substratum relationships. *In* V. H. Resh and D. M. Rosenberg (eds.), The ecology of aquatic insects, pp. 358–400. New York: Praeger.

Misonne, X.
1969. African and Indo-Australian Muridae: Evolutionary trends. Mus. Roy. l'Afrique Cent., Tervuren, Zool. 172: 219 pp., 27 pls.

Mondolfi, E., and G. Medina P.
1957. Contribución al conocimiento del "perrito de agua" (*Chironectes minimus* Zimmermann). Mem. Soc. Cienc. Nat. La Salle 17: 141–155.

Moore, W. J.
1966. Skull growth in the albino rat (*Rattus norvegicus*). J. Zool. London 149: 137–144.
1981. The mammalian skull. Cambridge: Cambridge University Press.

Morrison, D. F.
1976. Multivariate statistical methods, 2nd ed. New York: McGraw-Hill.

Moss, M. L.
1954. Growth of the calvaria in the rat. The determination of osseous morphology. Am. J. Anat. 94: 333–362.
1972. Regulation of skeletal growth. *In* R. J. Goss (ed.), Regulation of organ and tissue growth, pp. 127–142. New York: Academic Press.

Moss, M. L., and M. J. Baer
1956. Differential growth of the rat skull. Growth 20: 107–120.

Moyers, R. E., and F. L. Bookstein
1979. The inappropriateness of conventional cephalometrics. Am. J. Orthod. 75: 599–617.

Musser, G. G.
1964. Notes on geographic distribution, habitat, and taxonomy of some Mexican mammals. Occas. Pap. Mus. Zool. Univ. Michigan 636: 22 pp.
1982. Results of the Archbold Expeditions. No. 110. *Crunomys* and the small-bodied shrew rats native to the Philippine Islands and Sulawesi (Celebes). Bull. Am. Mus. Nat. Hist. 174: 1–95.

Musser, G. G., and A. L. Gardner
1974. A new species of the ichthyomyine *Daptomys* from Peru. Am. Mus. Novitates 2537: 23 pp.

Musser, G. G., and E. Piik
1982. A new species of *Hydromys* from western New Guinea. Zool. Meded. 56: 153–167.

Myers, C. W.
1969. The ecological geography of cloud forest in Panama. Am. Mus. Novitates 2396: 52 pp.

Nielson, A.
1950. The torrential invertebrate fauna. Oikos 2: 177–196.

Niethammer, V. G.
1970. Beobachtungen am Pyrenäen-Desman, *Galemys pyrenaica*. Bonn. zool. Beitr. 21: 157–182.

Nord, S. G.
1967. Somatotopic organization in the spinal trigeminal nucleus, the dorsal column nuclei and related structures in the rat. J. Comp. Neurol. 130: 343–356.

Nygren, W. E.
1950. Bolivar geosyncline of northwestern South America. Bull. Am. Assoc. Petrol. Geol. 34: 1998–2006.

Packard, R. L.
1960. Speciation and evolution of the pygmy mice, genus *Baiomys*. Univ. Kansas Publ. Mus. Nat. Hist. 9: 579–670.

Parsons, F. G.
1894. On the myology of the sciuromorphine and hystricomorphine rodents. Proc. Zool. Soc. London 1894: 251–295.
1896. Myology of rodents. II. An account of the myology of the Myomorpha, to-

gether with a comparison of the muscles of the various suborders of the rodents. Proc. Zool. Soc. London 1896: 159–192.

Patterson, B., and R. Pascual
1972. The fossil mammal fauna of South America. *In* A. Keast, F. C. Erk and B. Glass (eds.), Evolution, mammals and southern continents, pp. 247–309. Albany: SUNY Press.

Paynter, R. A. Jr., and M. A. Traylor Jr.
1977. Ornithological gazetteer of Ecuador. Cambridge, Mass.: Museum of Comparative Zoology, Harvard University.
1981. Ornithological gazetteer of Colombia. Cambridge, Mass.: Museum of Comparative Zoology, Harvard University.

Pearson, K.
1897. On a form of spurious correlation which may arise when indices are used in the measurement of organs. Proc. Roy. Soc. London 60: 489–502.

Pearson, O. P.
1958. A taxonomic revision of the rodent genus *Phyllotis*. Univ. Calif. Publ. Zool. 56: 391–496 + 13 pl.

Perrin, M. R., and B. A. Curtis
1980. Comparative morphology of the digestive system of 19 species of southern African myomorph rodents in relation to diet and evolution. South African J. Zool. 15: 22–33.

Peyre, A.
1956. Ecologie et biogeographie du desman (*Galemys pyrenaicus* G.) dans les Pyrénées Françaises. Mammalia 20: 405–418.

Pocock, R. I.
1914. On the facial vibrissae of Mammalia. Proc. Zool. Soc. London 1914: 889–912.
1921. On the external characters and classification of the Mustelidae. Proc. Zool. Soc. London 1921: 803–837.

Quay, W. B.
1954. The anatomy of the diastemal palate in microtine rodents. Misc. Publ. Mus. Zool. Univ. Michigan 86: 41 pp., 4 pls.

Rehkämper, G.
1981. Vergleichende Architektonik des Neocortex der Insectivora. Z. zool. Syst. Evolutionsforsch. 19: 233–263.

Reig, O. A.
1977. A proposed unified nomenclature for the enamelled components of the molar teeth of the Cricetidae (Rodentia). J. Zool. London 181: 227–241.
1978. Roedores cricétidos del Plioceno superior de la Provincia de Buenos Aires (Argentina). Publ. Mus. Mun. Cienc. Nat. Mar Plata "Lorenzo Scaglia" 2: 164–190.
1980. A new fossil genus of South American cricetid rodent allied to *Wiedomys*, with an assessment of the Sigmodontinae. J. Zool. London 192: 257–281.
1984. Distribuição geográfica e história evolutiva dos roedores muroideos sulamericanos (Cricetidae: Sigmodontinae). Rev. Brasil. Genet. 7: 333–365.

Rensberger, J. M.
1973. An occlusion model for mastication and dental wear in herbivorous mammals. J. Paleontol. 47: 515–528.

Repenning, C. A.
1967. Subfamilies and genera of the Soricidae. Geol. Surv. Prof. Pap. 565: iv + 74 pp.
1968. Mandibular musculature and the origin of the subfamily Arvicolinae. Acta Zool. Cracoviensia 13: 1–72.

Rinker, G. C.
1954. The comparative myology of the mammalian genera *Sigmodon, Oryzomys, Neotoma* and *Peromyscus* (Cricetinae), with remarks on their intergeneric relationships. Misc. Publ. Mus. Zool. Univ. Michigan 83: 124 pp.
1963. A comparative myological study of three subgenera of *Peromyscus*. Occas. Pap. Mus. Zool. Univ. Michigan 632: 18 pp.

Risnes, S.
1973. Mandibular movement capacity in the rat. Scand. J. Dent. Res. 81: 170–173.

Roberts, T. R.
1972. Ecology of fishes in the Amazon and Congo basins. Bull. Mus. Comp. Zool. 143: 117–147.

Rohlf, F. J.
1982. Consensus indices for comparing classifications. Math. Biosci. 59: 131–144.

Romankowowa, A.
1955. On the morphology of the hand of the mouse as a grasping organ. Zoologica Poloniae 6: 71–79.
1963. Comparative study of the structure of the os calcaneum in insectivores and rodents. Acta Theriol. 7: 91–126.

Ryan, J. M.
1986. Comparative morphology and evolution of cheek pouches in rodents. J. Morphol. 190: 27–41.

Ryder, J. A.
1877. The significance of the diameters of the incisors in rodents. Proc. Acad. Nat. Sci., Philadelphia 1877: 314–318.

Savage, D. E.
1951. A Miocene phyllostomatid bat from Colombia, South America. Univ. Calif.

Pub., Bull. Dept. Geol. Sci. 28: 357–366.

Savage. R. J. G.
1957. The anatomy of *Potamotherium* an Oligocene lutrine. Proc. Zool. Soc. London 129: 151–244.

Schmidly, D. J.
1972. Geographic variation in the white-ankled mouse, *Peromyscus pectoralis*. Southwestern Naturalist 17: 113–138.

Sharma, D. R., and S. Sivaram
1959. On the hyoid region of the Indian gerbils. Mammalia 23: 149–167.

Sibley, C. G., and J. E. Ahlquist
1985. Phylogeny and classification of New World suboscine passerine birds (Passeriformes: Oligomyodi: Tyrannides). *In* P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley (eds.), Neotropical ornithology (Ornithological Monograph 36, American Ornithological Union), pp. 396–428. Lawrence: Allen Press.

Simpson, G. G.
1950. History of the fauna of Latin America. Am. Sci. 38: 361–389.

Smith, J. M., and R. J. G. Savage
1959. The mechanics of mammalian jaws. School Sci. Rev. 40: 289–301.

Smith, K., and M. E. Lewis
1975. Environmental influences on the temperature of a small upland stream. Oikos 26: 228–236.

Sonntag, C. F.
1924. The comparative anatomy of the tongues of the Mammalia X. Rodentia. Proc. Zool. Soc. London 1924: 725–741.

Sprague, J. M.
1941. A study of the hyoid apparatus of the Cricetinae. J. Mammal. 22: 296–310.
1942. The hyoid apparatus of *Neotoma*. J. Mammal. 23: 405–411.

Stains, H. J.
1959. Use of the calcaneum in studies of taxonomy and food habits. J. Mammal. 40: 392–401.

Starrett, A., and G. F. Fisler
1970. Aquatic adaptations of the water mouse, *Rheomys underwoodi*. Los Angeles County Mus. Contrib. Sci. 182: 14 pp.

Statzner, B.
1976. Die Köcherfliegen-Emergenz (Trichoptera, Insecta) aus dem zentralafrikanischen Bergback Kalengo. Arch. Hydrobiol. 78: 102–137.

Stephan, H., and F. Dieterlen
1982. Relative brain size in Muridae with special reference to *Colomys goslingi*. Z. Säugetierkd. 47: 38–47.

Stephan, H., and H. J. Kuhn
1982. The brain of *Micropotamogale lamottei* Heim de Balsac, 1954. Z. Säugetierkd. 47: 129–142.

Stephens, L., and M. A. Traylor, Jr.
1983. Ornithological gazetteer of Peru. Cambridge, Massachusetts: Museum of Comparative Zoology, Harvard University.

Stirton, R. A.
1944. Tropical mammal trapping I. The water mouse *Rheomys*. J. Mammal. 25: 337–343.
1953. Vertebrate paleontology and continental stratigraphy in Colombia. Bull. Geol. Soc. Am. 64: 603–622.

Stout, J., and J. Vandermeer
1975. Comparison of species richness for stream-inhabiting insects in tropical and mid-latitude streams. Am. Nat. 109: 263–280.

Strauss, R. E., and F. L. Bookstein
1982. The truss: body form reconstruction in morphometrics. Syst. Zool. 31: 113–135.

Sweeney, B. W.
1984. Factors influencing life-history patterns of aquatic insects. *In* V. H. Resh and D. M. Rosenberg (eds.), The ecology of aquatic insects, pp. 56–100. New York: Praeger.

Tarasoff, F. J.
1972. Comparative aspects of the hind limbs of the river otter, sea otter and seals. *In* R. J. Harrison (ed.), Functional anatomy of marine mammals 1: 333–360. New York: Academic Press.

Tate, G. H. H.
1931. Random observations on habits of South American mammals. J. Mammal. 12: 248–256.
1939. Mammals of the Guiana region. Bull. Am. Mus. Nat. Hist. 76: 151–229.

Taylor, A. C., and E. O. Butcher
1951. The regulation of eruption rate in the incisor teeth of the white rat. J. Exp. Zool. 117: 165–188.

Tesh, R. B.
1970. Observations on the natural history of *Diplomys darlingi*. J. Mammal. 51: 197–199.

Thomas, O.
1893. On some mammals from central Peru. Proc. Zool. Soc. London 23: 333–341, 2 pl.
1897. Descriptions of four new South Amer-

ican mammals. Ann. Mag. Nat. Hist. 6(20): 218–221.
1905. Suggestions for the nomenclature of the cranial length measurements and of the cheek-teeth of mammals. Proc. Biol. Soc. Washington 18: 191–196.
1906a. A new aquatic genus of Muridae discovered by consul L. Soderström in Ecuador. Ann. Mag. Nat. Hist. 7(17): 86–88.
1906b. A third genus of the *Ichthyomys* group. Ann. Mag. Nat. Hist. 7(17): 421–423.
1919. The method of taking the incisive index in rodents. Ann. Mag. Nat. Hist. 9(4): 289–290.
1924a. On a new fish-eating rat from Bogota. Ann. Mag. Nat. Hist. 9(13): 164–165.
1924b. A new fish-eating rat from Ecuador. Ann. Mag. Nat. Hist. 9(13): 541–542.

Thorington, R. W., Jr.
1972. Proportions and allometry in the gray squirrel, *Sciurus carolinensis*. Nemouria, Occas. Pap. Delaware Mus. Nat. Hist. 8: 17 pp.

Tullberg, T.
1899. Ueber das System der Nagetiere. Nova Acta Reg. Soc. Upsaliensis, ser. 3, 18: i–v, 1–514, Al–18 + 57 pls.

Turnbull, W. P.
1970. Mammalian masticatory apparatus. Fieldiana (Geology) 18: 149–356.

van der Klaauw, C. J.
1931. The auditory bulla in some fossil mammals with a general introduction to this region of the skull. Bull. Am. Mus. Nat. Hist. 62: 352 pp.

Van Deusen, H. M.
n.d. *Crossomys moncktoni*. Unpublished manuscript summarizing field information and museum research. On file in Dept. of Mammalogy, American Museum of Natural History.

Van Valen, L.
1962. Growth fields in the dentition of *Peromyscus*. Evolution 16: 272–277.

Vilmann, H., and M. L. Moss
1979. Studies on orthocephalization. 2. Flexions of the rat head in the period between 14 and 60 days after gestation. Gegenbaurs morphol. Jahrb., Leipzig 125: 572–582.

Vorontsov, N. N.
1959. The system of hamster (Cricetinae) in the sphere of the world fauna and their phylogenetic relations (in Russian). Biul. Mosk. Obsh. Isp. Prir. Otd. Biol. 64: 134–137.
1979. Evolution of the alimentary system in myomorph rodents. New Delhi: Indian National Science Documentation Centre (published for the Smithsonian Institution and NSF).

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. Publ. Mus. Zool. Univ. Michigan 159: 41 pp.

Voss, R. S., J. L. Silva L., and J. A. Valdes L.
1982. Feeding behavior and diets of Neotropical water rats, genus *Ichthyomys* Thomas, 1893. Z. Säugetierk. 47: 364–369.

Vuilleumier, F., and D. Ewert
1978. The distribution of birds in Venezuelan paramos. Bull. Am. Mus. Nat. Hist. 162: 47–90.

Wagner, H. O.
1961. Die Nagetiere einer Gebirgsabdachung in Südmexiko und ihre Beziehungen zur Umwelt. Zool. Jahrb. Syst. 89: 177–242.

Wagner, J. A.
1843. Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen von Dr. Johann Christian Daniel von Schreber. Supplementenband 3: 614 pp. Erlangen (Germany).

Wahlert, J. H.
1974. The cranial foramina of protrogomorphous rodents; an anatomical and phylogenetic study. Bull. Mus. Comp. Zool. Harvard 146: 363–410.
1983. Relationships of the Florentiamyidae (Rodentia, Geomyoidea) based on cranial and dental morphology. Am. Mus. Novitates 2769: 23 pp.
1985. Cranial foramina of rodents. *In* W. P. Luckett and J.-L. Hartenberger (eds.), Evolutionary relationships among rodents, a multidisciplinary analysis, pp. 311–332. New York and London: Plenum Press.

Waite, P. M. E.
1973a. Somatotopic organization of vibrissal responses in the ventrobasal complex of the rat thalamus. J. Physiol. London 228: 527–540.
1973b. The responses of cells in the rat thalamus to mechanical movements of whiskers. J. Physiol. London 228: 541–561.

Ward, J. V., and J. A. Stanford
1982. Thermal responses in the evolutionary ecology of aquatic insects. Annu. Rev. Entomol. 27: 97–117.

Weijs, W. A.
1973. Morphology of the muscles of mastication in the albino rat, *Rattus nor-*

*vegicus*. Acta Morph. Neerl.-Scand. 11: 321–340.
1975. Mandibular movements of the albino rat during feeding. J. Morphol. 145: 107–124.
1980. Biomechanical models and the analysis of form: a study of the mammalian masticatory apparatus. Am. Zool. 20: 707–719.

Weijs, W. A., and R. Dantuma
1975. Electromyography and mechanics of mastication in the albino rat. J. Morphol. 146: 1–34.
1981. Functional anatomy of the masticatory apparatus in the rabbit (*Oryctolagus cunniculus* L.). Netherl. J. Zool. 31: 99–147.

Welker, C.
1976. Receptive fields of barrels in the somatosensory neocortex of the rat. J. Comp. Neurol. 166: 173–189.

Wernstedt, F. L.
1972. World climatic data. Lemont, Pennsylvania: Climatic Data Press.

Williams, T. R.
1966. Species succession in the river fauna of Mount Elgon, Uganda. J. Anim. Ecol. 35: 21P–22P.

Wilson, D. E.
1983. Checklist of mammals. *In* D. H. Janzen (ed.), Costa Rican natural history. Chicago: University of Chicago Press, pp. 443–447.

Wineski, L. E.
1985. Facial morphology and vibrissal movement in the golden hamster. J. Morphol. 183: 199–217.

Winge, H.
1891. *Habrothrix hydrobates* n. sp. en Vandrotte fra Venezuela. Vidensk. Medd. naturh. Foren. Kjobenhavn 5 (3): 20–27, 1 pl.
1941. The interrelationships of the mammalian genera, vol. 2 (translated from the Danish by E. Deichmann and G. M. Allen). Copenhagen: C. A. Reitzels.

Woods, C. A.
1972. Comparative myology of jaw, hyoid and pectoral appendicular regions of New and Old World histricomorph rodents. Bull. Am. Mus. Nat. Hist. 147: 115–198.

Woolsey, T. A.
1978. Some anatomical bases of cortical somatotopic organization. Brain Behav. Evol. 15: 325–371.

Woolsey, T. A., and H. Van der Loos
1970. The structural organization of layer IV in the somatosensory region (SI) in mouse cerebral cortex. Brain Res. 17: 205–242.

Wright, S.
1954. The interpretation of multivariate systems. *In* O. Kempthorne, T. A. Bancroft, J. W. Gowen, and J. L. Lush (eds.), Statistics and mathematics in biology, pp. 11–33. Ames: Iowa State College Press.
1968. Evolution and the genetics of populations, vol. 1. Genetic and biometric foundations. Chicago: University of Chicago Press.

Yablokov, A. V.
1974. Variability of mammals. New Delhi: Amerind Publishing Co. (for the Smithsonian Institution).

Yang, G., K. Manoharan, and A. K. Young
1969. Influence and degradation of dietary cellulose in caecum of rats. J. Nutr. 97: 260–264.

Zeman, W., and J. R. M. Innes
1963. Cragie's neuroanatomy of the rat. London: Academic Press.

Zucker, E., and W. I. Welker
1969. Coding of somatic sensory input by vibrissal neurons in the rat trigeminal ganglion. Brain Res. 12: 138–156.

Zwick, P.
1976. *Neoperla* (Plecoptera, Perlidae) emerging from a mountain stream in Central Africa. Int. Revue ges. Hydrobiol. 61: 683–697.

# BULLETIN OF
# THE AMERICAN MUSEUM
# OF NATURAL HISTORY

## VOLUME 188
## 1988

PUBLISHED BY ORDER OF THE TRUSTEES
NEW YORK : 1988

Edited by
BRENDA JONES

# CONTENTS OF VOLUME 188