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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 72

FAUNAL RELATIONSHIPS OF RECENT NORTH AMERICAN RODENTS

BY
EMMET T. HOOPER

ANN ARBOR
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CONTENTS

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INTRODUCTION

THE systematic zoologist early recognized the simple facts that, in animal distribution, each species has a characteristic geographic range, which may be large or small, and that, notwithstanding the variation among species in extent of distributional limitation, many species coincide in range, so that a group of species may be recognized as constituting a distributional category. Such categories represent groups of diverse taxonomic levels and geographic extents; in general, higher levels—genera and families—characterize realms or regions and continents, and lower taxonomic levels are characteristic of faunal areas and districts.

The larger distributional categories of most vertebrate animals are now rather well known. For that reason investigations aiming merely at defining the faunal composition of such distributional units are sterile as procedures for yielding new and significant information, unless they are based on newly collected ecological data.

The present study is a comparison of the major faunal assemblages of Recent rodents in the world, especially in regard to the affinities of North American rodents. The data on which it is based are available in several published reports. There is nothing new, other than the form of treatment for this particular group of mammals—the order Rodentia. The aim has been to bring together in condensed form certain data on the occurrences of families and genera of present-day rodents, to point out the amount of endemism on the generic and familial levels, and to indicate some affinities among the rodent faunas of the continents and other faunal regions. The order Rodentia is well suited for such a study because it is large and widely distributed. Three hundred and thirty-eight genera, representing thirty-two families, are recognized. In number of kinds and individuals rodents constitute a major fraction of the mammals of the world. They are native to all the principal continents and to most of the continental islands.

MATERIALS AND METHODS

The classification of mammals used is mainly that prepared by Simpson (1945) with a few emendations. The family Bathyergidae is placed in a separate series, Bathyergomorpha (Ellerman, 1940, 1941); Simpson listed it as ? Histrichomorpha, *incertae sedis*. (For present purposes it is unimportant whether the large subdivisions of the order Rodentia be termed series or suborders.) The families Anomaluridae and Pedetidae are in-

cluded in the series Myomorpha instead of ? Sciuromorpha, *incertae sedis,* as listed and the Ctenodactylidae in Myomorpha instead of ? Hystrichomorpha or ? Myomorpha, *incertae sedis,* although their position there remains doubtful. The name *Ammomys* is replaced by *Mesembriomys* (Muridae), see Ellerman (1941: 33); *Scarturus* is treated as a synonym of *Allactaga* (Dipodidae); *Acanthion* is considered a subgenus of *Hystrix* (Hystricidae); and *Stictomys* is regarded as a subgenus of *Cuniculus* (Dasyproctidae). *Tachyoryctes* is treated as a genus of the Cricetidae instead of the Rhizomyidae. *Platygeomys* is placed in the synonymy of *Cratogeomys* (Geomyidae), following Hooper (1946). *Hyosciurus* Tate and Archibald (Sciuridae), *Hylenomys* Thomas (Muridae), and *Melasmothrix* Miller and Hollister (Muridae), all omitted by Simpson, are listed as full genera.

The data on distribution of each genus are taken from Ellerman (1940, 1941), modified as required by the different taxonomic arrangement followed here or by certain facts of distribution (for some American genera) not available to Ellerman. Except for the southern limit of the Nearctic and the northern boundary of the Neotropical, the geographical limits of the six faunal regions are as he outlined them. The Palearctic region contains the land in the Old World north of the Yangtze River in eastern China, and, to the west, that roughly north of latitude 30 degrees north, through India, Iran, Iraq, and northern Africa. The African region includes all of Africa except the coastal part north of 30 degrees north latitude, Arabia, and Madagascar. The Indomalayan region consists of the remainder of the mainland of Asia south of the Palearctic region, all of the adjacent islands, and the islands of the East Indies except New Guinea, Australia, and the adjoining islands. The Australian region comprises the islands of New Guinea, the Moluccas, New Britain, the Solomons, Australia, and Tasmania. The limits of the Nearctic and Neotropical regions differ from those given by Ellerman. The Nearctic region includes all of North America north of the Central American countries, and the Neotropical region consists of Central America and South America.

Ellerman, following Flower and Lydecker (1891), included Mexico in the Neotropical region. When an attempt is made to establish on a continuous land mass definite geographical limits to two or more faunas, each one of which has its own range determined by an individual set of environmental factors, the faunal limits set must obviously be to a certain extent arbitrary. A faunal region, like other faunal categories, is a concept and as such is limited by definition. The defined limits should conform as closely as possible, however, to the range limits of most of the forms believed to constitute a fauna and to the approximate limits of the specific

environmental conditions with which the forms are associated. On both counts the Mexico–United States boundary is, for rodent distributions, a less satisfactory artificial limit beween the Neotropical and Nearctic regions, if only two regions are considered for the New World, than is a line across the Isthmus of Tehuantepec or at the Mexico–Central America boundary. The mountains and plateaus of Mexico, which make up the greater part of the country, are inhabited principally by boreal and sonoran kinds whose affinities are less with the lowland rodent fauna of Panama or Colombia than they are with the rodents in the United States. For the distribution of tropical and temperate rodents and their environments, the Mexico–Central America boundary is nearer the center of the transition band between the Nearctic and Neotropical regions than is the northern limit of Mexico, and for that reason is employed here to delimit the two regions. The Isthmus of Tehuantepec would be an even better boundary, but the available data on rodent distributions are based on political, rather than physiographic, divisions. The continent of Europe, as here understood, consists of all land in the Old World north of Africa and west of the Urals and Asia Minor. Australia includes that continent and the adjacent islands of Tasmania, New Guinea, the Solomons, New Britain, and the Moluccas. North America and South America are delimited at the Panama–Colombia boundary. The West Indies are included with North America.

The basic data for the present investigation are primarily the distributions of taxonomic units at the present time level. From these it is possible to determine patterns of distribution on a faunal or an areal basis, to compare each of the faunal or areal segments for amount and kind of similarity and dissimilarity of the component taxonomic units, to obtain information regarding centers of differentiation and dispersal of the units, and, with this and the available paleontological data, to postulate past movements of segments of the total fauna.

The occurrence on each continent and in each of the major faunal regions of the genera and, concomitantly, the families of Recent rodents is noted in Table I. Only genera and families are used, since the primary object here is to compare the faunas of large land masses. The familial and generic levels are most useful for that purpose. Categories higher than families are too inclusive to show the desired differences between faunas of two regions, and taxonomic groups below the genus are too narrow. Most of the lower categories are restricted to one continent or faunal region, and as a consequence little of the requisite information is to be obtained.

For a comparative study such as the present to have value the classification on which it is based must express phylogenetic relationships. Only

thus can the facts on distribution of a genus or family be data for phylogenetic lines. To show phylogenetic relationships certainly is the primary aim of any modern system of classification and one attained in the system used here in so far as information on the various rodents is available. The relationships of several genera are still obscure, but the affinities of most of them are reasonably clear at the familial and generic levels (for possible discrepancies at higher taxonomic levels, see Wood, 1947). Further study may result in a lower status in the taxonomic scale for a few forms now recognized as genera. Some South American forms are examples in point. Other forms may warrant higher rank. The present classification summarizes from a modern phylogenetic point of view present knowledge of the interrelationships of rodents.

TABLE I

OCCURRENCES OF THE GENERA OF RECENT RODENTS BY CONTINENTS AND BY FAUNAL REGIONS

The continents and faunal regions are abbreviated as follows: (*1*) Continents: Africa, Af; Asia, As; Australia, Au; Europe, Eu; North America, NA; South America, SA. (*2*) Faunal regions: African Region, ‖; Australian Region, §; Indomalayan Region, †; Nearctic Region, ¶; Neotropical Region, ‡; Palearctic Region, *.

SCIUROMORPH SERIES

Aplodontidae
- *Aplodontia*, NA¶

Sciuridae
- Sciurinae
  - *Sciurus*, As*, Eu*, NA¶‡, SA‡
  - *Syntheosciurus*, NA‡
  - *Microsciurus*, NA‡, SA‡
  - *Sciurillus*, SA‡
  - *Reithrosciurus*, As†
  - *Tamiasciurus*, NA¶
  - *Funambulus*, As*†
  - *Ratufa*, As†
  - *Protoxerus*, Af‖
  - *Epixerus*, Af‖
  - *Funisciurus*, Af‖
  - *Paraxerus*, Af‖
  - *Heliosciurus*, Af‖
  - *Myosciurus*, Af‖
  - *Callosciurus*, As*†
  - *Menetes*, As†
  - *Hyosciurus*, As†
  - *Rhinosciurus*, As†
  - *Lariscus*, As†
  - *Dremomys*, As*†
  - *Sciurotamias*, As*†
  - *Glyphotes*, As†
  - *Nannosciurus*, As†
  - *Atlantoxerus*, Af*
  - *Xerus*, Af‖
  - *Spermophilopsis*, As*
  - *Marmota*, As*†, Eu*, NA¶
  - *Cynomys*, NA¶
  - *Citellus*, As*, Eu*, NA¶
  - *Tamias*, NA¶
  - *Eutamias*, As*, NA¶
- Petauristinae
  - *Petaurista*, As*†
  - *Eupetaurus*, As*
  - *Sciuropterus*, As*, Eu*
  - *Glaucomys*, NA¶‡
  - *Eoglaucomys*, As*
  - *Hylopetes*, As†
  - *Aeretes*, As*
  - *Trogopterus*, As*†
  - *Belomys*, As†
  - *Pteromyscus*, As†
  - *Petaurillus*, As†
  - *Iomys*, As†

Geomyidae
- *Geomys*, NA¶
- *Thomomys*, NA¶
- *Pappogeomys*, NA¶
- *Cratogeomys*, NA¶
- *Orthogeomys*, NA¶‡
- *Heterogeomys*, NA¶‡
- *Macrogeomys*, NA‡
- *Zygogeomys*, NA¶

Heteromyidae
- Perognathinae
  - *Perognathus*, NA¶
  - *Microdipodops*, NA¶
- Dipodomyinae
  - *Dipodomys*, NA¶
- Heteromyinae
  - *Liomys*, NA¶‡
  - *Heteromys*, NA¶‡, SA‡

Castoridae
- *Castor*, As*, Eu*, NA¶

MYOMORPH SERIES
Anomaluridae
  Anomalurinae
    Anomalurus, Af‖
  Zenkerellinae
    Idiurus, Af‖
    Zenkerella, Af‖
Pedetidae
    Pedetes, Af‖
Cricetidae
  Cricetinae
    Oryzomys, NA¶‡, SA‡
    Melanomys, NA‡, SA‡
    Megalomys, SA‡
    Neacomys, NA‡, SA‡
    Scolomys, SA‡
    Nectomys, NA‡, SA‡
    Rhipidomys, NA‡, SA‡
    Thomasomys, SA‡
    Phaenomys, SA‡
    Chilomys, SA‡
    Tylomys, NA¶‡, SA‡
    Ototylomys, NA¶‡
    Nyctomys, NA¶‡
    Otonyctomys, NA¶
    Rhagomys, SA‡
    Reithrodontomys, NA¶‡, SA‡
    Peromyscus, NA¶‡
    Baiomys, NA¶‡
    Onychomys, NA¶
    Akodon, SA‡
    Zygodontomys, NA‡, SA‡
    Microxus, SA‡
    Podoxymys, SA‡
    Lenoxus, SA‡
    Oxymycterus, SA‡
    Blarinomys, SA‡
    Notiomys, SA‡
    Scapteromys, SA‡
    Scotinomys, NA¶‡
    Hesperomys, SA‡
    Eligmodontia, SA‡
    Graomys, SA‡
    Phyllotis, SA‡
    Irenomys, SA‡
    Chinchillula, SA‡
    Neotomys, SA‡
    Reithrodon, SA‡
    Euneomys, SA‡
    Chelemyscus, SA‡
    Holochilus, SA‡
    Sigmodon, NA¶‡, SA‡
    Sigmomys, SA‡
    Andiomys, SA‡
    Neotomodon, NA¶
    Neotoma, NA¶‡
    Nelsonia, NA¶
    Xenomys, NA¶
    Ichthyomys, SA‡
    Anotomys, SA‡
    Daptomys, SA‡
    Rheomys, NA¶‡, SA‡
    Neusticomys, SA‡
    Calomyscus, As*
    Phodopus, As*
    Cricetus, As*, Eu*
    Cricetulus, As*, Eu*
    Mesocricetus, As*, Eu*
    Mystromys, Af‖
    Myospalax, As*
  Nesomyinae
    (Madagascar)
    Macrotarsomys, Af‖
    Nesomys, Af‖
    Brachytarsomys, Af‖
    Eliurus, Af‖
    Gymnuromys, Af‖
    Hypogeomys, Af‖
    Brachyuromys, Af‖
    Tachyoryctes, Af‖
  Lophiomyinae
    Lophiomys, Af‖
  Microtinae
    Dicrostonyx, As*, Eu*, NA¶
    Synaptomys, NA¶
    Myopus, As*, Eu*
    Lemmus, As*, Eu*, NA¶
    Clethrionomys, As*, Eu*, NA¶
    Aschizomys, As*
    Eothenomys, As*†
    Anteliomys, As*†
    Alticola, As*†
    Hyperacrius, As*
    Dolomys, Eu*
    Arvicola, As*, Eu*
    Ondatra, NA¶
    Neofiber, NA¶
    Phenacomys, NA¶
    Pitymys, Eu*, NA¶
    Blanfordimys, As*
    Microtus, As*†, Af*, Eu*, NA¶‡
    Lagurus, As*, NA¶
    Prometheomys, Eu*
    Ellobius, As*
  Gerbillinae
    Gerbillus, As*†, Af*‖
    Tatera, As*†, Af*‖
    Taterillus, Af‖
    Desmodillus, Af‖
    Pachyuromys, Af*‖
    Ammodillus, Af‖
    Meriones, As*†, Af*‖, Eu*
    Brachiones, As*
    Psammomys, As*, Af*‖
    Rhombomys, As*
Spalacidae
    Spalax, As*, Af*, Eu*
Rhizomyidae
    Rhizomys, As*†
    Cannomys, As†
Muridae
  Murinae
    Hapalomys, As†
    Vandeleuria, As†

Micromys, As*†, Eu*
Apodemus, As*†, Af*, Eu*
Thamnomys, Af‖
Grammomys, Af‖
Carpomys, Ast
Batomys, Ast
Pithecheir, Ast
Hyomys, Au§
Conilurus, Au§
Zyzomys, Au§
Laomys, Au§
Mesembriomys, Au§
Oenomys, Af‖
Mylomys, Af‖
Dasymys, Af‖
Arvicanthis, Af*‖
Hadromys, Ast
Golunda, As*†
Pelomys, Af‖
Lemniscomys, Af*‖
Rhabdomys, Af‖
Hybomys, Af‖
Millardia, As*†
Pyromys, Ast
Dacnomys, Ast
Eropeplus, Ast
Stenocephalemys, Af‖
Aethomys, Af‖
Thallomys, Af‖
Rattus, As*†, Af*‖, Au§, Eu*
Nilopegamys, Af‖
Tryphomys, Ast
Gyomys, Au§
Leporillus, Au§
Pseudomys, Au§
Apomys, Ast
Melomys, Au§
Uromys, Au§
Coelomys, Ast
Malacomys, Af‖
Haeromys, Ast
Chiromyscus, Ast
Zelotomys, Af‖
Hylenomys, Af‖
Muriculus, Af‖
Mus, As*†, Af*‖, Eu*
Mycteromys, Ast
Leggadina, Au§
Colomys, Af‖
Nesoromys, Au§
Crunomys, Ast
Macruromys, Au§
Lorentzimys, Au§
Lophuromys, Af‖
Leimacomys, Af‖
Notomys, Au§
Mastacomys, Au§
Echiothrix, Ast
Melasmothrix, Ast
Acomys, Ast, Af*‖, Eu*
Uranomys, Af‖
Bandicota, As*†
Nesokia, As*†, Af*
Beamys, Af‖
Saccostomys, Af‖
Cricetomys, Af‖
Anisomys, Au§
Dendromurinae
Dendromus, Af‖
Malacothrix, Af‖
Prionomys, Af‖
Petromyscus, Af‖
Steatomys, Af‖
Deomys, Af‖
Otomyinae
Otomys, Af‖
Paratomys, Af‖
Phloeomyinae
Lenomys, Ast
Pogonomys, Au§
Chiropodomys, Ast, Au§
Mallomys, Ast, Au§
Phloeomys, Ast
Crateromys, Ast
Rhynchomyinae
Rhynchomys, Ast
Hydromyinae
Chrotomys, Ast
Celaenomys, Ast
Crossomys, Au§
Xeromys, Au§
Hydromys, Au§
Parahydromys, Au§
Leptomys, Au§
Pseudohydromys, Au§
Gliridae
Glirinae
Glis, Eu*
Muscardinus, As*, Eu*
Eliomys, As*, Af*‖, Eu*
Dryomys, As*, Eu*
Glirulus, As*
Myominus, As*
Graphiurinae
Graphiurus, Af‖
Platacanthomyidae
Platacanthomys, Ast
Typhlomys, Ast
Seleviniidae
Selevinia, As*
Zapodidae
Sicistinae
Sicista, As*, Eu*
Zapodinae
Zapus, As*, NA¶
Napaeozapus, NA¶
Dipodidae
Dipodinae
Dipus, As*, Eu*
Paradipus, As*
Eremodipus, As*
Jaculus, As*, Af*‖
Scirtopoda, As*, Eu*
Allactaga, As*, Af*, Eu*

Alactagulus, As*, Eu*
Pygeretmus, As*
Cardiocraniinae
Cardiocranius, As*
Salpingotus, As*
Euchoreutinae
Euchoreutes, As*
Ctenodactylidae
Ctenodactylus, Af*‖
Pectinator, Af‖
Massoutiera, Af*‖
Felovia, Af‖

HYSTRICOMORPH SERIES
Hystricidae
Hystricinae
Thecurus, As†
Hystrix, As*†, Af*‖, Eu*
Atherurinae
Atherurus, As*†, Af*‖
Trichys, As†
Erethizontidae
Erethizontinae
Erethizon, NA¶
Coendou, NA‡, SA‡
Echinoprocta, SA‡
Chaetomyinae
Chaetomys, SA‡
Caviidae
Caviinae
Cavia, SA‡
Kerodon, SA‡
Galea, SA‡
Microcavia, SA‡
Dolichotinae
Dolichotis, SA‡
Hydrochoeridae
Hydrochoerus, NA‡, SA‡
Dinomyidae
Dinomys, SA‡
Dasyproctidae
Cuniculinae
Cuniculus, NA‡, SA‡
Dasyproctinae
Dasyprocta, NA‡, SA‡
Myoprocta, SA‡
Chinchillidae
Lagostomus, SA‡
Lagidium, SA‡
Chinchilla, SA‡
Capromyidae
Capromys, NA‡ (Antilles)
Geocapromys, NA‡ (Antilles)
Procapromys, SA‡
Plagiodontia, NA‡ (Antilles)
Myocaster, SA‡
Octodontidae
Octodon, SA‡
Octodontomys, SA‡
Spalacopus, SA‡
Aconaemys, SA‡
Octomys, SA‡
Ctenomyidae
Ctenomys, SA‡
Abrocomidae
Abrocoma, SA‡
Echimyidae
Echimyinae
Proëchimys, NA‡, SA‡
Hoplomys, NA‡, SA‡
Euryzygomatomys, SA‡
Clyomys, SA‡
Carterodon, SA‡
Cercomys, SA‡
Mesomys, SA‡
Lonchothrix, SA‡
Isothrix, SA‡
Diplomys, NA‡, SA‡
Echimys, SA‡
Dactylomyinae
Dactylomys, SA‡
Kannabateomys, SA‡
Thrinacodus, SA‡
Thryonomyidae
Thryonomys, Af‖
Petromyidae
Petromys, Af‖

BATHYERGOMORPH SERIES
Bathyergidae
Georychus, Af‖
Cryptomys, Af‖
Heliophobius, Af‖
Bathyergus, Af‖
Heterocephalus, Af‖

COMPARISONS OF RODENT FAUNAS OF CONTINENTS

The data of Table I are grouped in Table II to show the number of genera represented on each continent. Each genus is counted once in arriving at a total. Endemic genera and genera represented on more than one continent are totaled separately; together they yield the count of genera per family and continent.

ASIA.—Asia has the largest number of genera, with representatives of 118 (35 per cent) of the 338 genera here recognized. About two-thirds

(eighty-eight) of the genera in Asia are members of the Muridae, Cricetidae, and Sciuridae. The remaining one-third is composed of a few genera of nine other families, the largest number of which are of the family Dipodidae. As is true on the other northern continents, the hystrichomorph rodents are poorly represented. Only four of the forty-nine genera of the hystrichomorph series have Asiatic forms and each of these occurs in the southern part of the continent.

AFRICA AND SOUTH AMERICA.—Africa and South America follow Asia in number of genera, having counts of eighty-nine and eighty-four (26 and 25 per cent) respectively, of the total genera of Recent rodents. As in the fauna of Asia, the larger segment in Africa (about two-thirds) is made up of representatives of the Muridae and Cricetidae. There are fewer genera of squirrels, eight as compared with twenty-eight in Asia. The remaining one-third of the African fauna consists of representatives of eleven other families—one bathyergid, two hystrichomorphs, and eight myomorphs. Although represented by an identical number of families and about the same number of genera as Africa, South America has less diversity of fauna. Eleven of the fourteen families (79 per cent) and thirty-nine of the eighty-four genera (46 per cent) represented there are hystrichomorphs. Only one family of the myomorph series is represented, but its genera account for 49 per cent of the total. One genus of the family Heteromyidae and three of Sciuridae complete the generic total.

NORTH AMERICA.—North America has sixty-nine of the 338 genera (20 per cent). Almost one-half (48 per cent) of these are myomorphs and most (thirty-one out of the thirty-three genera) belong to one family, Cricetidae. Twenty-five (36 per cent) are sciuromorph genera, divided among five of the twelve families on the continent. Eleven genera (16 per cent) are of the hystrichomorph series; all except one are also represented in South America or limited in occurrence to one of the Caribbean islands.

AUSTRALIA AND EUROPE.—Australia and Europe have the least representation, with twenty-six and thirty-four genera, respectively, or 8 per cent and 10 per cent of the total Recent genera. The totals are about the same for the two continents, but the diversity of the European fauna well exceeds that of Australia. All of the Australian rodents are referable to the family Muridae. In Europe nine families are represented by the thirty-four genera. Thirteen genera (38 per cent) are of the family Cricetidae, five (15 per cent) of Muridae, four (12 per cent) each of Sciuridae, Gliridae, and Dipodidae, and one genus each of the four other families on the continent.

TABLE II

ABSOLUTE NUMBER OF ENDEMIC (END.) AND NONENDEMIC (NONEN.) GENERA OF RECENT RODENTS ON EACH CONTINENT AND TOTAL NUMBER OF RECENT RODENTS IN EACH FAMILY

Family	Total Genera Per Family	Asia			Europe			N. America			S. America			Africa			Australia		
		End.	Nonen.	Total	End.	Nonen.	Total	End.	Nonen.	Total	End.	Nonen.	Total	End.	Nonen.	Total	End.	Nonen.	Total
Sciuromorph series																			
Aplodontidae	1	.....	.....	.....	.....	.....	.....	1	.....	1	.....	.....	.....	.....	.....	.....	.....	.....	.....
Sciuridae	43	23	5	28	.....	4	4	5	5	10	1	2	3	8	.....	8	.....	.....	.....
Geomyidae	8	.....	.....	.....	.....	.....	.....	8	.....	8	.....	.....	.....	.....	.....	.....	.....	.....	.....
Heteromyidae	5	.....	.....	.....	.....	.....	.....	4	1	5	.....	1	1	.....	.....	.....	.....	.....	.....
Castoridae	1	.....	1	1	.....	1	1	.....	1	1	.....	.....	.....	.....	.....	.....	.....	.....	.....
Myomorph series																			
Anomaluridae	3	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	3	.....	3	.....	.....	.....
Pedetidae	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	.....	1	.....	.....	.....
Cricetidae	99	12	14	26	2	11	13	15	16	31	31	10	41	14	5	19	.....	.....	.....
Spalacidae	1	.....	1	1	.....	1	1	.....	.....	.....	.....	.....	.....	.....	1	1	.....	.....	.....
Rhizomyidae	2	2	.....	2	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Muridae	92	27	7	34	.....	5	5	.....	.....	.....	.....	.....	.....	33	5	38	23	3	26
Gliridae	7	2	4	6	.....	4	4	.....	.....	.....	.....	.....	.....	1	1	2	.....	.....	.....
Platacanthomyidae	2	2	.....	2	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	2	2	.....	.....	.....
Seleviniidae	1	1	.....	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Zapodidae	3	.....	2	2	.....	1	1	1	1	2	.....	.....	.....	.....	.....	.....	.....	.....	.....
Dipodidae	11	7	4	11	.....	4	4	.....	.....	.....	.....	.....	.....	.....	2	2	.....	.....	.....
Ctenodactylidae	4	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	4	.....	4	.....	.....	.....
Hystrichomorph series																			
Hystricidae	4	2	2	4	.....	1	1	.....	.....	.....	.....	.....	.....	.....	2	2	.....	.....	.....
Erethizontidae	4	.....	.....	.....	.....	.....	.....	1	1	2	2	1	3	.....	.....	.....	.....	.....	.....
Caviidae	5	.....	.....	.....	.....	.....	.....	.....	.....	.....	5	.....	5	.....	.....	.....	.....	.....	.....
Hydrochoeridae	1	.....	.....	.....	.....	.....	.....	.....	1	1	.....	1	1	.....	.....	.....	.....	.....	.....
Dynomyidae	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	.....	1	.....	.....	.....	.....	.....	.....
Dasyproctidae	3	.....	.....	.....	.....	.....	.....	.....	2	2	1	2	3	.....	.....	.....	.....	.....	.....
Chinchillidae	3	.....	.....	.....	.....	.....	.....	.....	.....	.....	3	.....	3	.....	.....	.....	.....	.....	.....
Capromyidae	5	.....	.....	.....	.....	.....	.....	3	.....	3	2	.....	2	.....	.....	.....	.....	.....	.....
Octodontidae	5	.....	.....	.....	.....	.....	.....	.....	.....	.....	5	.....	5	.....	.....	.....	.....	.....	.....
Ctenomyidae	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	.....	1	.....	.....	.....	.....	.....	.....
Abrocomidae	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	.....	1	.....	.....	.....	.....	.....	.....
Echimyidae	14	.....	.....	.....	.....	.....	.....	.....	3	3	11	3	14	.....	.....	.....	.....	.....	.....
Thryonomyidae	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	.....	1	.....	.....	.....
Petromyidae	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	.....	1	.....	.....	.....
Bathyergomorph series																			
Bathyergidae	5	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	5	.....	5	.....	.....	.....
Total genera	338	78	40	118	2	32	34	38	31	69	64	20	84	71	18	89	23	3	26
Total families	32	2	10	12	0	9	9	2	10	12	6	8	14	6	8	14	0	1	1

ENDEMISM ON THE CONTINENTS

AUSTRALIA AND EUROPE.—On each continent except Europe more than one-half of the genera represented are restricted to the continent. Australia has no endemic families, but perhaps as could be expected on the basis of its small fauna and long isolation almost all (twenty-three of twenty-six) of the genera are confined there. On a percentage basis the incidence of endemism at the generic level is greater than for any other continent. The situation contrasts strongly with that of the European continent on which there is roughly an equal number of genera represented, but only 6 per cent (two of thirty-four) of the genera are endemic as compared with 88 per cent in Australia.

AFRICA AND SOUTH AMERICA.—The incidence of endemism in Africa and South America is similar. On each continent almost one-half of the families and three-fourths of the genera (80 per cent and 76 per cent, respectively) are found nowhere else. A large part of these on each continent are cricetids, but there the close resemblance of the faunas of the two regions ceases. In South America the remainder of the endemic genera except for one, *Sciurillus,* are hystrichomorph types in an array not seen elsewhere. In Africa, the endemic forms, exclusive of cricetids, are mostly murids and sciurids, with a few endemic genera in seven other families some of which, as the Bathyergidae and Ctenodactylidae, consist of highly specialized forms with apparently no close, living relatives.

ASIA.—Asia, with the most genera represented, has a high incidence of endemism approaching that of Australia. Seventy-eight (66 per cent) of the 118 genera are restricted to Asia. Twenty-seven (35 per cent) of these are murids, twenty-three (30 per cent) are sciurids, and twelve (15 per cent) are cricetids. The remaining sixteen genera are distributed among six other families. Only two families, the Rhizomyidae and Seleviniidae, are limited to that continent.

NORTH AMERICA.—Of the sixty-nine genera represented in North America thirty-eight (55 per cent) are restricted to the continent. Sixteen of the thirty-eight (42 per cent) genera belong to the myomorph series; all but one are members of the family Cricetidae. Eighteen (47 per cent) are sciuromorphs of five families, three of which are represented predominantly or exclusively in North America. Four of the endemic genera are hystrichomorphs; three comprise extant or recently extinct forms on Caribbean Islands.

COMPARISON OF RODENT FAUNAS OF THE MAJOR FAUNAL REGIONS

In his monumental work, Ellerman (1940: 47–74; 1941: 10–30) listed the genera of rodents on the basis of their occurrence in the zoogeographic

regions of the world. The regions are approximately those proposed by Sclater and adopted by Flower and Lydecker (1891: 96); their geographic limits correspond more closely to the range limits of rodent kinds than do continental boundaries. Compared with the rodent fauna of an entire continent, a regional assemblage more nearly reflects particular environmental conditions and the historical circumstances governing them, or at least closely correlated with them. Only in the case of the Australian Archipelago and faunal region do the limits of a faunal region and of a continent coincide. The absolute number of endemic and nonendemic genera of each family represented in the six faunal regions is listed in Table III.

NEOTROPICAL REGION.—The Neotropical region exceeds all others in total number of genera and families and in incidence of endemism. Fifteen (47 per cent) of the world total of thirty-two families are present there. Ten of the fifteen are confined to it, all of which are hystrichomorphs. The one hundred genera of this region constitute 30 per cent of the total genera of the world. Eighty-two of these are restricted to the Neotropical region and almost all are either representative of the family Cricetidae or of some hystrichomorph family. On a percentage basis this number is about equaled by the African region and is but slightly exceeded by the Australian region. Each of these regions, however, has fewer genera. Some of the Neotropical forms eventually will be treated as lower categories, but allowing for such procedure, it is apparent that the Neotropical region is a major center for the differentiation of cricetid and hystricomorph rodents.

AFRICAN REGION.—Of the southern regions, the African does not differ greatly from the Neotropical region in count of genera. It has eighty-one genera (24 per cent of the world total) representing twelve families (38 per cent of the total). Sixty-five (80 per cent) of the genera are restricted to the continent. There are representatives of each of the three families of hystrichomorph rodents known from outside the Neotropical region; two of these families are restricted to Africa, as are also five endemic genera of rodents of the family Bathyergidae and seven genera of squirrels. The remainder are all myomorph rodents and mostly represent the families Muridae and Cricetidae, particularly the former. About one-half of the total genera in the region and one-half of the count of endemics are murids; these fractions are exceeded only in the Indomalayan and Australian regions. In number of kinds and in incidence of endemism these three regions are the principal differentiation centers for the Muridae.

INDOMALAYAN REGION.—The Indomalayan region has slightly fewer genera than has the African. The total is seventy (21 per cent of

TABLE III

ABSOLUTE NUMBER OF ENDEMIC (END.) AND NONENDEMIC (NONEN.) GENERA OF RECENT RODENTS IN EACH FAUNAL REGION

Family	Palearctic			Nearctic			Neotropical			Indomalayan			African			Australian		
	End.	Nonen.	Total	End.	Nonen.	Total	End.	Nonen.	Total	End.	Nonen.	Total	End.	Nonen.	Total	End.	Nonen.	Total
Sciuromorph series																		
Aplodontiidae	..	..	..	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..
Sciuridae	6	10	16	3	5	8	3	2	5	13	7	20	7	..	7	..	..	..
Geomyidae	..	..	..	5	2	7	1	2	3	..	..	..	..	..	..	..	..	..
Heteromyidae	..	..	..	3	2	5	..	2	2	..	..	..	..	..	..	..	..	..
Castoridae	..	1	1	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..
Myomorph series																		
Anomaluridae	..	..	..	..	..	..	..	..	..	..	..	..	3	..	3	..	..	..
Pedetidae	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1	..	..	..
Cricetidae	16	14	30	9	17	26	36	12	48	..	7	7	13	5	18	..	..	..
Spalacidae	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Rhizomyidae	..	1	1	..	..	..	..	..	..	1	1	2	..	..	..	..	..	..
Muridae	..	11	11	..	..	..	..	..	..	25	10	35	31	5	36	23	3	26
Gliridae	5	1	6	..	..	..	..	..	..	..	..	..	1	1	2	..	..	..
Platacanthomyidae	..	..	..	..	..	..	..	..	..	2	..	2	..	..	..	..	..	..
Seleviniidae	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Zapodidae	1	1	2	1	1	2	..	..	..	..	..	..	..	..	..	..	..	..
Dipodidae	10	1	11	..	..	..	..	..	..	..	..	..	..	1	1	..	..	..
Ctenodactylidae	..	2	2	..	..	..	..	..	..	..	..	..	2	2	4	..	..	..
Hystrichomorph series																		
Hystrichidae	..	2	2	..	..	..	..	..	..	2	2	4	..	2	2	..	..	..
Erethizontidae	..	..	..	1	..	1	3	..	3	..	..	..	..	..	..	..	..	..
Caviidae	..	..	..	..	..	..	5	..	5	..	..	..	..	..	..	..	..	..
Hydrochoeridae	..	..	..	..	..	..	1	..	1	..	..	..	..	..	..	..	..	..
Dinomyidae	..	..	..	..	..	..	1	..	1	..	..	..	..	..	..	..	..	..
Dasyproctidae	..	..	..	..	..	..	3	..	3	..	..	..	..	..	..	..	..	..
Chinchillidae	..	..	..	..	..	..	3	..	3	..	..	..	..	..	..	..	..	..
Capromyidae	..	..	..	..	..	..	5	..	5	..	..	..	..	..	..	..	..	..
Octodontidae	..	..	..	..	..	..	5	..	5	..	..	..	..	..	..	..	..	..
Ctenomyidae	..	..	..	..	..	..	1	..	1	..	..	..	..	..	..	..	..	..
Abrocomidae	..	..	..	..	..	..	1	..	1	..	..	..	..	..	..	..	..	..
Echimyidae	..	..	..	..	..	..	14	..	14	..	..	..	..	..	..	..	..	..
Thryonomyidae	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1	..	..	..
Petromyidae	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1	..	..	..
Bathyergomorph series																		
Bathyergidae	..	..	..	..	..	..	..	..	..	..	..	..	5	..	5	..	..	..
Total genera	40	44	84	23	28	51	82	18	100	43	27	70	65	16	81	23	3	26
Total families	2	10	12	1	7	8	10	5	15	1	5	6	5	7	12	.....	1	1

the world total), of which forty-three (61 per cent) are restricted to the area. Except for two which represent the strictly Indomalayan family Platacanthomyidae, the genera all belong to families that are widespread in distribution. One of the families, Hystrichidae, is represented in the African and Palearctic regions as well; another, Rhizomyidae, has a genus in the Palearctic; the Muridae are also in the Palearctic, African, and Australian; and two, the Sciuridae and Cricetidae, are common to all regions except the Australian. There are only six families (19 per cent of total) in the entire Indomalayan region. By far the greatest part of the rodent fauna consists of squirrels (Sciuridae) and mice of the family Muridae. In total count of genera of Sciuridae (twenty) and in number of endemics (thirteen) of that family, this region exceeds all others. It is a region of great differentiation of the Muridae, closely followed in this respect by the African and Australian regions. Three murid genera are common to this and the African region.

AUSTRALIAN REGION.—The Australian faunal region and the Australian continent, including the adjacent islands as here defined, are identical. The fauna has already been discussed under the Comparisons of Rodent Faunas of Continents.

PALEARCTIC REGION.—Of the two northern regions, the Palearctic far exceeds the Nearctic in number and diversity of genera, with eighty-four genera (25 per cent of the world total) represented. These belong to twelve families (38 per cent of the total). One of these families, Hystrichidae, is a hystrichomorph type that is widely distributed in the Old World. Two, Sciuridae and Castoridae, are sciuromorphs that are common, the first to most of the world and the second to the Nearctic region. The other nine are myomorphs, two restricted to the region and seven common to other regions, principally the Indomalayan and African. Although the number of genera in each Palearctic family of the myomorph series is comparatively small, even in the widespread families Muridae and Cricetidae, the diversity at the familial level of the myomorph types in the Palearctic is unequaled elsewhere. This region is a major differentiation center for this series of the order Rodentia. In addition to those that are endemic, several nonendemic myomorph families are best developed there; of these the Dipodidae and Gliridae are represented by the most genera. Representatives of the family Sciuridae also make up an important part of the fauna. Most of them, however, also occur in other regions, and it seems clear that this region is of lesser importance as a differentiation center of the Sciuridae than is the Indomalayan region.

NEARCTIC REGION.—The relationships of the Nearctic rodent fauna are discussed in more detail in following paragraphs. The fauna has comparatively few genera and consists principally of cricetids and of five families

of the sciuromorph series. In this region, there are fifty-one genera (15 per cent of the total) representing eight families (25 per cent of the total). Twenty-three genera (45 per cent) and one family are restricted to the region.

AFFINITIES OF THE NORTH AMERICAN RODENT FAUNA

That the mammalian fauna of North America is composed of elements derived from, and interchanged with, faunal elements of other continents, especially of Eurasia and South America, is well established. The kind and amount of interchange with Eurasia and the general relationships of the Eurasian and North American faunas through the Cenozoic have been fully treated by Simpson (1947). He discussed many of the important factors which through time have influenced the movements of mammal kinds and effected the distribution patterns as seen today. Current ranges are the result of past events, but certainly many of the factors active in the past must also influence mammal occurrences at the present time. To derive past distributions from present ranges of morphological and ecological features may extend the facts too far, but it is worthwhile if for no other reason than that it yields a few reasonably probable estimates of histories of extant kinds to supplement data from the fossil record.

In the following discussions the amount of resemblance between the North American fauna and other faunas is expressed numerically. The index used is an expression of the extent of resemblance at one taxonomic level as measured by a proportion of groups common to two areas to groups not common to the two areas. It is a measure proposed by Simpson (1947: 672) and is written $\frac{100C}{N_1}$, where C stands for the number of units common to the two faunas, and N_1 for the total number of units in the smaller of the two faunas; the resultant is expressed as a percentage or index. It should be emphasized that the index expresses extent and not kind of resemblance.

AUSTRALIA, SOUTHERN ASIA, AND AFRICA.—Affinities of the North American fauna with the faunas of Australia, southern Asia (the Indomalayan region), and Africa are few and probably historically remote. The groups of rodents that inhabit these latter areas are mostly murids and members of other families apparently not closely related to the North American kinds. There are no families or genera common to North America and Australia. Two wide-ranging families, Sciuridae and Cricetidae, have representatives in Africa and the Indomalayan region as well as in North America. One genus (*Microtus*) of Cricetidae occurs in northern Africa as well as in North America (Table IV). The two families have a com-

TABLE IV

FAMILIES AND GENERA OF RECENT RODENTS COMMON TO NORTH AMERICA AND OTHER CONTINENTS

For each family and genus the known fossil history on each continent (data from Simpson, 1945) is indicated by the following abbreviations: (*1*) Continents: NA, North America; SA, South America; As, Asia; Eu, Europe; Af, Africa; (*2*) Geologic periods: Olig., Oligocene; Mioc., Miocene; Plioc., Pliocene; Pleist., Pleistocene; R, Recent.

NORTH AMERICA AND SOUTH AMERICA (8 common families, 20 common genera)
- Sciuridae (Mioc.–R, NA; R, SA)
  - *Sciurus* (Mioc.–R, NA; R, SA)
  - *Microsciurus* (R, NA, SA)
- Heteromyidae (Mioc.–R, NA; R, SA)
  - *Heteromys* (R, NA, SA)
- Cricetidae (Olig.–R, NA; Plioc.–R, SA)
  - *Oryzomys* (Pleist.–R, NA, SA)
  - *Melanomys* (R, NA, SA)
  - *Neacomys* (R, NA, SA)
  - *Nectomys* (R, NA, SA)
  - *Rhipidomys* (R, NA, SA)
  - *Tylomys* (R, NA, SA)
  - *Reithrodontomys* (Pleist.–R, NA; R, SA)
  - *Zygodontomys* (R, NA, SA)
  - *Sigmodon* (Plioc.–R, NA; R, SA)
  - *Rheomys* (R, NA, SA)
- Erethizontidae (Plioc.–R, NA; Olig.–R, SA)
  - *Coendou* (R, NA, SA)
- Hydrochoeridae (Pleist.–R, NA; Plioc.–R, SA)
  - *Hydrochoerus* (Pleist.–R, NA, SA)
- Dasyproctidae (R, NA, SA)
  - *Cuniculus* (R, NA, SA)
  - *Dasyprocta* (R, NA, SA)
- Capromyidae (R, NA; Mioc.–R, SA)
  - No common genus
- Echimyidae (Pleist.–R, NA; Olig.–R, SA)
  - *Proëchimys* (R, NA, SA)
  - *Hoplomys* (R, NA, SA)
  - *Diplomys* (R, NA, SA)

NORTH AMERICA AND ASIA (4 common families, 11 common genera)
- Sciuridae (Mioc.–R, NA; Pleist.–R, As)
  - *Sciurus* (Mioc.–R, NA; Pleist.–R, As)
  - *Marmota* (Plioc.–R, NA; Pleist.–R, As)
  - *Citellus* (Plioc.–R, NA; Pleist.–R, As)
  - *Eutamias* (Pleist.–R, NA; Plioc.–R, As)
- Castoridae (Olig.–R, NA; Mioc.–R, As)
  - *Castor* (Plioc.–R, NA, As)
- Cricetidae (Olig.–R, NA, As)
  - *Dicrostonyx* (R, NA; Pleist.–R, As)
  - *Lemmus* (R, NA, As)
  - *Clethrionomys* (Pleist.–R, NA, As)
  - *Microtus* (Pleist.–R, NA; R, As)
  - *Lagurus* (R, NA, As)
- Zapodidae (Plioc.–R, NA, As)
  - *Zapus* (Pleist.–R, NA; R, As)

NORTH AMERICA AND EUROPE (4 common families, 9 common genera)
- Sciuridae (Mioc.–R, NA, Eu)
  - *Sciurus* (Mioc.–R, NA, Eu)
  - *Marmota* (Plioc.–R, NA; Pleist.–R, Eu)
  - *Citellus* (Plioc.–R, NA; Pleist.–R, Eu)
- Castoridae (Olig.–R, NA, Eu)
  - *Castor* (Plioc.–R, NA, Eu)
- Cricetidae (Olig.–R, NA, Eu)
  - *Dicrostonyx* (R, NA; Pleist.–R, Eu)
  - *Lemmus* (R, NA; Pleist.–R, Eu)
  - *Clethrionomys* (Pleist.–R, NA, Eu)
  - *Microtus* (Pleist.–R, NA, Eu)
  - *Pitymys* (Pleist.–R, NA, Eu)
- Zapodidae (Plioc.–R, NA; Olig., Pleist.–R, Eu)
  - No common genus

NORTH AMERICA AND AFRICA (2 common families, 1 common genus)
- Sciuridae (Mioc.–R, NA; R, Af)
  - No common genus
- Cricetidae (Olig.–R, NA; R, Af)
  - *Microtus* (Pleist.–R, NA; R, Af)

NORTH AMERICA AND AUSTRALIA (no common family or genus)

paratively long history in North America and Europe, and to judge from the amount of differentiation and extensive distribution in Asia and Africa, they probably were represented on the two continents well before the time

indicated by the scantily known fossil record. The Sciuridae are known from the Miocene to Recent in North America and Europe, from the Pleistocene to Recent in Asia, but only from the Recent in Africa. Cricetidae have occurred in North America, Europe, and Asia since the Oligocene and in Africa since the Pliocene. Both families are probably of North American origin.

EUROPE.—There are comparatively few genera and families represented in North America and Europe, but several of them are common to the two continents. On this account the index of resemblance of North America to Europe is relatively as great as it is for any other Old World continent or faunal region; the index $\left(\frac{100C}{N_1}\right)$ is forty-four for families and twenty-six for genera. The taxonomic resemblance between North America and Asia is scarcely less; the index is thirty-three for families and sixteen for genera (Table V). Four families and nine genera

TABLE V

TAXONOMIC RESEMBLANCES

As measured by $\frac{100C}{N_1}$, for families and genera of Recent rodents, between North America and each of four other continental land masses, and between the Nearctic faunal region and each of four other faunal regions.

Continent	$\frac{100C}{N_1}$		Faunal	$\frac{100C}{N_1}$	
	Families	Genera	Region	Families	Genera
South America	67	29	Neotropical	63	33
Europe	44	26	Palearctic	50	24
Asia	33	16	Indomalayan	33	4
(Eurasia)	33	17	African	25	0
Africa	17	1.5			

are common to North America and Europe. Two of the families, Sciuridae and Cricetidae, occur over much of the world and have been represented on both continents since the Miocene and the Oligocene, respectively. The other two, Castoridae and Zapodidae, are confined to North America and Eurasia; the Castoridae date from the Oligocene on both continents and the Zapodidae from the Pliocene in North America and from the Oligocene and Pleistocene in Europe. All genera of these families which are common to both continents are Holarctic in distribution. The genus *Marmota* is represented by forms in the Indomalayan region, but these indicate their boreal predilection through the ecological situations in which they occur. The cricetid genera common to Europe and North America, namely *Dicrostonyx, Lemmus, Clethrionomys, Microtus,* and

Pitymys, are Holarctic in distribution, and within each genus there are morphologically similar forms on each continent. It seems likely that there was movement from one continent to the other late in geological history. None is known from epochs earlier than the Pleistocene. On the basis of similar evidence, the latest, but not necessarily the first, intercontinental movements of some species of *Sciurus, Marmota, Citellus* (Sciuridae), and *Castor* (Castoridae) could well have occurred in the same epoch. First occurrences of *Sciurus* and *Castor* are known to be earlier—in Pliocene time (Table IV).

ASIA.—The preceding remarks concerning the faunas of North America and Europe apply equally well in a comparison of the faunas of North America and Asia. There is slight difference in the list of families and genera common to the three continents. *Eutamias, Lagurus,* and *Zapus* are represented in Asia and North America but not in Europe and *Pitymys* occurs in Europe and North America but not in Asia. There are eleven genera common to Asia and North America and the same four families, mentioned above, common to all three continents. The index of resemblance of North America with Asia is thirty-three and sixteen for families and genera, respectively. The indices have essentially the same values for North America and Eurasia. The rodent fauna of northern Eurasia and northern North America consists in large part of representatives of nine genera, each of which has closely related species on the two land masses.

SOUTH AMERICA.—More southerly segments of the rodent fauna in North America are distinctly American. A large section consists of American families and genera that have attained their distinctness in the New World, and mainly in the western United States, Mexico, and Central America. Many of them have extensive ranges on the continent and have "spilled over" into suitable ecological situations in the contiguous faunal region and on the adjoining continent. For these reasons the North American continent has greater community of rodent forms with South America than with any other continent. Eight families and twenty genera are common to both (Table IV); the index is sixty-seven for families and twenty-nine for genera.

The amount of taxonomic resemblance between the Nearctic and Neotropical regions is also high (Table V). A list of the forms common to the two faunal regions contains five families and eighteen genera. Such a list differs from the one in Table IV in that it contains a higher percentage of the tropical forms of both North and South America. The following genera are common to the two continents, but are excluded from the Nearctic region, as here understood: *Microsciurus, Melanomys, Neacomys, Nectomys, Rhipidomys, Zygodontomys, Coendou, Hydrochoerus, Cuniculus, Dasyprocta, Proëchimys, Hoplomys,* and *Diplomys.* The following North

American genera enter the Neotropical region: *Glaucomys, Orthogeomys, Heterogeomys, Liomys, Ototylomys, Nyctomys, Peromyscus, Baiomys, Scotinomys, Neotoma,* and *Microtus.*

Part of the history of the forms common to North and South America is reasonably clear, as indicated by the morphological relationships of the genera, their present distributions and their occurrences in the fossil record. The present community of forms on the two continents was established in late geological time by the southward emigration of North American species and the northward emigration of South American kinds that long had been isolated on the continent but apparently were not a part there of the original mammalian fauna (Simpson, 1942: 326–27). The two continents apparently were separated in early Tertiary. A land connection probably similar to that now seen was re-established in Pliocene time (Simpson, 1940*a*, 1940*b*; Olson and McGrew, 1941; Scott, 1942). Until the continents were reunited the rodent fauna of South America seems to have consisted entirely of hystrichomorphs, whereas that of North America was composed of representatives of all the myomorph and sciuromorph families now represented on both continents, but was without hystrichomorphs. In Pliocene time North American rodents were added to the South American fauna (Scott, 1942; Simpson, 1940*a*, 1940*b*), and South American hystrichomorphs appeared on the North American continent (see Wilson, 1937). Insofar as the fossil record goes, it indicates a South American origin for the hystrichomorph genera and a North American differentiation and probable origin for the sciurid, heteromyid, and some if not all of the cricetid genera now represented in South America.

The morphological relationships and present distributions bear out the evidence obtained from the fossil record. The hystrichomorph genera, *Coendou, Hydrochoerus, Cuniculus, Dasyprocta, Proëchimys, Hoplomys,* and *Diplomys,* all have affinities in South America, where, as in the Tertiary, there still is an array of diverse forms not seen elsewhere in the world. None of the seven genera ranges far into North America, not even to the northern limit of the tropical conditions with which they are associated. The total extent of the range of each genus suggests that it originated in northern South America, and emigrated to the north late in geological time. The genus *Erethizon* is a disjunct now widely separated from its relatives and adapted to temperate conditions.

The relationships of the sciuromorph and myomorph genera are with types in North America and more remotely with forms in Eurasia. They are what Dunn (1931) might term "Old Northerns." In their relationships and ranges some of them are strictly North American forms which appear to have been exceedingly late (probably Pleistocene or even Recent) emigrants to South America, since only a few species of each genus occur

on the southern continent, and each of those species occurs only in the northern part. These genera are *Sciurus, Microsciurus, Heteromys,* and *Reithrodontomys.*

The remaining genera common to the two continents are tropical cricetines with ranges of varying sizes on both continents. Morphologically, they are, with allied forms, a group set apart from other New World cricetine rodents. These genera are *Oryzomys, Melanomys, Neacomys, Nectomys, Rhipidomys, Tylomys, Sigmodon, Zygodontomys* and *Rheomys.* Distinctive morphological features in some of them recall similar structures seen in forms in Eurasia. To judge from their ranges and relationships these and other South American cricetines were derived from early North American stocks. But whether the genera, as such, originated in North America or in South America is not known. They may have differentiated late in Tertiary time: (1) in the north, whence they were funneled southward into a Tertiary Central American peninsula (Schmidt, 1943); (2) in an insular Central America, separated by marine portals from South America (Simpson, 1940*a,* 1940*b;* Olson and McGrew, 1941) and the remainder of North America (Dickerson, 1918; Vaughan, 1919); or (3) in South America, from stocks that gained entrance to the continent after isthmian connections were re-established. From the amount of differentiation now seen in allied *Oryzomys*-like and *Akodon*-like forms in South America, it is probable that the nine genera above may have had a longer history in South America than did other North American emigrants, *Reithrodontomys* and *Heteromys,* for example. But their residency there need not date from a time earlier than Pliocene, when North American forms are first known from South America. The differentiation that has occurred, while involving many species, nevertheless is of a low taxonomic level and could well have taken place since mid-Pliocene and much of it even later. This seems particularly probable when it is considered that in South America the newly immigrant cricetine stocks probably found a large number of diverse and possibly unoccupied niches available to them. Under such favorable conditions evolution may well have been rapid, but a complete understanding of the history of the neotropical cricetines must come from the fossil record, which at present is inadequate.

PRINCIPAL FAUNAL UNITS OF NORTH AMERICAN RODENTS

In the course of the present study it has become clear that the Recent rodent fauna of North America is composed of three major units, which accord closely in distribution with the three divisions recognized by Merriam (1890) in his analysis of the biota of North America. (Their distributions are less in agreement with the zones described by Simpson, 1943*b*.) These major units of the North American rodent fauna are the boreal fauna of

high and middle latitudes, the arid western or sonoran fauna of Mexico and the western United States, and the tropical fauna of low latitudes and low elevations, excluding the interior plateau, of Mexico. Each of these rodent units appears to be natural in that it represents an aggregation of species and clusters of species—genera and families—that have generally similar distributions and environmental requirements, and common centers of maximum differentiation. If by reason of community in these features these are natural aggregations, then each has a history as a unit. Each consists of taxonomic segments derived at various times from other units on the continent or from South America or Eurasia. Species were added to and dropped from each unit as it evolved and responded to changes in climatic conditions in the geological past. Some now remain geographically separated from allied kinds. Other species are extinct either through annihilation or through evolution. But the major groups or phylogenetic lines now composing a unit probably have been associated for some time, some for several geological epochs.

The boreal unit consists of related eastern and western sets of species belonging to nineteen genera. The forms now occupy most of Canada and areas to the north, the coastal areas and higher mountains of the western United States, and much of the eastern section of the country. The eastern United States has been of minor importance as a differentiation or dispersal center for rodents. A few of the northern kinds have penetrated high mountain areas farther to the south; two species, *Glaucomys volans* and *Microtus guatemalensis,* have even reached Central America. Most species of each boreal genus are confined to northern parts of the continent. The affinities of all forms, except those of *Aplodontia* which apparently have no other close living relatives, are ultimately with Palearctic forms of Eurasia rather than with kinds in the sonoran or tropical faunal units of North America. Ten of the nineteen boreal genera are shared with Eurasia; eight are restricted to North America. They represent five families, but are predominantly squirrels of the subfamily Sciurinae and mice of the subfamily Microtinae. The boreal genera are: *Aplodontia* (Aplodontidae); *Sciurus, Tamiasciurus, Marmota, Tamias, Eutamias,* and *Glaucomys* (Sciuridae); *Castor* (Castoridae); *Dicrostonyx, Synaptomys, Lemmus, Clethrionomys, Ondatra, Phenacomys, Pitymys, Microtus,* and *Lagurus* (Microtinae, Cricetidae); and *Zapus* and *Napaeozapus* (Zapodidae). The genus *Erethizon* (Erethizontidae), now associated with the boreal unit, probably has not been a part of it for long. The species of the genus are tropical derivatives that are now adapted to temperate and boreal conditions and are geographically separated from their relatives in Central and South America.

The arid western or sonoran fauna occupies the arid mountains and interior plains, basins, and plateaus of most of the western United States and Mexico. It consists of species of twenty-three genera belonging to four families. Representatives of this faunal unit have spread northward and eastward to mingle with eastern and western boreal elements; others have spread southward into northern South America. The focal point of all the genera appears to be the arid region of the southern and western part of the continent, specifically the Mexican Plateau and adjoining Great Basin and Great Plains. The rodent forms comprising this faunal unit on the whole are not related to those of the boreal unit to the north and thereby to kinds in northern Eurasia. Instead, they are mostly indigenous forms, with remote affinities in southern Eurasia and closer relatives in Central and South America. One genus, *Citellus,* is represented in the Old World. The other twenty-two sonoran genera are exclusively American. Thirteen of them, eight and five, respectively, constitute the North American families Geomyidae and Heteromyidae. Only one genus, *Heteromys,* of these families is represented in South America. It is a late comer to that continent, probably in Pleistocene or even Recent time. The family Sciuridae is represented in the sonoran fauna by two genera, *Cynomys* and *Citellus,* both of which consist of species adjusted to arid conditions. (The subgenera *Citellus* and *Callospermophilus* of the genus *Citellus,* have boreal predilections, and for this and other morphological reasons, perhaps should be generically separate from the other subgenera of *Citellus.*) The remainder of the arid western unit is comprised of representatives of eight genera of the subfamily Cricetinae (Cricetidae): *Reithrodontomys, Peromyscus, Baiomys, Onychomys, Neotomodon, Neotoma, Nelsonia,* and *Xenomys.* All of these are endemic to North America.

The tropical unit is in the tropical lowlands of Mexico, the Antilles, Central America, and northern South America. A few kinds occur in the temperate climates at higher latitudes, but most are confined to tropical situations within the above-mentioned regions. Its species represent twenty-five genera belonging to seven families. All components of the fauna are exclusively American, with no close relatives outside the New World; and some of them, perhaps most of them, are South American in origin. The hystrichomorph segment, of which there are four families represented in the North American continent and one family in the Antilles, is clearly a South American group. The members moved into North America relatively recently; the fossil record indicates a Pliocene or Pleistocene invasion. The following are the tropical hystrichomorph genera in North America: *Coendou* (Erethizontidae); *Hydrochoerus* (Hydrochoeridae); *Cuniculus* and *Dasyprocta* (Dasyproctidae); *Proëchimys, Hoplomys* and *Diplomys* (Echimyidae); and, in the Antilles,

Capromys, Geocapromys, and *Plagiodontia* (Capromyidae). Two genera of squirrels, *Syntheosciurus* and *Microsciurus* (Sciuridae), are associated with the hystrichomorph types and other forms in the tropical fauna. That they are derived from northern forms and are late emigrants from North to South America seems probable from the distribution record of squirrels in current and geologic time. The rest of the tropical genera in North America consist of cricetine species which have affinities with forms in the sonoran fauna of North America and Eurasia. They are the "primitive Old Northern" forms (Dunn, 1931) of North American rodents. Facts of present and past distribution suggest that, although ultimately with northern affinities, they originated in tropical North or South America. All are known from fossil horizons at least as early, and mostly earlier, in North America, and not all occur in South America. They are presumed to be primarily North American tropical forms that have lately (Pliocene to Recent) moved into South America. The case is not clear, however, because the fossil record, particularly that of Central America and of northern South America, is inadequately known. The cricetine genera are *Oryzomys, Melanomys, Neacomys, Nectomys, Rhipidomys, Tylomys, Ototylomys, Nyctomys, Otonyctomys, Zygodontomys, Scotinomys, Sigmodon,* and *Rheomys.*

There is close correspondence between the present distribution of the three rodent faunal units and three major segments of the flora of North America, the Arcto-Tertiary flora, the Madro-Tertiary flora, and the Neotropical-Tertiary flora. The history of the three floral units in Tertiary time is reasonably clear (see summary by Chaney, 1947; Braun, 1947; and others in the same publication). The Arcto-Tertiary, confined to high latitudes in the early Tertiary, moved southward in Oligocene, Miocene, and Pliocene times in response to the progressive lowering of temperatures at middle and high latitudes. A regional diversity, in rodents as well as plants (Wilson, 1937), apparent in the Pliocene perhaps in response to seasonal rainfall, culminated in the two principal modern provinces of the flora: an eastern characterized by broadleaf deciduous forests and a western characterized by conifers and broadleafed evergreens and deciduous trees and shrubs.

The Madro-Tertiary moved northward from the Sierra Madre of Mexico, attained its widest distribution in the western United States during the Pliocene, and is now represented over much of the interior valleys, coastal lowlands, and mountains of the western United States and Mexico.

The Neotropical-Tertiary flora ranged northward to about 49 degrees north latitude in western North America during the Eocene and to progressively lower latitudes to the eastward. As the temperatures diminished in later Tertiary times, the northern limit of the flora, and probably

of its associated fauna, retreated southward. By Miocene time most of the tropical plant species in the eastern United States were eliminated, and by Pliocene time few tropical forms remained in the western United States. This flora has survived principally in northern South America, the Antilles, Central America, and Mexico, but relicts remain in southern parts of the eastern and western United States.

The correspondence at the present time level of the ranges of these important segments of the rodent fauna and of the flora of North America is not coincidence. Most rodents are directly dependent on plants for food, cover, and home sites. Many species depend on a particular floral aggregation, in which both kind of plant and the growth form of the vegetation are important. A modification in the distribution of the floral aggregation is followed by a similar change in the occurrence of the rodent kind. It is known that most of the rodent families now represented in North America were established on the continent by early or middle Tertiary (Simpson, 1947). By Pliocene time (Wilson, 1937) and probably earlier, there was regional diversity of rodent distribution. The associations of plants and rodent types probably were similar to those of today. It is logical to suppose that the ranges of the rodent faunas and of the floras were linked in the geological past as in the present. The units have been altered in detail through time and space—groups have been added and eliminated as the faunas and floras evolved and migrated—but it is probable that many essential elements and components of each fauna and flora have remained intact. The Tertiary history of the major vegetational units may well be the history of the principal rodent faunal units of North America.

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