

Geographical Distribution of Terrestrial Mammals in Middle America

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ABSTRACT: The 370 species of nonflying, nonmarine and noninsular mammals of Middle America (México, excluding Baja California, south through Panama) include 156 monotypic and 214 polytypic species. The distribution of these mammals is discussed with relation to their geographical affinities and their occurrence in principal areas. Major distributional barriers and areas of intergradation between subspecies in México northward of the Isthmus of Tehuantepec are defined.

Middle America, defined herein as being Central America including México, forms a narrow connection between North and South America. From the broad expanse of North America the continental mass narrows southeastwardly through México and ultimately to the present minimum width of approximately 40 miles at the Isthmus of Panamá. The restrictive nature of this corridor has been a major deterrent through time to inter-American movements by terrestrial organisms. Furthermore, movements were greatly discouraged — if not stopped — throughout most of the Tertiary when water gaps existed in this corridor (Mayr, 1946:8-9).

Insofar as mammals are concerned, Simpson (1950) has shown that these animals moved southward from Holarctica at various times, probably beginning in the late Mesozoic, to populate South America. He classes these immigrants into 3 groupings. Those considered by Simpson as "old-timers" reached South America in the late Mesozoic and early Tertiary and include present-day marsupials and edentates. Those considered as "old island hoppers" reached South America in mid-Tertiary (late Eocene to Miocene) and include primates, caviomorph rodents and procyonids (allies of the raccoon). Those that Simpson considered as "newcomers" reached South America in the late Pliocene and Quaternary and include Recent pan-American species of rabbits, squirrels, myomorph rodents, dogs, raccoons, weasels, cats, tapirs, peccaries and deer.

Following diversification in South America some mammals grouped as "old-timers" and "old island hoppers" moved northward beginning in the Pliocene and more abundantly in the Quaternary, when the present land bridge was re-established, until today Middle America and even parts of North America are inhabited by mammals having a direct affinity with the South American fauna. Species peculiar only to the Middle American area also developed. As a result, Middle America presently contains mammals differentiated locally and also species whose affinities are either South American or North American. The discussion presented here concerns the distribution of the species in these groups.

Three hundred and seventy species of Middle American mammals,

belonging to 9 terrestrial orders, are discussed in this report. Excluded are species of Chiroptera, Pinnipedia, Cetacea, Sirenia, species in the Mexican state of Baja California and insular species. These 370 mammals include 156 monotypic species and 214 polytypic species. This listing is derived from the text in Hall and Kelson (1959), except for changes in the status of some species in the following genera: *Chironectes* (Cabrera, 1958), *Lepus* (Anderson and Gaunt, 1962), *Sciurus* (Anderson, 1962), *Microsciurus* (Cabrera, 1961), *Perognathus* (Hall and Ogilvie, 1960), *Oryzomys* (Cabrera, 1961; Hall, 1960; Hershkovitz, 1960), *Peromyscus* (Hall and Alvarez, 1961; Hoffmeister and de la Torre, 1961), *Baiomys* (Packard, 1960), *Sigmodon* (Baker and Greer, 1962), *Microtus* (Baker and Greer, 1962), *Hydrochaeris* (Cabrera, 1961), *Speothos* (Hershkovitz, 1957), *Galictis* (Cabrera, 1958), *Spilogale* (Van Gelder, 1959), and *Tayassu* (Cabrera, 1961). Some range extensions recorded for species in the literature since 1959 also are included. In analyzing distributions of mammals the studies of Burt (1949), Dice (1943), Hershkovitz (1958), Hooper (1949), Leopold (1959) and Smith (1949) have been helpful.

Data concerning nomenclature and distribution were punched for each species on McBee key-sort cards. Places on key-sort cards were designated for the occurrence of species in the various political divisions of Central America. For México, in and northwestward of the Isthmus of Tehuantepec, places were designated for the major areas

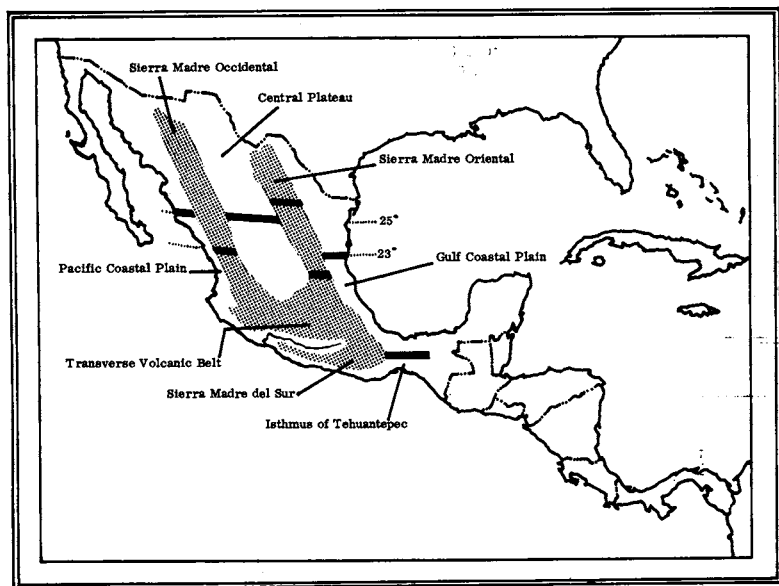


Fig. 1.—Middle America, showing the principal areas inhabited by mammals in México with major places which act as barriers to species and zones of intergradation between subspecies.

inhabited by mammals: the northern and southern parts of the Central Plateau, the Gulf Coastal Plain, the Pacific Coastal Plain, and the major mountain ranges (see Fig. 1). If the species have been subdivided into different subspecies within one major area or from one major area to another, this information also was recorded by punches. As a result, useful data as to the location of principal barriers to mammalian distribution and of major areas of intergradation between subspecies could be determined for both individual species and for groups of species. Financial assistance is acknowledged from the M.S.U. All-University Research Fund and the M.S.U. Development Fund. Victor Hogg drew the map.

GENERAL PATTERNS OF DISTRIBUTION

In Table I the 370 species of mammals are grouped according to orders. The majority of the species (251 or 71%) are Rodentia while, for example, only 35 Carnivora (9%) are present. The tapir (*Tapirus bairdii*) is the single representative of the order Perissodactyla.

Slightly less than one-half (156 or 42%) are monotypic species. Of the 214 polytypic species, geographic variation is conspicuous in most species of Marsupialia, Primates, Edentata, Lagomorpha, Artiodactyla, and Carnivora. Only 137 species (55%) of Rodentia have been shown to possess distinctive geographic subspecies.

Although the mammals of Middle America are, for the most part, fairly well understood taxonomically, there are still a number of poorly known groups. The species of such genera as *Cryptotis*, *Oryzomys*, *Sigmodon*, and *Tylomys* need additional study. Probably, as stated by Hall (*in* Hall and Kelson, 1959:vi), there are a number of mammals, now having full specific status, which, after additional collecting and study, may be shown to hold no more than subspecific rank. Certainly many of the 29 monotypic species of insectivores need to be studied more thoroughly. Consequently, any conclusions made herein — especially those having to do with monotypic species — may need some revision following systematic work. Even so, making a distinction be-

TABLE I.—Number of mammals in Middle America, excluding bats, marine mammals, insular species and those in Baja California

Orders	Monotypic species	Polytypic species	Totals
Marsupialia	2	9	11
Insectivora	29	8	37
Primates	2	6	8
Edentata	1	6	7
Lagomorpha	3	7	10
Rodentia	114	137	251
Carnivora	3	32	35
Perissodactyla	1	0	1
Artiodactyla	1	9	10
Totals	156	214	370

tween monotypic and polytypic species in this report seems justified in order to show especially differences in patterns of distribution and endemism.

Table II presents general distributional patterns for the 370 terrestrial species in Middle America. As expected, monotypic species (M) are generally much more restricted in distribution than polytypic species (P). This is further emphasized by the fact that 77 monotypic species are endemic to México, in and northwestward of the Isthmus of Tehuantepec, and 69 monotypic species are endemic to one or more of the political units of Middle America southeastward of this Isthmus. Of the 214 polytypic species, only 52 (24%) are endemic to one or the other of these two major regions. Although future studies may show that some monotypic species may have only subspecific status or may vary geographically and actually be classed as polytypic, the impressive

TABLE II.—General distributional patterns of monotypic (M) and polytypic (P) species of mammals

Orders	United States and southward into South America	United States and southward into Central America	United States and southward into Mexico*	Mexico* only	Mexico* and southward into South America	Mexico* and southward into Central America	Central America only	Central America and southward into South America
Marsupialia	M-0 P-1	M-0 P-0	M-0 P-0	M-0 P-0	M-0 P-2	M-0 P-2	M-2 P-0	M-0 P-4
Insectivora	M-0 P-0	M-0 P-0	M-0 P-3	M-14 P-3	M-0 P-0	M-1 P-2	M-14 P-0	M-0 P-0
Primates	M-0 P-0	M-0 P-0	M-0 P-0	M-0 P-0	M-0 P-2	M-0 P-0	M-1 P-1	M-1 P-3
Edentata	M-0 P-1	M-0 P-0	M-0 P-0	M-0 P-0	M-0 P-2	M-0 P-0	M-0 P-0	M-1 P-3
Lagomorpha	M-0 P-1	M-0 P-0	M-0 P-4	M-3 P-1	M-0 P-1	M-0 P-0	M-0 P-0	M-0 P-0
Rodentia	M-0 P-1	M-0 P-6	M-1 P-49	M-59 P-30	M-0 P-4	M-1 P-16	M-50 P-17	M-3 P-14
Carnivora	M-0 P-8	M-0 P-5	M-0 P-9	M-1 P-0	M-0 P-5	M-0 P-1	M-2 P-0	M-0 P-4
Perissodactyla	M-0 P-0	M-0 P-0	M-0 P-0	M-0 P-0	M-1 P-0	M-0 P-0	M-0 P-0	M-0 P-0
Artiodactyla	M-0 P-2	M-0 P-0	M-1 P-4	M-0 P-0	M-0 P-2	M-0 P-0	M-0 P-0	M-0 P-1
Totals	M-0 P-14	M-0 P-11	M-2 P-69	M-77 P-34	M-1 P-18	M-2 P-21	M-69 P-18	M-5 P-29

* In and northwestward of the Isthmus of Tehuantepec.

number of monotypic endemics reflects the variable habitats that have been available to mammals for adaptative radiation in Middle America.

If we include species that also occur in South America and in the United States, approximately one-half (74 species) of the 156 monotypic species occur only in Middle America southeastward of the Isthmus of Tehuantepec, while 79 are restricted to México, in and northwestward of the Isthmus. Three (only 2%) range into each

TABLE III.—Polytypic species occurring in South America and into Middle America but not so far as the Isthmus of Tehuantepec

Polytypic species (29)	Distribution in a northwestward direction from South America						
	Into Panama	Into Costa Rica	Into Nicaragua	Into Honduras, El Salvador	Into Guatemala	Into Yucatan Peninsula	Into Chiapas, Tabasco
<i>Chironectes minimus</i>	x	x	x	x	—	—	—
<i>Marmosa alstoni</i>	x	x	x	x	x	x	—
<i>M. mitis</i>	x	x	x	x	x	x	—
<i>Metachirus nudicaudatus</i>	x	x	x	—	—	—	—
<i>Aotus trivirgatus</i>	x	—	—	—	—	—	—
<i>Cebus capucinus</i>	x	x	x	x	—	—	—
<i>Ateles fusciceps</i>	x	—	—	—	—	—	—
<i>Myrmecophaga tridactyla</i>	x	x	x	x	x	x	—
<i>Bradypus griseus</i>	x	x	x	x	—	—	—
<i>Choloepus hoffmanni</i>	x	x	x	—	—	—	—
<i>Sciurus granatensis</i>	x	x	—	—	—	—	—
<i>Microsciurus alfari</i>	x	x	x	—	—	—	—
<i>M. flaviventer</i>	x	—	—	—	—	—	—
<i>Heteromys australis</i>	x	—	—	—	—	—	—
<i>Oryzomys albigularis</i>	x	—	—	—	—	—	—
<i>O. talamancæ</i>	x	x	—	—	—	—	—
<i>O. concolor</i>	x	x	—	—	—	—	—
<i>O. caliginosus</i>	x	x	x	—	—	—	—
<i>O. bicolor</i>	x	—	—	—	—	—	—
<i>Nectomys alfari</i>	x	x	x	—	—	—	—
<i>Hydrochaeris hydrochaeris</i>	x	—	—	—	—	—	—
<i>Dasyprocta punctata</i>	x	x	x	x	x	x	x
<i>Hoplomys gymnurus</i>	x	x	x	—	—	—	—
<i>Proechimys semispinosus</i>	x	x	x	—	—	—	—
<i>Speothus venaticus</i>	x	—	—	—	—	—	—
<i>Procyon cancrivorus</i>	x	x	—	—	—	—	—
<i>Bassaricyon gabbii</i>	x	x	x	—	—	—	—
<i>Felis tigrina</i>	x	x	—	—	—	—	—
<i>Mazama gouazoubira</i>	x	x	x	x	x	x	—
Totals at northern distributional limits	8	5	8	3	0	4	1

* Includes British Honduras.

region. In the case of the 214 generally wide-ranging polytypic species, 47 occur only in Middle America southeastward of the Isthmus of Tehuantepec, while 103 occur in México, in and northwestward of the Isthmus. Approximately 30 per cent (64 species) of the polytypic species occur in both regions.

MIDDLE AMERICAN MAMMALS THAT OCCUR ALSO IN SOUTH AMERICA

As one travels southeastward towards South America through subtropical and tropical parts of Middle America, an increasingly larger number of Neotropical mammals are observed. Although all mammals of Middle America that occur also in South America are included in this appraisal, it is not to be assumed that all species are of Neotropical origin but merely have this present distribution. Mammals known to occur in both areas include 6 monotypic and 61 polytypic species. This number represents only approximately 18 per cent of the total fauna.

MONOTYPIC SPECIES

Six Middle American monotypic species, that belong to 4 mammalian orders (Primates, Edentata, Rodentia, Perissodactyla), occur also in South America. Of these, Geoffroy's tamarin (*Saguinus geoffroyi*), the Darién pocket gopher (*Macrogeomys dariensis*), Rothschild's porcupine (*Coendou rothschildi*) and Darling's rat (*Diplomys darlingi*) live only in Panamá and eastward into South America. Only the tapir (*Tapirus bairdii*) ranges in Middle America as far northwestward as the Isthmus of Tehuantepec. The Central American five-toed armadillo (*Cabassous centralis*) reaches Guatemala. Perhaps the paucity in numbers in this category is partly the result of our meager knowledge of the mammalian fauna, especially at the Panamanian-Colombian border.

POLYTYPIC SPECIES

Sixty-one polytypic species belonging to 7 mammalian orders (see Tables III and IV) live in both Middle America and South America. Eighteen species belong to distinctly Neotropical orders (Marsupialia, Primates, Edentata), while some rodents, carnivores and ungulates also possess Neotropical affinities.

The ranges of 29 of the 61 polytypic species living also in South America do not reach the Isthmus of Tehuantepec (see Table III). Many of these species are widespread in tropical areas of South America. The majority (21 species) occur no farther northwestward into Middle America than Nicaragua.

Approximately one-half (32) of these polytypic species range northwestward into the Mexican area, beyond the Isthmus of Tehuantepec (see Table IV). The 18 species (belonging to 7 orders) which occur northwestward only as far as the Mexican area occupy, in México, only tropical and subtropical habitats in the Isthmus of Tehuantepec and, in some cases, along the two coastal plains. Of those species extending northwestward of the Isthmus, more live along the broader Gulf

Coastal Plain (14) than along the narrower Pacific Coastal Plain (7).

The 14 species reaching the United States include mostly wide-ranging carnivores. Only one rodent, the hispid cotton rat (*Sigmodon hispidus*), enjoys such an extensive distribution. Such ubiquitous species as the opossum (*Didelphis marsupialis*), eastern cottontail (*Sylvilagus floridanus*), gray fox (*Urocyon cinereoargenteus*), puma (*Felis concolor*), and white-tailed deer (*Odocoileus virginianus*) range northward into Canada. The presence of the margay (*Felis wiedii*) at the border between the United States and México is questionable, but the species does occur along the Gulf Coastal Plain in Tamaulipas. All 14 species live along the Gulf Coastal Plain and most probably used this avenue for their initial dispersal. At least 10 species also might have used the Pacific Coastal Plain for extensive movements, although most species have only limited distribution in Arizona and New México as compared with those occurring on the Gulf Coastal Plain in Texas. Five of the 14 species are confined in México to the coastal plains. The other 9 live also in other areas, with the puma and gray fox widespread in most parts of México.

MAMMALS COMMON TO CENTRAL AMERICA AND MEXICO IN AND
NORTHWESTWARD OF THE ISTHMUS OF
TEHUANTEPEC, BUT NOT FOUND IN SOUTH AMERICA

Two monotypic species and 21 polytypic species are distributed solely in Central America and in México, in and northwestward of the Isthmus of Tehuantepec. This assemblage represents only approximately 6 per cent of the 370 species in Middle America. Eleven other

TABLE IV.—Polytypic species occurring in South America and into the Mexican area northwestward of the Isthmus of Tehuantepec

Species ranging only as far as the Mexican area (18)	Species ranging into the United States (14)
<i>Philander opossum</i>	<i>Didelphis marsupialis</i>
<i>Caburmys derbianus</i>	<i>Dasyops novemcinctus</i>
<i>Alouatta villosa</i>	<i>Sylvilagus floridanus</i>
<i>Ateles geoffroyi</i>	<i>Sigmodon hispidus</i>
<i>Tamandua tetradactyla</i>	<i>Urocyon cinereoargenteus</i>
<i>Cyclopes didactylus</i>	<i>Nasua narica</i>
<i>Sylvilagus brasiliensis</i>	<i>Mustela frenata</i>
<i>Heteromys desmarestianus</i>	<i>Felis concolor</i>
<i>Oryzomys alfaroi</i>	<i>F. onca</i>
<i>Reithrodontomys mexicanus</i>	<i>F. pardalis</i>
<i>Agouti paca</i>	<i>F. wiedii</i>
<i>Potos flavus</i>	<i>F. yagouaroundi</i>
<i>Eira barbara</i>	<i>Tayassu tajacu</i>
<i>Galictis vittata</i>	<i>Odocoileus virginianus</i>
<i>Conepatus semistriatus</i>	
<i>Lutra annectens</i>	
<i>Tayassu albirostris</i>	
<i>Mazama americana</i>	

polytypic species having this distribution also range as far northward as the United States.

MONOTYPIC SPECIES

Of the two monotypic species that occur on both sides of the Isthmus of Tehuantepec, the Guatemalan small-eared shrew (*Cryptotis micrura*) occupies tropical habitats from Veracruz and Oaxaca southeastward into Costa Rica. The other species, the Oaxacan deer mouse (*Peromyscus oaxacensis*), apparently is found in only discontinuous mountainous areas of Oaxaca and Chiapas and southeastward.

POLYTYPIC SPECIES

Many of the polytypic species shared by both regions of Middle America are representatives of northern genera, which range widely in México, with 11 species occurring also in the United States. Species belonging to such genera as *Peromyscus*, *Canis* and *Mephitis* range as far southeastward as Costa Rica. Table V presents the distribution in Central America of the 21 species also found in México in and northwestward of the Isthmus of Tehuantepec but not reaching the United States. Most of these have continuous ranges across the Isthmus in tropical habitats and are fairly widely distributed in Central America. Some, for example, Saussure's shrew (*Sorex saussurei*), and the small-toothed harvest mouse (*Reithrodontomys microdon*), live in disjunct mountainous areas on either side of the lowlands of the Isthmus. The 11 wide-ranging species that occur as far northwestward as the United States (see Table VI) have continuous ranges in the lowlands across the Isthmus with the probable exception of the southern flying squirrel (*Glaucomys volans*), which lives only in disjunct highlands. Seven of these 11 species live southeastward at least as far as Honduras.

Tables V and VI present also the distribution in various major areas in México of polytypic mammals also found in Central America. Most polytypic species that span the Isthmus but do not range as far northwestward as the United States live chiefly on the two tropical coastal plains (see Table V). Two species, the variegated squirrel (*Sciurus variegatoides*) and Peters' climbing rat (*Tylomys nudicaudus*), occur only in the Isthmus area. Four species, Saussure's shrew (*Sorex saussurei*), Verapaz shrew (*Sorex veraepacis*), the small-toothed harvest mouse (*Reithrodontomys microdon*) and Sumichrast's harvest mouse (*Reithrodontomys sumichrasti*), have disjunct montane distributions on either side of the Isthmus. The plateau mouse (*Peromyscus melanophrys*) reaches Chiapas but enjoys its greatest distribution on the southern part of the Mexican Central Plateau. For the 11 species that also range into the United States (see Table VI), distribution in Mexican areas is fairly general, with at least 8 species occurring in desert or semidesert situations of the Mexican Central Plateau. All species, with the exception of the southern flying squirrel (*Glaucomys volans*), live on one or both of the coastal plains.

TABLE V.—Distribution in México, in and northwestward of the Isthmus of Tehuantepec, of endemic Middle American polytypic species occurring also southeastward of the Isthmus

Polytypic species (21)	Gulf Coast	Sierra Madre Oriental	Central Plateau	Sierra Madre Occidental	Pacific Coast	Trans-Mexican Volcanic Belt	Sierra Madre del Sur	Isthmus of Tehuantepec only	Limit in Southeastern Central America
<i>Marmosa canescens</i>					X				Yucatán Peninsula
<i>M. mexicanus</i>	X				X				Panamá
<i>Sorex saussurei</i>		X		X		X	X		Guatemala
<i>S. veraepacis</i>							X		Guatemala
<i>Sciurus aureogaster</i>	X								Chiapas
<i>S. deppii</i>	X								Costa Rica
<i>S. variegatoides</i>								X	Panamá
<i>Orthogeomys grandis</i>	X				X		X		Honduras
<i>Heterogeomys hispidus</i>	X				X				Guatemala
<i>Liomys pictus</i>	X				X				Guatemala
<i>Oryzomys fulvescens</i>	X				X			X	Panamá
<i>O. melanotis</i>	X				X				Yucatán Peninsula
<i>Tylomys nudicaudus</i>								X	Nicaragua
<i>Nyctomys sumichrasti</i>	X				X				Panamá
<i>Reithrodontomys microdon</i>									Panamá
<i>R. sumichrasti</i>	X					X	X		Panamá
<i>Baiomys musculus</i>									Nicaragua
<i>Peromyscus melanophrys</i>	X		X						Chiapas
<i>P. mexicanus</i>	X								Costa Rica
<i>Coendou mexicanus</i>	X				X				Panamá
<i>Bassarisca sumichrasti</i>	X				X				Panamá
Totals	12	1	1	1	10	3	5	3	

TABLE VI.—Distribution in México, in and northward of the Isthmus of Tehuantepec, of polytypic species ranging from the United States southeastward into Central America

Polytypic Species (11)	Gulf Coast	Sierra Madre Oriental	Central Plateau	Sierra Madre Occidental	Pacific Coast	Trans-Mexican Volcanic Belt	Sierra Madre del Sur	Southeastern Limit in Central America
<i>Glaucomys volans</i>	—	X	—	X	—	X	X	Honduras
<i>Oryzomys palustris</i>	X	—	?	—	X	—	—	Costa Rica
<i>Reithrodontomys fulvescens</i>	X	—	X	—	X	—	—	Costa Rica
<i>Peromyscus boylii</i>	—	X	X	X	X	X	X	Honduras
<i>P. leucopus</i>	X	—	X	—	X	—	—	Yucatán Peninsula
<i>Neotoma mexicana</i>	—	X	—	X	X	X	X	Honduras
<i>Canis latrans</i>	X	?	X	?	X	?	?	Costa Rica
<i>Procyon lotor</i>	X	X	X	X	X	X	X	Panamá
<i>Spilogale putorius</i>	X	—	X	—	—	—	—	Costa Rica
<i>Mephitis macroura</i>	—	X	X	X	X	X	X	Nicaragua
<i>Conepatus mesoleucus</i>	—	—	X	—	X	—	—	Nicaragua
Totals	6	5	8	5	9	5	5	

TABLE VII.—(continued)

Polytypic species (69)	DISTRIBUTION IN MEXICO								Totals
	Gulf Coast	Sierra Madre Oriental	Plateau, north	Plateau, south	Sierra Madre Occidental	Pacific Coast	Trans-Mexican Volcanic Belt	Sierra Madre del Sur	
<i>Onychomys leucogaster</i>	X	—	—	—	—	—	—	—	—
<i>O. torridus</i>	—	—	X	X	—	X	—	—	—
<i>Sigmodon fulviventris</i>	—	—	X	X	—	—	—	—	—
<i>S. ochrognathus</i>	—	X	—	—	?	—	—	—	—
<i>Neotoma albigula</i>	—	—	X	X	—	X	—	—	—
<i>N. lepida</i>	—	—	—	—	—	X	—	—	—
<i>N. micropus</i>	X	—	—	—	—	X	—	—	—
<i>Microtus mexicanus</i>	—	X	—	—	X	—	X	—	—
<i>Erethizon dorsatum</i>	—	X	—	—	X	—	—	—	—
<i>Canis lupus</i>	—	X	X	X	X	?	X	—	—
<i>Vulpes macrotis</i>	—	—	X	—	—	X	—	—	—
<i>Ursus americanus</i>	—	X	—	—	X	—	—	—	—
<i>U. arctos</i>	—	X	—	—	X	—	—	—	—
<i>Bassariscus astutus</i>	?	X	—	X	X	X	X	X	X
<i>Taxidea taxus</i>	—	—	X	X	—	X	—	—	—
<i>Mephitis mephitis</i>	X	X	X	—	X	—	—	—	—
<i>Conepatus leuconotus</i>	X	—	—	—	—	—	—	—	—
<i>Lynx rufus</i>	X	X	X	X	X	X	X	X	—
<i>Odocoileus hemionus</i>	—	—	X	X	—	X	—	—	—
<i>Antilocapra americana</i>	X	—	X	X	—	X	—	—	—
<i>Bison bison</i>	X	—	X	—	—	—	—	—	—
<i>Ovis canadensis</i>	—	X	X	—	X	—	—	—	—
Totals	23	17	42	30	19	32	10	5	1

MAMMALS DISTRIBUTED IN MEXICO, IN AND NORTHWESTWARD
OF THE ISTHMUS OF TEHUANTEPEC, AND NORTHWARD
INTO THE UNITED STATES

Ninety-six mammals (2 monotypic species and 94 polytypic species) are common to Middle America and the United States. This number represents approximately 26 per cent of all 370 mammals in Middle America. Of this group, the 2 monotypic species and 69 of the 94 polytypic species occur in México no further southeastward than the Isthmus of Tehuantepec.

MONOTYPIC SPECIES

Only two monotypic species are common to México and the United States. One, the Texas antelope squirrel (*Ammospermophilus interpres*), lives in an extensive area on the northern part of the Central Plateau. The other, Merriam's elk (*Cervus merriami*), a recently extinct species, probably occurred at one time in the Sierra Madre Occidental of Chihuahua (Hall and Kelson, 1959:1003).

POLYTYPIC SPECIES

Of the 103 polytypic species which occur in Middle America, only in and northwestward of the Isthmus of Tehuantepec, 69 (67%) also range into the United States. Of interest also is that almost one-half (94 species) of all of the 214 polytypic species in Middle America range into the United States (see Table II).

Table VII lists the 69 polytypic species which occur in the United States and southward into México, northwestward of the Isthmus of Tehuantepec. Most of these species inhabit places in northern México although one species, the ringtail (*Bassariscus astutus*), reaches the Isthmus of Tehuantepec. The area containing the most mammals common to both countries is the northern part of the Central Plateau. Forty-two of the 69 species occur in this area with continuous distributions into western United States. The majority of these 42 species are restricted to desert or semidesert. The two coastal plains also are well endowed with mammals having intercountry distribution; 23 species live on the Gulf Coastal Plain while 32 live on the Pacific Coastal Plain. Intercountry montane species are fewer than those occupying lowlands. The western Sierra Madre Occidental provides range for 19 species while the eastern Sierra Madre Oriental provides for 17 species. In both cases, the ranges of many montane species are interrupted by discontinuous highlands at the border of the two countries. The impressive number of species common to each of these countries emphasizes the role in mammalian speciation of the arid and semiarid parts of northern México and southwestern United States.

DISTRIBUTION OF ENDEMIC SPECIES

Almost all (148 of 156) of the monotypic species and one-third (73 of 214) of the polytypic species are endemic in Middle America.

TABLE VIII.—Distribution of monotypic species endemic to Middle America, east and south of the Isthmus of Tehuantepec

Monotypic species (69)	Chiapas, Tabasco	Yucatan Peninsula	Guatemala	Honduras, El Salvador	Nicaragua	Costa Rica	Panama
<i>Monodelphis melanops</i>	—	—	—	—	—	—	×
<i>Marmosa invicta</i>	—	—	—	—	—	—	×
<i>Sorex sclateri</i>	×	—	—	—	—	—	—
<i>S. stizodon</i>	×	—	—	—	—	—	—
<i>Cryptotis endersi</i>	—	—	—	—	—	—	×
<i>C. goodwini</i>	—	—	×	—	—	—	—
<i>C. gracilis</i>	—	—	—	—	—	×	—
<i>C. griseoventris</i>	×	—	—	—	—	—	—
<i>C. jacksoni</i>	—	—	—	—	—	×	—
<i>C. mayensis</i>	—	×	—	—	—	—	—
<i>C. mera</i>	—	—	—	—	—	—	×
<i>C. nigrescens</i>	—	—	—	×	?	×	—
<i>C. olivacea</i>	—	—	—	—	×	—	—
<i>C. orophila</i>	—	—	—	—	—	×	—
<i>C. tersus</i>	—	—	—	—	—	×	—
<i>C. zeteki</i>	—	—	—	—	—	—	×
<i>Aotus bipunctatus</i>	—	—	—	—	—	—	×
<i>Sciurus richmondi</i>	—	—	—	—	×	—	—
<i>Syntheosciurus brochus</i>	—	—	—	—	—	—	×
<i>S. poasensis</i>	—	—	—	—	—	×	—
<i>Microsciurus boquetensis</i>	—	—	—	—	—	—	×
<i>Orthogeomys pygacanthus</i>	—	—	—	×	—	—	—
<i>Macrogeomys matagalpae</i>	—	—	—	—	×	—	—
<i>M. underwoodi</i>	—	—	—	—	—	×	—
<i>Liomys adspersus</i>	—	—	—	—	—	—	×
<i>L. anthonyi</i>	—	—	×	—	—	—	—
<i>L. heterothrix</i>	—	—	×	×	—	—	—
<i>L. pinetorum</i>	×	—	—	—	—	—	—
<i>Heteromys gaumeri</i>	—	×	—	—	—	—	—
<i>H. goldmani</i>	×	—	×	—	—	—	—
<i>H. longicaudatus</i>	×	—	—	—	—	—	—
<i>Oryzomys aphantus</i>	—	—	—	—	—	×	—
<i>O. azuerensis</i>	—	—	—	—	—	—	×
<i>O. devius</i>	—	—	—	—	—	×	×
<i>O. gatunensis</i>	—	—	—	—	—	—	×
<i>Neacomys pictus</i>	—	—	—	—	—	—	×
<i>Nectomys dimidiatus</i>	—	—	—	—	×	—	—
<i>Rhipidomys scandens</i>	—	—	—	—	—	—	×
<i>Tylomys bullaris</i>	×	—	—	—	—	—	—
<i>T. fulviventer</i>	—	—	—	—	—	—	×
<i>T. panamensis</i>	—	—	—	—	—	—	×
<i>T. tumbalensis</i>	×	—	—	—	—	—	—
<i>T. watsoni</i>	—	—	—	—	—	×	×
<i>Ototylomys connectens</i>	—	—	×	—	—	—	—
<i>Otonyctomys hatti</i>	—	×	—	—	—	—	—
<i>Reithrodontomys brevirostris</i>	—	—	—	—	×	×	—

Of these, 87 mammals (69 monotypic species and 18 polytypic species) are confined to Middle America southeast of the Isthmus of Tehuantepec. Within México, in and northwest of the Isthmus of Tehuantepec, 111 endemic mammals (77 monotypic species and 34 polytypic species) live. These figures, as might be expected, show a high rate of endemism for the generally restricted monotypic species (94%) and a low rate for the generally wide-ranging polytypic species (24%).

ENDEMIC MONOTYPIC SPECIES

In Table VIII is presented a list of the 69 monotypic species confined to Middle America, southeast of the Isthmus of Tehuantepec. More than one-third (38%) are known from Panamá; endemics are least common in the Yucatán Peninsula (including British Honduras). Fifty species belong to the order Rodentia while 14 are insectivores.

Seventy-seven monotypic species are endemic to México, in and north of the Isthmus. In Table IX, these species are totaled according to the major areas in which they are now known to live. All but 7 species are restricted to a single major area. One species, the black-

TABLE VIII.—(continued)

Monotypic species (69)	Chiapas, Tabasco	Yucatan Peninsula	Guatemala	Honduras, El Salvador	Nicaragua	Costa Rica	Panamá
<i>R. creper</i>	—	—	—	—	—	×	×
<i>R. darienensis</i>	—	—	—	—	—	—	×
<i>R. rodriguezi</i>	—	—	—	—	—	×	—
<i>R. tenuirostris</i>	—	—	×	—	—	—	—
<i>Peromyscus allophylus</i>	×	—	—	—	—	—	—
<i>P. attilaneus</i>	—	—	×	—	—	—	—
<i>P. flavidus</i>	—	—	—	—	—	—	×
<i>P. grandis</i>	—	—	×	—	—	—	—
<i>P. hondurensis</i>	—	—	—	×	—	—	—
<i>P. lophurus</i>	×	—	×	—	—	—	—
<i>P. pirrensis</i>	—	—	—	—	—	—	×
<i>P. stirtoni</i>	—	—	—	×	—	—	—
<i>P. zarhynchus</i>	×	—	—	—	—	—	—
<i>Scotinomys harrisi</i>	—	—	—	—	—	×	—
<i>S. longipilosus</i>	—	—	—	—	—	×	—
<i>S. xerampelinus</i>	—	—	—	—	—	—	×
<i>Neotoma chrysomelas</i>	—	—	—	×	×	—	—
<i>Rheomys hartmanni</i>	—	—	—	—	—	—	×
<i>R. raptor</i>	—	—	—	—	—	—	×
<i>R. underwoodi</i>	—	—	—	—	—	×	×
<i>Microtus guatemalensis</i>	—	—	×	—	—	—	—
<i>Bassaricyon lasius</i>	—	—	—	—	—	×	—
<i>B. pauli</i>	—	—	—	—	—	—	×
Totals	11	3	10	6	6	17	26

eared mouse (*Peromyscus melanotis*), ranges, seemingly without geographic variation, in discontinuous montane areas in northeast, northwest and central México. More than one-half (41 species) of the endemics dwell in tropical areas, especially upper humid tropics, which occupy the lower mountain sides facing both coastal plains. Fifteen species occur in this situation facing the Gulf Coastal Plain. The southern part of the Central Plateau holds 15 species. The arid tropics of the Gulf Coastal Plain provides for only one endemic mammal, the Tamaulipas mole (*Scalopus inflatus*). This relative of the temperate-living eastern mole (*Scalopus aquaticus*) occupies only a marginal tropical area near the Río Grande in extreme northeastern Tamaulipas.

ENDEMIC POLYTYPIC SPECIES

Eighteen polytypic species (listed in Table X) are endemic to Middle America southeast of the Isthmus of Tehuantepec. Twelve species belong to genera with Neotropical affinities. Except for one primate, all species are rodents. Most species are recorded from more than one of the political divisions; some are widespread within the area. This list includes species in various areas: montane and tropical; with various adaptations: arboreal, terrestrial and fossorial. Eleven of the species occur in the variable habitats of Costa Rica.

The 34 polytypic species endemic to México, in and northwestward of the Isthmus, include 3 insectivores, 1 lagomorph and 30 rodents (see Table XI). As in the case of monotypic endemics, the southern part of the Central Plateau seems to provide an environment for diversification. Most of the 11 polytypic species known from this area are fossorial pocket gophers. The northern part of the Central Plateau lacks representative polytypic endemics. Fourteen endemics live in arid or humid tropical environments on the Pacific side while two live

TABLE IX.—Distribution of monotypic species endemic to México, in and northwest of the Isthmus of Tehuantepec

Orders	Distribution of species							
	Gulf Coast	Sierra Madre Oriental	Central Plateau	Sierra Madre Occidental	Pacific Coast	Trans-Mexican Volcanic Belt	Sierra Madre del Sur	Isthmus of Tehuantepec
Insectivora (14 species)	4	3	1	0	2	1	1	2
Lagomorpha (3 species)	0	0	0	0	0	1	1	1
Rodentia (59 species)	12	3	17	6	11	5	5	8
Carnivora (1 species)	0	0	0	0	1	0	0	0
Totals	16	6	18	6	14	7	7	11

on humid tropical mountain slopes on the Gulf side. Montane endemics are usually widespread, with the distribution of most species centered in the Trans-Mexican Volcanic Belt of south-central México and the Sierra Madre del Sur rather than in the northern mountains.

DISTRIBUTION AND GEOGRAPHIC VARIATION OF MEXICAN MAMMALS

Students of mammalian systematics have described numerous subspecies among the 167 polytypic, terrestrial species included herein as being found in México, in and northwest of the Isthmus of Tehuantepec. Taxonomists have used various means by which to distinguish geographic variation. Some have had large numbers of specimens to study; others have had few. It is not the purpose here to examine or criticize methodology, but to point out that subspecific names of Mexican mammals have been arrived at by no standardized plan. More often than not the describers made little effort to discuss ecological factors which might have played some causal role in the geographic variation. Even so, study of the distributions of subspecies of these mammals shows that there are some distinctive, over-all geographic patterns in this described variation. The boundary between two unlike habitats (for example, lowland and highland or grassland and desert) may be a common place of intergradation between subspecies of several

TABLE X.—Distribution of polytypic species endemic to Middle America, east and south of the Isthmus of Tehuantepec

Polytypic species (18)	Chiapas, Tabasco	Yucatan Peninsula*	Guatemala	Honduras, El Salvador	Nicaragua	Costa Rica	Panama
<i>Saimiri orstedii</i>	—	—	—	—	—	×	×
<i>Sciurus griseoflavus</i>	×	×	×	—	—	—	—
<i>S. yucatanensis</i>	×	×	×	—	—	—	—
<i>Macrogeomys cavator</i>	—	—	—	—	—	×	×
<i>M. cherriei</i>	—	—	—	—	—	×	—
<i>M. heterodus</i>	—	—	—	—	—	×	—
<i>Liomys crispus</i>	×	—	×	—	—	—	—
<i>L. salvini</i>	—	—	×	×	×	×	—
<i>Oryzomys bombycinus</i>	—	—	—	—	—	×	×
<i>Ototylomys brevirostris</i>	—	×	—	—	—	—	—
<i>O. phyllotis</i>	×	×	×	×	×	×	—
<i>Reithrodontomys gracilis</i>	×	×	×	×	×	×	—
<i>Peromyscus guatemalensis</i>	×	—	×	×	—	—	—
<i>P. nudipes</i>	—	—	—	—	—	×	×
<i>P. yucatanicus</i>	—	×	—	—	—	—	—
<i>Zygodontomys cherriei</i>	—	—	—	—	—	×	×
<i>Scotinomys tenguina</i>	×	?	×	×	×	×	×
<i>Rheomys thomasi</i>	×	—	?	×	—	—	—
Totals	8	6	8	6	4	11	6

* Includes British Honduras.

kinds of mammals occurring in both areas and may be a distributional barrier to others. It is the purpose here to appraise and define some of the major barriers to the dispersal of both monotypic and polytypic species and the major areas of intergradation in the geographic variation of polytypic species in México.

The principal distributional areas of México, in and northwest of the Isthmus of Tehuantepec, are grouped herein as subtropical and

TABLE XI.—Distribution of polytypic species endemic to México, in and northwestward of the Isthmus of Tehuantepec

Polytypic species (34)	Gulf Coast	Sierra Madre Oriental	Central Plateau	Sierra Madre Occidental	Pacific Coast	Trans-Mexican Volcanic Belt	Sierra Madre del Sur	Isthmus of Tehuantepec
<i>Sorex oreopolus</i>	—	—	—	×	—	×	×	—
<i>Cryptotis mexicana</i>	×	×	—	—	—	?	×	—
<i>C. pergracilis</i>	×	×	×	?	—	—	—	—
<i>Sylvilagus cunicularis</i>	—	—	×	—	×	?	?	—
<i>Eutamias bulleri</i>	—	×	—	×	—	—	—	—
<i>Citellus annulatus</i>	—	—	—	—	×	—	—	—
<i>C. odocetus</i>	—	—	—	—	×	—	—	—
<i>Sciurus colliaei</i>	—	—	—	—	×	—	—	—
<i>S. nelsoni</i>	—	—	—	—	—	×	—	—
<i>S. oculatus</i>	—	×	—	—	—	×	—	—
<i>S. polioopus</i>	—	—	—	—	×	×	×	—
<i>S. socialis</i>	—	—	—	—	×	—	—	×
<i>Zygoeomys trichopus</i>	—	—	—	—	—	×	—	—
<i>Pappogeomys bulleri</i>	—	—	×	—	×	—	—	—
<i>Cratogeomys fulvescens</i>	—	—	×	—	—	—	—	—
<i>C. gymnurus</i>	—	—	×	—	—	×	—	—
<i>C. merriami</i>	—	—	×	—	—	×	—	—
<i>C. perotensis</i>	—	—	×	—	—	×	—	—
<i>C. tylorhinus</i>	—	—	×	—	—	—	—	—
<i>C. zinseri</i>	—	—	×	—	—	—	—	—
<i>Perognathus goldmani</i>	—	—	—	—	×	—	—	—
<i>P. lineatus</i>	—	—	×	—	—	—	—	—
<i>P. pernix</i>	—	—	—	—	×	—	—	—
<i>Dipodomys phillipsii</i>	—	—	×	—	—	—	—	—
<i>Reithrodontomys chrysopsis</i>	—	—	—	—	—	×	—	—
<i>Peromyscus banderanus</i>	—	—	—	—	×	—	—	×
<i>P. hylocetes</i>	—	—	—	—	—	×	×	—
<i>P. megalops</i>	—	—	—	—	×	—	×	—
<i>P. perfulvus</i>	—	—	?	—	×	—	—	—
<i>Sigmodon alticola</i>	—	×	?	—	—	×	×	—
<i>S. planifrons</i>	—	—	—	—	×	—	—	—
<i>Neotomodon alstoni</i>	—	—	—	—	—	×	—	—
<i>Neotoma alleni</i>	—	—	—	—	×	—	—	—
<i>Nelsonia neotomodon</i>	—	—	—	×	—	—	—	—
Totals	2	5	11	3	14	12	6	2

tropical lowlands, including adjacent tropical mountain slopes bordering the 2 sea coasts, the semiarid and arid Central Plateau, and the sub-boreal and boreal mountain ranges (see Figure 1). Table XII totals the number of species found in each of these major areas. As might be expected, tropical areas are endowed with approximately twice as many species as montane areas. The remarkably large number of Plateau species emphasizes this area's frequently underestimated role in speciation of Mexican mammals.

COASTAL LOWLANDS AND THE CENTRAL PLATEAU

México, in and northwest of the Isthmus of Tehuantepec, has 3 major nonmontane areas: the Gulf Coastal Plain on the eastern side, the Pacific Coastal Plain on the western side and the elevated Central Plateau. Mountainous slopes and inland streamways bearing tropical and subtropical vegetation also are included with the appropriate coastal area. Although the 2 coastal plains may be blanketed with dense thorn shrub (in arid tropical situations) or with rain forest and jungle (in humid tropical situations), much of this lowland may be covered with desert shrub or open grassland, especially to the northward. These latter areas provide habitats not unlike some of those found on the generally more arid Central Plateau. Accordingly, there is considerable overlap in species composition between these 3 major areas.

GULF COASTAL PLAIN, NORTH OF THE ISTHMUS OF TEHUANTEPEC

The lowlands bordering the Gulf of México are broad to the northwestward, at the Texas border, and narrow to the southeastward, in Veracruz at the beginning of the Isthmus of Tehuantepec. Aridity is a feature of the temperate semidesert shrub and grassland in eastern Coahuila, Nuevo León and northwestern Tamaulipas. The arid subtropical shrub in eastern Tamaulipas extends southeastward, with a progressively increasing number of tropical plants, along the coast into Veracruz. Humid tropical conditions generally prevail in the Isthmus

TABLE XII.—Distribution of mammals in major habitats of México, in and northwest of the Isthmus of Tehuantepec

Habitat	Monotypic species	Polytypic species	Totals
Gulf Coastal Plain*	17	70	87
Pacific Coastal Plain*	15	84	99
Isthmus of Tehuantepec	13	63	76
Central Plateau	19	76	95
Sierra Madre Oriental	6	33	39
Sierra Madre Occidental	7	34	41
Trans-Mexican Volcanic Belt	7	35	42
Sierra Madre del Sur	7	26	33

* Not including Isthmus of Tehuantepec; including also submontane tropical habitats.

of Tehuantepec and along the borders of coastal streams. Northwestward the humid environment gradually moves inland and ultimately along the eastern face of the Sierra Madre Oriental. Humid tropical conditions in these foothills occur as far northwestward as southern Tamaulipas and perhaps even into southern Nuevo León. Eighty-seven mammals live in this area (see Table XII). The transition between the temperate open lands and the arid and humid tropical environments is an important area of intergradation between coastal subspecies. The most notable break seems to be at approximately 23° N latitude.

Monotypic species—Seventeen monotypic species (see Table XIII) occur along the Gulf side of México. The ranges of these species do not overlap latitude 23° N, and only one species, the Tamaulipas mole (*Scalopus inflatus*), lives north of this latitude. The other 16 live to the southward in more tropical areas, with 4 species ranging at least to the Isthmus of Tehuantepec. Most species occur in submontane humid tropical areas. This prominent humid belt along the east-facing slopes seems to have been an important place for speciation and, because of the disjunct nature of these areas, probably for the survival of relict species as well.

Polytypic species—Seventy polytypic species (totaled in Table XIV) live in coastal areas, including tropical vegetation in the foothills of the Sierra Madre Oriental. Few of these species are endemic to México, northwestward of the Isthmus of Tehuantepec. Most range either into the United States or southeastward in Central America or into both regions. As previously stated, the Gulf Coastal Plain has been a major avenue for north-south movements by lowland mammals.

TABLE XIII.—Distribution of monotypic species on the coastal plains of Mexico, west and northwest of the Isthmus of Tehuantepec

Gulf Coastal Plain (17)	Pacific Coastal Plain (15)
<i>Sorex macrondon</i> *	<i>Notiosorex gigas</i> *
<i>Cryptotis magna</i> *	<i>Cryptotis guerrensis</i> *
<i>C. micrura</i>	<i>Cratogeomys fumosus</i>
<i>C. nelsoni</i> *	<i>Liomys annectens</i> *
<i>Scalopus inflatus</i>	<i>L. guerrensis</i> *
<i>Heterogeomys lanius</i>	<i>Heteromys nigricaudatus</i> *
<i>Heteromys lepturus</i> *	<i>Reithrodontomys burti</i>
<i>H. temporalis</i>	<i>R. hirsutus</i>
<i>Tylomys gymnurus</i>	<i>Sigmodon alleni</i> *
<i>Peromyscus fuvvus</i> *	<i>Neotoma palatina</i>
<i>P. latirostris</i> *	<i>N. phenax</i>
<i>P. nelsoni</i> *	<i>Sigmodon guerrensis</i> *
<i>P. ochraventer</i> *	<i>Microtus umbrosus</i> *
<i>P. simulatus</i> *	<i>Xenomys nelsoni</i>
<i>Neotoma angustapalata</i> *	<i>Spilogale pygmaea</i>
<i>Microtus quasiater</i> *	
<i>Dasyprocta mexicana</i>	

* Submontane tropical in distribution.

Approximately 23° N latitude marks the boundary for the distributions of more than one-half (45 species) of these mammals. The 18 species found only to the northward include many species widely distributed in open, temperate lands of the American Southwest; among them are the desert cottontail (*Sylvilagus audubonii*), the black-tailed jack rabbit (*Lepus californicus*), the hispid pocket mouse (*Perognathus hispidus*), Merriam's pocket mouse (*Perognathus merriami*), the northern grasshopper mouse (*Onychomys leucogaster*), and the pronghorn (*Antilocapra americana*).

The 27 species found only southward of latitude 23° N are tropical in distribution. Mammals found here that range also into South America include the four-eyed opossum (*Philander opossum*), the woolly opossum (*Caluromys derbianus*), Geoffroy's spider monkey (*Ateles geoffroyi*), the tamandua (*Tamandua tetradactyla*), the forest rabbit (*Sylvilagus brasiliensis*), Alfaro's rice rat (*Oryzomys alfaro*), the spotted cavy (*Agouti paca*), the kinkajou (*Potos flavus*), the grison (*Galictis vittata*), the tayra (*Eira barbara*), and the red brocket (*Mazama americana*).

Seventeen of the 25 species that cross latitude 23° N show intergradation between subspecies in this general zone with distinctive, named subspecies on either side. Most rodents and even most carnivores vary geographically along this coastal strip. Forty-one of all species (52) that occur south of latitude 23° N also range at least as far southeastward as the Isthmus of Tehuantepec.

Forty of the 70 species live also on the Pacific Coastal Plain, with more than three-fourths (32 species) subspecifically different from their relatives on the Gulf side of México. Most of these 40 species probably obtained this bicoastal distribution by way of the Isthmus of Tehuantepec, although many of the mammals found only in the north-

TABLE XIV.—Distribution of polytypic species in the Gulf Coastal Plain, west and northwest of the Isthmus of Tehuantepec

Orders	Totals	North of 23° N only	South of 23° N only	Both North and South of 23° N	Geogr. var.	Also on Pacific Coast	Geogr. var. between Coasts
Marsupialia	4	0	3	1	1	2	1
Insectivora	3	1	1	1	0	1	1
Primates	1	0	1	0	0	1	0
Edentata	2	0	1	1	0	2	0
Lagomorpha	4	2	1	1	1	1	1
Rodentia	29	9	13	7	5	14	13
Carnivora	22	4	6	12	8	16	13
Artiodactyla	5	2	1	2	2	3	3
Totals	70	18	27	25	17	40	32

ern part of the Gulf Coast probably spread to the two coasts by way of the American Southwest. The population of the desert shrew (*Notiosorex crawfordi*), in the latter group, on the Pacific Coast may be specifically, instead of subspecifically, different from the population on the Gulf Coast and in southwestern United States (see Jones *et al.*, 1962:147-151).

Twenty-eight of the 70 species also occur on the Central Plateau, with 22 subspecifically different in each area. Ten (including 7 widely distributed carnivores) of the coastal species range into the higher parts of the adjacent Sierra Madre Oriental, with only 2 classed as being distinctive at the subspecific level.

PACIFIC COASTAL PLAIN, NORTH OF THE ISTHMUS OF TEHUANTEPEC

In contrast with the Gulf Coastal Plain, the lowlands bordering the Pacific Ocean are narrow, although broadening somewhat at the United States boundary in Sonora. Desert conditions in Sonora gradually grade into arid tropics to the southeastward with humid tropical environments found generally inland in the foothills of the Sierra Madre Occidental and along coastal stream courses. Insofar as mammalian distribution and geographic variation are concerned, the most conspicuous break is at approximately 25° N latitude, which separates generally desert conditions from arid tropical conditions. Submontane humid tropical areas are less prominent on the drier west-facing slopes of the Sierra Madre Occidental than on the wetter, east-facing slopes of the Sierra Madre Oriental on the Gulf side. Even so, some species are restricted to this kind of habitat in western México. Ninety-nine mammals live on the Pacific Coastal Plain (see Table XII).

Monotypic species—Fifteen monotypic species occur along the Pacific Coastal Plain (see Table XIII). At least 9 of these species occupy, wholly or partly, arid or humid tropical environments on the

TABLE XV.—Distribution of polytypic species on the Pacific Coastal Plain, west and north of the Isthmus of Tehuantepec

Orders	Totals	North of 25° only	South of 25° only	Both North and South of 25° N	Geogr. var.
Marsupialia	3	0	2	1	0
Insectivora	1	0	1	0	0
Primates	1	0	1	0	0
Edentata	2	0	2	0	0
Lagomorpha	3	1	1	1	1
Rodentia	50	22	20	8	8
Carnivora	20	2	7	11	4
Artiodactyla	4	2	0	2	1
Totals	84	27	34	23	14

western slopes of the Sierra Madre Occidental or inland along such major streams as the Río Balsas. All species present are endemic to this part of México. Only Burt's harvest mouse (*Reithrodontomys burti*) and the Sonoran wood rat (*Neotoma phenax*) occur north of latitude 25° N and inhabit arid, subtropical situations. No species ranges overlap this latitude.

Polytypic species—Eighty-four polytypic species live along the Pacific Coastal Plain (totaled in Table XV). As previously stated, the Gulf Coastal Plain probably has been the major avenue for north-south movements by lowland mammals. Even so, fewer polytypic species now live on the Gulf side (70 species) than on the Pacific side (84 species). Most of this majority on the Pacific Coast results from the presence of a large desert-living contingent (at least 20 species) that has flourished in Sonora and southwestern United States. On the Gulf Coast this southwestern element is much less conspicuous.

More than three-fourths (61 species) of the 80 mammals occur either north or south of latitude 25° N. Most of the 27 species confined to the northward of this latitude frequent arid shrub country and desert. Mammals of the American Southwest that reach this area include 7 species of pocket mice (genus *Perognathus*), 3 species of kangaroo rats (genus *Dipodomys*), 4 species of lowland mice (genus *Peromyscus*), and the kit fox (*Vulpes macrotis*).

The 34 species occurring only southeastward of latitude 25° N are generally tropical in distribution. Several species are endemic to the southern part of the Pacific Coast. These include the ring-tailed ground squirrel (*Citellus annulatus*), the Michoacán deer mouse (*Peromyscus banderanus*), the marsh mouse (*Peromyscus perfulvus*) and Allen's wood rat (*Neotoma alleni*). Many of these tropical species range inland considerable distances along such streams as the Río Balsas.

Of the 23 species whose distributions cross latitude 25° N, 14 have been found to exhibit geographic variation in the area, with zones of intergradation between distinctive subspecies occurring at or near this latitude. As might be expected, this line marks a subspecific division for all 8 rodents. These include the localized species, Collie's squirrel (*Sciurus colliaei*) and the Sinaloan pocket mouse (*Perognathus pernix*).

Of 53 species that occur southward of latitude 25° N, 42 range southeastward at least to the Isthmus of Tehuantepec. Thirty-five of all 84 coastal species live also on the Central Plateau, with 25 considered as being different subspecies in each area. Only 13 (mostly carnivores) of the coastal species occur in the highlands of the adjacent Sierra Madre Occidental.

ISTHMUS OF TEHUANTEPEC

This narrow strip of land, only approximately 130 miles wide (north to south), has long been a busy avenue to intercontinental movements by mammals. Although montane and other nontropical mammals

must have passed through this corridor in the geologic past, the present low, hilly relief in the Isthmus now supports mostly tropical-adapted inhabitants. The northern Gulf side is generally humid tropical environment while the southern Pacific side is generally arid tropical environment. The border between these areas marks a zone of intergradation between subspecies for some polytypic species and a barrier for other species. At the present time 13 monotypic species and 63 polytypic species are known to live in the Isthmus (see Table XII).

Monotypic species—Thirteen monotypic species (see Table XVI) live in the hilly lowlands of the Isthmus. Although collecting of mammals in this area has been confined principally to the vicinity of railroads and recently constructed highways, there are sufficient data on distribution to detect a division of the monotypic species into Gulf-side and Pacific-side groups. Species such as the Tehuantepec jack rabbit (*Lepus flavigularis*) are found in the open, mixed grass and shrub of the arid tropical lowlands on the Pacific side. The Mexican agouti (*Dasyprocta mexicana*) seems to be confined to dense rain forest on the Gulf side.

Polytypic species—Of the 63 polytypic species present (totaled in Table XVII), less than one-half (27 species) are confined to one side of the Isthmus or the other. The 17 species that appear to be restricted to the Pacific side include mammals that seem adapted best to the arid tropical western coast of México. Among these are the grayish mouse-opossum (*Marmosa canescens*), the sociable squirrel (*Sciurus socialis*), Desmarest's spiny pocket mouse (*Heteromys desmarestianus*), the Michoacán deer mouse (*Peromyscus banderanus*), the plateau mouse (*Peromyscus melanophrys*), and the spotted skunk (*Spilogale putorius*).

Ten species are confined to the humid tropical area of the Gulf side of the Isthmus. Included are such rain forest species as the woolly opossum (*Caluromys derbianus*), the forest rabbit (*Sylvilagus*

TABLE XVI.—Distribution of monotypic species in the Isthmus of Tehuantepec

Species (13)	Gulf side only	Pacific side only	Both Gulf and Pacific sides
<i>Cryptotis celatus</i>	—	×	—
<i>C. frontalis</i>	—	×	—
<i>C. micrura</i>	—	—	×
<i>Lepus flavigularis</i>	—	×	—
<i>Orthogeomys cunicularis</i>	—	×	—
<i>Heteromys lepturus</i>	×	—	—
<i>H. temporalis</i>	×	—	—
<i>Tylomys gymnurus</i>	×	—	—
<i>Peromyscus sloeops</i>	—	×	—
<i>Sigmodon macdougalli</i>	—	×	—
<i>S. macrodon</i>	—	×	—
<i>Dasyprocta mexicana</i>	×	—	—
<i>Tapirus bairdii</i>	—	—	×
Totals	4	7	2

brasiliensis), the howler monkey (*Alouatta villosa*), the spotted cavy (*Agouti paca*), and the white-lipped peccary (*Tayassu albirostris*). Many of the Gulf-side species range into South America.

More than one-half (36 species) of the 63 polytypic species range across the Isthmus. Current knowledge indicates that 15 of the 36 species are divisible into different subspecies in the 2 somewhat contrasting areas. Among the 11 rodents with this distribution, most of the 5 species that do not show geographic variation within the Isthmus are strictly tropical animals with less extensive northward distributions than most of the 7 species that vary geographically within the area. Among the species in the latter group are the marsh rice rat (*Oryzomys palustris*), the white-footed mouse (*Peromyscus leucopus*), and the hispid cotton rat (*Sigmodon hispidus*), which are distributed as far northward as temperate areas of the United States.

CENTRAL PLATEAU

Earlier it was pointed out that the Mexican Central Plateau is inhabited by a number of endemic species, especially the southern part (see Tables IX and XI). Probably the variability of the area from the United States border southward to the Valley of México has been a factor in speciation, since the country possesses, for example, irregular and dissected topography, desert shrub, grasslands, interior basins, riparian growth, volcanic badlands, and rocky uplands. The most conspicuous break in mammalian distribution seems to occur in the vicinity of latitude 25° N (see Baker, 1956, and Baker and Greer, 1962). This line separates somewhat the more arid northern desert country (Mesa del Norte) from the more humid southern area (Mesa Central). Even the elevated western grasslands on the eastern slopes of the Sierra Madre Occidental are separated in this area by the deep canyon of the Río Nazas in west-central Durango. Ninety-five terrestrial mammals are recorded from the Central Pla-

TABLE XVII.—Distribution of polytypic species in the Isthmus of Tehuantepec

Orders	Totals	Gulf side only	Pacific side only	Both Gulf and Pacific sides	Geographic variation
Marsupialia	5	2	1	2	0
Primates	2	1	0	1	0
Edentata	3	0	0	3	0
Lagomorpha	2	1	0	1	1
Rodentia	27	3	13	11	7
Carnivora	20	2	3	15	5
Artiodactyla	4	1	0	3	2
Totals	63	10	17	36	15

teau; these include 19 monotypic species (see Table XVIII) and 76 polytypic species (see Table XIX).

Monotypic species—All but one of the 19 monotypic species living on the Central Plateau (see Table XVIII) are rodents. The single insectivore is the obscurely known Tlalpam small-eared shrew (*Cryptotis soricina*) from the Valley of México. Three rodents are fossorial pocket gophers, which may owe their distinctive natures to isolation in scattered, suitable soil deposits in the southern part of the Mexican tableland. Some species, such as the Mexican prairie dog (*Cynomys mexicanus*) and the ornate kangaroo rat (*Dipodomys ornatus*), are characteristic of grasslands. The Texas antelope squirrel (*Ammospermophilus interpres*) and species of mice (genus *Peromyscus*) and of wood rats (genus *Neotoma*) live in rocky situations. Four monotypic species live only north of latitude 25° N while 15 occur to the southward; none overlaps this line. To the northward, 2 species, Nelson's kangaroo rat (*Dipodomys nelsoni*) and Goldman's wood rat (*Neotoma goldmani*), are, for the most part, confined to interior basins, chiefly the Bolsón de Mapimí, in Chihuahua, Coahuila and Durango. The placing of Thomas' rice rat (*Oryzomys fulgens*) in Plateau habitat is questionable.

Polytypic species—Of the 76 species (totaled in Table XIX), 39 are restricted either to the area north of 25° N latitude (15 species) or to that part of the Central Plateau south of this latitude (24 species). Twenty-six of the 37 overlapping species have distinguishable

TABLE XVIII.—Distribution of monotypic species on the Central Plateau

Species (19)	North of 25° N only	South of 25° N only
<i>Cryptotis soricina</i>	—	×
<i>Ammospermophilus interpres</i>	×	—
<i>Citellus perotensis</i>	—	×
<i>Cynomys mexicanus</i>	×	—
<i>Pappogeomys alcorni</i>	—	×
<i>Cratogeomys irolonis</i>	—	×
<i>C. varius</i>	—	×
<i>Dipodomys nelsoni</i>	×	—
<i>D. ornatus</i>	—	×
<i>Liomys bulleri</i>	—	×
<i>Oryzomys fulgens</i>	—	×
<i>Reithrodontomys hirsutus</i>	—	×
<i>Peromyscus bullatus</i>	—	×
<i>P. mekisturus</i>	—	×
<i>Sigmodon melanotis</i>	—	×
<i>Neotoma goldmani</i>	×	—
<i>N. latifrons</i>	—	×
<i>N. montezumae</i>	—	×
<i>N. nelsoni</i>	—	×
Totals	4	15

subspecies on either side of this division line. As in the case of monotypic species, this line assumes considerable importance in distribution with all but 11 of the 76 species being some way affected.

Forty-four (85%) of the 52 mammals that range northward of latitude 25° N occur also in the United States. Of course there is a broad avenue of open lands into the United States at the northern border of México. Thirty species (20 subspecifically different) live also on the Gulf Coastal Plain, while 31 species (23 subspecifically different) occur also on the Pacific Coastal Plain. Most of these species are characteristic of open lands and probably reached these three areas by way of the open, northern end of the Central Plateau. To the southward, the open land becomes almost surrounded by marginal, forested mountains to the east, south and west. Herein, at least 11 endemic polytypic species (see Table XI) reside. Even so, one seemingly characteristic species, aptly called the plateau mouse (*Peromyscus melanophrys*), is distributed also southeastward across the Balsas Basin and the Isthmus of Tehuantepec and into Chiapas. Fourteen species, mostly wide-ranging carnivores, live also in the mountains to the eastward (Sierra Madre Oriental) and to the westward (Sierra Madre Occidental).

Of the 15 species that are restricted to the northward of latitude 25° N, most occur only sparingly on the Central Plateau (in northeastern Chihuahua and northwestern Coahuila). These include such species as the black-tailed prairie dog (*Cynomys ludovicianus*), the desert pocket gopher (*Geomys arenarius*), Merriam's pocket mouse (*Perognathus merriami*) and the northern grasshopper mouse (*Onychomys leucogaster*). The beaver (*Castor canadensis*) reaches this area only along the Río Grande and some of its tributaries. The bison (*Bison bison*) is included although there is some question as to whether it ever reached the Central Plateau proper. Two species, the kit fox (*Vulpes macrotis*) and the mule deer (*Odocoileus hemionus*), range

TABLE XIX.—Distribution of polytypic species on the Central Plateau

Orders	Totals	North of 25° N only	South of 25° N only	Both North and South of 25° N	Geographic variation
Marsupialia	1	0	1	0	0
Insectivora	1	0	1	0	0
Edentata	1	0	1	0	0
Lagomorpha	4	0	1	3	3
Rodentia	50	10	18	22	17
Carnivora	14	2	2	10	6
Artiodactyla	5	3	0	2	0
Totals	76	15	24	37	26

widely in the northern part of the Central Plateau; both occur somewhat south of latitude 25° N, the latter at least into northern San Luis Potosí (Dalquest, 1953:211).

As in the case of monotypic species, the southern part of the Central Plateau provides room for diversification of polytypic species of pocket gophers. Seven of the 20 rodents listed as occurring only southward of latitude 25° N are pocket gophers, mostly belonging to the genus *Cratogeomys*. Some species, such as the brush mouse (*Peromyscus boylii*) and the piñon mouse (*Peromyscus truei*), occur in scattered uplands in the southern area, but reside only in the marginal mountains north of latitude 25° N.

The ecological situations that species, which range throughout the Central Plateau, may occupy are grasslands, shrub lands and rocky areas. Species that have more or less continuous ranges in grasslands that border the eastern face of the Sierra Madre Occidental include the white-sided jack rabbit (*Lepus callotis*), the banner-tailed kangaroo rat (*Dipodomys spectabilis*), the northern pygmy mouse (*Baiomys taylori*) and the Zacatecan cotton rat (*Sigmodon fulviventor*). Desert shrub lands that generally are widespread eastward of the grasslands are homes for such polytypic species as Nelson's pocket mouse (*Perognathus nelsoni*), Merriam's kangaroo rat (*Dipodomys merriami*), and the cactus mouse (*Peromyscus eremicus*). Such species as the rock squirrel (*Citellus variegatus*), the plateau mouse (*Peromyscus melanophrys*) and the white-ankled mouse (*Peromyscus pectoralis*) occupy rocky areas, including numerous man-made rock fences.

THE MOUNTAINS

Montane areas listed herein include sub-boreal and boreal habitats generally covered with nontropical deciduous and evergreen forests. The allocation of some mammals to strictly montane areas (instead, for example, to montane tropical areas) was difficult owing to the paucity of published ecological information. Certainly, Goldman's (1951) accounts of collecting localities in México proved of utmost value in assigning many species to specific areas.

For purposes of studying the montane distribution of mammals, the Mexican highlands, northwest of the Isthmus of Tehuantepec, are arranged in 4 groups (see Table XII and Fig. 1). The 3 northern groups, the Sierra Madre Oriental on the east, the Sierra Madre Occidental on the west, and the intermediate Trans-Mexican Volcanic Belt form a U-shaped escarpment on 3 sides of the Central Plateau. The Sierra Madre del Sur extends to the southward from the latter mountains into Guerrero and Oaxaca, but the 2 are at least partly separated by the valley of the Río Balsas.

SIERRA MADRE ORIENTAL

The Sierra Madre Oriental is an irregular series of mountains bordering the Gulf Coastal Plain in eastern México, from northern Coahuila southward at least into west-central Veracruz and Hidalgo,

where it joins the Trans-Mexican Volcanic Belt. The deeply entrenched Río Grande separates this highland from Trans-Pecos mountains in western Texas. Southwardly, 2 places where elevations decline sufficiently to isolate some montane habitats also form important breaks in mammalian distribution. One is at approximately 26° N latitude, in southern Coahuila and adjacent Nuevo León (see Baker, 1956). The other is at approximately 22° N latitude in extreme southern Tamaulipas and adjacent San Luis Potosí. Thirty-nine species live in these mountains (see Table XII).

Monotypic species—Six monotypic species occur in the Sierra Madre Oriental (see Table XX). All are confined only to these mountains, except for the black-eared mouse (*Peromyscus melanotis*), which enjoys also an extensive distribution in the mountains of central and northwestern México. This species ranges northward in the Sierra

TABLE XX.—Distribution of monotypic species in the major mountainous regions of México, North of the Isthmus of Tehuantepec

Species (26)	Sierra Madre Oriental	Trans-Mexican Volcanic Belt	Sierra Madre Occidental	Sierra Madre del Sur
<i>Sorex milleri</i>	x	—	—	—
<i>Cryptotis alticola</i>	—	x	—	—
<i>C. fossor</i>	—	—	—	x
<i>C. obscura</i>	x	—	—	—
<i>Scalopus montanus</i>	x	—	—	—
<i>Romerolagus diazi</i>	—	x	—	—
<i>Sylvilagus insonus</i>	—	—	—	x
<i>Citellus madrensis</i>	—	—	x	—
<i>Sciurus alleni</i>	x	—	—	—
<i>S. apache</i>	—	—	x	—
<i>S. nayaritensis</i>	—	—	x	—
<i>Cratogeomys angustirostris</i>	—	x	—	—
<i>C. neglectus</i>	—	x	—	—
<i>Peromyscus angustirostris</i>	x	—	—	—
<i>P. lepturus</i>	—	—	—	x
<i>P. melanocarpus</i>	—	—	—	x
<i>P. melanotis</i>	x	x	x	—
<i>P. oaxacensis</i>	—	—	—	x
<i>P. polius</i>	—	—	x	—
<i>P. thomasi</i>	—	—	—	x
<i>Sigmodon leucotis</i>	—	—	x	—
<i>S. melanotis</i>	—	x	—	—
<i>S. vulcani</i>	—	x	—	—
<i>Microtus fulviventris</i>	—	—	—	x
<i>M. umbrosus</i>	—	—	—	x
<i>Cervus merriami</i>	—	—	x	—
Totals	6	7	7	8

Madre Oriental only as far as the vicinity of 26° N. The Coahuilan mole (*Scalopus montanus*) is confined northward of latitude 26° N. Miller's shrew (*Sorex milleri*) crosses this line but does not extend southward of southern Nuevo León, north of latitude 22° N. Allen's squirrel (*Sciurus alleni*) occupies montane areas in between latitudes 26° N and 22° N. The other 2 species (listed in Table XX) are found

TABLE XXI.—Distribution of polytypic species in the Sierra Madre Oriental

Species (33)	South to 26° N only	North to 26° N only	Both north and south of 26° N	Geographic variation	South of 26° N but north of 22° N only	North to 22° N only	Both north and south of 22° N	Geographic variation
<i>Sorex saussurei</i>	—	×	—	—	—	—	×	—
<i>Cryptotis mexicana*</i>	—	—	—	—	—	×	—	—
<i>Sylvilagus floridanus</i>	—	—	×	×	—	—	×	—
<i>Eutamias bulleri</i>	—	×	—	—	×	—	—	—
<i>E. dorsalis</i>	×	—	—	—	—	—	—	—
<i>Citellus variegatus</i>	—	—	×	—	—	—	×	×
<i>Sciurus oculatus</i>	—	—	—	—	—	×	—	—
<i>Glaucomys volans</i>	—	—	—	—	—	—	×	—
<i>Thomomys umbrinus</i>	—	—	×	×	—	—	×	×
<i>Reithrodontomys megalotis</i>	—	×	—	—	—	—	×	—?
<i>Peromyscus boylii</i>	—	—	×	×	—	—	×	×
<i>P. difficilis</i>	—	—	×	×	—	—	×	×
<i>P. pectoralis</i>	—	—	×	—	×	—	—	—
<i>P. truei</i>	—	×	—	—	×	—	—	—
<i>Sigmodon alticola</i>	—	—	—	—	—	×	—	—
<i>S. ochrognathus</i>	×	—	—	—	—	—	—	—
<i>Neotoma mexicana</i>	—	—	×	×	—	—	×	×
<i>Microtus mexicanus</i>	—	×	—	—	—	—	×	×
<i>Erethizon dorsatum</i>	×	—	—	—	—	—	—	—
<i>Canis lupus</i>	—	—	×	—	—	—	×	—?
<i>Urocyon cinereoargenteus</i>	—	—	×	—	—	—	×	×
<i>Ursus americanus</i>	—	—	×	—?	×	—	—	—
<i>U. arctos</i>	×	—	—	—	—	—	—	—
<i>Bassariscus astutus</i>	—	—	×	×	—	—	×	×
<i>Procyon lotor</i>	—	—	×	—	—	—	×	×
<i>Nasua narica</i>	—	—	×	—	—	—	×	—
<i>Mustela frenata</i>	—	—	×	—	—	—	×	—
<i>Mephitis macroura</i>	—	—	×	—	—	—	×	×
<i>M. mephitis</i>	×	—	—	—	—	—	—	—
<i>Felis concolor</i>	—	—	×	—	—	—	×	—
<i>Lynx rufus</i>	—	—	×	×	—	—	×	—
<i>Odocoileus virginianus</i>	—	—	×	×	—	—	×	×
<i>Ovis canadensis</i>	×	—	—	—	—	—	—	—
Totals	6	5	18	8	4	3	20	11

* Possibly confined to montane tropical habitat.

southward of latitude 22° N in the mountains of western Veracruz or Hidalgo and near the junction with the Trans-Mexican Volcanic Belt.

Polytypic species—Thirty-three polytypic species live in the Sierra Madre Oriental (see Table XXI). Of the 29 species that occur in the vicinity of latitude 26° N, 11 do not cross this line, while 8 of the 18

TABLE XXII.—Distribution of polytypic species in the Trans-Mexican Volcanic Belt in central Mexico

Species (35)	Only in Trans. Vol. Belt	Geogr. var.	Also in Sierra Madre Oriental	Geogr. var.	Also in Sierra Madre Occidental	Geogr. var.	Also in Sierra Madre del Sur	Geogr. var.
<i>Sorex oreopolus</i>	—	×	—	—	×	×	×	—
<i>S. saussurei</i>	—	×	×	—	×	—	×	×
<i>S. vagrans</i>	—	—	—	—	×	×	—	—
<i>Sylvilagus floridanus</i>	—	×	×	×	×	×	—	—
<i>Citellus variegatus</i>	—	—	×	×	—	×	—	—
<i>Sciurus nelsoni</i>	×	×	—	—	×	—	—	—
<i>S. oculatus</i>	—	×	×	×	—	—	—	—
<i>S. polioopus</i>	—	×	—	—	×	×	×	×
<i>Glaucomys volans</i>	—	—	×	—	×	×	×	×
<i>Thomomys umbrinus</i>	—	×	×	×	×	×	—	—
<i>Zygoeomys trichopus</i>	×	×	—	—	—	—	—	—
<i>Cratogeomys gymnurus</i>	—	×	—	—	—	—	—	—
<i>C. merriami</i>	—	×	—	—	—	—	—	—
<i>C. perotensis</i>	—	×	—	—	—	—	—	—
<i>Reithrodontomys chrysopsis</i>	×	×	—	—	—	—	—	—
<i>R. megalotis</i>	—	×	×	×	×	×	×	×
<i>R. microdon</i>	—	—	—	—	—	—	×	×
<i>R. sumichrasti</i>	—	×	—	—	—	—	×	×
<i>Peromyscus boylüi</i>	—	—	×	—	×	×	×	—
<i>P. difficilis</i>	—	—	×	×	×	×	×	×
<i>P. hyllocetes</i>	—	—	—	—	—	—	×	×
<i>P. truei</i>	—	—	×	×	×	×	×?	×
<i>Sigmodon alticola</i>	—	—	×	—	—	—	×	×
<i>Neotomodon alstoni</i>	×	×	—	—	—	—	—	—
<i>Neotoma mexicana</i>	—	×	×	×	×	×	×	×
<i>Microtus mexicanus</i>	—	×	×	×	×	×	—	—
<i>Canis lupus</i>	—	—	×	—	×	—	—	—
<i>Urocyon cinereoargenteus</i>	—	—	×	×	×	×	×	×
<i>Bassariscus astutus</i>	—	×	×	×	×	—	×	×
<i>Procyon lotor</i>	—	—	×	×	×	×	×	—
<i>Mustela frenata</i>	—	×	×	×	×	×	×	—?
<i>Mephitis macroura</i>	—	—	×	×	×	×	×	—
<i>Felis concolor</i>	—	—	×	×?	×	—	×	×
<i>Lynx rufus</i>	—	—	×	×	×	×	×	—
<i>Odocoileus virginianus</i>	—	×	×	×	×	×	×	×
Totals	4	20	22	17	23	19	21	15

that do cross have distinctive subspecies on either side. The 6 species found only to the northward also have extensive ranges in western North America. Of the 5 species confined to the southward of latitude 26° N, 2 range no further southward in the mountains than latitude 22° N. One of these, Buller's Chipmunk (*Eutamias bulleri*), has its nearest relative in the Sierra Madre Occidental in western México. Of the 27 species that live in the vicinity of 22° N, do not cross the area of this latitude, while 11 of the 20 that do cross have named subspecies on either side. As expected, most of the 16 species that occur throughout the entire length of the mountains are ubiquitous carnivores.

TRANS-MEXICAN VOLCANIC BELT

This series of highlands, featuring disjunct, lofty volcanic peaks, crosses south-central México from the edge of the Gulf Coastal Plain in Veracruz to the end of the Pacific Coastal Plain in Jalisco, Colima and Michoacán. These highlands meet the southern ends of the Sierra Madre Oriental, on the east, and the Sierra Madre Occidental, on the west. The valley of the Río Balsas is conspicuous along much of the southern boundary of this volcanic belt. Not all boreal areas are continuous throughout this east-west mountainous chain; consequently, many mammals have disjunct distributions. Forty-two mammals live in this montane belt (see Table XII).

Monotypic species—Seven monotypic species (see Table XX) occur in the Trans-Mexican Volcanic Belt. Six are endemic while the seventh, the black-eared mouse (*Peromyscus melnotis*), occurs also in the Sierra Madre Oriental and the Sierra Madre Occidental (see Table IX).

Polytypic species—Thirty-five polytypic species (see Table XXII) live in the Trans-Mexican Volcanic Belt. Approximately two-thirds of these species are shared in common with each of the 3 other mountain chains; 1 insectivore, 6 rodents, 7 carnivores and 1 deer are distributed in each area. Three-fourths or more of these mammals have distinctive subspecies in each area. Although differences are slight, the mammalian fauna of the Trans-Mexican Volcanic Belt bears closer resemblance to those of the Sierra Madre Oriental and the Sierra Madre Occidental than to the fauna in the Sierra Madre del Sur. The effects of numerous isolated montane habitats in the irregular volcanic belt are emphasized by the presence of 4 endemic polytypic species as well as subspeciation within the area in 13 of the other 32 species. Many species displaying geographic variation, such as the Mexican long-tailed shrew (*Sorex oreopolus*), Nelson's squirrel (*Sciurus nelsoni*), Sumichrast's harvest mouse (*Reithrodontomys sumichrasti*), the volcano mouse (*Neotomodon alstoni*), and the Mexican vole (*Microtus mexicanus*), are restricted to boreal situations which because of their altitudinal requirements are found only in the disjunct highest parts of this east-west range.

SIERRA MADRE OCCIDENTAL

The elongated Sierra Madre Occidental is a massive, elevated, forested plateau throughout much of its extent in northwestern México. At present, the highland environments near the northern border of Chihuahua and eastern Sonora are not continuous with those in the mountains in western United States. Still, the western mountains of these two countries have in common most of the polytypic species found

TABLE XXIII.—Distribution of polytypic species in the Sierra Madre Occidental

Species (34)	North of 23° N only	South of 23° N only	Both north and south of 23° N	Geographic variation
<i>Sorex oreopolus</i>	—	—	×	—
<i>S. saussurei</i>	—	—	×	—
<i>S. vagrans</i>	—	—	×	×
<i>Sylvilagus floridanus</i>	—	—	×	—
<i>Eutamias bulleri</i>	—	—	×	×
<i>E. dorsalis</i>	×	—	—	—
<i>Citellus variegatus</i>	—	—	×	—
<i>Sciurus aberti</i>	×	—	—	—
<i>S. arizonensis</i>	×	—	—	—
<i>Glaucomys volans</i>	—	—	×	×
<i>Thomomys umbrinus</i>	—	—	×	×
<i>Reithrodontomys megalotis</i>	—	—	×	—
<i>Peromyscus boylii</i>	—	—	×	—
<i>P. truei</i>	—	—	×	—
<i>P. difficilis</i>	—	—	×	—
<i>Sigmodon ochrognathus</i>	×	—	—	—
<i>Neotoma mexicana</i>	—	—	×	×
<i>Nelsonia neotomodon</i>	—	—	×	—
<i>Microtus mexicanus</i>	—	—	×	×
<i>Erethizon dorsatum</i>	×	—	—	—
<i>Canis lupus</i>	—	—	×	—
<i>Urocyon cinereoargenteus</i>	—	—	×	×?
<i>Ursus americanus</i>	×	—	—	—
<i>U. arctos</i>	×	—	—	—
<i>Bassariscus astutus</i>	—	—	×	—
<i>Procyon lotor</i>	—	—	×	—
<i>Nasua narica</i>	—	—	×	—
<i>Mustela frenata</i>	—	—	×	—
<i>Mephitis macroura</i>	—	—	×	×?
<i>M. mephitis</i>	×	—	—	—
<i>Felis concolor</i>	—	—	×	—
<i>Lynx rufus</i>	—	—	×	×?
<i>Odocoileus virginianus</i>	—	—	×	—
<i>Ovis canadensis</i>	×	—	—	—
Totals	9	0	25	9

on the Mexican side and have been an important avenue in the past for north-south movements of montane plants and animals. To the southward, these mountains meet the Trans-Mexican Volcanic Belt in central Jalisco. Forty-one mammals are recorded (see Table XII).

The Sierra Madre Occidental is a formidable escarpment bordering the Pacific Coastal Plain. The chief break, which affects mammalian distribution, in this highland is the canyon of the Río Mezquital-Río San Pedro at approximately 23° N latitude (see Baker and Greer, 1962). This river system bisects the mountains in a northeast-southwest direction and drains part of the Central Plateau in southern Durango and flows into the Pacific Ocean by way of the state of Nayarit. The valley of the Río Grande de Santiago, which empties into the Pacific Ocean in southern Nayarit and also cuts through the mountains in the vicinity of 21° 50' N latitude seems to be only of minor importance as a deterrent to the distribution of montane mammals.

Monotypic species—Seven monotypic species occur in the Sierra Madre Occidental (see Table XX). Except for the wide-ranging black-eared mouse (*Peromyscus melanotis*), all species are confined to the area, except for the recently extinct Merriam's elk (*Cervus merriami*), which also lived in southwestern United States. The Nayarit squirrel (*Sciurus nayaritensis*) is the only monotypic species restricted southward of latitude 23° N, while the ranges of 2 species, the black-eared mouse (*Peromyscus melanotis*) and the white-eared cotton rat (*Sigmodon leucotis*), overlap this division. The other 4 species occur to the northward.

Polytypic species—Thirty-four polytypic species (see Table XXIII) live in montane habitats of the Sierra Madre Occidental. Nine of these are confined to the north side of latitude 23° N. Those living to the northward also range into the United States; several are distributed no further southward in México than Chihuahua. Nine of the 25 species that cross latitude 23° N are divisible into distinct subspecies on either side. Several of these montane mammals; for example, the Mexican long-tailed shrew (*Sorex oreopolus*), Saussure's shrew (*Sorex saussurei*), the vagrant shrew (*Sorex vagrans*), and the Mexican vole (*Microtus mexicanus*), seem absent in the mountainous country between central Durango and Jalisco or Michoacán. This hiatus appears to result from the present lack of suitable boreal habitats in Nayarit and adjacent parts of southern Durango and northern Jalisco. The canyon of the Río Mezquital-Río San Pedro, in the vicinity of latitude 23° N, seems to be a highly effective barrier to north-south movements of tree squirrels. The polytypic species, Abert's squirrel (*Sciurus aberti*), and the monotypic species, the Apache squirrel (*Sciurus apache*), live to the northward in pine-oak forests, even to the vicinity of the north rim of this canyon, while the monotypic species, the Nayarit squirrel (*Sciurus nayaritensis*), lives in practically the same kind of habitat in the vicinity of this deep canyon but to the southward (see Baker and Greer, 1962).

Mammals common to both the Sierra Madre Oriental and the

Sierra Madre Occidental—Table XXIV lists the 29 polytypic species shared by each of these mountain systems (see McVaugh, 1952, for discussion of distribution of some plants in the same areas). Twenty-two of these mammals are separable into distinctive subspecies in each of the two ranges. At least 20 (some of which not being confined to montane habitats alone) occur also in the interconnecting Trans-Mexican Volcanic Belt. The distribution in northern México of such montane species as Saussure's shrew (*Sorex saussurei*), probably the southern flying squirrel (*Glaucomys volans*), the Zacatecas deer mouse (*Peromyscus difficilis*), the piñon mouse (*Peromyscus truei*), the Mexi-

TABLE XXIV.—Polytypic species occurring in both the Sierra Madre Oriental and Sierra Madre Occidental of Mexico

Species (29)	Geographic variation	Also in Transverse Volcanic Belt	Also in the United States
<i>Sorex saussurei</i>	—	×	—
<i>Sylvilagus floridanus</i>	×	×	×
<i>Eutamias bulleri</i>	×	—	—
<i>E. dorsalis</i>	×	—	×
<i>Citellus variegatus</i>	×	×	×
<i>Glaucomys volans</i>	×	×?	×
<i>Thomomys umbrinus</i>	×	×	×
<i>Reithrodontomys megalotis</i>	×	×	×
<i>Peromyscus boylii</i>	×	×	×
<i>P. difficilis</i>	×	×	×
<i>P. truei</i>	—?	×	×
<i>Sigmodon ochrognathus</i>	×	—	×
<i>Neotoma mexicana</i>	×	×	×
<i>Microtus mexicanus</i>	×	×	×
<i>Erethizon dorsatum</i>	—	—	×
<i>Canis lupus</i>	×	×?	×
<i>Urocyon cinereoargenteus</i>	×	×	×
<i>Ursus americanus</i>	×	—	×
<i>U. arctos</i>	—?	—	×
<i>Bassariscus astutus</i>	×	×	×
<i>Procyon lotor</i>	×	×	×
<i>Nasua narica</i>	—	—?	×
<i>Mustela frenata</i>	×	×	×
<i>Mephitis macroura</i>	—	×	×
<i>M. mephitis</i>	×	—	×
<i>Felis concolor</i>	×?	×	×
<i>Lynx rufus</i>	×	×	×
<i>Odocoileus virginianus</i>	×	×	×
<i>Ovis canadensis</i>	—	—	×
Totals	22	20	27

can wood rat (*Neotoma mexicana*), and the Mexican vole (*Microtus mexicanus*) follows the U-shaped pattern of these 3 mountain groups. Other species, such as the cliff chipmunk (*Eutamias dorsalis*), the yellow-nosed cotton rat (*Sigmodon ochrognathus*), the porcupine (*Erethizon dorsatum*), the black bear (*Ursus americanus*), and the mountain sheep (*Ovis canadensis*), reached the two northern ranges by way of the United States. Populations of Buller's chipmunk (*Eutamias bulleri*) presently are isolated from one another in the two mountainous areas on either side of the Central Plateau. This species may have spread from one area to the other by way of a transplateau route (see Baker, 1956:146).

TABLE XXV.—Distribution of polytypic species in the Sierra Madre del Sur

Species (26)	Only in Sierra Madre del Sur	Also in Trans-Mexican Volcanic Belt	Geographic Variation	Also in Sierra Madre de Chiapas	Geographic Variation
<i>Sorex oreopolus</i>	—	×	×	—	—
<i>S. saussurei</i>	—	×	×	×	×
<i>S. veraepacis</i>	—	—	—	×	×
<i>Cryptotis mexicana</i>	—	×	×	—	—
<i>Sciurus poliopus</i>	—	×	×	—	—
<i>Glaucomys volans</i>	—	×	×	×	—
<i>Orthogeomys grandis</i>	×	—	—	—	—
<i>Reithrodontomys megalotis</i>	—	×	×	—	—
<i>R. microdon</i>	—	—	—	×	×
<i>R. sumichrasti</i>	—	×	×	×	×
<i>Peromyscus boylii</i>	—	×	—	×	—
<i>P. difficilis</i>	—	×	×	—	—
<i>P. hylocetes</i>	—	×	×	—	—
<i>P. megalops</i>	×	—	—	—	—
<i>P. truei</i>	—	×	×	—	—
<i>Sigmodon alticola</i>	—	×	×	—	—
<i>Neotoma mexicana</i>	—	×	×	×	×
<i>Urocyon cinereoargenteus</i>	—	×	×	×	×
<i>Bassariscus astutus</i>	—	×	×	—	—
<i>Procyon lotor</i>	—	×	—	×	—?
<i>Nasua narica</i>	—	—?	—	×	×
<i>Mustela frenata</i>	—	×	×	×	×
<i>Mephitis macroura</i>	—	×	—	×	—
<i>Felis concolor</i>	—	×	×	×	—
<i>Lynx rufus</i>	—	×	—	—	—
<i>Odocoileus virginianus</i>	—	×	×	×	×
Totals	2	21	17	14	9

SIERRA MADRE DEL SUR

Irregular highlands in Guerrero and western Oaxaca are included in the Sierra Madre del Sur. These mountains are separated from more northern mountains largely by the valley of the Río Balsas and from the highlands of Chiapas, to the eastward, by hilly tropical lowlands in the Isthmus of Tehuantepec. In the Sierra Madre del Sur, forests of oaks and other nontropical deciduous trees, conifers and even some subalpine areas provide variable habitats for montane species. Our knowledge of mammals of these mountains is less complete than for those in highlands in northern México. The 33 species (see Table XII) have affinities with mammals in either or both the Trans-Mexican Volcanic Belt and the Chiapan highlands.

Monotypic species—Eight monotypic species (listed in Table XX) live in the Sierra Madre del Sur. Of interest is the presence of 2 voles (genus *Microtus*), each belonging to a different subgenus. One of these, *Microtus umbrosus*, may be restricted to montane tropical habitat (Goldman, 1951:349). One species, the Oaxacan deer mouse (*Peromyscus oaxacensis*), also is found in Chiapas and southeastward; all other monotypic species are endemic in the Sierra Madre del Sur.

Polytypic species—Table XXV lists the 26 polytypic species that live in the Sierra Madre del Sur. Most species (21) occur also in the Trans-Mexican Volcanic Belt, with 17 assignable to different subspecies in the 2 areas. Of 14 species living also in the mountains of Chiapas, most (9 species), except for ubiquitous carnivores, are classified as different subspecies from those in the Sierra Madre del Sur. Three mammals common to these 2 mountain masses, are absent from the Trans-Mexican Volcanic Belt. Species, such as the Mexican small-eared shrew (*Cryptotis mexicana*), the large pocket gopher (*Orthogeomys grandis*), all carnivores and the white-tailed deer (*Odocoileus virginianus*), are recorded both from the mountains and from tropical areas.

SUMMARY

The 370 species of nonflying, nonmarine mammals of Middle America, excluding species on offshore islands and in the Mexican state of Baja California, include 156 monotypic and 214 polytypic species. The fauna contains mammals whose affinities are either South American, North American or secondarily diversified within Middle America. Rodents comprise 71 per cent of the total. The gradual crowding of mammalian habitats as Middle America narrows in a southeastward direction is a principal factor governing mammalian distribution in the area. This crowding has had less effect on mammals that live in the continuous coastal lowlands than on those that occur in montane areas, including submontane tropical situations. These montane areas lack continuity in several places from north to south, allowing for isolation of many sub-boreal and boreal species, as well as of species in submontane tropical habitats. The following statements summarize some of the findings concerning mammalian distribution in Middle America:

1. The hilly tropical lowland of the narrow Isthmus of Tehuantepec provides a major break in present-day mammalian distribution in Middle America. Only 2 per cent of the monotypic species and 30 per cent of the polytypic species cross this narrow corridor. More Middle American mammals are confined to the area in and northwest of the Isthmus (79 monotypic and 103 polytypic species) than to the area southeast of the Isthmus (74 monotypic and 47 polytypic species). Only 6 per cent (2 monotypic and 21 polytypic species) of the mammalian fauna, endemic to Middle America, cross the Isthmus.

2. Six monotypic and 61 polytypic species in Middle America (18% of all species) also occur in South America. Of these, 5 monotypic and 29 polytypic species range no further northwestward than Middle America southeast of the Isthmus of Tehuantepec. One monotypic species reaches the Isthmus while 32 polytypic species range into the Isthmus and northwestward in México, 14 of the species occurring also in the United States. All species common to Middle America and South America are adapted for life in tropical environments. Probably the principal route of movements in México of these intercontinental species has been along the Gulf Coastal Plain rather than the Pacific Coastal Plain.

3. Two monotypic species and 32 polytypic species are distributed in or on both sides of the Isthmus of Tehuantepec in Middle America but are not known to occur in South America. Eleven polytypic species range northward into the United States. Although most of these have continuous distributions in the tropical environment across the Isthmus, a few have disjunct montane distributions.

4. Two monotypic and 94 polytypic species in Middle America (26% of all the species) occur also in the United States. Of the 2 monotypic and 69 polytypic species which occur no further southeastward in México than the Isthmus of Tehuantepec, 1 monotypic and 42 polytypic species range in México on to the Central Plateau. Twenty-three polytypic species occur on the Gulf Coastal Plain while 32 occur on the Pacific Coastal Plain. Species common to the disjunct montane areas of the 2 countries include 17 polytypic species in the eastern Sierra Madre Oriental and 1 monotypic and 19 polytypic species in the western Sierra Madre Occidental. The impressive number of species common to each of these countries shows the similarity of the habitats, at least at and near their common boundaries, and also the role in mammalian speciation of the semiarid and arid parts of northern México and southwestern United States.

5. The variable habitats of Middle America allow for a large number of monotypic species, of which 95 per cent (148 of 156 species) are endemic, although it is suspected that some may lose their monotypic status when further taxonomic evaluations are made. In contrast, only 33 per cent (73 of 214 species) of the more wide-ranging polytypic species are restricted to Middle America. Southeast of the Isthmus of Tehuantepec, Panamá accommodates more endemic monotypic species than any other political area, while Costa Rica is inhabited by more

endemic polytypic species. In and northwest of the Isthmus of Tehuantepec the submontane humid tropical habitat, especially on the Gulf side of México, and the southern part of the Central Plateau are the principal living places for endemic monotypic species, while the latter area is also important for endemic polytypic species.

6. The coastal lowlands, including adjacent tropical slopes of the mountains, and the Central Plateau are inhabited by more than twice as many species of mammals as the mountainous areas of México.

7. The coastal lowlands on both the Gulf and the Pacific sides are characterized by semidesert or desert at the northern border of México. Accordingly, a large contingent of mammals of the American Southwest occur there. Southeastwardly, these coastal areas become tropical, generally arid along the coast and generally humid inland along the seaward slopes of the mountains. Although the change in a southward direction of the temperate semidesert or desert conditions into tropical ones is gradual, this transition area marks the north-south geographical boundary for many species. It also is a zone of intergradation between subspecies of many polytypic species whose distributions overlap the area. On the Gulf side this break is at approximately 23° N latitude; on the Pacific side the break is at approximately 25° N latitude.

8. The transition between the generally humid Gulf side of the Isthmus of Tehuantepec and the generally arid Pacific side marks the geographical boundary for some tropical species and is a zone of intergradation between subspecies for some others that live on both sides.

9. The transition in the vicinity of 25° N latitude between the more arid northern part of the Central Plateau and the more humid southern part marks the north-south geographical boundary for the distribution of many Plateau mammals and also is an area of intergradation between subspecies of many polytypic species occurring throughout the Central Plateau. The large number of mammals (95 species) known from the Central Plateau emphasizes its importance in mammalian speciation.

10. Montane areas in central and northern México are fashioned in a U-shape, with the Sierra Madre Oriental on the east, the Trans-Mexican Volcanic Belt on the south, and the Sierra Madre Occidental on the west. At least 21 mammals are distributed throughout these ranges. In addition, the two northern ranges have some mammals found also to the northward in western United States. Conspicuous breaks in these two northern ranges disrupt mammalian distributions, serving as distinct barriers to some species and zones of intergradation between subspecies for other species. In the eastern Sierra Madre Oriental breaks of significance to montane mammalian distribution occur at the border with the United States and southward at approximately 26° N latitude and at 22° N latitude. In the western Sierra Madre Oriental breaks occur at the border with the United States and southward at approximately 23° N latitude and, to a lesser extent, at 21° 50' N latitude.

11. The Trans-Mexican Volcanic Belt contains isolated highlands

allowing for some geographic variation in polytypic species of the area and some endemism among monotypic species. The mammalian fauna of this mountainous belt shows close affinity to the two northern ranges as well as to the partially isolated Sierra Madre del Sur to the southward. Most polytypic species common to these different mountain masses are separable in each area as distinctive subspecies.

12. The mammals found in the Sierra Madre del Sur have a closer relationship with those found in the Trans-Mexican Volcanic Belt than with those eastward across the lowland of the Isthmus of Tehuantepec in the mountains of Chiapas. Even so, 1 monotypic and 14 polytypic species (including some ubiquitous carnivores) are common to the Sierra Madre del Sur and the mountains of Chiapas, with 9 polytypic species separable into distinctive subspecies in each area.

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