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(Marsupialia: Didelphidae) in North and
Middle America**

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The Systematics of the Genus *Didelphis* (Marsupialia: Didelphidae) in North and Middle America

Alfred L. Gardner

Opossums of the genus *Didelphis* are characterized by dense underfur and long guard hair, five toes on each foot with an opposable and clawless hallux, a naked prehensile tail except for a furred short basal portion, and a well-developed marsupium in females. The genus is known from Pliocene deposits of South America and now occurs from central Argentina north to southern Canada at elevations ranging from sea level on both the Atlantic and Pacific coasts to more than 3,000 meters in the mountains of México and South America. Ecologically, they are usually associated with moist forests or woodlands near water in a wide variety of habitats that include the temperate pine-oak forest, prairie and mesquite grassland, chaparral, subtropical and tropical cloud forest, rain forest, tropical evergreen and tropical deciduous forest, savanna, thorn forest, and tropical scrub.

I became interested in *Didelphis* after finding that chromosomal material prepared from Costa Rican *D. marsupialis* indicated a karyotype differing markedly from that reported for *D. marsupialis* from the United States (Shaver, 1962; Biggers *et al.*, 1965). However, the karyotype of the Costa Rican specimens is indistinguishable from those of *D. paraguayensis* (= *D. albiventris*), *D. aurita* (= *D. marsupialis aurita*), *Lutreolina crassicaudata*, and *Philander opossum* reported by Biggers *et al.* (1965), Dreyfus and Campos (1941), and Saez (1931, 1938). This information indicates greater chromosomal variation within a single species than is known to exist among several species in three distinct genera. The primary purpose of this study was to examine the taxonomic, cytogenetic, and evolutionary implications of the two chromosomal patterns in *Didelphis*.

Linnaeus' (1758:54) genus *Didelphis* was intricately composite and included all of the then known American marsupials. *Didelphis marsupialis*, the first species Linnaeus listed under this genus, was also composite and included all of the large opossums. Thomas (1888:316) designated *D. marsupialis* Linnaeus as the type species and (p. 323) restricted *marsupialis* to include only two forms, "*marsupialis* var. *typica*" and "*marsupialis* var. *azarae*." Subsequent attempts to fix the identity of *D. marsupialis* Linnaeus (restricted) resulted in conflicting opinion and confusion, even to rejecting the name *Didelphis* because its type species was considered indeterminable (Alston, 1879-1882:196, footnote; Allen, 1897:43; Rehn, 1900:576). Allen (1900:185-188) retained the name *Didelphis* and decided that *marsupialis* was best applied to the Virginia opossum, citing Linnaeus' reference to Tyson (1704:1565-1575) on the anatomy of opossums definitely known to have come from Virginia.

Thomas (1901:144-145) pointed out that Linnaeus' primary reference for *marsupialis* was *Philander* Seba (1734:64, t. 39) and that the animal depicted on Seba's plate 39 is clearly a *Didelphis* and probably came from Guiana as did most of Seba's South American animals. Rehn (1901:147-149), passing over Linnaeus' reference to Seba, decided that the reference to Hernandez should be given priority over the reference to Tyson and thus he retained the name *Didelphis virginiana* Kerr, 1792, for the Virginia opossum and applied *marsupialis* to Mexican specimens of *Didelphis*. Rehn's treatment was followed by Allen (1901) who made the first serious attempt to review the extent of variation within North and Central American *Didelphis*. In this publication, Allen recognized *D. virginiana* and *D. virginiana pigra* Bangs, 1898, and made the following changes: considered the names *D. breviceps* Bennett, 1833, and *D. pruinoso* Wagner, 1843, to be junior synonyms of *D. californica* Bennett, 1833, which name he referred to *D. marsupialis*; described as new *D. m. texensis* from Texas, *D. m. tabascensis* and *D. yucatanensis* from México, and *D. richmondi* from Nicaragua; and was responsible for the *nomen nudum*, *Didelphis nelsoni* (p. 160). Allen still rejected Linnaeus' reference to Seba despite Thomas' insistence (1901:153) to the contrary. The following year, Allen (1902) examined the variation within South American species of *Didelphis* and reviewed the nomenclature of the genus, at which time he accepted Thomas' earlier conclusions and cited Seba as the primary reference for *D. marsupialis* Linnaeus (restricted), thereby shifting the type locality of *marsupialis* from "the region about the city of México" (1901:169) to northeastern South America.

Allen (1902) also resurrected Oken's names for the large opossums of North and South America, applying *D. paraguayensis* to the white-eared South American species and *D. mesamericana* to the Mexican populations, and recognized two groups within *Didelphis* (1902:256-257). Allen's *marsupialis*-group included: *D. virginiana* and *D. virginiana pigra* restricted to the United States; *D. mesamericana* in central and western México, *D. mesamericana texensis* in the Rio Grande valley of Texas and México, *D. mesamericana tabascensis* in southern México and Guatemala; *D. yucatanensis* in the Yucatán peninsula, *D. yucatanensis cozumelae* Merriam, 1901, on Cozumel Island; *D. richmondi* in Nicaragua; *D. marsupialis* with seven subspecies in Panamá and South America, of which only the names *D. marsupialis caucae* Allen, 1900 (= *D. m. etensis* Allen, 1902, *fide* Handley, 1966) and *D. marsupialis battyi*, Thomas, 1902, apply to Central American *Didelphis*.

His *paraguayensis* group included *D. paraguayensis* with four subspecies, all currently assigned to, or regarded as synonyms of, *D. albiventris* Lund, 1841 (see Hershkovitz, 1969:54). The name *D. m. particeps* Goldman, 1917, was later assigned to the population on Isla del Rey (= Isla San Miguel), Panamá.

With minor modifications, this arrangement persisted until Hershkovitz (1951: 550) reduced the number of species to two: *Didelphis azarae* Temminck, 1825 (a name which Hershkovitz, 1969:54, later considered a composite and replaced with *D. albiventris*), restricted to South America, and *D. marsupialis* in North, Central, and South America. Hershkovitz ostensibly recognized *D. m. californ-*

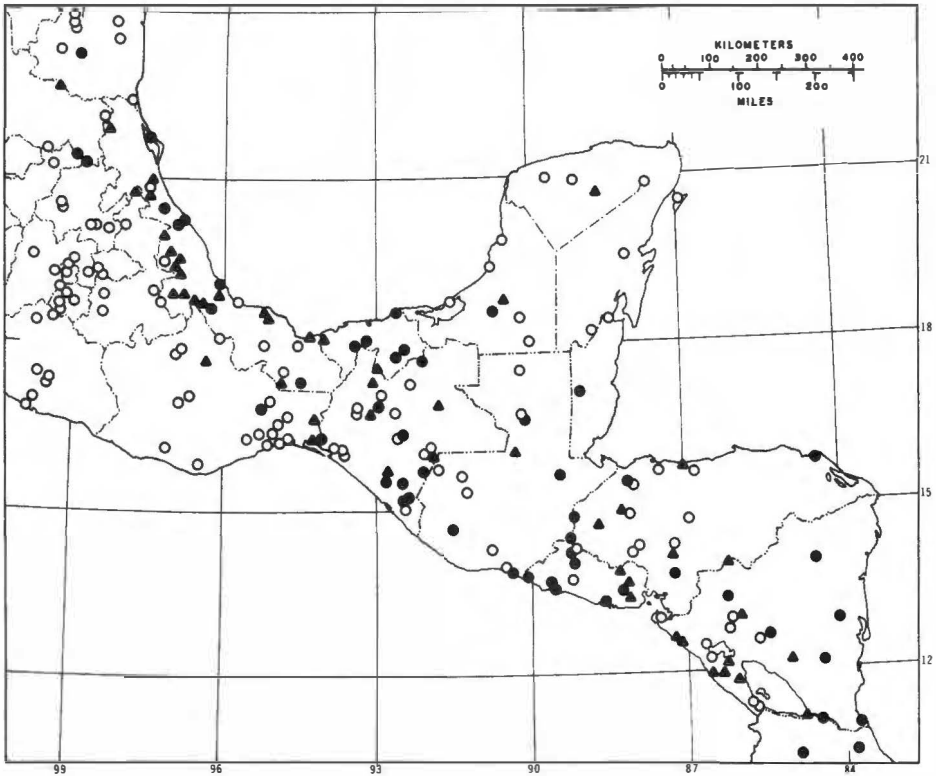


FIG. 1.—Map of México and Central America including the zone of sympatry between *Didelphis virginiana* and *D. marsupialis*. Plotted localities are based on specimens examined: open circle, *virginiana*; solid dot, *marsupialis*, and triangle, both species.

ica (*mesamericana* Oken, 1816, being unavailable under current rules of zoological nomenclature) as transitional between the temperate subspecies *virginiana* from Canada and the United States and *marsupialis* from Costa Rica, Panamá, and South America. Hall and Kelson (1952:323-324, 1959:5-9), probably considering Hershkovitz's treatment unsupported and extreme, retained all of the names for North and Central American opossums recognized by Allen (1902) as subspecies of *D. marsupialis*, except that they used the name *californica* in place of *mesamericana* (in the subspecific sense).

As a consequence of my investigations, *D. virginiana* is recognized as a distinct species occurring in tropical, subtropical, and temperate habitats of North America from southern Canada to the southwestern border of Nicaragua and Costa Rica. *Didelphis marsupialis* is a tropical species, the range of which extends from southern Tamaulipas, México, to the northern border of Argentina. A third species, *D. albiventris*, is a subtropical and temperate species restricted to South America.

Studying animals of known karyotype, I found a number of distinctive non-chromosomal features useful in distinguishing *virginiana* and *marsupialis*. These

features include differences in cranial morphology, hair pattern, color pattern, and behavior.

Major emphasis has been placed on the Mexican and Central American populations of both species. This region includes the zone of sympatry and ranges of the nine subspecies of *D. marsupialis* recognized by Hall and Kelson (1959). I have given little attention to populations of *D. virginiana* occurring north of the Rio Grande valley of southern Texas.

MATERIAL AND METHODS

Specimens

The number of specimens examined exceeds 2800. Of these, 1754 are from México and Central America. The majority of the approximately 1000 additional specimens represent *Didelphis virginiana* from the United States. A smaller number represent South American *D. marsupialis* and *D. albiventris*, examined but not tabulated. Abbreviations preceding the names of institutions listed below are used in the text beyond to identify the source of specimens examined.

AMNH—American Museum of Natural History

CAS—California Academy of Sciences

IB—Instituto de Biología, Universidad Nacional Autónoma de México

KU—University of Kansas, Museum of Natural History

LACM—Los Angeles County Museum

LSUMZ—Louisiana State University, Museum of Zoology

MCZ—Museum of Comparative Zoology, Harvard

MSB—University of New Mexico, Museum of Southwestern Biology

MSC—McNeese State College

MVZ—University of California at Berkeley, Museum of Vertebrate Zoology

TCWC—Texas A&M University, Texas Cooperative Wildlife Collections

TTU—The Museum, Texas Tech University

UA—University of Arizona

UCLA—University of California at Los Angeles

UMMZ—University of Michigan, Museum of Zoology

USNM—National Museum of Natural History (formerly the U.S. National Museum)

Measurements

All measurements are in millimeters. Those of total length, tail, hind foot, and ear are those recorded by the preparator. Measurements of the following skull dimensions were taken using parallel-jawed dial calipers graduated in twentieths of a millimeter (0.05):

Greatest length of skull.—The greatest length obtainable in the midline of the skull from the anterior surface of the premaxillary bones to the posteriormost extensions of the skull, usually the lambdoidal crests.

Condylbasal length.—The distance, in the midline of the skull, from the anterior surface of the premaxillary bones to a line connecting the posterior margins of the occipital condyles.

Palatal length.—The distance, in the midventral line of the skull, from the anterior surface of the premaxillary bones to the posterior margin of the palate.

Zygomatic breadth.—The greatest spread of the zygomatic arches, measured on the squamosal bones at a right angle to the long axis of the skull.

Interorbital constriction.—The least distance across the skull between the orbits.

Postorbital constriction.—The least distance across the skull behind the postorbital processes of the frontal bones.

Breadth across canines.—The breadth between the lateral margins of the upper canines, taken at the level of the palate.

Breadth across molars.—The greatest distance between the outer margins of the third upper molars (M3-M3).

Breadth of brain case.—The least distance across the brain case behind the zygomatic arches immediately anterior to the lateral expansion of the lambdoidal crests.

Breadth of palatal shelf.—The breadth of the free posterior extension of the hard palate.

Length of maxillary toothrow.—The greatest distance from the anterior face of the upper canine to the posterior face of the last upper molar (M4).

Length of upper molar series.—The distance between the anterior face of the first upper molar (M1) and the posterior face of the last upper molar (M4).

Length of mandible.—The length of one ramus of the lower jaw, measured from the anteriormost point (excluding incisors) to the posteriormost surface of the mandibular condyle.

Length of lower molar series.—The distance between the anterior face of the first lower molar (m1) and the posterior face of the last lower molar (m4).

Breadth of rostrum across jugals.—The breadth across the skull between the common point of juncture between the lacrimal, jugal, and maxillary bones.

Greatest breadth of nasals.—The greatest breadth across the expanded base of the nasal bones.

Breadth of rostrum across frontals.—The breadth across the skull between the junctures of the maxillofrontal suture and the lacrimals.

All measurements have been segregated on the bases of age class and sex of the individual. Measurements were entered on IBM code sheets and transferred to IBM cards for computer analysis. The mean, range, standard deviation, and coefficient of variation were determined for each sample. Measurements from selected samples are presented in tabular form in Appendix I. The samples consist of individuals of one sex and the three oldest age classes (ages 4, 5, and 6). Specimens from different localities were grouped in order to increase sample size. Grouped localities are from the same geographic region and are generally within the limits of the Biotic Provinces as construed by Goldman and Moore (1946) for México and by Ryan (1963) for Central America.

A computerized least squares analysis of variance utilizing the values of 17 cranial measurements was used to determine the significance of difference between geographically sympatric population samples of *virginiana* and *marsupialis*. In this analysis the species samples were not segregated on the basis of sex or age class.

Chromosome Preparations

The animals used for chromosomal analysis were treated using the techniques described by Patton (1967). Chromosomal material from Louisianan and Texan specimens of *D. virginiana* was prepared in the laboratory. All other chromosomal preparations were made under field conditions in México, Costa Rica, and Perú. For comparative purposes, slides were prepared also from *D. albiventris* in Perú.

Slides were stained with Giemsa, and cover slips were affixed with Permount. The dried mounted slides were scanned under a microscope, and certain meta-

phases were marked and later photographed. Pictures of individual chromosomes were cut from photographs and arranged according to size in *marsupialis* and *albiventris*, or on the bases of morphology and size in *virginiana*. Negatives of selected slides were projected on writing paper by means of a photographic enlarger, and the chromosome images were outlined in pencil and measured to determine relative chromosomal lengths. The diploid number, fundamental number, and chromosome morphology were determined by standard methods (Patton, 1967).

Representative slides of chromosomal material with the corresponding voucher specimens are deposited in the Louisiana State University Museum of Zoology.

AGE CLASSES

Specimens were assigned to one of seven age classes based on tooth eruption and wear. Specimens lacking a fully erupted M1 were regarded simply as immature. All remaining individuals were assigned to age classes based on the following criteria: age class 1, M1 as well as m1 and sometimes m2 are fully developed; 2, M2 as well as m2 and sometimes m3 are in position; 3, M3 are in position and the permanent premolars are erupting; 4, the permanent premolars and m4 are in position; 5, all teeth erupted, but M4 shows little wear regardless of that on the other teeth; and 6, M4 moderately to excessively worn.

The sequence of tooth eruption proceeds rapidly until attainment of the fourth age class, then seems to lag until the positioning of the last upper molar. Individuals in age classes four to six were considered sexually mature and used in the computer analysis of cranial measurements.

VARIATION

Geographic Variation

Seasonal variation.—Primarily, any seasonal variation is expressed in length and density of the fur, the pelage being longer and thicker in late autumn and winter than during other times of the year. The differences are most pronounced in populations from the United States and at higher elevations in México. Populations from higher northern latitudes and higher elevations also vary seasonally in breeding activity, young individuals being absent during the winter and early spring (see Reynolds, 1945, regarding some United States populations). Most Mexican and Central American opossums from lower elevations and more southerly latitudes do not vary seasonally in fur quality and reproductive activity, probably because of the milder climates in these regions.

Dichromatism.—The two color phases (gray and black) occurring in the three species of *Didelphis* result from the color of guard hairs. The dark color phase is uncommon to rare in most United States populations, but increases in frequency along the Gulf Coast and in southern Texas and is common in Latin American populations (see Table 1). The gray phase predominates in most Mexican and Central American populations of *virginiana*, with its greatest frequency at upper elevations in the Mexican highlands. According to Allen (1901:172), the black

TABLE 1.—Percentage of regional population samples of *Didelphis virginiana* and *D. marsupialis* in the gray (G) or black (B) color phase; N= number.

Region	<i>D. virginiana</i>			<i>D. marsupialis</i>		
	N	G	B	N	G	B
Texas (except southern portion).	73	85	15			
Southern Texas and northeastern México (Tamaulipas, Coahuila, and Nuevo León).	89	46	54			
Eastern México (San Luis Potosí, and Veracruz).	32	78	22	47	48	52
Northwestern México (Sonora, Sinaloa, Chihuahua, and Durango).	65	42	58			
Western México (Nayarit, Jalisco, Colima, and Michoacán).	72	56	44			
Mexican Highlands (Hidalgo, México, Distrito Federal, Puebla and Morelos).	44	96	04			
Southern México (Guerrero and Oaxaca).	77	74	26			
México east of the Isthmus of Tehuantepec (Tabasco, Campeche, Quintana Roo, Yucatán, and Chiapas).	58	84	16	38	30	70
Northern Central America (Guatemala, El Salvador, Honduras, and Nicaragua).	105	85	15	89	37	63
Southern Central America (Costa Rica, and Panamá).				201	53	47

phase occurred in the material he examined from southern Texas at a "ratio of five to one of the gray phase." However, the samples I examined from the same region (which included the specimens examined by Allen) have a dark to gray phase ratio of approximately one to one, which, because of Allen's sample, still may be biased in favor of dark individuals. All of Allen's specimens were collected before the turn of the century by workers who were undoubtedly familiar with the very pale-colored opossums of the eastern United States. I suggest that these workers were more likely to make museum specimens of odd or unusual individuals (*i.e.*, black phase) in preference to those in the more familiar gray phase.

Didelphis marsupialis, on the other hand, is represented by samples in which one-half to two-thirds of the specimens are in the dark phase. Nevertheless, all 15 individuals of two litters of Mexican *marsupialis* born in captivity to a gray phase female from about 5 km. W El Naranjo, San Luis Potosí, that was bred to a dark phase male from about 1 km. W Fortún, Veracruz, were in the gray phase. However, a litter of 10 born to a female from one of the first two litters backcrossed to the male from Fortún contained three in the dark phase and seven in the gray phase.

Length of extremities.—*Didelphis virginiana* varies in the length of the tail relative to the length of the head and body. As outlined by Allen (1901:150), the tail is less than 70 per cent as long as the head and body in animals from northeastern United States. The tail increases from north to south in absolute and relative length, averaging 73 per cent along the Gulf Coast to 82 per cent in southern

Texas. This relative length of the tail is maintained throughout Mexican and Central American populations except in Sonora and Sinaloa, where the average tail length approximates 93 per cent of the head and body length.

The increase in tail length (and size of the ear) from north to south in the United States follows the well-known ecological principle that the length of extremities tends to be shorter in colder climatic zones than in warmer ones. In contrast to this generality, populations from the Mexican highlands at elevations up to 3000 meters along the Transvolcanic Axis and near México City have the tail slightly longer (about 85 per cent) than do adjacent populations at lower elevations. The greater tail length in northwestern Mexican populations (about 93 per cent) possibly allows increased heat radiation and therefore would be advantageous for animals in the hotter, drier habitats of that region.

The length of the tail relative to the length of the head and body approximates 102 per cent in all age groups of *marsupialis* from northern Veracruz to Panamá. No geographic variation in tail length is discernible in the Mexican and Central American samples of this species.

Color pattern.—Allen's (1901:150-152) discussion of the geographic variation in coloration is accurate and generally complete as regards *D. virginiana*. Briefly, *virginiana* in the central and northern United States is characterized by pale body color, an almost all white head, black ears tipped with flesh color, white forefeet, white toes on hind feet, and the black basal portion of the naked tail short or absent. Specimens from populations in the southeastern United States and along the Gulf Coast are characterized by generally darker color, an almost all white head except for dark facial markings, flesh colored tips of the ears reduced or absent, white on forefeet restricted to the toes, white on hind feet restricted to the terminal phalanges or absent from one or both feet, and the black base of the naked portion of tail longer (up to 20 per cent of the unfurred portion in some individuals). Individuals from southern Texas and northeastern México have even darker coloration, the white color on the head often restricted to the cheek region, ears usually black, feet black, and 25 to 50 per cent of the naked portion of tail pigmented with melanin. Nearly all other Mexican and Central American specimens of *virginiana* have a dark head with white cheeks, black toes and ears, and about 50 per cent of the naked tail black. A few individuals from populations along the southern margin of the Mexican Plateau have up to four-fifths of the unfurred portion of the tail black.

The greatest shifts in color pattern in *virginiana* occur between the populations in northeastern México and south central Texas. These changes, from north to south, include: the replacement of the white head of northern animals by a much darker head, which retains, however, a distinctly white cheek; the reduction or loss of pale ear tips; the complete loss of white on the feet and toes; and an increase in the extent of black pigment on the tail. A greater incidence of dark individuals and an increase in tail length are associated with these character shifts.

The only geographic variation in color pattern noted in *marsupialis* is in the extent of black pigment beyond the haired base of the tail. The black color covers from 20 to 30 per cent of the unfurred portion of the tail in *marsupialis* from

México through Honduras. A few Nicaraguan specimens have up to one-half of the naked portion of the tail black, and populations south of the southern limits of *virginiana*, in Costa Rica and Panamá, commonly have half or more of the tail black.

Nongeographic Variation

Skulls exhibit an unusual amount of individual variation, much of it dependent on age and sex. Allen (1901:152-159) dwelt at length on a number of features subject to individual variation, compiling two lists of large skulls that warrant comment. The first list included 21 of the largest males from a series of about 200 from such diverse areas as New Jersey, Florida, and western and southern México. His second list included 12 of the largest females from the same series, again from equally diverse and widely separated geographic areas, including Nicaragua. Allen's purpose in presenting this information was primarily to demonstrate sexual dimorphism in size. Secondarily, he pointed out that large (and old) opossums came from several widely separated localities and suggested that these regions shared some kind of protective environment allowing individuals to reach old age and attain large size. I was able to examine these specimens and found that, with a single exception on each list, all the animals are *virginiana*. The two exceptions, a male from Frontera, Tabasco, México, and a female from Greytown, Nicaragua (the holotype of *D. richmondi*), are both *marsupialis*.

During the course of this study, I observed that: 1) differences in skull size between the sexes usually do not become pronounced until about age class 4; 2) skulls with low, poorly developed cranial crests that were assigned to age classes 4, 5, and 6 on the basis of tooth eruption, are smaller than the average for the same age—the size differences, although apparent in both sexes, being remarkable in some males; and 3) those skulls with broken or excessively worn teeth belonging, on the basis of tooth eruption, to relatively young animals, are also smaller than the average for their age class. Allen (1901) noted that skulls of males were usually larger and more robust, with greater development of cranial crests than skulls of females. However, he offered no satisfactory explanation for skulls of old males of the same or smaller size than those of average-sized females, nor did he explain the occasional female skull that has the size and configuration of the skull of a large adult male.

Ontogenetic variation in skull development is pronounced. It is well known that the skull and certain postcranial skeletal elements of opossums increase in size throughout the life of the individual (see Lowrance, 1949). An examination of an opossum skull, particularly if the bones have separated, reveals that most of the sutures are the "overlapping" type with relatively smooth surfaces of articulation between the bones. Therefore, some changes in skull dimensions may occur through a shifting of the margins of the bones relative to each other. These changes in positional and proportional relationships plus the continued deposition of bone throughout the life of the individual suggest that local environmental influences might exert a profound effect upon cranial morphology. Probably the

effect of diet is provided by the skulls of two young (age class 2) male *marsupialis* from El Salvador with unusually worn teeth. Label information, MVZ 130305 and 130306, records stomach contents as "seeds" and "coffee beans," respectively—hardly optimum foods.

In an attempt to explain at least some of the variation (especially that considered to be independent of genetic influence) exhibited by *Didelphis* and outlined in the preceding observations, I have formulated the following hypothesis: Mammals that have indiscriminate food habits have a broader range of morphological variation. Opossums of this genus are opportunistic omnivores, apparently lacking restrictive dietary requirements. Therefore, individuals are able to grow and become reproductively mature utilizing marginal food sources. Diets deficient in certain nutrients are reflected by a slower growth rate and smaller size, independent of age and sex. Marginal foods with abrasive qualities accelerate attrition of the teeth, eventually affecting the longevity of the animal. Size differences between sexes become accentuated following the attainment of reproductive maturity (age class 4 in females), suggesting that the nutritional load placed on pregnant and lactating females diverts energy sources that would otherwise contribute to increased growth. The existence of male-sized females could be exemplified by either the availability of an unusually good food source or the reduction of fecundity due to a variety of factors from less breeding activity to complete sterility.

Didelphis virginiana and *D. marsupialis* were compared using a computerized least squares analysis of variance in an attempt to assess the extent of interspecific variation. The measurements of 17 cranial dimensions were analyzed for each species sample from the geographic zone of sympatry (see Fig. 1). All *virginiana* from the zone of sympatry assigned to the three oldest age classes (ages 4, 5, and 6) were compared to a similarly derived sample of *marsupialis*. The F values (Table 2) ranged from 2.20 to 137.58. Values of F greater than 3.89 with one degree of freedom are significant at the five per cent level and values greater than 6.81 with one degree of freedom are significant at the one per cent level. Any values of F approximating 13 indicate a probability of about one-twentieth of one per cent that the differences between samples are not significant. Eleven of the 17 values for F are greater than 13 and seven exceed 50. The results of this analysis support the conclusion that *D. virginiana* and *D. marsupialis* are separate species distinguishable on the bases of nonmensural and nonchromosomal characters.

The length of the upper molar series was the only variate not significant at the five per cent level ($F = 2.20$). This measurement and that of the length of maxillary toothrow were restricted to individuals of age classes 5 and 6. These two measurements were not taken on specimens in age class 4 because the fourth upper molar is not yet in position. In spite of the restricted sample, the F value of 24.49 for the length of maxillary toothrow has an extremely low probability and likely reflects interspecific differences in spacing between the canine and the anterior permanent premolars. The breadth across upper canines ($F = 5.73$) was the only measurement with a probability between five and one per cent.

Measurements of individuals comprising the sympatric species samples were reanalyzed for standard statistics (mean, standard deviation, and coefficient of

TABLE 2.—Values of *F* from the least squares analysis of variance comparing samples of *Didelphis marsupialis* and *D. virginiana* from the geographic zone of sympatry in México and Central America. The species samples (*N*) for each of the 17 cranial variates compared include individuals of both sexes in the three oldest age classes (4, 5, and 6).

Variate	<i>D. marsupialis</i>	<i>D. virginiana</i>	<i>F</i> *
	<i>N</i>	<i>N</i>	
Greatest length of skull	210	197	52.94
Condylobasal length	201	186	43.87
Palatal length	207	196	19.17
Zygomatic breadth	193	187	50.40
Interorbital constriction	206	193	10.10
Postorbital constriction	209	196	8.51
Breadth across canines	196	177	5.73
Breadth across molars	196	175	69.00
Breadth of brain case	206	194	137.58
Breadth of palatal shelf	181	184	76.75
Length of maxillary toothrow	175	155	24.49
Length of upper molar series	170	155	2.20
Length of mandible	207	193	46.27
Length of lower molar series	196	177	8.69
Breadth of rostrum across jugals	197	186	72.93
Greatest breadth of nasals	200	187	93.86
Breadth of rostrum across frontals	192	184	10.62

**F* values (one degree of freedom) exceeding 3.89 are significant at the 5 per cent level and those exceeding 6.81 are significant at the 1 per cent level.

variation—see Table 7 in Appendix I); however, each sample was segregated on the bases of sex and age class (4, 5, and 6). Values for greatest length of skull, length of palate, zygomatic breadth, and breadth of brain case (Figs. 2, 3, and 4), and the data in Table 7 illustrate differences in cranial size between age classes and sexes of each species. Although skulls of *virginiana* are often larger than skulls of *marsupialis*, especially in age class 6, cranial measurements alone usually will not serve to assign specimens to either species. Size differences between age classes 4 and 5 are comparable between the sexes, but the size differences between 5 and 6 are considerably less in females than in males. Females in age class 6 of both species reflect the deceleration in growth rate that I have attributed to increased nutritional demands of pregnancy and lactation. Broken lines have been added connecting the means of each sample in the graphs in Fig. 2 to emphasize these growth trends.

These data also indicate a faster growth rate in *virginiana*, with individuals often attaining larger size than in *marsupialis* of comparable sex and age class. Interspecific differences in growth rate, however, may not be entirely due to primary genetic differences. *Didelphis virginiana* successfully utilizes a wide variety of habitats from sea level to elevations over 10,000 feet, whereas *marsupialis* is restricted to warm humid regions at relatively low elevations. Local habitats that are restrictive or intolerable to *marsupialis* occur within the geographic zone of sympatry. Therefore, average environmental diversity favoring *virginiana* could account for some of the observed size differences through the influences of vary-

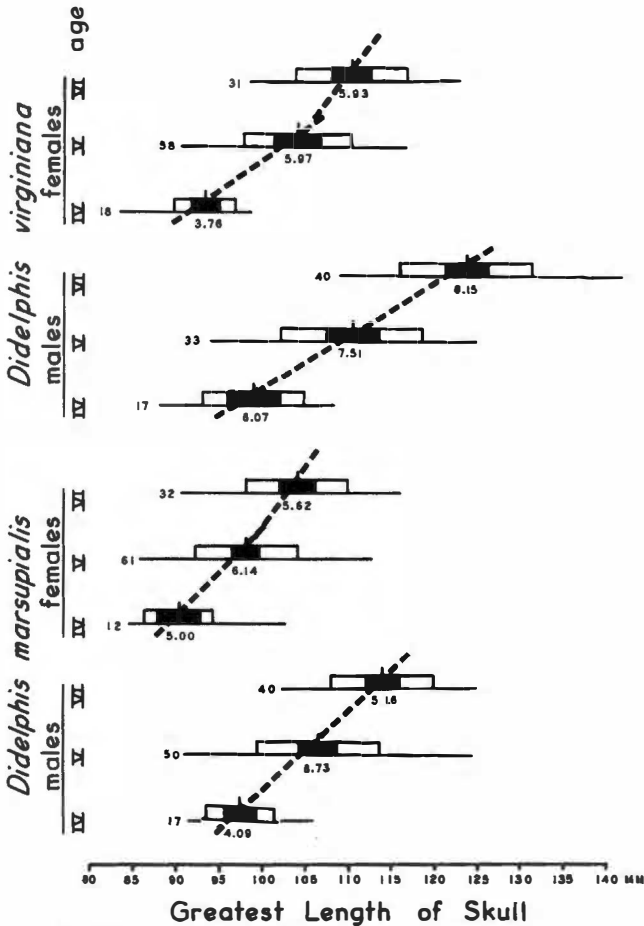


FIG. 2.—Graphs of the cranial measurement, greatest length of skull, for samples from geographically sympatric populations of *Didelphis virginiana* and *D. marsupialis*. Species samples are segregated by sex and age class (roman numerals: age classes 4, 5, and 6); horizontal line, range; short vertical line, mean; solid boxes, two standard errors on each side of the mean; open and solid boxes, one standard deviation on each side of the mean; sample size at left of range; coefficient of variation below each graph; broken lines joining means of each age class sample within each sex illustrate growth patterns.

ing dietary regimes, severity of parasite infestations, extent of predator exposure, and other factors associated with different habitats that could affect morphogenesis and bias population age structure.

CHROMOSOMES

Didelphids are separable, on the basis of diploid numbers, into 14, 18, and 22-chromosome groups. The 14-chromosome group is comprised of *Marmosa*, *Metachirus*, *Dromiciops*, and *Caluromys*—the latter regarded by Reig (1955) as two of the three surviving genera of the otherwise extinct Microbiotheriinae. The 12

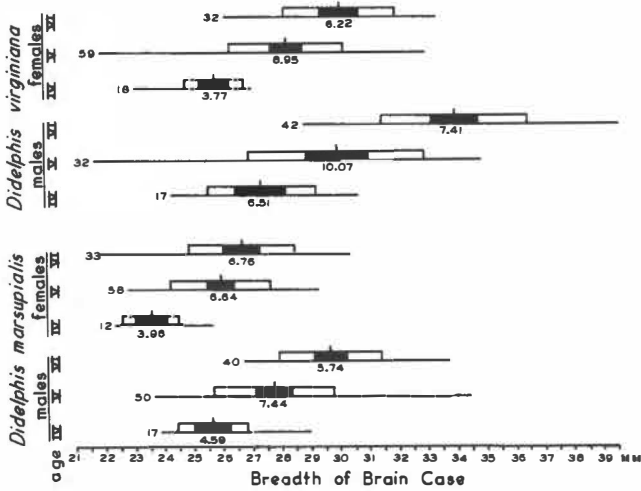


FIG. 3.—Graphs of the cranial measurements, length of palate and zygomatic breadth, for samples from geographically sympatric populations of *Didelphis virginiana* and *D. marsupialis*. See Fig. 2 for description of graphs.

species of this group whose chromosomes have been studied have essentially the same karyotype with four pairs of biarmed and two pairs of uniarmed autosomes, a small submetacentric X, and a minute acrocentric Y chromosome. Two species of *Monodelphis* are the only New World marsupials known to have 18 chromosomes. Their karyotype (Reig and Bianchi, 1969) differs from that of the

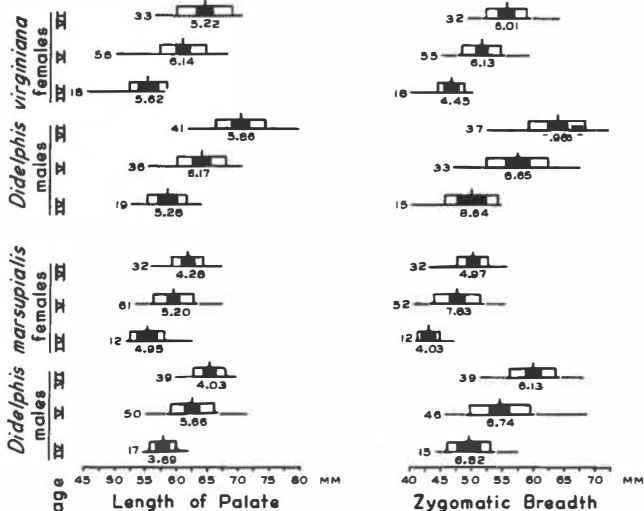


FIG. 4.—Graphs of the cranial measurement, breadth of brain case, for samples from geographically sympatric populations of *Didelphis virginiana* and *D. marsupialis*. See Fig. 2 for description of graphs.

① *Didelphis albiventris*, Cordillera Carpish, Depto. Huánuco, Perú.



② *Didelphis marsupialis*, 13 km. N Huixtla, Chiapas, México.



③ *Didelphis virginiana*, Edinburg, Hidalgo Co., Texas.



FIG. 5.—Karyotypes of three species of *Didelphis*: *D. albiventris*, E slope Cordillera Carpish, Departamento de Huánuco, Perú, LSUMZ 14009; *D. marsupialis*, ca. 13 km. N Huixtla, Chiapas, México, LSUMZ 11912; and *D. virginiana*, Edinburg, Hidalgo County, Texas, LSUMZ 13393.

14-chromosome group by having four additional pairs of medium-sized unarmed autosomes, a very small acrocentric X chromosome, and two instead of four pairs of large biarmed autosomes. The 22-chromosome group includes *Didelphis*, *Philander*, *Chironectes*, and *Lutreolina*. Six of the seven species in this group have chromosomal complements consisting entirely of unarmed elements like the karyotype described below for *D. marsupialis*, except that *L. crassicaudata* has a medium-sized metacentric X chromosome. The distinctive and unique chromosomal pattern characterizing the seventh species of the group, *D. virginiana*, is described below.

Karyotype Analysis

Karyotypes of the three species of *Didelphis* are shown in Fig. 5. The number of individuals analyzed, their provenance, sex, chromosome numbers, and fundamental numbers (numbers of autosomal arms), as well as the morphological types of chromosomes for each species are summarized in Table 3. The karyotype descriptions are as follows:

Didelphis marsupialis.—The diploid number is 22 and the fundamental number is 20. The three pairs of large and the seven pairs of medium-sized autosomes are all acrocentric. The X and Y chromosomes are small acrocentrics, although the X is about four times the size of the Y.

Didelphis albiventris.—The diploid number, fundamental number, and morphology of the chromosomes are identical to those described for *D. marsupialis*, except that the Y chromosome is minute.

Didelphis virginiana.—The diploid number is 22, and the fundamental number is 32. The autosomes are three pairs of large subtelocentrics, three pairs of

TABLE 3.—Somatic chromosome numbers and morphological types for the three species of *Didelphis*.

Species	Chromosomes*							
	Sex		Autosomes					
	♂	♀	2n	FN	ST	A	X	Y
<i>Didelphis albiventris</i>								
Perú	1	3	22	20		10	A	A
<i>Didelphis marsupialis</i>								
México	5	6	22	20		10	A	A
Costa Rica	1	2	22	20		10	A	A
Perú	5	2	22	20		10	A	A
<i>Didelphis virginiana</i>								
Louisiana	7	3	22	32	6	4	SM	A
Texas	2		22	32	6	4	SM	A
México	6	3	22	32	6	4	SM	A

*Autosome numbers refer to numbers of homologous pairs; A=acrocentric, SM=submetacentric, ST=subtelocentric, 2n=diploid number, and FN=fundamental number.

TABLE 4.—Analysis of mean chromosome length for 21 metaphases from a female specimen of *Didelphis virginiana* (LSUMZ 15107) from El Salto, San Luis Potosí, México. Mean chromosome lengths are also expressed as a percentage of the total diploid complement length (per cent TCL).

Chromosome	Short arm (S)		Long arm (L)		Arm ratio (L/S)	Chromosome length %-TCL
	Mean*	%-TCL	Mean*	%-TCL		
1	7.67	1.18	39.29	6.05	5.12	7.24
2	7.14	1.10	37.52	5.78	5.25	6.88
3	7.24	1.11	36.00	5.55	4.97	6.66
4	6.67	1.02	34.57	5.33	5.18	6.35
5	6.67	1.02	33.57	5.17	5.03	6.20
6	6.76	1.04	31.95	4.92	4.73	5.96
7	7.00	1.07	27.57	4.25	3.94	5.33
8	6.57	1.01	26.62	4.10	4.05	5.11
9	7.00	1.07	25.62	3.95	3.66	5.03
10	6.76	1.04	24.90	3.84	3.68	4.88
11	6.67	1.02	24.57	3.79	3.68	4.81
12	6.33	0.97	23.90	3.68	3.78	4.66
13**			23.05			3.55
14**			22.48			3.46
15**			21.67			3.34
16**			20.86			3.21
17**			19.81			3.05
18**			18.57			2.86
19**			17.14			2.64
20**			16.09			2.48
X	8.48	1.30	12.95	2.00	1.53	3.30
X	7.81	1.20	11.81	1.82	1.52	3.02

*Expressed in measurement units.

**Acrocentric chromosomes.

TABLE 5.—Comparison of chromosome (C) lengths of *Didelphis virginiana* (V), *D. marsupialis* (M), and a modified chromosomal complement (long arm only) of "virginiana" (L). Means (\bar{X}) are expressed in measurement units for 21 metaphases from a female *virginiana* from El Salto, San Luis Potosí (LSUMZ 15107), and 23 metaphases from a female *marsupialis* from Fortín, Veracruz (LSUMZ 15104). Mean chromosome lengths are also expressed as a percentage of the total diploid complement length (per cent TCL).

C	<i>virginiana</i> N=21		<i>marsupialis</i> N=23		"virginiana" N=21		Difference	
	\bar{X}	% TCL	\bar{X}	% TCL	\bar{X}	% TCL	(V-M)	(L-M)
1	47.00	7.24	55.00	8.12	39.29	7.14	-0.88	-0.98
2	44.62	6.87	51.83	7.65	37.52	6.82	-0.78	-0.83
3	43.29	6.66	49.00	7.23	36.00	6.54	-0.57	-0.69
4	41.19	6.34	46.17	6.82	34.57	6.28	-0.48	-0.54
5	40.24	6.19	43.91	6.48	33.57	6.10	-0.29	-0.38
6	38.52	5.93	41.22	6.09	31.95	5.80	-0.16	-0.29
7	31.90	4.91	32.39	4.78	27.57	5.01	0.13	0.23
8	29.14	4.49	30.74	4.54	26.62	4.84	-0.05	0.30
9	27.86	4.29	29.39	4.34	25.62	4.65	-0.05	0.31
10	27.05	4.16	28.70	4.24	24.90	4.52	-0.08	0.28
11	26.33	4.05	27.83	4.11	24.57	4.46	0.06	0.35
12	25.90	3.99	27.04	3.99	23.90	4.34	0.00	0.35
13	25.24	3.89	26.48	3.91	23.05	4.19	-0.02	0.28
14	24.76	3.81	25.74	3.80	22.48	4.08	0.01	0.28
15	24.33	3.75	25.22	3.72	23.67	3.94	0.03	0.22
16	23.91	3.68	24.52	3.62	20.86	3.79	0.06	0.17
17	23.00	3.54	24.17	3.57	19.81	3.60	-0.03	-0.03
18	22.43	3.45	23.09	3.40	18.57	3.37	0.05	-0.03
19	21.81	3.36	21.78	3.22	17.14	3.11	0.14	-0.11
20	19.95	3.07	19.97	2.95	16.10	2.92	0.12	-0.03
X	21.48	3.30	12.17	1.80	12.95	2.35	1.50	0.55
X	19.57	3.02	11.04	1.63	11.81	2.15	1.39	0.52

medium-sized subtelocentrics, and four pairs of medium-sized acrocentric chromosomes. The X is a smaller, medium-sized submetacentric, and the Y is a small acrocentric. The metaphase chromosomes are analyzed in Table 4.

Comparison of Karyotypes

A comparison of the chromosomes of *virginiana* with those of *marsupialis* suggests that the six pairs of biarmed autosomes of *virginiana* arose through a series of pericentric inversions, inasmuch as there is a difference in fundamental number without a corresponding change in diploid number. However, the short arms of the autosomes of *virginiana* are so short that they could represent accumulations of extraneous material on the chromosomes. Also the submetacentric X chromosome of *virginiana* is similar to the metacentric X of *Lutreolina crassicaudata*, which Reig (personal communication) thinks may represent an isochromosome (term defined by Darlington, 1939). Therefore, if the short autosomal arms represent additional material and the larger X chromosome arose through the forma-

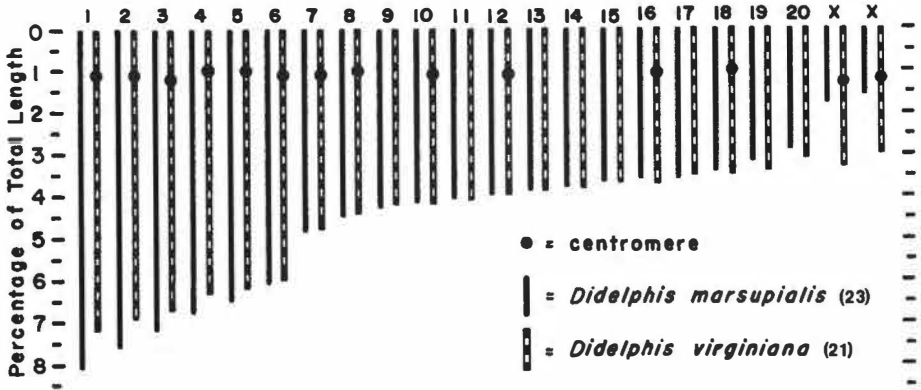


FIG. 6.—A comparison of the chromosome lengths of *Didelphis marsupialis* and *D. virginiana*. The mean length of each chromosome (averages of 23 metaphases for *D. marsupialis* and 21 metaphases for *D. virginiana*) is expressed as a percentage of the total diploid complement length. Autosomes are arranged by size. Centromere position is indicated for biarmed chromosomes.

tion of an isochromosome, the long arms of the autosomes and X chromosome of *virginiana* should approximate the lengths of the chromosomes of *marsupialis*.

The chromosome lengths of *virginiana* and *marsupialis* are compared with each other (see Fig. 6) and with a modified chromosomal complement of *virginiana* (biarmed chromosomes represented by the long arms only) in Table 5. The average chromosome length is the ranking criterion used in making these comparisons, inasmuch as it is the only method applicable to the all-uniarmed chromosomes of *marsupialis*. The mean length in measurement units for each chromosome is also expressed as a percentage of the total diploid complement length (per cent TCL). The values for the modified chromosomal complement of *virginiana* were derived by tabulating and ranking the long arm measurements as though each represented a whole chromosome. The differences between percentage of TCL values (Table 5) were calculated for comparison of the normal complement of *marsupialis* with the normal complement of *virginiana* and the modified complement of *virginiana*.

A breakdown of the difference values for chromosome lengths in the *virginiana* versus *marsupialis* comparison shows that 15 chromosomes differ by less than 0.20 and eight chromosomes differ by less than 0.06. Values for the modified *virginiana* versus the normal *marsupialis* comparison reveal greater differences between chromosome lengths inasmuch as 15 of the 20 autosomes differ by more than 0.20. These findings support the hypothesis that the biarmed autosomes of *virginiana* were probably derived through a series of pericentric inversions in a *marsupialis*-like ancestor, although they do not explain the differences seen between the longer autosomes or the X chromosomes of the two species (Fig. 6). I consider the karyotype of *virginiana* to be derived from the *marsupialis*-like karyotype because the latter is shared by five of the six other American marsupials with 22 chromosomes. However, because a minimum of two breaks had to

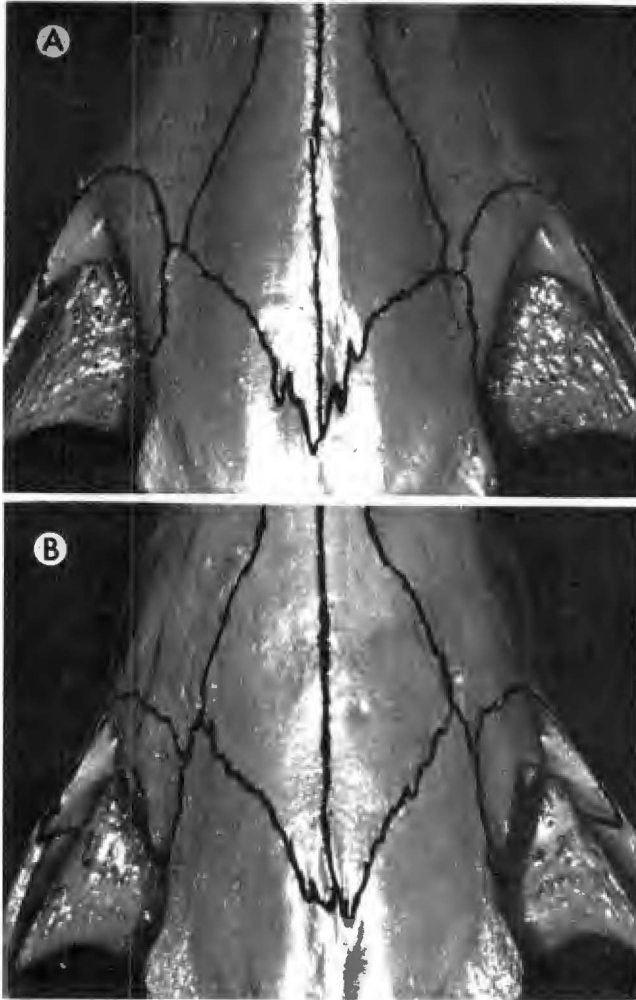


FIG. 7.—Dorsal views of the naso-frontal region of a skull of *Didelphis virginiana* and a skull of *D. marsupialis*: A, *D. virginiana* from 2 mi. S Grosse Tete, Iberville Parish, Louisiana, LSUMZ 6067; B, *D. marsupialis* from 1 km. W Fortín, Veracruz, México, LSUMZ 15104.

occur in each chromosome for each pericentric inversion, a large number of chromosomal fractures probably took place in the evolution of the *virginiana* karyotype. Multiple breaks would allow for extensive chromosomal rearrangements and would explain the six pairs of submetacentric autosomes by a series of pericentric inversions and the larger submetacentric X chromosomes through one or more unequal translocations—probably with the larger autosomes, inasmuch as they are comparatively shorter in *virginiana*.

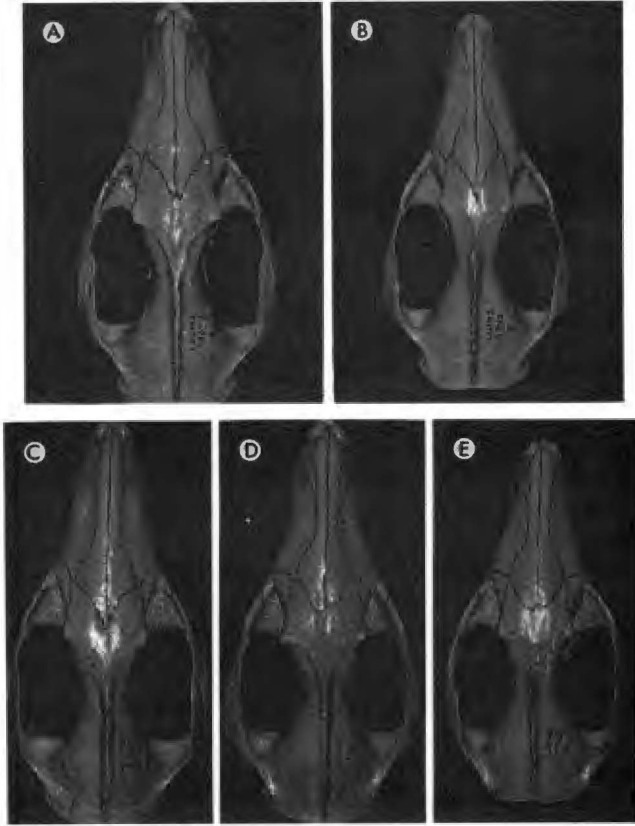


FIG. 8.—Dorsal views of two skulls of *Didelphis marsupialis* and three skulls of *D. virginiana*. *Didelphis marsupialis*: A, 1 km. W Fortún, Veracruz, México, LSUMZ 15104; B, Xilitla, San Luis Potosí, México, LSUMZ 2742. *Didelphis virginiana*: C, 2 mi. S Grosse Tete, Iberville Parish, Louisiana, LSUMZ 6067; D, 1 mi. E Teapa, Tabasco, México, LSUMZ 7314; E, Bledos, San Luis Potosí, México, LSUMZ 4763.

CHARACTERS OF TAXONOMIC VALUE

Chromosomal features provided the primary characters of taxonomic significance used in this study. Subsequent examination of individuals of known karyotype revealed a number of other features useful for distinguishing *D. virginiana* and *D. marsupialis*. These include differences in cranial morphology, color pattern, hair pattern, and behavior.

The taxonomic characters used by Allen (1901) were the extent of black on the base of the tail, the ratio of the head and body length to tail length, and features of the nasals, particularly of the posterior margin, all of which he applied to characterize species and subspecies of *Didelphis*. I have found, however, that Allen's characters are of limited value except for distinguishing some populations

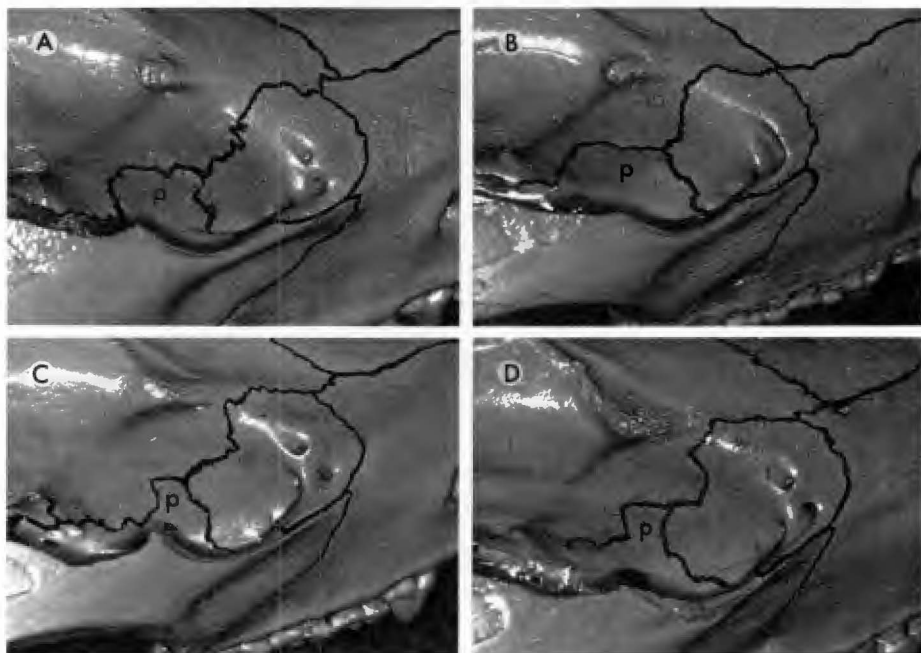


FIG. 9.—Lateral view of the orbital region of *Didelphis virginiana* and *D. marsupialis* comparing the widths of the palatine. *Didelphis virginiana*: A, 1 mi. E Teapa, Tabasco, México, LSUMZ 14009; B, Bledos, San Luis Potosí, México, LSUMZ 4763. *Didelphis marsupialis*: C, 1 km. W Fortín, Veracruz, México, LSUMZ 15104; D, Xilitla, San Luis Potosí, México, LSUMZ 2742.

of *virginiana*. The characters I consider to be the most important from a practical point of view are those which, in addition to delineating geographic variation, facilitate the identification of prepared specimens in collections.

Cranial Characters

Naso-lacrimal region.—The relationship of the lateral margin of the nasal bones to the medial border of the lacrimal bones, and of both to the maxillo-frontal suture, is useful for distinguishing *virginiana* from *marsupialis*. The lateralmost extent of each nasal in *virginiana*, where intercepted by the maxillo-frontal suture, is aligned with, or anterior to, the point where the same suture meets the lacrimal (Figs. 7A, 8C and D, 10B). The lateral point on the nasal bones of *marsupialis* where met by the maxillo-frontal suture is always anterior to the point where this suture intercepts the lacrimal (Figs. 7B, 8A and B, 11B).

The naso-lacrimal features are variable, particularly in *virginiana*, where these characters will occasionally seem *marsupialis*-like, but in such cases the dorsal lacrimo-frontal suture will usually be bowed medially (Fig. 8D). Contact between the nasals and lacrimals, seen in only one deformed *marsupialis* skull, is a common feature of *virginiana* (Fig. 8E).



FIG. 10.—Three views of a skull of *Didelphis virginiana* from Edinburg, Hidalgo County, Texas, LSUMZ 13393: A, dorsal view of skull; B, dorsal view of naso-frontal region; and C, lateral view of orbital region (P=palatine).

Nasal bones.—Typically, *marsupialis* has narrow nasals that terminate posteriorly in an acute angle. The nasals of *virginiana* are generally broader and, in Mexican and Central American populations, commonly terminate in a rounded or truncated angle. However, the size and configuration of the nasals are subject to considerable individual variation in both species and have limited taxonomic value when used alone.

Lacrimo-jugal region.—The configuration of the posterior extension of the lacrimal bone that forms the lower anterior margin of the orbit, and its relationship to the underlying jugal, is the cranial character most often serving to separate *virginiana* from *marsupialis*. The lacrimal of *virginiana* recedes from the outer margin of the jugal before terminating, usually in a rounded point (Figs. 7A, 8C, 10B). Also, in *virginiana*, the lacrimal appears to be set down into a shallow depression in the jugal (Fig. 9A and B). The lacrimal of *marsupialis* recedes only slightly from the outer margin of the jugal before terminating in a strong and sometimes squared point (Figs. 7B, 8A and B, 11B), and the lacrimal usually appears to lie on top of, rather than down into, the jugal (Fig. 9C and D).

Inner wall of orbit.—The sutural pattern formed by the dorsal extension of the palatine bones that make up part of the inner wall of the orbit, is a valuable aid in separating the two species. The dorsal extension of the orbital portion of the palatine is usually broad in *virginiana* (Figs. 9A and B, 10C), whereas it is always

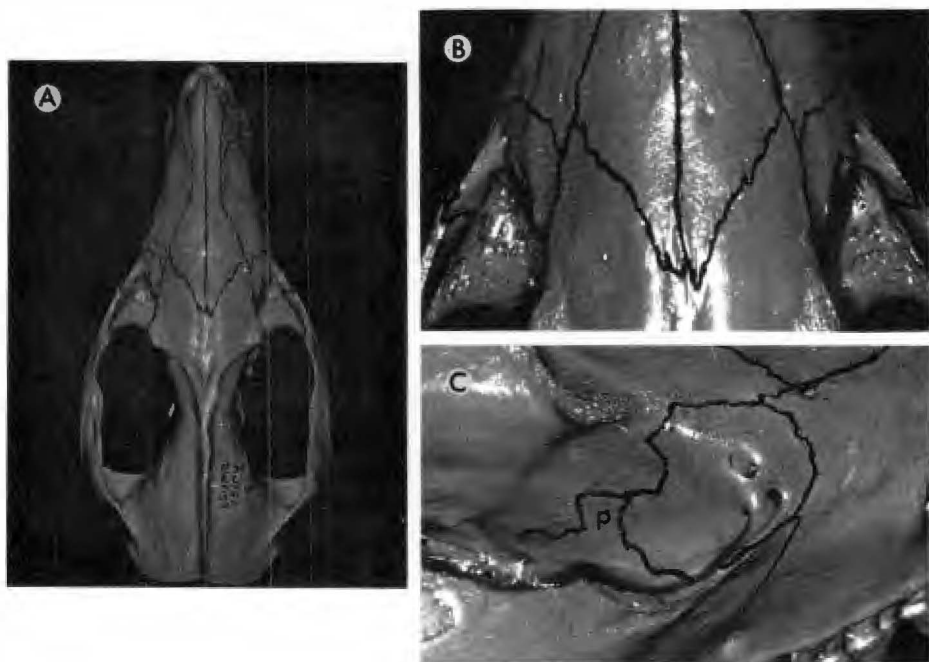


FIG. 11.—Three views of a skull of *Didelphis marsupialis* from 1 km. E Fortín, Veracruz, México, LSUMZ 15104: A, dorsal view of skull; B, dorsal view of naso-frontal region; C, lateral view of orbital region (P = palatine).

narrow in *marsupialis* (Figs. 9C and D, 11C), sometimes becoming a narrow point or occasionally absent entirely.

External Characters

Color pattern.—Perhaps the most distinctive and easily observed external character separating *virginiana* and *marsupialis* is the hair color of the cheek region. The white cheek in Mexican and Central American *virginiana* is bordered behind by the darker color of the sides of the head and neck and above by a dark band extending from the ear through the eye. Dark individuals often have a few black hairs scattered through the otherwise white cheek. The cheek color is usually buff in *marsupialis*; however, it can vary from pale yellow to a deep buffy orange, and much of the hair is tipped with dark brown or black, imparting an overall dusky appearance. The paler color of the cheek region is not clearly set off from the rest of the head, as it is in *virginiana*.

Davis (1944:374) noted that the buffy cheek color of the Mexican opossums he assigned to *D. mesamericana tabascensis* (= *D. marsupialis*) did not appear to be due to what Allen (1901:173) termed adventitious staining, but he did not attribute any special importance to this observation. The extent of the black pigmented basal portion of the tail, as discussed under the section on geographic variation, can be used to separate most Mexican *virginiana* from sympatric

marsupialis, but this character is too variable for broader application. The color pattern combination of a short black tail base, a white face, flesh-colored ear tips, and white toes is unique to *virginiana* in southern Canada and all of the United States except the southeastern and Gulf coastal states.

Hair pattern.—Two hair patterns, inconspicuous in prepared specimens, involve the relative distribution of the guard hair and the length of the furred base of the tail. Living *marsupialis* often have a “razorback” appearance because guard hairs tend to be concentrated along the midline, whereas in *virginiana*, guard hairs are more evenly distributed over the dorsum. The furred base of the tail of adults is longer in *marsupialis* than in *virginiana*.

Behavior

Individuals of *marsupialis* display an elaborate series of protracted movement patterns and sounds when threatened by larger mammals. More pronounced in males than in females, the movement pattern consists of turning the head from side to side so that the weight is shifted alternately from one front foot to the other. The lateral movements of the head and foreparts of the body are interrupted at irregular intervals by forward lunges, accompanied by growling and hissing sounds. This stereotyped bluffing behavior reminiscent of that of *Phylander opossum* may be continued for several minutes. The bluffing response by *virginiana* is less extreme than that of *marsupialis*, characterized by much less body movement, and an abbreviated lunging-growling-hissing pattern.

I have seen examples of “playing possum” by individuals of *virginiana* when cornered or caught in a trap. However, I have never seen this behavior in *marsupialis*. When caught in steel traps, these opossums are always active when approached, whereas *virginiana* often lies on its side with the mouth open, commences salivating, and will sometimes defecate and urinate.

Several of the *virginiana* used in the chromosomal analyses were captured by grabbing the tail. Thus caught, these opossums did little more than growl and move their bodies from side to side. I was not able to catch *marsupialis* in this manner, but those who have caught *Didelphis* this way in areas where *virginiana* does not occur (south of Nicaragua) have reported active, biting, aggressive reactions quite unlike those of the more docile *virginiana*.

Another behavioral trait, tail coiling, was observed in *marsupialis*, and *Phylander opossum* but not seen in *virginiana*. In a threatened situation, *marsupialis* tightly coils the tail, sometimes drawing it up under the body. Under similar circumstances, *virginiana* does not coil the tail.

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 1902. *Didelphis marsupialis cauae*, Allen, Bull. Amer. Mus. Nat. Hist., 16:257.
 1902. *Didelphis marsupialis etensis* Allen, Bull. Amer. Mus. Nat. Hist., 16:257.
 1902. *Didelphis mes-americana tabascensis*, Allen, Bull. Amer. Mus. Nat. Hist., 16:257.
 1917. *Didelphis marsupialis particeps* Goldman, Proc. Biol. Soc. Washington, 30:107.
 1920. *D[idelphis] m[arsupialis] richmondi*, Goldman, Smithsonian Misc. Coll., 69:46.
 1924. *Didelphis mesamericana mesamericana*, Miller, Bull. U. S. Nat. Mus., 128:3 (part).
 1951. [*Didelphis marsupialis*] *californica*, Hershkovitz, Fieldiana, Zool., Chicago Mus. Nat. Hist., 31:548 (part).
 1953. *Didelphis marsupialis mesamericana*, Dalquest, Louisiana State Univ. Studies, Biol. Ser., 1:20 (part).

Holotype.—Adult female (skin with skull), AMNH 14192, taken by J. H. Batty.

Type locality.—Cali, Upper Cauca Valley, Colombia.

Distribution.—From central Tamaulipas in eastern México at elevations generally under 4500 feet, through eastern San Luis Potosí, Veracruz, eastern Puebla and Oaxaca to the Isthmus of Tehuantepec, thence southward from coast to coast through México and Central America to northern and western Colombia, western Ecuador, and northwestern Perú. The distribution of *D. marsupialis cauae*, as determined from specimens examined, is indicated by Fig. 12.

Description.—Body size large; tail long (usually longer than head and body); color pattern variable with head and body usually dark except for pale-colored

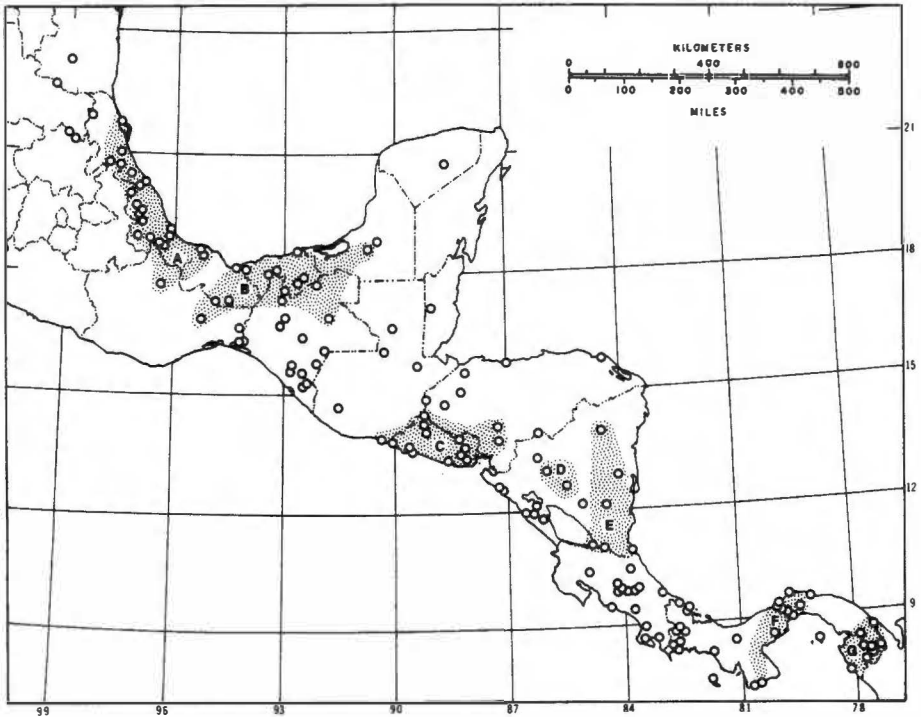


FIG. 12.—Distribution map for *Didelphis marsupialis* in México and Central America as determined by specimens examined.

base of rostral vibrissae and cheek (pale yellow to orange-buff); ears, lower legs, and feet black; proximal portion of tail black (up to 50 per cent of bare tail in southern populations); dichromatic; skull long and narrow, with nasals usually pointed posteriorly. The characters used to separate this species from *virginiana* are discussed under Characters of Taxonomic Value.

Remarks.—This subspecies is poorly characterized, and an adequate diagnosis awaits a thorough analysis of the species throughout its range. In spite of the common and widespread occurrence of *marsupialis*, numbers of specimens sufficient for detailed studies of variation are, with few exceptions, unavailable. The extreme amount of variation due to various combinations of age and sexual, ontogenetic, and dietary influences necessitates relatively large numbers of specimens for the successful analysis of geographic variation.

Consistently, opossums of this species have been confused with individuals of the species *virginiana*. J. A. Allen, the first to attempt a revision of the genus, was confused regarding the morphological identity of *D. marsupialis* (*sensu stricto*) as exemplified by his description of *D. yucatanensis* (1901:178). I found that the holotype (USNM 108299) is a specimen of *virginiana*, yet the two paratypes (USNM 108298 and 108300) from the type locality (Chichén Itzá, Yucatán) are both specimens of *marsupialis*. These two specimens are also the only examples

of *marsupialis* that I have seen from the Yucatán Peninsula proper. The majority of the Chiapan specimens Allen referred to *D. marsupialis tabascensis* are *virginiana*, and all his specimens of *D. richmondi* are clearly referable to *marsupialis*.

Hall and Dalquest (1963:195) claimed that all of the specimens they included under *D. m. californica* except the one from 2 km. E Perote were intergrades between *californica* and *D. m. tabascensis*. Examination of these specimens failed to reveal any intergrades. Ten of these fourteen specimens are referable to *D. m. cauae* (*tabascensis* as understood by Hall and Dalquest).

Measurements.—Cranial measurements from seven selected samples (A to G on the distribution map in Fig. 12) are presented in Appendix I.

Specimens examined.—Mexican and Central American specimens examined are listed in Appendix II.

***Didelphis virginiana virginiana* Kerr**

1758. *Didelphis marsupialis* Linnaeus, Syst. Nat., ed. 10, p. 54 (part).

1792. *Didelphis virginiana* Kerr, An. King., p. 193.

1795. *D[idelphis] pilosissima* Link, Beytrage zur Naturgeschichte, p. 67.

1795. *D[idelphis] illinensium* Link, Beytrage zur Naturgeschichte, p. 67.

1806. *Didelphis Woapink* Barton, Facts, observations and conjectures relative to the question of the opossum of North America, p. 2.

1888. *Didelphys marsupialis* var. *typica* Thomas, Cat. Marsup. Monotr. British Mus., p. 323 (part).

1902. *Did[elphis] boreo-americana* Allen, Bull. Amer. Mus. Nat. Hist., 16:252 (*ex* Oken, 1816).

1951. [*Didelphis marsupialis*] *virginiana*, Hershkovitz, Fieldiana, Zool., Chicago Nat. Hist. Mus., 31:550.

Holotype.—Based on "Virginian Opossum" of Pennant, 1781, Hist. Quadrupeds, p. 301, pl. 34.

Type locality.—Virginia.

Distribution.—From southern Ontario (Peterson and Downing, 1956), southern New Hampshire, northern Vermont, northern New York, central Michigan, north central Wisconsin (Long and Copes, 1968), and central Minnesota southward to South Carolina, Georgia, Alabama, Mississippi, and Louisiana, and westward to south central Texas, eastern Colorado, and western Nebraska. Introduced populations in California (Grinnell, 1933), Oregon, Washington, Idaho, Arizona (Hock, 1952), New Mexico (Sands, 1960), and western Colorado (see Fig. 14).

Description.—Size large, ears small, and tail short (usually under 70 per cent of head and body); face white with dusky color of dorsum sometimes extending forward in a narrow V-shaped wedge to between eyes; eyering dusky; lower legs black; distal half of forefeet and toes of hind feet white; remaining portion of feet black; ears black, conspicuously tipped with white or flesh color; black base of tail short (usually less than 20 per cent of bare tail); dichromatic (dark phase uncommon to rare); skulls of adults usually broad with wide nasals terminating posteriorly in a point.

Remarks.—The introduced populations in California, western Colorado,

Oregon, and Washington are successfully established and expanding their distribution. Introduced opossums in Arizona apparently have died out, and the status of the populations in New Mexico and Idaho is unknown. Miller (1899) and Seton (1929) have chronicled some of the northward expansions of range of *virginiana*, and reports of additional distributional records are common in the recent literature.

This form and its southern representative, *pigra*, probably differentiated from the darker Mexican form, *D. v. californica*, while in at least partial isolation in southeastern regions of the United States during the Wisconsin glaciation.

***Didelphis virginiana pigra* Bangs**

1898. *Didelphis virginiana pigra* Bangs, Proc. Boston Soc. Nat. Hist., 28:172.
 1951. [*Didelphis marsupialis*] *virginiana*, Hershkovitz, Fieldiana, Zool., Chicago Nat. Hist. Mus., 31:550.
 1952. *Didelphis marsupialis pigra*, Hall and Kelson, Univ. Kansas Publ., Mus. Nat. Hist., 5:322.

Holotype.—Adult female (skin with skull), MCZ 3500, taken on 31 January 1896 by O. Bangs.

Type locality.—Oak Lodge, on east Peninsula opposite Micco, Brevard Co., Florida.

Distribution.—From coastal Texas (vicinity of Lavaca Bay, Calhoun County) eastward along the Gulf Coast through Louisiana, Mississippi, and Alabama to Georgia, then north into South Carolina (Beaufort County) and south throughout Florida (see Fig. 14).

Description.—Like *D. v. virginiana* except for longer tail (usually exceeding 70 per cent of head and body) and generally darker color overall; head pale, with a V-shaped dusky patch extending forward between eyes; dark eyering expanded in front of eye and extending posteriorly as an indistinct stripe to light color at base of ears; white cheek blending into grayer postocular stripe above and into darker color of sides of head and neck behind; lower legs and feet black; toes of forefeet white; white of hind toes restricted to tips or entirely absent; ears black, pale color of ear tips reduced or absent; black base of tail up to 30 per cent or more of bare tail; dichromatic but dark phase uncommon; skull as in *D. v. virginiana*.

Remarks.—This weakly differentiated subspecies intergrades with the paler and shorter-tailed northern subspecies, *virginiana*, and the much darker Texan and Mexican subspecies, *californica*, to the west. *Didelphis v. pigra* differs from *virginiana* primarily by the almost all black ears and toes on hind feet, longer tail, darker overall coloration, and greater frequency of the dark color phase. These features occur infrequently throughout the range of *virginiana* but have their greatest expression in the populations assigned to *pigra* along the Gulf Coast and in Georgia, southern South Carolina, and Florida. The extent of genetic influence from the darker populations of southern Texas is unknown (see the account of *D. v. californica*).

***Didelphis virginiana californica* Bennett**

1833. *Didelphis Californica* Bennett, Proc. Zool. Soc. London, p. 40.
 1833. *Didelphis breviceps* Bennett, Proc. Zool. Soc. London, p. 40.
 1843. *Didelphis pruinosa* Wagner, Suppl. Schreber's Saug., 3:40.
 1888. *Didelphys marsupialis* var. *typica* Thomas, Cat. Marsup. Monotr. British Mus., p. 323 (part).
 1901. *Didelphis marsupialis* Allen, Bull. Amer. Mus. Nat. Hist., 14:166 (not Linnaeus, 1758).
 1901. *Didelphis marsupialis texensis* Allen, Bull. Amer. Mus. Nat. Hist., 14:172.
 1901. *Didelphis marsupialis tabascensis* Allen, Bull. Amer. Mus. Nat. Hist., 14:173 (part).
 1902. *Did[elphis] mes-americana*, Allen, Bull. Amer. Mus. Nat. Hist., 16:251 (ex Oken, 1816).
 1902. *Didelphis mes-americana texensis*, Allen, Bull. Amer. Mus. Nat. Hist., 16:256.
 1902. *Didelphis mes-americana tabascensis*, Allen, Bull. Amer. Mus. Nat. Hist., 16:257.
 1903. *Didelphis yucatanensis* Bangs, Bull. Mus. Comp. Zool., 39:157 (not Allen, 1901).
 1951. *Didelphis marsupialis californica*, Hershkovitz, Fieldiana, Zool., Chicago Mus. Nat. Hist., 31:548.

Holotype.—Skull, sex unknown, British Museum (Natural History) 55.12.26.190, taken by J. Coulter.

Type locality.—"That part of California which adjoins to Mexico" (probably southern Mexican Plateau—see *Remarks*).

Distribution.—From Aransas and Val Verde counties, Texas, in the east, and north-central Sonora, in the west, southward throughout México (except the central Mexican Plateau and the Yucatán Peninsula), Guatemala, British Honduras, Honduras, and El Salvador, and through central and western Nicaragua to the southwestern border of Nicaragua; probably occurs in northwestern Costa Rica. The distribution of *D. v. californica*, as determined by specimens examined, is outlined on the map in Fig. 13.

Description.—Size medium to large, ears large and tail long (from 80 to 90 per cent of head and body); dark body color extending forward over top of head in a V-shaped wedge to between eyes; dark eyering with prominent ocular stripe extending from in front of eye to pale colored spot at base of ear; white cheek region distinctly outlined above by postocular stripe and behind by darker color of sides of head and neck; black legs, feet, and ears (a few individuals from north-eastern México and the Rio Grande Valley of Texas have irregularly white-tipped ears); extensive black pigmentation on tail (usually more than 30 per cent, and sometimes more than 50 per cent of bare tail); dichromatic, with dark phase common; long, broad skulls in adults with narrow nasals usually terminating posteriorly in a rounded or truncated point; postorbital processes not unusually prominent.

Remarks.—The use of Bennett's name, *californica*, for this subspecies depends on the specific identity of the type, notwithstanding the alleged type locality. Mr. John Edwards Hill of the Mammal Section of the British Museum (Natural History) compared the skulls of Bennett's holotypes of *D. californica* and *D. breviceps* with several detailed photographs of *marsupialis* and *virginiana*, accompanied by descriptions that I sent to him, and concluded that both *californica* and *breviceps* are referable to *virginiana*. Information on the label of the holotype,

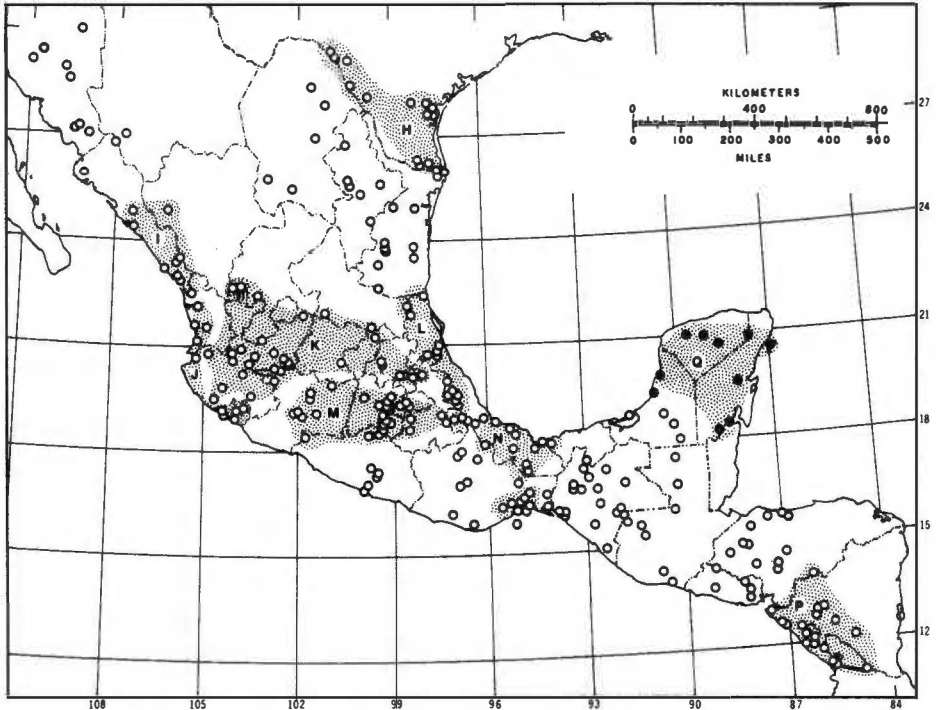


FIG. 13.—Distribution map for *Didelphis virginiana californica* and *D. v. yucatanensis* in the United States, México, and Central America as determined by specimens examined. *Didelphis v. californica*, open circles; *D. v. yucatanensis*, solid dots.

written by Oldfield Thomas, states that it was “taken from one of the types of *D. californica* Benn. D. Z. S. 1833, p. 40” (J. E. Hill, personal communication). J. A. Allen (1902:256; footnote), mentioned having examined Bennett’s holotypes in the British Museum (Natural History) and stated, “a skull . . . of one of the two specimens on which *D. californica* Bennett was based (the skins are not extant) resembles, in the character of the nasals, the Vera Cruz type of Mexican opossum, named by me *D. m. tabascensis*. The type of *D. breviceps* . . . is a rather young specimen . . . the skull . . . was found to agree in the form of the nasals with Sinaloa specimens of corresponding age.” In this same footnote, Allen interpreted Bennett’s material “from that part of California which adjoins to Mexico” as “unquestionably Sonoran.” Bailey (1933:243) also implied that Sonora, México was the probable source of Bennett’s holotypes, and Hershkovitz (1951:550) restricted the type locality to that state. Obviously, Sonora was selected for the type locality because of its proximity to California; however, although the type of *californica* may actually have come from Sonora, the probability is greater, for reasons given beyond, that it came from elsewhere in México.

Bennett (1833) named five species in addition to *D. californica* and *D. breviceps* and assumed that they all came from the same region. These include a hog-nosed skunk, a spotted ground squirrel, a tree squirrel, and a jack rabbit. With the

exception of the skunk (*Mephitis nasuta*—a name apparently overlooked in the literature), they have been reported on as follows: *Spermophilus spilosoma*, type locality restricted to Durango, Durango, by Howell (1938:122); *Spermophilus macrourus*, referred to *Citellus variegatus variegatus* (Erxleben) by Howell (1938:136) *Sciurus nigrescens*, referred to *S. aureogaster nigrescens* by Musser (1970:15) who recommends that the type locality can be restricted to the mountains south and southeast of the town of Aquixtla, in northern Puebla; and *Lepus nigricaudatus*, considered a synonym of *Lepus callotis* Wagler by Hall (1951:187) and Anderson and Gaunt (1962:9). Obviously, these are mammals of the southern portions of the Mexican Plateau and would appear to support Allen's (1901:169) allegation that the specimens Bennett described were collected by the English botanist, David Douglas, "on his journey across Mexico," except that Douglas never travelled in the present Republic of México.

During the time Douglas was in western North America, he visited the present state of California twice (22 December 1830 to 18 August 1832 and approximately from 4 to 29 November 1833), spending most of his time in the region around and north of Monterey. He journeyed south to Santa Barbara, possibly as far as the mission of San Buenaventura (Ventura), in late April and May 1831 (see McKelvey, 1955:299-341, 393-427), but never travelled south of the present state of California and, therefore, could not have collected the specimens described by Bennett (1833). This conclusion is supported by Vigors' (1833:65) report on bird skins that were part of the same collection "recently" obtained by the Zoological Society of London from "California." Among these was an *Ortyx* (= *Cyrtonyx*) *montezumae* and a *Psittacara* (= *Aratinga*)—birds that definitely did not come from California. It should be noted that neither Bennett nor Vigors mentioned Douglas in their reports although he was the only collector sending material to London from western North America at that time.

Although the subsequent association of this collection of mammals and birds with Douglas is very likely correct, I believe that these specimens were actually the work of the Irish botanist, Thomas Coulter. Coulter was a physician and administrator for the English-owned Real del Monte Mining Company in México from 1825 to 1828. He travelled widely on the Mexican Plateau while working for the mining company (McVaugh, 1943) and later visited northwestern México, California, and Arizona (Coville, 1895; McKelvey, 1955:428-442). Coulter reached Monterey, California, by ship from western México in late November 1831. There he met Douglas and the two became friends and worked together during the winter and following spring of 1831-1832. In August 1832, Douglas left California for Hawaii where, during his short stay (7 to 12 September), he shipped all of his California collections to London. Douglas did not return to California until November 1833 on his return to Hawaii from the vicinity of the Columbia River (after the reports by Bennett, 26 March 1833, and Vigors, 11 June 1833 had been read).

As far as I have been able to determine, there were only two people Douglas met in California prior to shipping his collections to London who could possibly have provided the mammals reported on by Bennett. One is the German collector,

Ferdinand Deppe, who is known to have travelled in México and who collected mammals and birds (McKelvey, 1955:426). However, at the time of their meeting in 1832, Deppe was involved in commercial ventures along the west coast between Acapulco, México, and Monterey, California. Coulter, on the other hand, had just come from several years of extensive travels in México that encompassed southern portions of the Mexican Plateau where most if not all of the specimens in question undoubtedly were collected. Douglas probably sent some of Coulter's material with his own, and herein must be the association between Douglas and the specimens reported on by Bennett (1833) and Vigors (1833). Several events of the time likely contributed to the present confusion surrounding the origin of these specimens. First, after learning of the resignation of Joseph Sabine from the secretaryship of the Horticultural Society of London, Douglas sent in his own resignation as collector for the Society (McKelvey, 1955:410) when he shipped his California collection to London. In doing so, Douglas terminated his obligation and, therefore, further communication with the Society. Second, after returning to North America from his short stay in Hawaii, Douglas lost nearly everything he had, including his journals, in an accident on the Fraser River, British Columbia, on 13 June 1833. Third, Douglas died in the Hawaiian Islands in 1834 before he could return to England. Finally, when Coulter returned to Ireland from California in 1834 by way of México, he had the misfortune to lose all of his journals and manuscripts between London and Dublin. Also, Coulter may not have been aware of the reports by Bennett and Vigors to the Zoological Society of London inasmuch as he lived in Ireland and was primarily concerned with putting his plant collections in order, or perhaps Coulter did not claim any responsibility for the "California" collection because he feared that to do so might have detracted from Douglas; nevertheless, there is no record that he was even aware that Douglas would be credited with these specimens.

Howell (1938:123) suggested that the holotype of *Spermophilus pilosoma* might have been collected by George Tradescant Lay, the naturalist on the *Blossum* commanded by Captain Beechey, when he visited Tepic, Nayarit, in late 1827 or early 1828; however, supportive evidence is lacking. Furthermore, the birds from the voyage of the *Blossum* had already been reported on in 1828 by Vigors (1830:352-358) before his later (1833) account of the birds in the "California" collection.

As was pointed out by Davis (1944:375) and Hall and Kelson (1952:322), Allen (1901:170-172) allied *D. m. texensis* (herein considered a synonym of *D. v. californica*) with Mexican populations of *Didelphis*, which he separated from United States populations on "differences of degree" and not absolute characters. Allen relied heavily on the predominance of the dark phase (see the discussion of dichromatism in the section dealing with geographic variation) and the more pronounced head markings to distinguish *D. marsupialis texensis* from *D. virginiana*, and he relied on the configuration of the nasals for distinguishing *D. m. texensis* from *D. m. marsupialis*. However, with the exception of the relative color phase frequencies, these characters are found in all populations of Latin American *virginiana*.

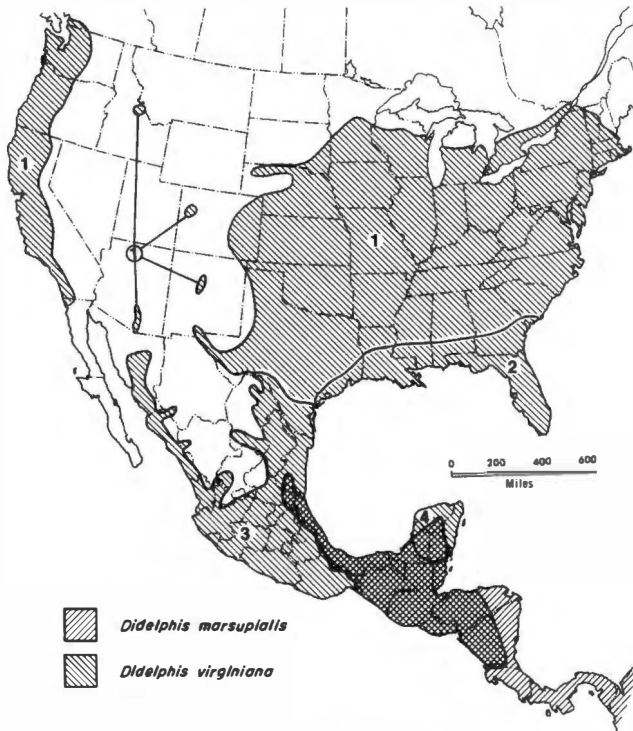


FIG. 14.—Map showing combined distribution of *Didelphis marsupialis* and *D. virginiana* in North and Middle America. Subspecies of *D. virginiana*: 1, *D. v. virginiana*, including introduced populations; 2, *D. v. pigra*; 3, *D. v. californica*; and 4, *D. v. yucatanensis*.

Didelphis mesembrinus (Hall and Kelson, 1952:322) is a *nomen nudum* used with reference to the common Mexican opossum, and was probably a *lapsus calami* for *mesamericana*. Hall and Kelson's (1952) interpretation of "Sycamore Creek" as equivalent to Fort Worth, Texas, is in error as far as USNM 24359/31765 is concerned. The label for this specimen reads "mouth of Sycamore Creek" and undoubtedly refers to where Sycamore Creek joined the Rio Grande in Kinney Co., Texas, in 1890 when the specimen was collected (this region is now under the Amistad Reservoir).

Measurements.—Cranial measurements from nine selected samples (H to P on the map in Fig. 13) are presented in Appendix I.

Specimens examined.—See Appendix II.

***Didelphis virginiana yucatanensis* Allen**

1901. *Didelphis yucatanensis* Allen, Bull. Amer. Mus. Nat. Hist., 14:178.
 1901. *Didelphis yucatanensis cozumelae* Merriam, Proc. Biol. Soc. Washington, 14:101.
 1946. *Didelphis marsupialis yucatanensis*, Goldman and Moore, J. Mamm., 26:360.
 1951. *Didelphis marsupialis californica*, Hershkovitz, Fieldiana, Zool., Chicago Mus. Nat. Hist., 31:548.
 1952. *Didelphis marsupialis cozumelae*, Hall and Kelson, Univ. Kansas Publ., Mus. Nat. Hist., 5:324.

Holotype.—Adult male (skin with skull), USNM 108299, taken 1 February 1901 by E. W. Nelson and E. A. Goldman.

Type locality.—Chichén Itzá, Yucatán, México.

Distribution.—Most of Campeche, all of Yucatán and Quintana Roo (including Isla Cozumel). The distribution of *D. v. yucatanensis*, as determined by specimens examined, is shown in Fig. 13.

Description.—Size small to medium, tail over 80 per cent of head and body length; color as in *D. v. californica* with from 40 to 60 per cent of bare tail black; skull small with prominent postorbital processes.

Remarks.—Three of the 10 specimens Allen (1901:178-179) originally assigned to *yucatanensis* belong to the species *marsupialis* and include two of the three specimens Allen had before him from the type locality. These specimens (USNM 108297, 108298, and 108300) are those with tail ratios (with head and body) exceeding 100 per cent (Allen, 1901:178). I hesitate to recognize on the basis of size a subspecies of any *Didelphis* represented by so few specimens, and were it not for the greater development of the postorbital processes characterizing the majority of the specimens assigned herein to *yucatanensis*, I would not separate subspecifically this population from *californica*.

Measurements.—Cranial measurements (Q on map in Fig. 13) are presented in Appendix I.

Specimens examined.—See Appendix II.

PALEOGEOGRAPHY AND EVOLUTION

Fossil Record

Marsupials were part of the Tertiary North American fauna until the early Miocene. The earliest record for any member of the genus *Didelphis* is from Pliocene deposits in South America. For the remainder of the Tertiary and until Pleistocene times, didelphids are known only from South American deposits. Marsupials reappear (represented by *Didelphis*) in the fossil record of North America during the Sangamon Interglacial Stage of the Pleistocene (Hibbard *et al.*, 1965). Post-Wisconsin remains of *Didelphis* are widespread in the United States and México.

Origin and Dispersal Pattern

Clemens (1968) did not regard *Didelphis* as an archetypal marsupial. Instead, on the basis of the derived nature of several morphological characters, particularly features of dentition, he considered *Didelphis* to be a relatively late evolutionary product of a South American radiation from an *Alphadon*-like ancestor.

Clemens' (1968:16) statement that after the establishment of a Panamanian land bridge between North and South America in the Pliocene, "some groups of South American marsupials dispersed northward into Central and North America" is in accord with Simpson's (1965) views on the origin and dispersal of northern mammals with South American affinities. The post-Pleistocene dispersal of opossums appears to have been rapid in the United States. Changes in

the prehistoric distribution of *Didelphis*, as determined by remains from archeological sites, have been summarized by Guilday (1958). His oldest positive record (p. 43) is from the Indian Knoll site in western Kentucky and is judged to date back three to four thousand years, and the most northern records of occurrence are in northern West Virginia and northern Ohio, dated from 1400 to 1600 AD. At present, the northern limits of the opossum include Massachusetts, southern Ontario, central Michigan, central Wisconsin, and central Minnesota.

Present Distribution

The distribution of North and Central American *Didelphis* is summarized by the map in Fig. 14 and is presented in greater detail for *marsupialis* and *virginiana* in Figs. 12 and 13, respectively, which are based on specimens examined. Distributional patterns suggest that Pleistocene and Recent records for *Didelphis* in the United States represent *virginiana*. The southern limits for *virginiana* coincide with the southern extent of the northern highlands of Middle America and are near the southern end of the seasonally arid tropical deciduous forests of the Pacific slope and coastal plain of México and Central America. The fact that *virginiana* does not also occur in the mountains of Cost Rica and western Panamá argues against the hypothesis that *virginiana* dispersed northward from South America to occupy its present range. Its absence is significant because the Cordillera Talamanca was uplifted during Miocene times and today supports subtropical and temperate habitats at higher elevations that are unpopulated by marsupials. On the other hand, if *Didelphis* did spread northward from South America after the establishment of the Panamanian land bridge during the late Pliocene, the trip required over two million years to complete, according to the Sangamon record and the potassium-argon dates (Evernden *et al.*, 1964), which indicate that the Pleistocene began about 2.5 million years ago. This evidence and the unusual ability of *virginiana* to occupy successfully an extremely broad array of ecological situations, clearly indicate a North American origin for the species.

The other species, *marsupialis*, is a typical Neotropical opossum that reaches the northernmost limits of its distribution in the isolated remnants of the humid montane and wet tropical forests of eastern San Luis Potosí and Tamaulipas, México. Throughout its range, *marsupialis* is associated with warm, humid, tropical forest habitats at moderate and lower elevations (usually below 4000 feet in México and Central America). The present distribution of *marsupialis* (Fig. 12) almost exactly coincides with that of another typical tropical marsupial, *Philander opossum*.

Herskovitz (1958:608) considered *Didelphis* to be a Neotropical excurrent to the Nearctic. Recently (1969), he suggested a number of alternative explanations for the origin and dispersal of *Didelphis*. The concept of *Didelphis* as a member of an early Middle American "Stratum III" descendant from overseas or island-hopping South American "Stratum II" ancestors is the most probable of Herskovitz's (1969:17) alternatives.

In South America, *marsupialis* occurs throughout the warm humid tropical forests at moderate to lower elevations. *Didelphis albiventris* is found in subtropical and temperate habitats at moderate to upper elevations, at lower elevations in higher latitudes from the Brazilian Shield to central Argentina, and along the arid coast of northern Perú. *Didelphis marsupialis* probably differentiated in Middle America from a South American stock represented today by *albiventris*, then successfully reinvaded South America with the establishment of the Panamanian land bridge, and displaced *albiventris* throughout the tropical lowlands. The dispersal southward and subsequent establishment of *marsupialis*, facilitated by the fluctuations of the Pleistocene climates and tropical forest vegetation (see Haffer, 1969), probably restricted *albiventris* to habitats that were marginal to uninhabitable for *marsupialis*. This hypothesis explains the origin of the isolated populations of *albiventris* on the Guiana Shield (Hershkovitz, 1969:54). The relative homogeneity of *marsupialis* throughout its range suggests a rather recent establishment of its present distributional pattern, although it may also reflect genetic conservatism.

Speciation of Didelphis virginiana

The northern distributional limits of *D. marsupialis*, in what is now México, undoubtedly were affected by the increasing aridity during the late Pliocene and the periodic fluctuations of climates and displacement of habitats during the Pleistocene. The absence of any unequivocal remains of *Didelphis* in North America until just preceding the last continental glaciation suggests that either the tropical habitats occupied by *marsupialis* were not conducive to the preservation of hard parts or that the temperate-tolerant *virginiana* had not yet evolved.

Superficially, the derivation of *virginiana* from a *marsupialis* progenitor in North or Central America seems unlikely. Herein lies the probable significance of the unusual karyotype of *virginiana*. I believe that *virginiana* achieved reproductive isolation from its progenitor, *marsupialis*, through a series of chromosomal rearrangements, a method called "quantum evolution" by Simpson (1961) and "saltational speciation" by Lewis (1966). This evolutionary scheme is quite unlike the concept of species formation as an extension of ecogeographic race formation through the continued gradual accumulation of genetic differences followed by the refinement of isolating mechanisms.

The differences in chromosome pattern between *virginiana* and *marsupialis* are unusual for the following reasons: 1) as a rule, American marsupials are evolutionarily conservative with regard to changes in karyotypes, as demonstrated by the presence of only three basic chromosomal patterns; 2) when changes have occurred in the karyotypes, they have been primarily of the "Robertsonian" type, involving either centric fusions or dissociations, the latter course being the most likely because the oldest groups have the lowest chromosomal number, 14, and the conservative fundamental number, 20; 3) with the exception of *virginiana*, opossums in the 22-chromosome group (at least six species in four genera, including two species of *Didelphis*) have nearly identical karyotypes; 4) *virginiana*

is unique inasmuch as it is the only known American marsupial in which pericentric inversions have played a role in the evolution of its karyotype. The stable nature of didelphid karyotypes suggests that either the frequency of inversions and translocations is very low or the selective pressures against the establishment of altered chromosomal patterns is very great. Undoubtedly, the circumstances leading to the establishment of the distinctive and unique karyotype of *virginiana* were unusual.

These conditions probably enforced the isolation of a small inbreeding population of *marsupialis*. The overall consequences of obligatory inbreeding include decreased vigor, higher frequency of abnormal development, and reduced fecundity. The less fit individuals resulting under such circumstances would be removed through competition with normal opossums if spatial isolation were not also a factor. Lewis (1966:170), in outlining his model for saltational speciation, cited evidence supporting the idea that an additional consequence of inbreeding is extensive chromosome breakage—a prerequisite for deriving the karyotype of *virginiana* from that of *marsupialis*.

The prime essential under these conditions is the ability to produce offspring and not the ability to compete with normal individuals. Competition becomes a factor as soon as particular gene sequences arise that facilitate the survival of those individuals with the new combinations. Then, carriers of nonadaptive combinations will be selected against through competition with their better adapted siblings. This selection would have the added effect of rapidly fixing the adaptive rearrangements in the population. A byproduct of these events in the evolution of the modified chromosomal pattern in *virginiana* was the establishment of reproductive isolation from its parental species, *marsupialis*. If hybridization occurred after renewed contact between the two populations, then secondary barriers reducing or eliminating hybridization could be expected to have developed.

Geographic Origin of Didelphis virginiana

Cooling Pleistocene climates at the onset of each glacial stage caused *marsupialis* to withdraw its range to lower elevations and lower latitudes. The entrapment of small populations of these opossums probably occurred repeatedly throughout the Pleistocene. The probable effects of shifting Quaternary climates in México are discussed by Martin (1958). Additional evidence for climatic fluctuations and the effect on vegetational zones and animal associates is presented for eastern México by Martin and Harrell (1957), and for western México by Duellman (1965). A series of environmental conditions that probably existed in Michoacán and adjacent areas in western México, both during periods of maximum glaciation and at the height of glacial retreat, are outlined by Duellman (1965:697). This information for western México suggests greatly altered local climates and shifting vegetational zones during the Pleistocene, accentuated because of the mountainous physiography of the region. The climate of the broad eastern lowlands was probably little affected by the temperature fluctuations occurring at higher elevations. In fact, as far as *marsupialis* is concerned, the lowering of the seas as much as 100 meters, with a rise in overall humidity associated

with the stages of glacial maxima, increased the extent of available lowland habitats. Quaternary events in México are largely inferred from what has been learned of these events in the United States, and even less is known about Central America. Therefore, a geographic site where *virginiana* underwent differentiation is difficult to suggest. I do not believe that *virginiana* evolved in Central America because it is unlikely that spatial isolation from *marsupialis* could have been achieved there. Areas in the United States are not seriously considered as sites of differentiation, although Florida was undoubtedly important in the subsequent evolution of populations of *virginiana* in the United States. The Florida Peninsula is rejected because I do not believe that the ecological extremes in this area during the glacial stages would have had any appreciable effect on a *marsupialis* isolate, partly because of the lack of topographic diversity, if indeed *marsupialis* occurred in this region. The persistence of xeric habitats and dry climates in northeastern México and southern Texas throughout the Pleistocene and Recent (as postulated by Martin and Harrell, 1957) would have prevented the dispersal of *marsupialis* into the southeastern United States.

In its ecological tolerances, *virginiana* differs from *marsupialis* primarily in its ability to inhabit cold and arid habitats. The survival of an otherwise tropical opossum in western México during the Pleistocene climatic fluctuations required acclimation to both of these environmental stresses. The major climatic shifts that took place in western México in the Pleistocene caused the elevational depression of temperate habitats, perhaps as much as 1000 meters, during glacial stages. Two additional climatic shifts profoundly affected biotic communities. These were the changes related to cooler temperatures and pluvial conditions during glacial maxima alternating with the changes related to warmer temperatures and increased aridity during interglacial stages. Therefore, I postulate that the speciation of *virginiana* from a Pleistocene isolate of *marsupialis* occurred in western México. Although the Balsas basin of Michoacán and Guerrero seems the most likely site for these events to take place, other locations in western México may have been involved. The boreal climates of the highlands adjacent to the Balsas basin during glacial stages would have reinforced the isolation of a small population of incipient *virginiana* in the Balsas basin with periodic seasonal cold fronts extending southward from glaciated higher peaks along the Transvolcanic Axis. Cold stress would also have kept the population level low. Probably, the long-term effects of low population numbers, effective isolation from progenitor stocks, and forced inbreeding influenced the speciation of *virginiana* and aided in selecting for individuals with broad ecological tolerances.

Exactly when during the Pleistocene *virginiana* evolved is unknown. Fossil material of Sangamon interglacial age from the United States suggests that *virginiana* differentiated sometime earlier, perhaps during the Illinoian glacial age.

Didelphis virginiana has been able to expand its distribution until now it occupies a variety of habitats, including the cool, arid Mexican Plateau, the cool, humid mountains of southern México and Central America, the temperate habitats of the United States with its severe winters in the northern States, and the hot arid deserts and desert scrub forests of Sonora and Sinaloa. It occurs sym-

patrically with *marsupialis* in the warm tropical lowlands of eastern and southern México and Central America as far south as southwestern Nicaragua (see Fig. 1).

SUMMARY AND CONCLUSIONS

When J. A. Allen (1902) published his second revisionary study of the genus *Didelphis*, he recognized three species with a total of nine subspecies as occurring in North and Central America. Subsequently, Goldman (1917) added another subspecies from Isla San Miguel, Panamá. However, considerable confusion existed regarding the true identities of the named species and subspecies of *Didelphis*, due in part to the great amount of individual variation exhibited by these opossums. Hershkovitz (1951), in an attempt to resolve some of the taxonomic problems surrounding members of the genus, recognized only two species of *Didelphis*. One of these, *albiventris*, is a temperate zone species restricted to South America. The other species he called *D. marsupialis* and gave its distribution as southern Canada to northern Argentina. In North America, he recognized *D. marsupialis virginiana*, stating that it intergraded with the nominate subspecies found in Costa Rica, Panamá, and South America through a series of Mexican and northern Central American populations to which he applied the name *californica*. Hall and Kelson (1952, 1959) considered Hershkovitz's action to be extreme and, although following his recognition of a single species, *D. marsupialis*, in North and Central America, chose to recognize 11 subspecies occurring north of Colombia.

I became interested in *Didelphis* after finding that an analysis of chromosomal material prepared from Costa Rican specimens revealed a karyotype unlike that reported for opossums supposedly of the same species from the United States. Didelphids can be separated into three groups, based on the number of chromosomes, and often, distinct species in different genera are characterized by the same karyotype. The karyotype of the Costa Rican *Didelphis* is like those of six species (including *D. albiventris*) in four genera from South America. It consists of 22 acrocentric chromosomes with three pairs of large and seven pairs of medium-sized autosomes, a small X chromosome, a minute Y chromosome, and a fundamental number of 20. Although specimens of *Didelphis* from the United States also have 22 chromosomes, they have three pairs of large and three pairs of medium-sized submetacentrics, four pairs of medium-sized acrocentrics, a medium-sized submetacentric X, a small acrocentric Y, and a fundamental number of 32. This chromosomal information implied a greater amount of variation within a single species than is known to exist between different genera in the same chromosome group, a strange situation, inasmuch as American opossums are conservative regarding karyotypic variation.

The examination of other chromosomal material collected from opossums in Louisiana, Texas, México, and Perú confirmed the existence of two very different karyotypes in North and Central American species of *Didelphis*. Through the study of opossums of known karyotype, I found several features, including differences in cranial structure, color pattern, hair pattern, and behavior, useful in separating these two kinds of opossum by gross morphology. Then I examined

over 2800 museum specimens of *Didelphis* in order to determine the distribution of the two kinds in North and Central America, and record variation within and between populations. As a result, I recognize *virginiana* as being distinct from *marsupialis* and occurring from southern Canada southward through the United States and México to southwestern Nicaragua in a wide variety of habitats at elevations from sea level to more than 11,000 feet. *Didelphis marsupialis* is widely distributed throughout the lowlands of South and Central America, as far north as Tamaulipas in eastern México, usually occurring in tropical forests at elevations below 4500 feet.

An analysis of the different karyotypes suggests that the karyotype of *virginiana* was derived from that of *marsupialis* through a series of pericentric inversions and translocations and is unique in this respect among American marsupials.

Didelphis was thought to have expanded its range northward into Central and North America from South America after the formation of the Panamanian land bridge during Pliocene times. However, a review of the North American Pleistocene fossil record fails to reveal any remains of *Didelphis* until the Sangamon Interglacial Stage, nearly two million years after the establishment of a land connection between the two continents. An examination of the distributions and ecological affinities of *virginiana* and *marsupialis* supports Hershkovitz's (1969) hypothesis that *Didelphis* was probably in Middle America before the Pliocene closing of the Panamanian seaway.

The present distribution of *virginiana*, with its ability to utilize a broad array of ecological situations, its fossil record, and its unique karyotype, suggest that *virginiana* differentiated in México from a *marsupialis* isolate under the environmental influences of fluctuating Pleistocene climates and habitats. Under the combined influences of isolation, inbreeding, and low population numbers due to periodic seasonal environmental stress, individuals in a small population of *marsupialis* could be expected to show decreased vigor, increased frequency of abnormal development (including chromosomal breakage), and a tendency toward a greater tolerance to severe climates. An increased frequency of chromosomal breakage would help explain the evolution of the karyotype found in *virginiana*.

On this basis, I advance the hypothesis that *virginiana* arose from *marsupialis* primarily as the result of a number of chromosomal rearrangements that either greatly reduced hybrid fecundity or brought about intersterility between the two species when they achieved secondary contact. This evolutionary mechanism has been called quantum evolution (Simpson, 1961) or saltational speciation (Lewis, 1966).

These remarks suggest that *D. virginiana* is unique among didelphids in ways other than its karyotype. Therefore, I recommend that the wealth of information on *virginiana* that is accumulating from studies of its morphology, reproductive physiology, cytogenetics, cellular physiology, and biochemistry be reevaluated in light of the probable evolutionary history of the species. Also, data derived

from such studies on *virginiana* should not be interpreted *ipso facto* as characterizing other marsupials.

The oldest available name for the single Mexican and Central American subspecies of *marsupialis* that I recognize in this study is *D. m. cauae* Allen, 1900. I have assigned populations of *virginiana* to three subspecies in addition to the nominate subspecies, which is found throughout eastern and midwestern regions of the United States north to Ontario, Canada, and had been introduced into several western states. *Didelphis v. pigra* Bangs, 1898, occurs along the Gulf Coastal Plain of Texas and Louisiana to Florida, Georgia, and South Carolina. *Didelphis v. californica* Bennett, 1833, occurs from southern Texas and Tamaulipas in the east, and Sonora in the west, throughout most of México and Central America to southwestern Nicaragua. This subspecies is absent on the north central Mexican Plateau and is replaced on the Yucatán Peninsula by the smaller *D. v. yucatanensis* Allen, 1901.

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APPENDIX I—CRANIAL MEASUREMENTS

Cranial measurements are presented in Table 6 for selected samples of *Didelphis marsupialis* and *D. virginiana* from southern Texas, México, and Central America. Table 7 gives cranial measurements for the species samples from the geographic zone of sympatry in México and Central America (see Fig. 1). Measurements (described under Material and Methods) of these specimens were the basis for the least squares analysis of variance. Values for the measurements greatest length of skull, palatal length, zygomatic breadth, and breadth of brain case in Table 7 are also graphed in Figs. 2, 3, and 4.

Each sample in Table 6, indicated by its appropriate letter, includes specimens from several localities representing large geographic areas, but generally from within the same physiographic region. The areas covered by the samples representing the following taxa are:

Didelphis marsupialis cauae (Fig. 12).—*Sample A*, Veracruz and Oaxaca in eastern México except the Isthmus of Tehuantepec; *sample B*, the lowlands of southern México including Campeche, Tabasco, northern Chiapas, and the Isthmus of Tehuantepec of Veracruz and Oaxaca; *sample C*, El Salvador, the Department of Santa Rosa in Guatemala, and the Pacific versant of Honduras; *sample D*, central Nicaragua; *sample E*, the Caribbean lowlands of Nicaragua; *sample F*, central Panamá including the Canal Zone and the Provinces of Colón, San Blas, Panamá, Veraguas, Coclé, and Los Santos; *sample G*, eastern Panamá in the Provinces of San Blas and Darién.

Didelphis virginiana californica (Fig. 13).—*Sample H*, Texas south of Aransas and Val Verde Counties; *sample I*, northwestern México from Culiacán, Sinaloa to Acaponeta, Nayarit; *sample J*, western México including Nayarit (except Acaponeta), Pacific slope of Jalisco, and Colima; *sample K*, the Mexican Plateau including Zacatecas, Jalisco, southern San Luis Potosí, northwestern Michoacán, Queretaro, Hidalgo, and northwestern Puebla; *sample L*, eastern México including southeastern Tamaulipas, eastern San Luis Potosí, and Veracruz west of longitude 96°00'; *sample m*, the Transvolcanic Axis of México including Michoacán, México, Puebla, Morelos, Distrito Federal, and northern Guerrero; *sample N*, Veracruz and northern Oaxaca in eastern México; *sample O*, the Pacific versant of the Isthmus of Tehuantepec in Oaxaca; *sample P*, the central highlands and Pacific versant of Nicaragua.

Didelphis virginiana yucatanensis (Fig. 13).—*Sample Q*, northern British Honduras and the Yucatán Peninsula of México including Isla Cozumel.

TABLE 6.—Measurements of 17 cranial dimensions for selected samples of *Didelphis marsupialis caucea* (Samples A to G—see Fig. 12), *D. virginiana californica* (samples H to P—see Fig. 13), and *D. virginiana yucatanensis* (sample Q—see Fig. 13). The mean (\bar{X}), standard deviation (SD), extremes, coefficient of variation (CV), and sample size (N) is given for each sex.

Sample	Males					Females				
	\bar{X}	SD	Extremes	CV	N	\bar{X}	SD	Extremes	CV	N
	<i>Didelphis marsupialis caucea</i>									
	<i>Greatest length of skull</i>									
A	108.68	9.06	91.00-123.60	8.33	21	100.64	7.67	85.65-112.90	7.62	22
B	114.59	7.20	101.80-124.90	6.29	14	99.81	5.80	93.40-107.65	5.81	8
C	106.65	7.83	95.45-121.65	7.34	13	101.05	9.65	84.40-116.15	9.55	12
D	106.30	7.67	94.25-121.55	7.22	20	93.15	6.12	86.15-105.70	6.57	17
E	109.68	7.32	97.80-123.00	6.68	17	101.14	6.77	91.40-115.10	6.69	18
F	105.36	9.21	88.15-120.10	8.74	23	96.78	7.31	83.80-111.60	7.56	23
G	108.64	9.98	97.10-128.35	9.18	10	101.23	7.76	92.55-116.90	7.67	12
	<i>Condylobasal length</i>									
A	105.42	8.27	88.70-116.95	7.85	21	98.80	6.95	85.55-110.45	7.04	22
B	110.75	6.56	98.85-119.95	5.92	14	98.16	5.47	92.05-104.55	5.58	8
C	102.80	7.14	92.65-117.50	6.95	12	97.88	8.06	83.00-107.50	8.24	12
D	102.39	6.74	91.85-114.75	6.58	17	91.98	5.95	85.30-103.50	6.47	17
E	106.04	6.80	95.50-118.40	6.40	16	98.78	6.53	89.25-110.95	6.61	17
F	101.76	8.72	85.50-115.80	8.57	23	94.58	6.70	82.45-107.50	7.08	22
G	105.16	9.12	94.40-123.10	8.68	10	99.33	7.45	91.70-114.60	7.50	12

TABLE 6.—Continued.

Sample	Males					Females				
	\bar{X}	SD	Extremes	CV	N	\bar{X}	SD	Extremes	CV	N
						<i>Length of upper molar series</i>				
A	20.37	.97	18.45-21.65	4.77	17	20.31	.66	19.40-21.50	3.24	17
B	20.30	.56	19.40-21.35	2.76	11	20.46	.73	19.10-21.60	3.59	7
C	20.13	.37	19.60-20.85	1.85	12	20.08	.48	19.40-20.70	2.40	11
D	20.31	.71	18.95-21.40	3.49	15	20.39	.79	18.95-21.30	3.85	10
E	20.63	.80	19.70-22.40	3.89	15	19.78	.65	18.40-20.55	3.27	14
F	20.27	.80	18.60-21.85	3.93	18	19.58	.51	18.95-20.60	2.60	13
G	20.37	1.09	18.80-21.40	5.36	5	19.90	.44	19.00-20.65	2.23	11
						<i>Length of mandible</i>				
A	86.62	6.95	73.80-97.80	8.02	20	81.27	6.70	64.50-92.00	8.25	22
B	92.06	5.91	81.60-99.50	6.42	13	80.93	5.01	75.40-87.50	6.19	8
C	85.11	6.30	74.75-98.20	7.40	14	80.66	6.95	68.00-89.05	8.62	12
D	86.46	6.78	76.65-99.90	7.84	19	75.62	5.60	68.45-86.25	7.40	17
E	88.47	6.01	78.90-100.30	6.80	17	81.68	5.82	72.80-94.00	7.12	18
F	84.63	7.41	70.40-96.40	8.75	24	78.73	6.09	67.15-90.50	7.74	23
G	88.33	7.67	77.30-103.25	8.69	10	81.41	6.02	74.80-94.10	7.39	12
						<i>Length of lower molar series</i>				
A	22.16	1.07	20.40-23.70	4.81	19	21.99	.74	20.70-23.25	3.38	21
B	22.26	.92	20.50-23.60	4.11	13	22.44	.71	21.15-23.50	3.17	8
C	21.92	.57	20.90-23.00	2.60	13	21.90	.63	20.90-22.70	2.88	12
D	22.19	.73	21.15-23.35	3.28	19	22.41	.70	20.95-23.45	3.13	14
E	22.40	.82	21.00-23.80	3.66	16	21.74	.91	20.45-23.80	4.17	15
F	22.10	.90	20.70-23.80	4.08	24	21.58	.79	20.15-22.80	3.67	19
G	22.42	.67	21.10-23.60	3.01	9	21.80	.44	21.15-22.60	2.03	12

TABLE 6.—Continued.

Sample	Males					Females				
	\bar{X}	SD	Extremes	CV	N	\bar{X}	SD	Extremes	CV	N
						<i>Breadth of rostrum across jugals</i>				
A	27.37	2.54	22.10-31.25	9.27	21	25.65	2.22	22.50-30.35	8.64	21
B	29.10	2.26	26.50-33.65	7.78	13	25.84	1.21	24.75-28.40	4.68	8
C	27.70	2.11	24.45-31.00	7.61	12	25.59	1.70	22.10-27.25	6.53	12
D	27.81	3.29	22.30-34.50	11.84	18	24.30	1.92	21.50-27.80	7.88	17
E	27.22	2.16	23.60-32.10	7.95	17	25.76	1.60	23.35-28.40	6.20	15
F	26.52	3.25	20.55-35.00	12.27	23	25.54	2.43	20.95-29.65	9.51	21
G	27.64	3.48	22.45-33.35	12.60	9	26.07	2.03	22.75-30.30	7.77	12
						<i>Greatest breadth of nasals</i>				
A	14.34	1.60	11.50-16.40	11.14	21	13.32	1.34	11.35-16.10	10.05	22
B	15.38	1.33	13.20-17.45	8.68	14	13.33	.87	12.30-14.90	6.56	8
C	14.47	1.38	12.30-17.20	9.55	14	13.28	.76	12.25-14.35	5.74	11
D	15.53	2.10	12.20-19.50	13.55	18	12.50	1.30	10.60-15.60	10.42	17
E	15.13	1.36	12.80-18.30	9.02	17	13.80	1.15	12.20-15.50	8.35	15
F	14.25	1.76	11.00-19.50	12.36	23	13.53	1.79	11.45-18.10	13.20	21
G	15.34	2.52	11.80-19.55	16.44	8	13.52	1.85	11.60-17.40	13.69	12
						<i>Breadth of rostrum across frontals</i>				
A	16.66	1.82	13.85-19.85	10.93	19	15.62	1.72	11.10-18.60	11.01	22
B	18.19	1.83	15.60-21.40	10.07	13	15.66	1.21	14.55-17.85	7.74	7
C	17.30	1.64	15.45-20.30	9.49	13	15.82	1.07	13.50-17.20	6.76	12
D	18.75	2.70	14.70-25.60	14.39	18	15.68	1.49	13.80-18.50	9.48	17
E	17.59	1.53	15.20-21.55	8.72	17	16.39	1.22	14.40-18.25	7.44	15
F	17.07	2.15	13.40-23.25	12.57	23	16.00	2.20	11.80-19.80	13.73	21
G	18.08	2.96	14.15-23.30	16.38	8	16.77	2.06	13.80-20.40	12.28	11

TABLE 6.—Continued.

Sample	Males					Females				
	\bar{X}	SD	Extremes	CV	N	\bar{X}	SD	Extremes	CV	N
	<i>Didelphis virginiana</i>									
	<i>Greatest length of skull</i>									
H	109.45	11.78	91.85-139.10	10.76	21	100.56	5.16	92.25-108.40	5.13	10
I	108.42	7.91	90.80-121.85	7.29	18	99.59	7.69	85.10-114.50	7.72	22
J	108.98	11.25	85.00-130.00	10.33	25	97.32	9.50	84.20-111.30	9.75	12
K	104.77	7.00	92.50-115.00	6.68	18	98.77	7.34	86.70-117.55	7.43	18
L	110.31	15.22	89.20-142.10	13.80	16	101.27	6.15	92.60-110.65	6.07	10
M	108.38	10.97	90.70-125.70	10.12	13	96.68	7.81	81.40-104.80	8.08	17
N	112.93	11.20	88.00-124.50	9.92	13	110.33	7.99	95.40-120.50	7.24	8
O	115.02	11.43	90.90-134.70	9.94	20	98.48	3.91	92.35-104.50	3.97	9
P	115.56	11.49	94.70-133.55	9.94	35	104.21	7.56	93.40-119.25	7.26	54
Q	102.47	6.60	89.80-115.30	6.44	15	91.79	8.87	77.85-108.90	9.67	8
	<i>Condylbasal length</i>									
H	104.87	10.27	90.35-138.80	9.79	20	97.13	4.52	91.25-103.80	4.65	8
I	104.74	7.27	88.55-116.00	6.94	18	96.48	6.25	83.10-105.80	6.48	20
J	106.09	9.83	84.10-124.85	9.26	23	95.06	8.54	83.10-106.80	8.98	12
K	103.10	8.57	90.75-127.75	8.31	19	96.74	7.18	83.55-114.50	7.42	18
L	106.74	12.87	88.40-135.00	12.06	16	99.34	6.36	90.20-107.85	6.40	9
M	105.93	9.85	89.25-118.50	9.30	13	94.79	7.38	80.30-103.50	7.79	17
N	109.06	11.45	86.60-123.15	10.50	13	107.66	7.25	93.90-116.65	6.74	8
O	108.61	10.92	89.85-126.00	10.05	13	95.75	3.60	91.60-101.45	3.76	5
P	111.28	10.42	93.65-129.50	9.36	34	101.38	7.02	81.25-116.10	6.92	52
Q	99.16	7.15	87.40-113.10	7.21	13	89.61	7.76	77.10-104.60	8.66	8

TABLE 6.—Continued.

Sample	Males					Females				
	\bar{X}	SD	Extremes	CV	N	\bar{X}	SD	Extremes	CV	N
	<i>Breadth across canines</i>									
H	20.31	2.39	16.00-25.10	11.78	20	17.56	.92	16.25-19.55	5.22	10
I	19.54	1.88	15.80-23.45	9.63	18	17.50	1.52	14.70-20.70	8.69	21
J	19.90	2.57	15.20-25.30	12.92	23	17.25	1.86	14.85-20.10	10.76	13
K	19.64	2.32	15.90-25.25	11.80	19	17.33	1.39	15.20-21.40	8.02	19
L	20.18	3.45	15.60-28.15	17.10	16	18.12	1.34	16.45-20.45	7.40	9
M	20.16	2.33	16.30-24.40	11.55	13	17.11	1.68	13.90-19.70	9.81	17
N	20.96	2.82	14.85-24.50	13.47	12	19.77	1.04	18.00-21.45	5.25	9
O	21.42	2.35	16.80-26.05	10.97	26	17.39	1.47	15.10-20.00	8.47	11
P	20.99	2.36	17.05-25.40	11.25	31	18.35	1.37	15.60-21.55	7.44	51
Q	19.09	1.97	17.20-23.90	10.34	14	16.09	1.31	13.90-18.00	8.16	9
	<i>Breadth across molars</i>									
H	31.55	1.67	29.10-34.90	5.28	21	29.98	1.33	27.95-32.60	4.43	10
I	30.59	1.15	28.45-33.40	3.76	17	29.22	1.06	27.70-31.80	3.63	21
J	30.56	1.39	28.00-33.30	4.55	24	29.33	1.45	27.00-31.35	4.95	12
K	30.85	1.28	28.85-33.35	4.15	19	29.84	.87	27.50-31.15	2.93	18
L	31.85	2.04	28.45-35.45	6.42	14	31.29	1.21	29.50-33.50	3.86	9
M	31.46	.87	30.00-33.60	2.77	12	29.60	1.27	27.30-31.00	4.30	15
N	32.72	2.49	27.50-36.10	7.60	12	32.17	3.04	24.30-34.30	9.44	9
O	31.90	1.47	29.00-34.85	4.60	25	29.87	1.00	27.40-30.90	3.33	10
P	31.65	1.38	29.10-34.70	4.37	32	30.78	1.19	27.15-33.00	3.85	48
Q	28.99	2.08	22.90-31.10	7.17	14	26.14	2.88	21.60-29.50	11.00	8

TABLE 6.—Continued.

Sample	Males					Females				
	\bar{X}	SD	Extremes	CV	N	\bar{X}	SD	Extremes	CV	N
						<i>Breadth of brain case</i>				
H	30.12	3.53	24.90-38.00	11.70	20	27.61	1.00	26.40-29.00	3.64	10
I	30.11	2.23	25.60-34.10	7.41	18	27.81	2.22	23.35-31.60	7.99	22
J	30.03	3.08	23.75-36.60	10.25	25	27.31	2.50	24.40-31.70	9.14	13
K	29.49	1.94	26.50-33.50	6.57	18	27.95	2.25	23.40-33.80	8.06	18
L	30.52	4.47	21.60-39.50	14.66	19	28.13	1.79	26.10-31.30	6.36	10
M	30.17	3.52	21.70-34.40	11.68	14	27.38	2.23	23.40-30.20	8.15	17
N	31.08	3.14	24.20-34.90	10.10	13	29.18	2.38	24.55-31.50	8.16	9
O	31.41	3.27	25.80-37.90	10.42	18	26.29	1.49	24.00-28.10	5.67	6
P	31.53	3.69	24.10-38.50	11.71	33	28.33	2.11	23.00-33.30	7.44	54
Q	27.61	2.20	23.60-32.55	7.99	14	24.51	3.03	20.95-30.40	12.38	8
						<i>Breadth of palatal shelf</i>				
H	17.42	1.24	15.70-20.00	7.14	18	16.83	.76	15.65-17.90	4.52	9
I	16.78	.73	15.40-17.90	4.38	16	16.40	.96	14.95-18.10	5.83	17
J	16.90	1.22	15.10-19.35	7.25	22	16.65	1.37	14.60-18.50	8.21	13
K	17.03	.84	16.00-18.30	4.91	14	16.75	.95	15.10-18.00	5.67	19
L	17.39	1.43	15.20-19.55	8.23	15	17.63	1.05	16.35-20.05	5.94	9
M	17.12	.90	15.20-17.95	5.26	10	16.72	1.15	14.50-18.15	6.91	16
N	17.64	1.27	15.00-19.25	7.20	13	18.01	2.17	13.75-20.60	12.06	8
O	17.65	1.11	15.60-19.30	6.30	21	16.33	.57	15.40-17.30	3.51	7
P	17.66	1.07	14.85-19.25	6.03	31	17.38	1.07	14.60-19.45	6.14	52
Q	16.38	.74	14.80-17.60	4.50	13	15.58	1.07	14.20-17.55	6.88	9

TABLE 6.—Continued.

Sample	Males					Females				
	\bar{X}	SD	Extremes	CV	N	\bar{X}	SD	Extremes	CV	N
						<i>Length of maxillary toothrow</i>				
H	44.05	2.69	37.95-51.10	6.11	18	41.03	1.90	37.75-43.50	4.62	8
I	43.43	1.56	40.50-46.25	3.60	16	40.91	1.49	38.80-43.40	3.65	20
J	43.95	1.84	40.15-46.65	4.20	22	41.31	1.06	39.50-43.00	2.56	8
K	43.67	1.94	39.50-48.50	4.43	16	41.89	1.09	40.00-43.65	2.61	15
L	45.74	2.95	41.25-50.15	6.44	13	43.20	.81	42.00-44.65	1.86	7
M	44.81	1.57	43.10-47.10	3.50	11	41.50	1.91	38.10-43.65	4.60	13
N	46.97	2.74	43.00-51.80	5.84	9	45.43	2.72	39.10-48.50	5.98	9
O	45.68	3.11	39.55-50.65	6.82	25	41.66	3.58	34.05-47.75	8.58	10
P	45.34	2.64	39.60-51.70	5.81	29	42.22	1.21	39.40-44.60	2.88	43
Q	41.18	1.93	37.60-44.85	4.68	13	38.61	2.39	37.20-43.90	6.18	7
						<i>Length of upper molar series</i>				
H	20.89	.76	19.35-22.40	3.65	17	20.28	1.01	18.95-21.65	4.96	7
I	20.62	.86	19.00-22.00	4.15	16	19.89	.75	18.10-20.85	3.76	20
J	20.66	.62	19.70-21.95	3.00	21	19.86	.52	18.80-20.55	2.64	8
K	20.47	.71	19.45-21.80	3.46	14	20.16	.55	19.35-21.00	2.73	14
L	20.81	.85	19.25-22.40	4.07	14	20.95	.47	20.40-21.85	2.25	7
M	20.81	.39	20.25-21.40	1.85	11	19.90	.69	18.40-20.90	3.45	13
N	21.22	1.07	20.00-23.05	5.03	7	21.06	.89	19.10-21.90	4.23	9
O	21.91	2.13	19.05-28.80	9.72	23	19.82	.58	18.40-20.45	2.95	10
P	20.43	.95	18.05-22.15	4.64	30	19.79	.76	17.80-21.50	3.85	45
Q	18.96	.76	17.85-20.30	3.99	13	18.53	.55	17.90-19.30	2.96	7

TABLE 6.—Continued.

Sample	Males					Females				
	\bar{X}	SD	Extremes	CV	N	\bar{X}	SD	Extremes	CV	N
H	86.83	9.46	73.30-109.00	10.89	20	80.77	4.46	74.40-87.40	5.52	10
I	87.02	6.48	74.05-97.90	7.45	18	79.79	6.31	68.55-92.50	7.91	23
J	87.52	8.71	68.85-104.00	9.95	26	79.14	7.73	68.00-89.90	9.76	13
K	85.98	7.69	74.55-106.70	8.94	19	80.37	6.17	68.50-96.45	7.68	19
L	89.16	11.48	71.70-112.70	12.88	18	81.65	5.12	74.80-89.00	6.27	10
M	88.52	8.49	73.50-102.75	9.59	14	78.23	6.95	65.10-85.95	8.89	17
N	89.30	9.57	70.15-100.45	10.72	14	88.69	7.07	76.90-99.20	7.97	10
O	92.31	9.16	71.75-110.40	9.92	25	81.46	5.19	73.85-90.60	6.37	12
P	92.88	10.02	76.80-116.90	10.79	34	84.00	6.16	66.10-95.50	7.33	53
Q	81.57	5.94	71.95-92.90	7.28	16	73.18	6.77	62.35-86.95	9.25	9
						<i>Length of lower molar series</i>				
H	22.85	1.19	21.25-27.00	5.22	19	22.51	1.41	20.00-23.95	6.27	8
I	22.37	.96	21.00-24.20	4.27	18	21.77	.55	20.15-22.55	2.52	21
J	22.47	.71	20.90-23.50	3.15	24	21.95	.84	20.75-23.30	3.82	11
K	22.43	.78	21.25-23.50	3.48	19	22.10	.61	20.90-23.25	2.77	19
L	23.17	.91	21.55-25.05	3.92	18	22.88	.67	22.25-24.00	2.94	8
M	22.65	.54	21.60-23.30	2.38	12	22.08	.96	20.35-23.85	4.36	16
N	23.23	.80	22.30-25.00	3.43	10	23.09	.72	21.65-23.90	3.11	9
O	23.37	1.05	21.15-24.85	4.50	25	22.17	.59	20.60-22.70	2.65	12
P	22.32	.95	20.35-23.70	4.26	33	21.73	.89	20.00-24.00	4.11	50
Q	21.13	.88	19.30-22.40	4.18	16	20.37	.82	19.00-22.00	4.03	9

TABLE 6.—Continued.

Sample	Males					Females				
	\bar{X}	SD	Extremes	CV	N	\bar{X}	SD	Extremes	CV	N
	<i>Breadth of rostrum across jugals</i>									
H	29.01	3.48	23.20-36.30	11.99	16	26.67	1.87	23.75-28.65	7.02	10
I	27.74	2.86	22.70-34.00	10.30	18	25.02	2.14	21.85-30.70	8.56	20
J	28.10	3.11	22.10-34.55	11.07	23	25.06	2.75	21.40-28.60	10.97	13
K	26.88	2.69	22.60-34.20	10.02	19	25.43	2.12	21.90-31.35	8.34	19
L	28.25	4.03	22.05-36.50	14.26	16	26.19	2.14	22.70-29.35	8.16	10
M	28.08	2.67	24.10-33.25	9.52	13	24.36	1.99	20.00-28.20	8.17	17
N	29.05	3.40	23.20-35.10	11.71	14	27.90	1.07	26.10-29.00	3.84	8
O	30.49	3.54	22.95-35.50	11.61	25	26.40	2.22	23.00-29.30	8.39	10
P	31.24	3.75	23.95-38.15	12.00	35	27.84	2.37	20.65-32.30	8.52	50
Q	26.74	2.77	21.75-33.00	10.35	16	23.28	1.97	20.00-27.10	8.48	9
	<i>Greatest breadth of nasals</i>									
H	16.07	2.25	12.80-22.25	14.00	16	14.85	.98	13.60-17.00	6.59	10
I	15.97	1.96	12.45-18.50	12.27	18	14.03	1.28	11.90-16.95	9.13	20
J	15.61	2.01	11.05-19.60	12.86	25	14.12	1.56	11.90-16.30	11.07	13
K	14.98	1.96	12.50-19.40	13.09	19	14.26	.91	13.20-16.90	6.39	19
L	15.69	2.21	12.40-20.40	14.12	18	13.85	1.19	12.30-16.20	8.59	10
M	15.22	1.94	12.45-18.60	12.75	13	13.62	1.50	11.30-16.30	11.02	17
N	16.47	1.79	13.90-19.90	10.85	14	15.36	1.15	13.50-17.40	7.50	8
O	16.82	2.12	11.95-20.50	12.62	26	14.75	1.46	13.20-18.20	9.89	11
P	17.15	2.29	12.25-23.25	13.35	35	15.06	1.74	11.05-20.10	11.58	50
Q	14.67	1.33	12.65-17.60	9.03	15	13.08	1.88	10.15-16.70	14.40	8

TABLE 6.—Continued.

Sample	Males					Females					
	\bar{X}	SD	Extremes	CV	N	\bar{X}	SD	Extremes	CV	N	
	<i>Breadth of rostrum across frontals</i>										
H	18.11	2.64	13.65-25.05	14.56	16	16.48	1.17	14.80-18.05	7.07	10	
I	17.20	1.64	14.00-19.55	9.53	18	15.49	1.30	13.25-17.90	8.39	20	
J	16.89	1.89	13.20-20.75	11.18	23	15.25	1.56	13.10-17.40	10.20	13	
K	16.21	1.81	13.45-19.40	11.14	19	15.27	1.17	13.20-18.60	7.67	19	
L	17.42	2.39	13.60-22.10	13.73	16	15.13	1.24	13.05-16.90	8.17	10	
M	17.00	2.09	14.20-21.50	12.31	13	14.42	1.53	11.40-17.10	10.61	17	
N	17.75	1.73	14.10-19.90	9.72	14	17.27	.76	16.10-18.30	4.42	8	
O	19.14	2.22	14.55-23.25	11.58	25	16.36	1.39	15.00-19.40	8.52	11	
P	19.53	2.35	14.00-25.10	12.03	34	16.78	1.87	11.05-21.65	11.17	50	
Q	16.22	1.50	14.35-19.70	9.27	16	14.28	1.94	11.00-18.00	13.56	8	

TABLE 7.—Measurements of 17 cranial dimensions for samples of *Didelphis virginiana* and *D. marsupialis* from the geographic zone of sympatry (see Fig. 1). Each species sample, identified in the left margin, is subdivided on the bases of sex and age class (4, 5, and 6). The first line for the measurements of each subdivision gives the mean plus or minus one standard deviation, the second line the extremes, and the third line the coefficient of variation and the sample size (in parentheses).

Species	Males			Females		
	Age class 4	Age class 5	Age class 6	Age class 4	Age class 5	Age class 6
<i>D. virginiana</i>	99.07 ± 6.02	110.56 ± 8.30	123.90 ± 7.64	93.48 ± 3.52	104.23 ± 6.23	110.75 ± 6.57
	88.00—108.35	94.00—125.00	109.05—142.10	83.40—98.90	90.60—117.00	98.85—123.40
	6.07 (17)	7.51 (33)	6.15 (40)	3.76 (18)	5.97 (58)	5.93 (31)
<i>D. marsupialis</i>	97.43 ± 3.99	106.63 ± 7.18	114.12 ± 5.90	90.37 ± 4.52	98.32 ± 6.04	104.19 ± 5.86
	91.25—105.70	91.00—124.70	102.30—124.90	84.40—102.75	85.68—112.90	90.55—116.15
	4.09 (17)	6.73 (50)	5.16 (40)	5.00 (12)	6.14 (61)	5.62 (32)
<i>D. virginiana</i>	96.56 ± 5.01	106.53 ± 7.23	118.68 ± 7.24	91.34 ± 3.26	101.60 ± 5.86	107.46 ± 5.92
	86.60—105.50	91.50—119.30	105.15—135.00	81.25—95.70	88.75—113.20	96.85—117.95
	5.19 (17)	6.79 (29)	6.10 (38)	3.60 (17)	5.77 (56)	5.51 (30)
<i>D. marsupialis</i>	95.23 ± 3.84	105.53 ± 6.74	110.25 ± 5.35	88.87 ± 4.04	96.33 ± 5.73	101.90 ± 4.70
	89.70—102.30	88.70—119.90	100.80—119.95	83.00—99.70	85.55—110.45	89.50—110.95
	4.03 (17)	6.51 (48)	4.85 (37)	4.54 (12)	5.94 (58)	4.61 (31)

Greatest length of skull

Condylobasal length

TABLE 7.—Continued.

Species	Males			Females		
	Age class 4	Age class 5	Age class 6	Age class 4	Age class 5	Age class 6
<i>D. virginiana</i>	58.65 ± 3.10	64.11 ± 3.96	70.60 ± 4.14	55.06 ± 3.10	61.22 ± 3.76	64.82 ± 3.39
	52.50 — 64.00	55.55 — 70.75	62.00 — 80.05	45.65 — 58.30	49.50 — 68.50	57.10 — 71.10
	5.28 (19)	6.17 (36)	5.86 (41)	5.62 (18)	6.14 (58)	5.22 (33)
<i>D. marsupialis</i>	58.15 ± 2.15	62.68 ± 3.55	65.47 ± 2.65	55.47 ± 2.75	59.76 ± 3.11	62.08 ± 2.66
	54.85 — 62.20	55.10 — 71.45	60.05 — 70.00	52.00 — 62.80	53.35 — 67.55	56.15 — 67.60
	3.69 (17)	5.66 (50)	4.03 (39)	4.95 (12)	5.20 (61)	4.28 (32)
		<i>Zygomatic breadth</i>				
<i>D. virginiana</i>	50.26 ± 4.34	57.70 ± 4.99	64.38 ± 4.48	46.99 ± 2.10	51.40 ± 3.15	55.18 ± 3.32
	40.60 — 55.10	47.30 — 67.95	52.70 — 72.50	41.60 — 50.65	45.00 — 59.30	48.90 — 63.65
	8.64 (15)	8.65 (33)	6.96 (37)	4.45 (18)	6.13 (55)	6.01 (32)
<i>D. marsupialis</i>	49.77 ± 3.40	54.87 ± 4.80	60.30 ± 3.70	43.35 ± 1.75	48.06 ± 3.77	50.34 ± 2.51
	44.35 — 57.60	45.85 — 68.70	51.65 — 68.20	41.25 — 47.50	40.90 — 55.85	43.45 — 56.15
	6.82 (15)	8.74 (46)	6.13 (39)	4.03 (12)	7.83 (52)	4.97 (32)
		<i>Interorbital constriction</i>				
<i>D. virginiana</i>	18.93 ± 1.41	20.85 ± 2.01	23.66 ± 1.76	17.34 ± 1.11	19.18 ± 1.62	20.34 ± 1.40
	16.65 — 21.20	15.55 — 24.60	20.10 — 28.10	14.10 — 18.85	16.50 — 22.85	17.25 — 23.05
	7.45 (19)	9.64 (37)	7.55 (42)	6.40 (18)	8.45 (56)	6.88 (32)
<i>D. marsupialis</i>	18.65 ± 1.46	20.46 ± 1.87	22.17 ± 2.13	17.61 ± 1.07	18.58 ± 1.45	19.53 ± 1.16
	16.20 — 20.00	16.40 — 24.00	18.77 — 29.60	15.75 — 19.25	16.00 — 22.35	16.65 — 21.30
	7.82 (17)	9.13 (49)	9.60 (40)	6.07 (12)	7.80 (61)	5.94 (31)

TABLE 7.—Continued.

Species	Males				Females			
	Age class 4	Age class 5	Age class 6		Age class 4	Age class 5	Age class 6	
<i>D. virginiana</i>	11.14 ± .60	11.18 ± .49	11.50 ± .49	<i>Postorbital constriction</i>	11.14 ± .47	11.52 ± .57	11.68 ± .71	
	10.25—12.35	10.30—12.70	10.60—12.65		10.30—11.75	10.20—13.05	10.55—13.70	
	5.39 (20)	4.38 (35)	4.26 (42)		4.22 (18)	4.95 (58)	6.08 (33)	
	11.32 ± .43	11.41 ± .42	11.51 ± .50		11.48 ± .46	11.74 ± .49	11.76 ± .52	
<i>D. marsupialis</i>	10.65—12.20	10.25—12.15	10.40—12.45	10.35—12.15	10.65—12.80	10.90—12.60		
	3.80 (17)	3.68 (51)	4.34 (40)	4.01 (12)	4.17 (60)	4.42 (33)		
<i>D. virginiana</i>	17.95 ± 1.51	20.34 ± 1.91	22.89 ± 1.91	<i>Breadth across canines</i>	16.76 ± .67	18.18 ± 1.30	19.71 ± 1.07	
	14.85—20.75	16.35—24.60	19.55—28.15		15.60—18.00	15.45—21.15	17.90—21.70	
	8.41 (19)	9.39 (31)	8.34 (34)		4.00 (17)	7.15 (53)	5.43 (31)	
	17.36 ± 1.12	19.19 ± 1.40	20.94 ± 1.38		15.34 ± .73	16.86 ± 1.32	18.09 ± .88	
	15.90—19.10	16.00—23.50	18.75—24.75		14.35—16.55	14.55—21.10	16.30—19.90	
6.45 (15)	7.30 (47)	6.59 (38)	4.76 (9)	7.83 (60)	4.86 (31)			
<i>D. virginiana</i>	30.88 ± 1.83	31.68 ± 1.50	32.50 ± 1.72	<i>Breadth across molars</i>	29.32 ± 1.89	31.02 ± 1.26	31.63 ± 1.35	
	27.50—35.45	29.00—36.00	28.70—36.10		24.30—31.65	27.90—33.70	29.10—34.30	
	5.93 (16)	4.73 (33)	5.29 (35)		6.45 (14)	4.06 (53)	4.27 (29)	
	29.44 ± 1.36	30.21 ± 1.44	30.61 ± 1.16		29.00 ± .68	29.52 ± 1.31	30.00 ± 1.04	
	27.35—31.65	26.90—33.35	28.35—33.35		27.60—29.75	26.95—33.30	27.50—31.80	
4.62 (14)	4.77 (50)	3.80 (34)	2.34 (11)	4.44 (60)	3.47 (31)			

TABLE 7.—Continued.

Species	Males			Females		
	Age class 4	Age class 5	Age class 6	Age class 4	Age class 5	Age class 6
<i>D. virginiana</i>	27.24 ± 1.78	29.85 ± 3.01	33.89 ± 2.51	25.76 ± .97	28.15 ± 1.96	30.02 ± 1.87
	24.30 — 30.60	21.60 — 34.80	28.75 — 39.50	23.00 — 27.00	21.80 — 32.90	26.05 — 33.30
<i>D. marsupialis</i>	6.53 (17)	10.08 (32)	7.41 (42)	3.77 (18)	6.95 (59)	6.22 (32)
	25.65 ± 1.18	27.75 ± 2.07	29.66 ± 1.73	23.56 ± .93	25.88 ± 1.72	26.62 ± 1.80
<i>D. marsupialis</i>	23.85 — 29.00	23.65 — 34.50	26.70 — 33.70	22.30 — 25.65	22.70 — 29.25	21.90 — 30.30
	4.59 (17)	7.44 (50)	5.74 (40)	3.96 (12)	6.64 (58)	6.76 (33)
<i>D. virginiana</i>	16.26 ± .93	17.57 ± 1.01	18.40 ± .84	16.36 ± .83	17.45 ± 1.09	18.27 ± 1.30
	14.85 — 17.80	15.50 — 19.25	16.60 — 20.15	14.60 — 17.90	15.40 — 20.45	13.75 — 20.60
<i>D. marsupialis</i>	2.95 (16)	3.75 (34)	3.55 (33)	3.30 (17)	5.05 (55)	6.85 (32)
	15.68 ± .75	16.56 ± 1.05	16.96 ± .86	15.52 ± .70	16.48 ± 1.04	17.20 ± .81
<i>D. marsupialis</i>	14.55 — 16.65	13.85 — 18.40	15.10 — 18.30	14.25 — 16.70	13.40 — 19.50	15.70 — 19.25
	4.78 (15)	6.34 (46)	5.07 (30)	4.51 (12)	6.31 (53)	4.71 (28)
<i>D. virginiana</i>	44.49 ± 2.44	46.95 ± 2.35	46.95 ± 2.35	42.44 ± 1.70	43.38 ± 2.18	43.38 ± 2.18
	38.85 — 49.10	38.85 — 49.10	42.70 — 51.80	39.20 — 47.30	39.10 — 48.50	39.10 — 48.50
<i>D. marsupialis</i>	5.48 (34)	5.01 (40)	5.01 (40)	4.01 (56)	5.03 (32)	5.03 (32)
	43.71 ± 1.90	44.78 ± 1.75	44.78 ± 1.75	41.81 ± 1.60	42.63 ± 1.44	42.63 ± 1.44
<i>D. marsupialis</i>	39.70 — 47.25	41.70 — 48.40	41.70 — 48.40	38.20 — 45.70	39.65 — 45.40	39.65 — 45.40
	4.35 (50)	3.91 (40)	3.91 (40)	3.83 (59)	3.38 (30)	3.38 (30)

*Breadth of brain case**Breadth of palatal shelf**Length of maxillary toothrow*

TABLE 7.—Continued.

Species	Males			Females		
	Age class 4	Age class 5	Age class 6	Age class 4	Age class 5	Age class 6
	<i>Length of upper molar series</i>					
<i>D. virginiana</i>	20.52 ± .93	20.81 ± .96	20.81 ± .96	20.19 ± .95	20.19 ± .95	20.04 ± 1.03
	18.05—22.40	18.90—23.05	18.90—23.05	17.80—22.20	17.80—22.20	18.35—23.10
	4.53 (34)	4.61 (39)	4.61 (39)	4.71 (58)	4.71 (58)	5.14 (31)
	20.39 ± .77	20.36 ± .71	20.36 ± .71	20.13 ± .70	20.13 ± .70	20.06 ± .57
<i>D. marsupialis</i>	18.45—22.40	19.20—21.65	19.20—21.65	18.40—21.60	18.40—21.60	19.20—21.20
	3.78 (51)	3.49 (35)	3.49 (35)	3.48 (60)	3.48 (60)	2.84 (29)
	<i>Length of mandible</i>					
<i>D. virginiana</i>	79.74 ± 4.72	89.06 ± 6.28	99.86 ± 6.98	75.02 ± 2.83	83.89 ± 5.33	89.14 ± 5.22
	70.15—88.75	75.10—98.75	86.05—116.90	66.10—78.60	72.95—96.30	79.60—99.20
	5.92 (20)	7.05 (36)	6.99 (39)	3.77 (18)	6.35 (58)	5.86 (33)
	78.28 ± 3.48	85.66 ± 5.97	91.77 ± 4.77	72.44 ± 3.78	79.49 ± 5.23	84.41 ± 4.08
<i>D. marsupialis</i>	72.85—85.00	73.80—100.75	82.10—100.30	68.00—82.30	64.50—92.00	73.85—94.00
	4.45 (17)	6.97 (50)	5.20 (38)	5.22 (12)	6.58 (62)	4.83 (33)
	<i>Length of lower molar series</i>					
<i>D. virginiana</i>	23.09 ± .91	22.52 ± .80	22.68 ± 1.04	22.69 ± 1.03	22.19 ± 1.00	21.84 ± 1.14
	21.25—25.05	20.35—24.30	21.10—25.00	21.05—24.00	20.40—24.20	20.00—25.40
	3.94 (17)	3.55 (32)	4.59 (36)	4.54 (14)	4.51 (57)	5.40 (30)
	22.78 ± .50	22.16 ± .83	21.98 ± .78	22.34 ± .61	21.93 ± .77	21.85 ± .74
<i>D. marsupialis</i>	22.00—23.80	20.60—23.70	20.40—23.60	21.75—23.80	20.45—23.50	20.70—23.45
	2.19 (16)	3.75 (50)	3.55 (36)	2.73 (9)	3.51 (60)	3.39 (30)

TABLE 7.—Continued.

Species	Males						Females					
	Age class 4	Age class 5	Age class 6	Age class 4	Age class 5	Age class 6	Age class 4	Age class 5	Age class 6	Age class 4	Age class 5	Age class 6
	<i>Breadth of rostrum across jugals</i>											
<i>D. virginiana</i>	25.51 ± 1.92	28.71 ± 2.71	32.89 ± 2.67	24.59 ± 1.51	27.49 ± 2.00	29.33 ± 1.82	22.05 - 30.20	23.20 - 33.40	28.05 - 38.15	20.65 - 26.90	23.55 - 31.60	25.90 - 32.60
	7.53 (19)	9.44 (35)	8.12 (39)	6.10 (17)	7.28 (55)	6.21 (30)	25.24 ± 2.00	26.72 ± 1.97	29.47 ± 1.97	23.19 ± 1.08	25.39 ± 1.80	26.62 ± 1.41
<i>D. marsupialis</i>	22.30 - 29.15	22.10 - 31.25	25.70 - 34.50	21.50 - 25.50	21.80 - 30.35	23.00 - 28.40	7.92 (15)	7.37 (44)	6.68 (40)	4.66 (11)	7.09 (58)	5.30 (32)
	<i>Greatest breadth of nasals</i>											
<i>D. virginiana</i>	14.48 ± 1.34	15.85 ± 1.64	18.06 ± 1.85	13.09 ± .94	14.80 ± 1.68	15.51 ± 1.14	12.25 - 17.30	12.05 - 19.35	14.00 - 23.25	11.05 - 15.05	12.15 - 20.10	13.00 - 17.40
	9.25 (19)	10.35 (35)	10.24 (41)	7.18 (17)	11.35 (55)	7.35 (30)	13.04 ± .96	14.47 ± 1.46	15.81 ± 1.34	11.76 ± .89	13.22 ± 1.22	14.06 ± .89
<i>D. marsupialis</i>	11.55 - 15.50	11.50 - 17.70	13.90 - 19.50	10.60 - 13.40	11.10 - 16.60	12.20 - 15.60	7.36 (16)	10.09 (48)	8.48 (40)	7.57 (10)	9.23 (58)	6.33 (32)
	<i>Breadth of rostrum across frontals</i>											
<i>D. virginiana</i>	15.96 ± 1.18	17.67 ± 1.98	20.16 ± 1.91	14.55 ± 1.40	16.62 ± 1.76	17.16 ± 1.34	14.00 - 18.10	13.50 - 21.15	16.50 - 25.10	11.05 - 16.35	13.15 - 21.65	13.65 - 20.10
	7.39 (18)	11.21 (35)	9.47 (38)	9.62 (17)	10.59 (55)	7.81 (30)	15.60 ± 1.24	17.09 ± 1.76	18.62 ± 2.05	14.90 ± 1.03	15.70 ± 1.51	16.75 ± 1.08
<i>D. marsupialis</i>	14.10 - 18.45	13.85 - 20.35	14.35 - 25.60	13.50 - 16.70	11.10 - 19.20	14.40 - 18.55	7.92 (15)	10.30 (45)	11.01 (40)	6.91 (11)	9.62 (55)	6.45 (32)

APPENDIX II—SPECIMENS EXAMINED

Localities in the following lists of specimens examined are arranged from north to south and from west to east within each political unit. Localities in italics were not plotted separately on the distribution maps (Figs. 12 and 13) because undue crowding would have resulted; instead, they are included under the symbol for the preceding unitalicized locality. Place names included in each plotted locality citation are listed in the Gazetteer. Localities within quotation marks were not located by me. Each specimen listed is identified by its catalogue number and the initials of the institution where it is housed.

Didelphis marsupialis caucea

Specimens examined (613).—MEXICO: Tamaulipas: Ejido Santa Isabel, 2 km. W Pan American Highway, 1 (KU 57524). San Luis Potosí: *ca.* 5 km. W (by road) El Naranjo, *El Salto*, Río Naranjo, 3 (AMNH 176700, 176702; LSUMZ 4773); Río Axtla, 3 km. W Axtla, 1 (KU 19048); *ca.* 2 km. W Xilitla, 2 (LSUMZ 15102, 15103); *Xilitla*, 3 (LSUMZ 2742-2744); 3 km. N Tamazunchale, 1 (KU 19049); "Rancho Sabinal," 1 (LSUMZ 7853). Hidalgo: 4 km. E San Felipe Orizatlán, 1 (TTU 18181); Veracruz: 6.5 km. NNW El Higo, 1 (IB 10773); Hacienda Tamiahua, Cabo Rojo, 2 (KU 82834, 82835); 17 km. NW Tuxpan, 2 (KU 82836, 82837); 9 km. NW Tuxpan, 1 (KU 82838); Tuxpan, 1 (KU 82839); 5 km. S Tihuatlán, 2 (KU 23395, 23397); Papantla, 2 (USNM 93043, 93044); 9 km. E Papantla, 1 (KU 23398); 9 km. NW Nautla, 1 (KU 23399); 3 km. SW San Marcos, 2 (KU 23400, 23401); 4 km. W Tlapacoyan, 1 (KU 23402); 1 mi. NE Las Minas, 1 (USNM 329398); ½ mi. NW Las Minas, 1 (USNM 329399); 5 km. N Jalapa, 2 (TCWC 1925, 1926); 2 km. W Jico, 1 (KU 19054); Mirador, 5 (USNM 58687-58691); Boca del Río, 1 (TCWC 2748); 4 km. WNW Fortín, 3 (KU 17683-17685); Río Metlac, 1 km. W Fortín, 2 (LSUMZ 15104, 15105); 3 km. SE Orizaba, 3 (KU 19055-19057); Potrero Viejo, 1 (KU 32048); 24 mi. S Veracruz, 4 (AMNH 203557-203559, 203561); 15 km. ESE San Juan de la Punta, 2 (KU 19060, 19061); Río Blanco, 20 km. W Piedras Negras, 2 (KU 10951, 10962); 15 mi. N San Andrés Tuxtla, 2 (AMNH 172154, 172168); 15 km. NE Catemaco, 4 (IB 7923-7925, 7932); San Andrés Tuxtla, 1 (AMNH 172165); 3 km. E San Andrés Tuxtla, 4 (KU 23404-23406, 24001); Catemaco, 3 (AMNH 172151; USNM 65543, 65957); Lake Catemaco, 3 (AMNH 172169, 172174, 172176); Agua Dulce, 1 (USNM 271103); 20 km. E Jesús Carranza, 2 (KU 23407-23408); 60 km. ESE Jesús Carranza, 1 (KU 23410). Puebla: Metlaltoyuca, 1 (USNM 92979). Oaxaca: 10 km. S Yetla, 1 (KU 99528); Santo Domingo (Mts. near), 1 (USNM 73321); 1 km. N Cerro Baúl, Ranch Carlos Minné, 37 km. NW (by road) Risa de Oro (Chiapas), 1 (CAS 14634); Tapanatepec, 1 (IB 2475); "8 mi. S Veracruz" [*sic*], 2 (AMNH 172152, 172155); "Oaxaca" (general designation), 1 (AMNH 26597). Tabasco: 15 km. NW [*sic*] Alvaro Obregón, 1 (KU 19064); Frontera, 2 (USNM 100507, 100508); La Venta, 1 (USNM 271104); 15 mi. W, 6 mi. N Villa Hermosa, 1 (KU 66270); 6 mi. S Cardenas, 3 (KU 66271-66273); 10 mi. E, 19 mi. N Mascuspana, 1 (KU 66274); 4 mi. N, 2 mi. E Macuspana, 1 (KU 66275); 5 mi. SE Macuspana, 2 (KU 66276, 66277); 6.5 km. NE Teapa, 1 (IB 8089); Teapa, 6 (IB 7561, 7563; USNM 100510, 100511, 100513, 100512—holotype of *D. marsupialis tabascensis* Allen, 1901); 1 mi. E Teapa, 2 (LSUMZ 7312, 8094); Río Puyacatengo, 15 km. E Teapa, 1 (IB 6958); "Tabasco" (general designation), 1 (USNM 10196/38687). Chiapas: 16 mi. NW Palenque, 1 (TCWC 16282); *ca.* 5 km. S Solusuchiapa, 1 (LSUMZ 11913); 3 mi. SSE Soyaló, 1 (TCWC 8273); 2 mi. E El Real, 1 (KU 66278); Tuxtla, 4 (USNM 76205-76208); 4 mi. NE Chiapa de Corzo, 1 (TCWC 8272); 5 mi. S Chiapa, 1 (AMNH 172173); 20 mi. W Comitán, 1 (AMNH 172156); 3 km. E Risa de Oro, 1 (LSUMZ 11911); 18 mi. E Zapaluta, 1 (TCWC 8271); 25 mi. SE Comitán, 1 (AMNH 172166); 24 mi. SSE Zapaluta (5 mi. W Hwy. 190), 2 (TCWC 8933, 8934); cerca Finca Prusia, 1 (IB 7); Paval, 20 km. NE Mapastepec, 1 (IB 9); Finca La Esperanza, 45 km. N Huixtla, 1 (IB 10); Finca Germania, 24 km. NE Huixtla, 1 (IB 11); Río Huixtla, *ca.* 13 km. N Huixtla, 1 (LSUMZ 11912); "16 mi. N Chiapas-

Guatemala border [sic]," 1 (AMNH 172162). Campeche: Apazote, near Yahaltuma, 1 (USNM 108297); 7.5 km. W Escarcega, 1 (KU 91449). Yucatán: Chichén Itzá, 2 (USNM 108298, 108300).

BRITISH HONDURAS: Central Farm, 1 (USNM 360463).

GUATEMALA: Toocoq, 15 km. SE La Libertad, 1 (KU 81962); Chinaja, 1 (KU 81964); Chimoacán, 3 (AMNH 79097-79099); Finca Selache [sic] [ca. 6 mi. S Cipres], 3 (AMNH 68520, 68521, 68542); Astillero, 4 (KU 64596-64599); "Guatemala" (general designation), 2 (USNM 61214, 61215).

EL SALVADOR: San José del Sacare, 1 (MVZ 130277); Colima, 1 (MVZ 130278); N slope Mt. Cacaguatique, 1 (MVZ 98151); *Mt. Cacaguatique*, 6 (MVZ 130304-130309); Barra de Santiago, 1 (MVZ 130273); Hacienda Chilata, 6 (MVZ 98158-98161, 130315, 130316); ¾ mi. NE Divisadero, 1 (MVZ 130280); *Carolina Mine*, 4 km. W Divisadero, 1 (MVZ 130284); *Monte Cristo Mine*, 1½ mi. W Divisadero, 2 (MVZ 98149, 130282); 1 mi. W Divisadero, 1 (MVZ 130281); 10 mi. W La Libertad, 1 (TCWC 6620); Volcán de San Miguel, 2 (MVZ 130314, 130315); SW edge Lake Olomega, 2 (MVZ 98153, 98157); Puerto del Triunfo, 6 (MVZ 130317-130322).

HONDURAS: Patuca, 1 (USNM 36065); 7 mi. W La Ceiba, 1 (TCWC 14511); 2 mi. W San Pedro Sula, 1 (TCWC 11088); 7 km. N Santa Bárbara, 1 (TCWC 18551); *Santa Bárbara*, 1 (AMNH 123289); Copán, 1 (TCWC 18550); Las Flores, Gracias, 23 (AMNH 128975, 128977-128990, 128992, 128993, 129693-129696, 129699, 129700); 1 km. NW Nuevo Ocotepaque, 1 (TCWC 18011); Tegucigalpa, 1 (AMNH 126761); El Zapote, [7 km. S] Sabana Grande, 1 (AMNH 126763); "Patuca River," 1 (USNM 21012/36060); "Las Ventanas, Lake Yojoa," 1 (AMNH 126138).

NICARAGUA: Bonanza, 10 (KU 96362, 96363, 99397-99403, 99405); 4½ km. N, 2 km. E Jalapa, 11 (KU 110604-110613, 110617); 2 km. E Yalí, 1 (KU 105880); Hacienda La Trampa, 16 km. E, 5½ km. N Jinotega, 3 (KU 99422, 99424; USNM 338812); *Santa María de Ostuma*, 1 (KU 105881); *Finca Tepeyac*, 10½ km. N, 9 km. E Matagalpa, 46 (KU 104518-104522, 104524-104532, 104555-104573, 104575; USNM 337527-337529, 337532-337534, 337538, 337540, 337542-337545); Kurinwas River, 12° 52' N, 84° 03' W, 1 (USNM 392858); Hacienda San Isidro, 10 km. S Chinandega, 3 (KU 104545, 104547, 104551); Santa Rosa, 17 km. N, 15 km. E Boaco, 1 (KU 110629); San Antonio, 3 (KU 105883, 105884, 114460); 3 mi. SW Managua, 1 (KU 70184); 1 km. N, 2½ km. W Villa Somoza, 1 (KU 110648); El Recreo, 13 (KU 104419-104426; USNM 337655-337659); *S side Río Mico*, *El Recreo*, 18 (KU 110631-110647, 114462); Hacienda Azacualpa, 5 km. N, 2 km. W Villa El Carmen, 3 (KU 108218-108220); 3 km. N, 4 km. W Diriamba, 2 (KU 110649, 114463); Hacienda Mecatepe, 2 km. N, 11½ km. E Nandaime, 1 (KU 108144); *La Calera*, 3 km. S, 5 km. W *Nandaime*, 1 (KU 108145); La Esperanza, 5 km. S, 3½ km. E San Carlos, 14 (KU 108221-108230; USNM 361208, 361210, 361211, 361213); Toro Rapids, 1 (AMNH 136926); Greytown, 4 (USNM 33134/45138, 33135/45139, 33137/45141, 45140—holotype of *D. richmondi* Allen, 1901); "Río Coco," 1 (AMNH 29256); "Lavala [= Savala]," 4 (AMNH 28324, 28327, 28961, 29323); "Río Escondido, 50 mi. from Bluefields," 1 (USNM 36486/48855); "Nicaragua" (general designation), 3 (AMNH 136947; USNM 337539, 337546).

COSTA RICA: Cariari, 1 (LSUMZ 12635); Monteverde, 1 (LACM 26241); Alajuela, 1 (AMNH 177084); San José, 10 (AMNH 3654, 3675, 10095; USNM 9070/38861, 9071/37941, 9072/38855, 9073/38862, 9074/37942, 9075/38863, 15969); *San Pedro Montes de Oca*, 1 (AMNH 139250); *Universidad de Costa Rica, San Pedro*, 1 (LSUMZ 11433); *Hatillo*, 2 (LACM 24539, 24540); Santa Teresa Peralta, 1 (AMNH 140336); Finca Lornessa, 2 km. NW Santa Ana, 2 (LSUMZ 14458, 14459); *Santa Ana*, 1 (LSUMZ 12632); Cartage, 1 (KU 26929); IICA, Turrialba, 4 (LSUMZ 9336; USNM 284467-284469); 5 km. SE Turrialba, 1 (KU 26921); Pandora, 2 (LACM 26028; USNM 284466); San Gerónimo Pirris, 3 (AMNH 124819; USNM 250318, 250480); Finca Ligia, Parrita, 1 (LACM 26680); Pozo Azul, 1 (AMNH 19204); San Isidro del General, 10 (AMNH 139240-139248; LACM 25797); 4 mi. NE Palmar, 1 (TCWC 10577); *Palmar*, 6 (AMNH 139305-139310); Camp Seattle, Osa Peninsula, 1 (LACM 23989); 9 mi. ENE Puerto Golfito, 1 (TCWC 10585); "Talamanca,"

2 (USNM 12210/14210, 14213); "Costa Rica" (general designation), 4 (USNM 8808/37940, 61199, 105272, 256466).

PANAMA: Porto Bello, 1 (USNM 171486); Nievecita Farm, 1 (USNM 291145); Mandinga, 1 (USNM 305163); Boca del Drago, 3 (USNM 315089-315091); Fort Sherman, 2 (USNM 296197, 296351); *Colón*, 1 (USNM 296196); Almirante, 14 (USNM 315075-315088); Mojinga Swamp, 1 (USNM 301149); *Camp Piña*, 9 (UA 5285; USNM 301148, 301383-301387, 302461, 302464); *Río Indio*, near *Gatún*, 4 (USNM 170899-170902); *Fort Davis*, 4 (USNM 296348-296350, 302328); *Gatún*, 9 (AMNH 36705-36709; USNM 171058, 171224, 171235, 171734); *Lion Hill*, 2 (USNM 172735, 172736); Cerro Azul (La Zumbadora), 30 (UA 7298; USNM 302454-302460, 302462, 302463, 302658-302664, 303086-303088, 305162, 305164, 305165, 306455-306460); Barro Colorado, 3 (USNM 256175, 256176, 257316); Juan Mina Station, *Río Chágres*; 1 (AMNH 164492); *Río Chágres*, 1 (AMNH 147758); *Río Mandinga*, 2 mi. W *Gamboa*, 1 (USNM 296199); *Madden Road*, 2 (USNM 301147, 301150); *Empire*, 3 (USNM 178724, 179552, 179553); Red Tank, 1 (USNM 301388); *Fort Clayton*, 6 (USNM 296198, 296347, 296352-296354, 301146); *Curundu*, 2 (USNM 297882, 297883); *Corozal*, 1 (UA 7297); *Ancón*, 1 (USNM 171984); *Quarry Heights*, 1 (USNM 303289); *Fort Kobbe*, 3 (USNM 296346, 297881, 298705); Cerro Punta, 5 (USNM 314191-314194, 322988); Palo Santo, 1 (USNM 291102); Boquete, 2 (AMNH 18916, 27023); Armila, 4 (USNM 335041-335044); El Valle, 1 (MVZ 118730); 6 mi. E El Valle (*Prov. Coclé*), 1 (USNM 304730); 2 mi. E Concepción, 1 (TCWC 10578); Boquerón, 27 (AMNH 18917, 18918, 18921, 27024-27041, 27682, 29669-29673); Santa Fé, *Río Santa María*, 2 (USNM 304731, 304732); 1 mi. SW Progreso, 8 (USNM 362353-362360); *Río Chucunaque*, 2 (USNM 306461, 306462); San Miguel Island, 1 (MCZ 8439—holotype of *D. marsupialis particeps* Goldman, 1917); Bambito, 1 (USNM 314195); Guabala, 1 (USNM 331074); 1 mi. S *Guabala*, 2 (USNM 331072, 331073); 2 mi. NE *Talé*, 1 (USNM 331076); El Real, 3 (AMNH 37568, 37627; USNM 309334); Tacarcuna, 1 (USNM 309334); Capetí, 1 (AMNH 38181); *Cituro*, 2 (AMNH 38172, 38173); Boca de *Río Paya*, 2 (USNM 306463, 306464); Mount Pirre, near head of *Río Limón*, 1 (USNM 179052); *Cana*, 8 (USNM 179050, 179051, 179058, 179165, 179913-179915, 180732); Jaqué, jct. *Río Jaqué* and *Río Imamada*, 3 (USNM 362350-362352); 8 mi. E *Jaqué*, 1 (USNM 362349); *Isla Coiba*, 3 (AMNH 18922, 27021, 27022); *Guánico*, 10 (USNM 298704, 322979-322987); Cerro Hoya, 1 (USNM 322978); "Panamá" (general designation), 2 (AMNH 63358; USNM 33175).

Didelphis virginiana californica

Specimens examined (869).—UNITED STATES: Texas: *Val Verde County*: Del Rio, 4 (USNM 18341/25222, 18342/25223, 126881, 127586); Devil's River, 1 (USNM 117533). *Kinney County*: Mouth of Sycamore Creek, 1 (USNM 24359/31765); Ft. Clark, 11 (USNM 63130-63135, 143135-143139). *Maverick County*: Eagle Pass, 1 (USNM 24358/31764). *Dimmit County*: Catarina, 2 (TCWC 4472, 20838); San Rogue Creek, 8 mi. E Catarina, 1 (TCWC 6571). *Jim Wells County*: Alice, 1 (USNM 31414/43279). *Aransas County*: Rockport, 3 (AMNH 7274/5878, 7275/5879, 14826). *Nueces County*: Nueces River, 1 (USNM 31909/43770); Nueces Bay, 3 (USNM 31908/43769, 43547, 43805); Corpus Christi, 7 (AMNH 1021, 3519, 3520; USNM 31415/43280, 99907, 99908, 116956); 11 mi. SE Corpus Christi, 1 (TCWC 779). *Hidalgo County*: Edinburg, 1 (LSUMZ 13393); ca. 6 mi. S Mission, 1 (LSUMZ 15161). *Willacy County*: 2 mi. E Sebastian, 1 (UA 17586). *Cameron County*: Brownsville, 12 (AMNH 3286/2565, 182979; KU 36-38; UCLA 11571; USNM 29791/41871, 32691/44614, 33131/45135, 33132/45136, 41820, 33133/45137—holotype of *D. marsupialis texensis* Allen, 1901); 16 mi. SE Brownsville, 1 (USNM 14909/38852); "Washington Co., Long Point," 1 (USNM 7740); "Washington Co.," 1 (USNM 7495); "Lower Rio Grande," 1 (USNM 1171); "Cameron Co." (general designation), 2 (UCLA 11575, 11576).

Mexico: Sonora: Oputo, 1 (USNM 251115); Ures, 1 (UCLA 51069); Hermosillo, 1 (USNM 33705/45740); 1 mi. S El Novillo, east bank *Río Yaqui*, 1 (MSB 19055); 1 mi. E Soyopa, 1 (UA 265); Tesia, 1 (UCLA 16946); Camoa, *Río Mayo*, 4 (MVZ 85261-85264);

½ mi. N La Aduana, 1 (MSB 9356); "Alamos region," 1 (MSC 902). Chihuahua: near Batopilas, 1 (USNM 96224). Coahuila: La Gacha, 1 (KU 67277); ½ mi. S Sabinas, 1 (KU 34543); Monclova, 1 (KU 34890); 1 mi. SW San Pedro de Las Colonias, 1 (KU 40194); 1 mi. N San Lorenzo, 1 (KU 40195). Nuevo León: near Golondrinas, 1 (USNM 33033); Hacienda la Barranca, Río San Juan, 1 (KU 100195); 20 km. NW Montemorelos, 1 (TCWC 2749); Monterrey, 5 (IB 1239; USNM 25558/32951, 25559/32952, 25560/32953, 25735/33135); *El Obispado, Monterrey*, 1 (IB 1193); Aguaje del Lobo, 10 mi. S Monterrey, 1 (MVZ 91164); "Hacienda Vargas, Río San Juan," 2 (KU 100196, 100197); "Rancho Chapotal, Río San Juan," 1 (KU 100198). Tamaulipas: Matamoros, 4 (USNM 138/1121, 1401, 1402, 1404); El Mulato, 5 (UMMZ 61548-61551, 61562); San Fernando, 1 (KU 88267); Villa Mainero, 2 (KU 88265, 88266); 36 km. N, 10 km. W Ciudad Victoria (1 km. E El Barretal on Río Purificación), 2 (AMNH 146770; KU 36938); 12 km. N, 4 km. W Ciudad Victoria (near Laredo-Ciudad México Highway), 1 (KU 36939); Victoria, 1 (USNM 119995); 3 mi. N Soto la Marina, 1 (KU 54914); Sierra de Tamaulipas, 10 mi. W, 2 mi. S Piedra, 7 (KU 54915-54921); 4 mi. N Jaumave, 1 (KU 54922); Altamira, 5 (USNM 92962-92964, 94092, 95962). Sinaloa: Sierra de Choix, 50 mi. NE Choix, 1 (USNM 96225); 3 mi. NE San Miguel, 1 (KU 84943); Culiacán, 1 (USNM 96820); 3 mi. N El Dorado, 1 (KU 75183); El Batel, 70 km. NE Mazatlán, 2 (MVZ 106114, 106115); 1 km. NE Santa Lucía, 7 (KU 93973-93979); 1 km. E Santa Lucía, 1 (KU 67278); *Copala*, 7 (LACM 8809-8813, 8963, 8964); 6 mi. SW [sic] Mazatlán, 1 (AMNH 146986); near Mazatlán [9 mi. SE Mazatlán], 2 (USNM 96821, 96822); Rosario, 1 (USNM 91170); Escuinapa, 47 (AMNH 24033-24045, 24715, 24717-24730, 24821-24826, 24862-24870, 25947, 25948; USNM 98077); "Sinaloa" (general designation), 1 (UA 9058). Durango: Chacala, 1 (USNM 96819). Zacatecas: San Juan Capistrano, 1 (USNM 90988); 8 mi. S Moyahua, 1 (CAS 13136). San Luis Potosí: El Salto, Río Naranjo, 3 (AMNH 176701; LSUMZ 2741, 15107); ca. 5 km. W (by road) El Naranjo, 1 (LSUMZ 15106); 19 km. SW Ebano, 1 (LSUMZ 4774); Bledos, 12 (LSUMZ 4761-4772); Hacienda Capulín, 1 (LSUMZ 4684). Nayarit: Acaponeta, 1 (USNM 91169); 5 mi. SSW Rosa Morada, 1 (KU 64450); 9 km. E San Blas, 1 (IB 5719); *Crucero de Solquipa, ca. 8 mi. E (by road) San Blas*, 1 (LSUMZ 11902); ½ mi. N Alticama [sic], 2 (KU 36364, 36365); *Alticama [sic]*, 1 (KU 36366); Tepic, 1 (USNM 88143); 8 mi. SSW Las Varas, 1 (KU 64451). Jalisco: 5 mi. NE Huejuquilla, 1 (KU 109467); La Mesa María de León, 1 (KU 107131); Chinampas, 1 (KU 112030); San Sebastián, 1 (USNM 88142); 1 mi. WNW Tequila, 1 (KU 36921); Etzatlán, 11 (USNM 34501/46586-34511/46595); 2 mi. SW Tapatlán, 3 (KU 63135-63137); 2.5 mi. E Tepatlán, 3 (KU 62302-62304); 3 mi. N Guadalajara, 1 (KU 30817); *Guadalajara*, 6 (AMNH 16625-16630); 5 mi. SW Arandas, 1 (KU 62305); 4 mi. NNE Puerto Vallarta, 3 (KU 64452-64454); Ameca, 2 (USNM 87059, 87060); Huascato, 1 (AMNH 115621); 3 mi. ENE Santa Cruz de las Flores, 1 (KU 30818); 19 mi. SW *Guadalajara*, 2 (KU 36362, 36363); Ocotlán, 1 (USNM 120098); 1 mi. S Ocotlán, 1 (KU 30820); Atemajac, 2 (USNM 34338/46429, 34339/46430); 2.5 mi. NNE Autlán, 1 (KU 30819); 8 mi. S Purifaction [sic], 1 (KU 33316); 2 mi. N Ciudad Guzmán, 4 (KU 30821, 36367-36369); *Zapotlán*, 1 (USNM 33517/45562); "Estancia," 6 (AMNH 25181-25183, 25185-25187); "Las Canoas," 1 (AMNH 26017); "Los Masos," 4 (AMNH 27243-27246); "Río Santa María," 2 (AMNH 25184, 25188); "Wakenakili" [sic], 1 (AMNH 25852). Guanajuato: Celaya, 2 (USNM 78428, 78481). Queretaro: Jalpan, 1 (USNM 81449). Hidalgo: Tasquillo, 3 (IB 12; TCWC 2750, 2751); Ixmiquiltán [sic], 1 (USNM 81726); Pachuca, 4 (USNM 26418/33831, 26419/33832, 51865, 52699); Río [sic] del Monte, 1 (USNM 26420/33833); Tulancingo, 2 (USNM 55581, 55582). Veracruz: 6.5 km. NNW El Higo, 1 (IB 10775); 1 km. NNE *El Higo*, 1 (IB 10774); Tuxpan, 1 (KU 82840); 12½ mi. N Tihuatlán, 1 (KU 88268); 5 km. S Tihuatlán, 4 (KU 23392-23394, 23396); 4 km. W Tlapacoyan, 1 (KU 23403); 2 km. E Perote, 1 (KU 19050); Las Vigas, 1 (USNM 54280); 5 km. N Jalapa, 2 (KU 19052, 19053); Jico, 1 (USNM 54989); Mirador, 1 (USNM 58692); Río Atoyac, 8 km. NW Potrero, 2 (KU 17686, 17688); 24 mi. S Veracruz, 1 (AMNH 203560); Orizaba, 10 (USNM 7846/38853, 58159-58165, 58415, 58416); Maltrata, 1 (USNM 65395); 7 km. SE San Juan de la Punta, 2 (KU 19058, 19059); Río Blanco, 20 km. W Piedras Negras, 4 (KU

17687-17690, 19063); Alvarado, 1 (AMNH 172164); 15 mi. N San Andrés Tuxtla, 3 (AMNH 172157-172159); *Tapalapan*, *Sierra San Andrés Tuxtla*, 1 (MVZ 121179); 15 km. NE Catemaco, 2 (IB 7922, 7933); *Catemaco*, 2 (IB 7930; USNM 65956); *Lake Catemaco*, 2 (AMNH 172167, 172174); 1 km. E *Catemaco*, 1 (IB 7926); 1 km. S *Catemaco*, 1 (IB 7949); Coatzacoalcos, 1 (KU 66269); Pasa Nueva, 2 (AMNH 17175, 17176); Minatitlán, 1 (USNM 78123); 20 km. ENE Jesús Carranza, 1 (KU 32049); 25 km. SE Jesús Carranza, 2 (KU 32050, 32051); 34 km. SE *Jesús Carranza*, 1 (KU 23409). Colima: Colima, 7 (USNM 23269/45274, 45294-45298, 45300); 4 mi. SW *Colima*, 1 (KU 39458); 5 km. NE Santiago, 1 (KU 87660); Hacienda Magdalena, 8 (AMNH 171912-171918; USNM 45299); Manzanillo, 9 (USNM 32635/44558-32640/44562, 32645/44568, 32646/44569, 33226/45231); Armeria, 8 (USNM 33264/45269-33268/45273, 45291-45293); "Colima" (general designation), 1 (USNM 7022). Michoacán: Hacienda El Molino, Negrete, 1 (USNM 20443/35673); Jiquilpan, 1 (KU 62306); Querendaro, 4 (USNM 35526/47810-35528/47812, 50832); 1 km. S Tzintzuntzan, 1 (IB 7921); 3 mi. N Pátzcuaro, 1 (MVZ 100063); 2 mi. W *Pátzcuaro*, 1 (MVZ 100066); La Salada, 2 (USNM 126166, 126167); 2 mi. N Nueva Italia, 2 (KU 39459, 39460); near La Huacana, 1 (USNM 126688); 1¼ mi. S Tacámbaro, 1 (MVZ 100074); 1 mi. E, 6 mi. S *Tacámbaro*, 1 (MVZ 100067). México: Teotihuacán, 1 (IB 7456); San Cayetano, 2 (IB 1312, 7072); Salazar, 1 (USNM 36169/48513); Amecameca, 1 (USNM 51506). Distrito Federal: Bosque de Chapultepec [Ciudad México], 3 (IB 5, 437; KU 27979; *Pedregal de San Angel* [Ciudad México], 3 (IB 137, 796, 8736); Tlapan, 4 (KU 66268; USNM 50062-50064). Morelos: Joya de Atexcapa, Lagunas de Zempoala, 1 (IB 1344); *Cerro Cuautepeitl*, *Lagunas de Zempoala*, 3 (IB 1967-1969); *Cerro Zempoala*, 1 (IB 9758); Cuernavaca, 1 (USNM 20921/36033); Xiutepec, 1 (IB 7069); *Yautepec*, 2 (USNM 51124, 51125); *Las Estacas*, 1 (IB 6); Alpuyeca, 3 (TCWC 4502-4504); Tequisquitengo, 7 (AMNH 143565-143571). Puebla: Metlatoyuca, 1 (USNM 92978); Huachinango [sic], 1 (USNM 93042); Río Otlati, 15 km. NW San Martín, 1 (TCWC 2753); San Martín, 2 (USNM 55579, 55580); Chalchicomula, 1 (USNM 53489); Atlixco, 2 (USNM 55320, 55321); 4 mi. W Matamoros, 1 (KU 62307). Guerrero: El Limón, 1 (USNM 126715); Los Sabinos, 17 km. E Teloloapan, 1 (IB 6473); Buena Vista de Cuellar, 1 (KU 66267); 1 mi. NW Omilteme, 1 (USNM 329397); Acahuizotla, 3 (TCWC 4964, 4965, 5161); Agua de Obispo, 2 (KU 99527; TCWC 5392); Río Aguacatillo, 30 km. N Acapulco, 1 (TCWC 2752); Acapulco, 6 (USNM 70616-70620, 70657); "Ahuehuepa," 1 (IB 7070). Oaxaca: Tuxtepec, 5 (USNM 65423, 65424, 65542, 65954, 65955); Reyes, 3 (USNM 69590-69592); *Cuicatlán*, 5 (IB 7068; KU 32022; USNM 69798-69800); Vista Hermosa, 1 (KU 99529); 3 mi. ESE Oaxaca, 2 (KU 68617, 68618); *Oaxaca*, 1 (USNM 68196); 15 mi. SW Oaxaca, 1 (KU 54345); Guichicovi, 1 (USNM 73491); La Gloria (Santa María Chimalapa), 1 (AMNH 145639); 3 km. SW Colonia Rudolfo Figueroa [Cerro Baul], 1 (CAS 14633); La Ventosa, 2 (AMNH 148964, 148965); Juchitán, 1 (USNM 9374/8660); Cerro de Mixtequilla, 2 (AMNH 145175, 145176); *Las Pilas* (between *Cajón de Piedra* and *Tehuantepec*), 1 (AMNH 145177); *Las Cuevas*, 3 (AMNH 143470, 145952, 145954); *Guiengola*, 1 (AMNH 145630); *Salazar*, 8 (AMNH 143468, 143469, 145182, 145631-145634, 145953); *La Presa*, 2 (AMNH 145635, 145636); *Mixtequilla*, 7 (AMNH 143920-143926); *Las Tejas*, 2 (AMNH 145637, 145638); *San Antonio*, 5 (AMNH 145641, 145955, 145957-145959); *Tehuantepec*, 3 (AMNH 145628; USNM 73490, 73492); *Cerro del Tigre*, 1 (AMNH 145956); San Dionisio, Buena Vista, 1 (AMNH 145951); Tapanatepec, 2 (AMNH 176703; IB 2475); Tenango [25 mi. W Tehuantepec], 3 (AMNH 148966-148968); Boca del Río, 12 (AMNH 148952-148963); San Mateo del Mar, 1 (USNM 73708); *Santa María del Mar*, 4 (AMNH 145629, 145179-145181); Jamaica Junction, km. 212 on Puerto Escondido Rd., 1 (CAS 14309); *Sinai*, 10 km. E *Nopala*, 1 (CAS 14939); Chalalapa, 1 (KU 62308); "Gueladú (Jalapa)," 1 (AMNH 148951); "Potrero Gueladú," 1 (AMNH 145178); "Distrito de Tehuantepec" (general designation), 1 (AMNH 143974). Tabasco: La Venta, 1 (USNM 271102); Teapa, 1 (USNM 100509); 1 mi. E *Teapa*, 1 (LSUMZ 7314). Chiapas: ca. 5 km. S Solusuchiapa, 3 (LSUMZ 11906-11908); Tumbala, 4 (USNM 76211-76214); *Yajalon*, 1 (USNM 76210); Pueblo Nuevo Solistahuacán, 1 (AMNH 172153); Ocuilapa, 1

(USNM 76203); El Real, 34 km. NE Altimirano, 1 (TCWC 8931); *Yaxoquintela*, 37 km. NE Altimirano, 1 (TCWC 8932); Ocozocauatla, 1 (USNM 76202); Tuxtla, 1 (USNM 76204); San Cristóbal, 2 (AMNH 172160; USNM 76209); San Bartolomé, 2 (USNM 133187, 133206); Valley of Comitán, [=Hda. Juncana, ca. 22 mi. SE Comitán], 1 (USNM 76716); 4 mi. S La Trinitaria, 1 (TCWC 8248); San José, 28 mi. ESE Comitán, 2 (MVZ 113484, 113485); 6 mi. NW Tonalá, 1 (KU 68619); 14 km. NE Tonalá, 1 (IB 7931); Finca Ocuilapa, 10 km. SE Tonalá, 3 (LSUMZ 11903-11905); Cerca Finca Prusia, 1 (IB 8); Huehuetan, 4 (USNM 77687, 77688, 77875, 78001). Campeche: 1 km. SW Puerto Real, Isla del Carmen, 1 (KU 91450); Apazote, near Yahaltuma, 1 (USNM 108296); La Tuxpeña, 2 (USNM 181261, 181262); 65 km. S, 128 km. E Escarcega, [Laguna Alvarado], 1 (KU 93806).

GUATEMALA: Chuntuqui, 4 (USNM 244907-244910); Libertad, 5 (USNM 244911-244914, 251161); Chinaja, 2 (KU 81963, 81967); Nenton, 1 (USNM 76717); *Jacaltenango*, 3 (USNM 76713-76715); Barillas, 231 km. (by road) N Quetzaltenango, 2 (LACM [DRP 1276, 1386]); *El Benado* [sic], *Río Ixcán*, 16 km. E Barillas, 1 (LACM [DRP 1309]); 1 mi. NE Nebaj, 1 (KU 64594); Finca Valles Lirios, Escuintla, 1 (USNM 275678); 5 mi. S Chiquimulilla, 1 (KU 64595); "Guatemala" (general designation), 3 (USNM 61211-61213).

EL SALVADOR: Los Esesmiles, 3 (MVZ 130274-130276); N slope Mt. Cacaquatique, 1 (MVZ 98152); San Salvador, 1 (USNM 238705); 2 mi. N Divisadero, 1 (MVZ 130283); *Divisadero*, 2 (MVZ 98150, 130279); Río San Miguel, 3 (MVZ 130310-130312); *Lake Olomega*, 6 (MVZ 130298-130303); *SW edge Lake Olomega*, 3 (MVZ 98154-98156).

HONDURAS: 7 mi. W La Ceiba, 1 (TCWC 14510); Lacetilla [sic], 1 (TCWC 11090); Yaruca, 1 (MCZ 10611); Chemelición [sic], 1 (USNM 148748); *La Limon* [= *La Lima*], 1 (TCWC 11089); 7 km. N Santa Bárbara, 1 (TCWC 18552); El Jaral, Lake Yojó, 1 (AMNH 126139); *Santa Bárbara*, 2 (AMNH 123284, 123285); El Caliche Cedros, 2 (AMNH 127565, 127566); Las Flores, Gracias, 6 (AMNH 128974, 128976, 128988, 129691, 129692, 129697); Las Flores Archaga, 8 (AMNH 126140, 126141, 126189, 126194, 128475-128478); *El Manteadito*, *Intibuca* [4 mi. NE San José], 1 (AMNH 126193); Muin, *Intibuca* [11 km. N Marcala], 1 (AMNH 126191); *El Horno*, *Intibuca* [5 km. N Marcala], 2 (AMNH 126190, 126192); Tegucigalpa, 2 (AMNH 123286, 126762); "Honduras" (general designation), 1 (USNM 19463).

NICARAGUA: 1½ km. N, 1 km. E Jalapa, 3 (KU 110614-110616); *Jalapa*, 1 (AMNH 29254); 6½ km. N, 1 km. E Cosiguina, 1 (KU 114458); *El Paraiso*, 1 km. N Cosiguina, 1 (KU 114459); Hacienda La Trampa, 16 km. E, 5½ km. N Jinotega, 23 (KU 99405-99421, 99423, 99425-99429); *Santa María de Ostuma*, 11 (KU 110618-110628); *Finca Tepeyac*, 10½ km. N, 9 km. E Matagalpa, 4 (KU 104523; USNM 337530, 337531, 337541); Matagalpa 7 (AMNH 28405, 28406, 28962, 29251-29253, 29257); 2 mi. SE Darío, 1 (TCWC 10579); 8 km. N, 12 km. E Boaco, 1 (KU 110630); Hacienda San Isidro, 10 km. S Chinandega, 23 (KU 104533, 104534, 104536-104540, 104542-104544, 104546, 104548-104550, 104552-104554; USNM 337521-337526); San Antonio, 11 (KU 97319-97329); Hacienda Las Colinas, 4 km. WNW Puerto Momotombo, 13 (KU 104327-104330, 104350; UA 2505-2508; USNM 334582-334584, 337654); Hacienda Corpus Christi, Chiltepec [sic], 16 (UA 2499; USNM 332423-332427, 332429-332434, 334578-334581); 5 km. N Sabana Grande, 1 (KU 97330); 1 km. N Sabana Grande, 1 (KU 114461); 3 mi. SW Managua, 11 (KU 70180-70183, 70185-70191); 5 mi. SW Managua, 1 (KU 70192); 10 mi. SW Managua, 1 (KU 70193); Villa Somoza, 1 (KU 104427); Hacienda Azacualpa, 5 km. N, 2 km. W Villa El Carmen, 6 (KU 108213-108215, 108217; USNM 361205, 361206); 3 km. N, 4 km. W Diriamba, 1 (KU 110650); Hacienda Mecatepe, 2 km. N, 11½ km. E Nandaime, 10 (KU 108133-108140, 108142, 108143); *La Calera*, 3 km. S, 5 km. W Nandaime, 1 (KU 108146); Finca Amayo, 13 km. S, 14 km. E Rivas, 31 (KU 97331, 97333-97344, 105651, 104652-104666; USNM 337846, 337848); Sapoá, 1 (KU 105882); La Esperanza, 5 km. S, 3 ½ km. E San Carlos, 1 (USNM 361209); "Río Coco," 2 (AMNH 29255, 29272); "Lavalá [= Savalá]," 2 (AMNH 28408, 28410); "Peña Blanca," 1 (AMNH 29782); "Nicaragua" (general designation), 2 (USNM 253502, 332428).

Didelphis virginiana yucatanensis

Specimens examined (43).—MEXICO: Yucatán: Mérida, 6 (AMNH 30524; USNM 11422/37937, 11423/37938, 11424/37475, 11425/37939, 11850/38854); Izamal, 1 (USNM 172068); Chichén Itzá, 8 (AMNH 30524, 91172, 91174, 91176, 91177, 91180, MCZ 12370; USNM 108299—holotype of *D. v. yucatanensis* Allen, 1901); ca. 1 km. E Chichén Itzá, 2 (LSUMZ 11909, 11910); "Yucatán Peninsula," 1 (MCZ 12301). Campeche: Campeche, 1 (USNM 100531); Champotón, 1 (KU 91447); 5 km. S Champotón, 1 (KU 91448). Quintana Roo: Pueblo Nuevo X-can, 2 (KU 91438, 91439); 3.5 km. N San Miguel, Isla Cozumel, 10 (KU 91428-91437); "Cozumel Island," 6 (USNM 108494-108497, 108498—holotype of *D. yucatanensis cozumelae* Merriam, 1901, 108499); 4 km. NNE Felipe Carrillo Puerto, 1 (KU 91446); Xcopen, 1 (MCZ 13200).

BRITISH HONDURAS: Corozal, 2 (AMNH 146585, 146586).

APPENDIX III—GAZETTEER

The following place names and geographic or topographic features are those to which reference is made in this report for specimens of *Didelphis* from México and Central America. The spellings and coordinates given for localities were taken from several sources and all coordinates were checked on the following maps: The American Geographical Society's "Map of Hispanic America. . . ." scale 1:1,000,000; the Atlas Geográfico de la Republica Mexicana, scale 1:500,000; maps of the "Estados Unidos Mexicanos" prepared by the Departamento Geográfico Militar, scale 1:500,000, first edition, 1958 (southern México); United States Air Force "World Aeronautical Chart," scale 1:1,000,000; maps of Costa Rica prepared by the Instituto Geográfico de Costa Rica, scale 1:50,000. Coordinates for most of the Panamanian localities were taken from Fairchild and Handley (1966).

When a locality is known by two or more names, the additional names are enclosed in brackets. If specimen label information gave a place name for a locality other than one in current use, the locality referred to is entered separately under each name. Latitude north of the equator and longitude west of Greenwich are provided for all localities; however, in several instances the coordinates are indicated as only approximate (*ca.*), but represent my best estimate on the basis of available information. Countries, states within México, and localities within Mexican states and Central American countries are listed in alphabetical sequence. The appropriate departamento or provincia is listed for each Central American locality.

BRITISH HONDURAS

Central Farm, Cayo, *ca.* 17°08' N, 89°00' W
 Corozaal, Corozaal, 18°22' N, 88°24' W

COSTA RICA

Alajuela, Alajuela, 10°01' N, 84°12' W
 Camp Seattle, Osa Peninsula, Puntarenas,
ca. 8°41' N, 83°28' W
 Cariari, Limón, 10°22' N, 83°44' W
 Cartago, Cartago, 9°52' N, 83°55' W
 Hatillo, San José, 9°55' N, 84°06' W
 Monteverde, Puntarenas, *ca.* 10°18' N,
 84°50' W
 Palmar, Puntarenas, *ca.* 8°58' N, 83°58' W
 Pandora, Limón, 9°45' N, 82°57' W
 Parrita (San Gerónimo Pirris), Puntarenas,
 9°31' N, 84°20' W
 Pozo Azul, Puntarenas, 9°30' N, 84°20' W
 Puerto Golfito, Puntarenas, 8°39' N, 83°
 11' W
 San Gerónimo Pirris (Parrita), Puntarenas,
 9°31' N, 84°20' W
 San Isidro del General (Ureña), San José,
 9°23' N, 83°43' W

San José, San José, 9°56' N, 84°05' W
 San Pedro, Montes de Oca, San José, 9°
 56' N, 84°03' W
 Santa Ana, San José, 9°56' N, 84°11' W
 Santa Teresa, Peralta, Cartago, 9°58' N,
 83°37' W
 Turrialba, Cartago, 9°54' N, 83°41' W

EL SALVADOR

Barra de Santiago, Ahuachapán, 13°47' N,
 90°03' W
 Chilata (Hacienda Chilata), Sonsonate, 13°
 39' N, 89°34' W
 Colima, Cuscatlán, 13°59' N, 89°06' W
 Divisadero, Morazán, 13°36' N, 88°04' W
 Lake Olomega, San Miguel, *ca.* 13°23' N,
 88°03' W
 La Libertad, Libertad, 13°29' N, 89°19' W
 Los Esesmiles, Chalatenango, 14°17' N,
 89°07' W
 Mount Cacaquatique, San Miguel, 13°48' N,
 88°14' W
 Puerto del Triunfo, Usulután, 13°16' N,
 88°32' W

Río San Miguel, San Miguel, *ca.* 13°25' N,
88°08' W
San José del Sacare, Chalatenango, 14°15'
N, 89°10' W
San Salvador, San Salvador, 13°42' N, 89°
12' W
Volcán de San Miguel, San Miguel, *ca.* 13°
25' N, 88°15' W

GUATEMALA

Astillero, Santa Rosa, 13°51' N, 90°21' W
Barillas, Huehuetenango, 15°48' N, 91°
19' W
Chimoxán, Alta Verapaz, *ca.* 15°38' N,
89°39' W
Chinaja, Alta Verapaz, 16°02' N, 90°13' W
Chiquimulilla, Santa Rosa, 14°01' N, 90°
23' W
Chuntuqui, El Petén, 17°31' N, 90°09' W
Ciprés (Finca Ciprés), Suchitepéquez, *ca.*
14°38' N, 91°29' W
Escuintla, Escuintla, 14°17' N, 90°46' W
Jacaltenango, Huehuetenango, 15°40' N,
91°44' W
Libertad (La Libertad), El Petén, 16°47' N,
90°07' W
Nebaj, El Quiché, 15°24' N, 91°08' W
Nenton, Huehuetenango, 15°48' N, 91°
45' W
Toocoq, El Petén, 16°41' N, 90°02' W

HONDURAS

Chamelecón, Cortés, 15°24' N, 88°01' W
Copán, Copán, 14°51' N, 89°11' W
El Caliche Cedros, Francisco Morazán, 14°
42' N, 86°57' W
El Jaral, Cortés, 14°57' N, 88°01' W
La Ceiba, Atlantida, 15°47' N, 86°50' W
La Lima, Cortés, *ca.* 15°22' N, 87°43' W
Lancetilla, Atlantida, 15°42' N, 87°28' W
Las Flores Archaga, Distrito Central, *ca.*
14°17' N, 87°11' W
Las Flores (Las Flores Pucca), Lempira,
14°39' N, 88°37' W
Marcala, La Paz, 14°11' N, 88°00' W
Nueva Ocotepeque, Ocotepeque, 14°24' N,
89°12' W
Patuca, Gracias a Diós, 15°50' N, 84°18' W
Sabana Grande, Francisco Morazán, 13°
48' N, 87°15' W
San José, La Paz, 14°15' N, 87°56' W
San Pedro Sula, Cortés, 15°29' N, 88°01' W

Santa Bárbara, Santa Bárbara, 14°55' N,
88°14' W
Tegucigalpa, Distrito Central, 14°06' N,
87°13' W
Yaruca, Atlantida, 15°36' N, 86°46' W

MEXICO

Campeche

Apazote, 18°43' N, 90°23' W
Campeche, 19°51' N, 90°33' W
Chamotón, 19°20' N, 90°43' W
Escarcega, 18°37' N, 90°43' W
La Tuxpeña (La Tuxpana), 18°27' N, 90°
04' W
Puerto Real, 18°46' N, 91°31' W

Chiapas

Chiapa (Chiapa de Corzo), 16°42' N 93°
01' W
Comitán, 16°24' N, 92°27' W
El Real, 16°54' N, 91°46' W
Finca Prusia, 15°44' N, 92°44' W
Huehuetan, 15°01' N, 92°24' W
Huixtla, 15°08' N, 92°28' W
La Trinitaria (Zapaluta), 16°07' N, 92°
03' W
Mapastepec, 15°27' N, 92°54' W
Ocuilapa, 16°53' N, 93°19' W
Ocozocuaula, 16°46' N, 93°22' W
Palenque, 17°31' N, 91°59' W
Pueblo Nuevo Solistahuacán, 17°08' N,
92°53' W
Risa de Oro, 16°20' N, 94°03' W
San Bartolomé, 16°20' N, 92°34' W
San Cristóbal (San Cristóbal de las Casas),
16°45' N, 92°38' W
San José (San José del Arco), 16°02' N,
91°49' W
Solusuchiapa, *ca.* 17°26' N, 93°02' W
Soyaló, 16°54' N, 92°56' W
Tonalá, 16°05' N, 93°45' W
Tumbala, 17°18' N, 92°20' W
Tuxtla (Tuxtla Gutierrez), 16°45' N, 93°
07' W
Yajalon, 17°16' N, 92°20' W
Yaxoquintela, *ca.* 16°54' N, 91°46' W
Zapaluta (La Trinitaria), 16°07' N, 92°
03' W

Chihuahua

Batopilas, 27°01' N, 107°44' W

Coahuila

La Gacha, 28°22' N, 101°31' W
 Monclova, 26°55' N, 101°25' W
 Sabinas, 27°51' N, 101°07' W
 San Lorenzo, 25°29' N, 102°11' W
 San Pedro de las Colonias, 25°45' N, 102°59' W

Colima

Armeria, 18°56' N, 103°58' W
 Colima, 19°15' N, 103°45' W
 Hacienda Magdalena (Pueblo Juárez), 19°10' N, 103°57' W
 Manzanillo, 19°03' N, 104°20' W
 Santiago, 19°07' N, 104°21' W

Distrito Federal

Ciudad México, 19°25' N, 99°10' W
 Tlapan (Tlapam), 19°17' N, 99°10' W

Durango

Chacala, 24°49' N, 106°44' W

Guanajuato

Celaya, 20°31' N, 100°37' W

Guerrero

Acahuizotla, 17°21' N, 99°28' W
 Acapulco, 16°51' N, 99°55' W
 Agua de Obispo, ca. 17°16' N, 99°31' W
 Buena Vista de Cuellar, 18°27' N, 99°25' W
 El Limón, ca. 18°28' N, 101°50' W
 Los Sabinos, ca. 18°23' N, 99°45' W
 Omilteme, 17°33' N, 99°40' W

Hidalgo

Ixmiquilpan (Ixmiqulpan), 20°29' N, 99°14' W
 Pachuca, 20°07' N, 98°44' W
 Río del Monte (Reál del Monte), 20°08' N, 98°39' W
 San Felipe Orizatlán, 21°11' N, 98°37' W
 Tasquillo, 20°33' N, 99°18' W
 Tulancingo, 20°05' N, 98°22' W

Jalisco

Ameca, 20°33' N, 104°03' W
 Arandas, 20°42' N, 102°21' W
 Atemajac, 20°11' N, 103°42' W

Autlán, 19°46' N, 104°24' W
 Chinampas, 21°49' N, 101°49' W
 Ciudad Guzmán (Zapotlán), 19°32' N, 103°28' W
 Etzatlán, 20°46' N, 104°05' W
 Guadalajara, 20°40' N, 103°21' W
 Huascato, 20°32' N, 102°14' W
 Huejuguilla (Huejuguilla el Alto), 22°38' N, 103°53' W
 La Mesa María de León, ca. 22°25' N, 103°24' W
 Ocotlán, 20°21' N, 102°46' W
 Puerto Vallarta, 20°36' N, 105°16' W
 Purification (Purificación), 19°32' N, 104°38' W
 San Sebastián, 20°47' N, 104°51' W
 Santa Cruz de las Flores, ca. 20°28' N, 103°31' W
 Tapatlán, 20°48' N, 102°46' W
 Tequila, 20°53' N, 103°49' W
 Zapotlán (Ciudad Guzmán), 19°32' N, 103°28' W

México

Amecameca, 19°07' N, 98°46' W
 Salazar, 19°19' N, 99°24' W
 San Cayetano, ca. 19°25' N, 100°01' W
 Teotihuacan, ca. 19°37' N, 98°53' W

Michoacán

El Molino (Hacienda El Molino), 20°18' N, 102°28' W
 Jiquilpan, 19°49' N, 102°43' W
 La Huacana, ca. 18°58' N, 101°50' W
 La Salada, ca. 19°07' N, 102°00' W
 Nueva Italia, 19°02' N, 102°06' W
 Pátzcuaro, 19°30' N, 101°36' W
 Querendero, 19°48' N, 100°53' W
 Tacámbaro, 19°14' N, 101°22' W
 Tzintzuntzan, 19°38' N, 101°35' W

Morelos

Alpuyeca, 18°44' N, 99°16' W
 Cerro Zempoala, ca. 19°00' N, 99°20' W
 Cuernavaca, 18°55' N, 99°14' W
 Lagunas de Zempoala, ca. 19°02' N, 99°18' W
 Las Estacas, 18°53' N, 99°00' W
 Tequisquitengo, 18°37' N, 99°16' W
 Jiutepec (Jiutepec), 18°53' N, 99°11' W
 Yautepac, 18°52' N, 99°04' W

Nayarit

Acaponeta, 22°30' N, 105°22' W
 Alticama (Aticama), 21°29' N, 105°12' W
 Las Varas, 21°12' N, 105°08' W
 Rosa Morada (Rosamorada), 22°08' N, 105°12' W
 San Blas, 21°32' N, 105°17' W
 Tepic, 21°31' N, 104°54' W

Nuevo León

Golondrinas, 26°43' N, 100°30' W
 La Barranca (Hacienda La Barranca), 25°36' N, 99°18' W
 Montemorelos, ca. 25°11' N, 99°50' W
 Monterrey, 25°40' N, 100°18' W

Oaxaca

Boca del Río, ca. 16°12' N, 95°09' W
 Cerro Baúl, ca. 16°33' N, 94°10' W
 Cerro de Mixtequilla, ca. 16°27' N, 95°15' W
 Cerro del Tigre, 16°21' N, 95°13' W
 Chacalapa, 15°49' N, 96°27' W
 Cuicatlán (San Juan Bautista Cuicatlán), 17°48' N, 96°58' W
 Guichicovi, 16°58' N, 95°06' W
 Guiengola, ca. 16°22' N, 95°22' W
 Jamaica Junction, 16°09' N, 97°06' W
 Juchitán, 16°26' N, 95°02' W
 La Gloria (Santa María Chimalapa), 16°43' N, 94°45' W
 La Presa, ca. 16°22' N, 95°18' W
 La Ventosa, 16°35' N, 94°56' W
 Las Cuevas, ca. 16°23' N, 95°20' W
 Las Pilas, ca. 16°24' N, 95°18' W
 Las Tejas, ca. 16°22' N, 95°21' W
 Mixtequilla (Santa María Mixtequilla), 16°23' N, 95°15' W
 Oaxaca (Oaxaca de Juárez), 17°04' N, 96°43' W
 Reyes (Reyes Papalo or Concepción), 17°50' N, 96°53' W
 Salazar, ca. 16°22' N, 95°20' W
 San Antonio, ca. 16°20' N, 95°27' W
 San Dionisio (San Dionisio del Mar), 16°20' N, 94°46' W
 San Mateo del Mar, 16°12' N, 95°00' W
 Santa María del Mar, 16°14' N, 94°52' W
 Santo Domingo (Santo Domingo Petapa), 16°50' N, 95°07' W
 Nopala (Santos Reyes Nopala), 16°06' N, 97°10' W

Tapanatepec (San Pedro Tapanatepec), 16°23' N, 94°11' W
 Tehuantepec, 16°20' N, 95°13' W
 Tenango, 16°16' N, 95°35' W
 Tuxtepec, 18°05' N, 96°06' W
 Vista Hermosa, 17°43' N, 96°22' W
 Yetla (San Mateo Yetla), 17°45' N, 96°24' W

Puebla

Atlixco, 18°54' N, 98°26' W
 Chalchicomula (Ciudad Serdán), 18°59' N, 97°27' W
 Huachinango (Huauchinango), 20°11' N, 98°03' W
 Matamoros (Izúcar de Matamoros), 18°36' N, 98°28' W
 Metlaltoyuca, 20°45' N, 97°51' W
 San Martín (San Martín Texmelucan), 19°17' N, 98°27' W

Queretaro

Jalpan, 21°14' N, 99°29' W

Quintana Roo

Felipe Carrillo Puerto (Santa Cruz de Bravo), 19°35' N, 88°03' W
 Pueblo Nuevo X-can, ca. 20°52' N, 87°17' W
 San Miguel, Isla Cozumel, 20°31' N, 86°57' W
 Xcopen, 18°11' N, 88°43' W

San Luis Potosí

Axtla, 21°27' N, 98°52' W
 Bledos, 21°51' N, 101°07' W
 Ebano, 22°12' N, 98°23' W
 El Naranjo (Naranjos), 22°31' N, 99°20' W
 El Salto, 22°36' N, 99°24' W
 Hacienda Capulín, 21°30' N, 99°37' W
 Tamazunchale, 21°16' N, 98°47' W
 Xilitla, 21°23' N, 99°01' W

Sinaloa

Copala, 23°23' N, 105°56' W
 Culiacán, 24°48' N, 107°24' W
 El Batel, 23°27' N, 105°49' W
 El Dorado, 24°18' N, 103°23' W
 Escuinapa, 22°50' N, 105°47' W
 Mazatlán, 23°12' N, 106°26' W
 Rosario, 23°00' N, 105°52' W

San Miguel, 25°56' N, 109°03' W
 Santa Lucía, 23°27' N, 105°53' W
 Sierra de Choix, ca. 26°46' N, 108°03' W

Sonora

Alamos, 27°02' N, 108°57' W
 Camoa, ca. 27°13' N, 109°18' W
 El Novillo, ca. 28°55' N, 109°36' W
 Hermosillo, 29°05' N, 110°57' W
 La Aduana, ca. 27°03' N, 109°01' W
 Oputo, 30°09' N, 109°22' W
 Soyapa, 28°45' N, 109°38' W
 Tesia, 27°09' N, 109°24' W
 Ures, 29°26' N, 110°24' W

Tabasco

Alvaro Obregón (Frontera), 18°32' N,
 92°39' W
 Cardenas, 17°59' N, 93°23' W
 Frontera (Alvaro Obregón), 18°32' N,
 92°39' W
 La Venta, 18°06' N, 94°01' W
 Macuspana, 17°45' N, 92°40' W
 Teapa, 17°33' N, 92°57' W
 Villa Hermosa, 17°59' N, 92°55' W

Tamaulipas

Altamira, 22°23' N, 97°56' W
 Ejido Santa Isabel, 23°14' N, 99°00' W
 El Mulato, 24°54' N, 98°57' W
 Jaumave, 23°24' N, 99°23' W
 Matamoros, 25°55' N, 97°30' W
 Piedra, 23°30' N, 98°06' W
 San Fernando, 24°51' N, 98°09' W
 Soto la Marina, 23°46' N, 98°15' W
 Victoria (Ciudad Victoria), 23°45' N,
 99°07' W
 Villa Mainero, 24°34' N, 99°36' W

Veracruz

Agua Dulce, 18°09' N, 94°08' W
 Alvarado, 18°47' N, 95°45' W
 Boca del Río, 19°06' N, 96°07' W
 Catemaco, 18°25' N, 95°06' W
 Coatzacoalcos, 18°08' N, 94°24' W
 El Higo, 21°46' N, 98°22' W
 Fortín, 18°54' N, 97°00' W
 Hacienda Tamiahua, 21°44' N, 97°33' W
 Jalapa, 19°31' N, 96°55' W
 Jesús Carranza (Santa Lucrecia), 17°
 26' N, 95°01' W
 Jico, 19°25' N, 97°00' W

Las Minas, 19°41' N, 97°07' W
 Las Vigas, 19°38' N, 97°05' W
 Maltrata, 18°47' N, 97°16' W
 Minatitlán, 17°59' N, 94°33' W
 Mirador, 19°17' N, 96°54' W
 Nautla, 20°13' N, 96°46' W
 Orizaba, 18°51' N, 97°05' W
 Papantla, 20°27' N, 97°19' W
 Pasa Nueva, 17°59' N, 95°11' W
 Perote, 19°34' N, 97°14' W
 Piedras Negras, 18°46' N, 96°11' W
 Potrero, 18°53' N, 96°47' W
 Potrero Viejo, 18°52' N, 96°55' W
 San Andrés Tuxtla, 18°27' N, 95°13' W
 San Juan de la Punta, 18°49' N, 96°44' W
 San Marcos, 20°12' N, 96°57' W
 Tapalapan, ca. 18°37' N, 95°39' W
 Tihuatlán, 20°43' N, 97°33' W
 Tlapacoyan, 19°58' N, 97°13' W
 Tuxpan, 20°57' N, 97°24' W
 Veracruz, 19°12' N, 96°08' W

Yucatán

Chichén Itzá, 20°40' N, 88°34' W
 Izamal, 20°56' N, 89°01' W
 Mérida, 20°58' N, 89°37' W

Zacatecas

Moyahua, 21°16' N, 103°10' W
 San Juan Capistrano, 22°37' N, 104°
 05' W

NICARAGUA

Boaco, Boaco, 12°27' N, 85°43' W
 Bonanza, Zelaya, 13°57' N, 84°32' W
 Chinandega, Chinandega, 12°37' N, 87°
 11' W
 Cosiguina, Chinandega, 12°55' N, 87°
 30' W
 Dario, Matagalpa, 12°42' N, 86°08' W
 Diriamba, Carazo, 11°53' N, 86°15' W
 El Recreo, Zelaya, 12°07' N, 84°24' W
 Greytown (San Juan del Norte), Río San
 Juan, 10°56' N, 83°43' W
 Hacienda La Trampa, Jinotega, ca. 13°08'
 N, 85°54' W
 Jalapa, Nueva Segovia, 13°55' N, 86°
 09' W
 Managua, Managua, 12°08' N, 86°12' W
 Matagalpa, Matagalpa, 12°59' N, 85°
 53' W
 Momotombo, León, 12°25' N, 86°37' W

Nandaime, Granada, 11°46' N, 86°02' W
 Rivas, Rivas, 11°26' N, 85°51' W
 Sabana Grande, Managua, 12°06' N, 86°
 12' W
 San Antonio, Chinandega, 12°31' N, 87°
 04' W
 San Carlos, Río San Juan, 11°08' N, 84°
 47' W
 Santa María de Ostuma, Matagalpa, ca. 13°
 00' N, 85°56' W
 Sapoa, Rivas, 11°15' N, 85°38' W
 Toro Rapids, Río San Juan, 11°02' N, 84°
 28' W
 Villa El Carmen, Managua, 11°56' N,
 86°31' W
 Villa Somoza, Chontales, 12°08' N, 84°
 58' W
 Yalí, Jinotega, 13°19' N, 86°10' W

PANAMA

Almirante, Bocas del Toro, 9°18' N, 82°
 24' W
 Ancón, Canal Zone, 8°57' N, 79°34' W
 Armila, San Blas, 8°40' N, 77°27' W
 Bambito, Chiriquí, 8°15' N, 82°37' W
 Barro Colorado, Canal Zone, 9°09' N, 79°
 51' W
 Boca del Drago, Bocas del Toro, 9°26' N,
 82°20' W
 Boquerón, Chiriquí, 8°31' N, 82°34' W
 Boquete, Chiriquí, 8°47' N, 82°25' W
 Camp Piña, Canal Zone, 9°16' N, 80°00' W
 Cana, Darién, 7°47' N, 77°42' W
 Capetí, Darién, 8°04' N, 77°33' W
 Cerro Azul (La Zumbadora), Panamá, 9°
 14' N, 79°21' W
 Cerro Hoya, Los Santos, 7°18' N, 80°42' W
 Cerro Punta, Chiriquí, 8°53' N, 82°34' W
 Cituro, Darién, 8°00' N, 77°36' W
 Colón, Colón, 9°21' N, 79°55' W
 Concepción, Chiriquí, 8°31' N, 82°37' W
 Corozal, Canal Zone, 8°58' N, 79°35' W
 Curundu, Canal Zone, 8°59' N, 79°33' W
 El Real, Darién, 8°06' N, 77°45' W
 El Valle, Coclé, 8°36' N, 80°08' W
 Empire, Canal Zone, 9°03' N, 79°41' W
 Fort Clayton, Canal Zone, 8°59' N, 79°
 36' W
 Fort Davis, Canal Zone, 9°15' N, 79°56' W
 Fort Kobbe, Canal Zone, 8°54' N, 79°36' W
 Fort Sherman, Canal Zone, 9°21' N, 79°
 57' W
 Gamboa, Canal Zone, 9°06' N, 79°42' W
 Gatún, Canal Zone, 9°15' N, 79°56' W
 Guabala, Chiriquí, 8°13' N, 81°44' W
 Guánico, Los Santos, 7°20' N, 80°30' W
 Isla Coiba, Veraguas, 7°26' N, 81°45' W
 Jaqué, Darién, 7°31' N, 78°10' W
 Juan Mina, Canal Zone, 9°09' N, 79°40' W
 Lion Hill, Canal Zone, 9°13' N, 79°54' W
 Madden Road, Canal Zone, ca. 9°05' N, 79°
 38' W
 Mandinga, San Blas, 9°29' N, 79°05' W
 Mojinga Swamp, Canal Zone, 9°18' N, 79°
 59' W
 Mount Pirri (Cerro Pirre), Darién, 7°51' N,
 77°44' W
 Nievécita Farm, Bocas del Toro, ca. 9°35'
 N, 82°43' W
 Palo Santo, Chiriquí, 8°49' N, 82°40' W
 Porto Bello, Colón, 9°41' N, 79°41' W
 Progreso, Chiriquí, 8°29' N, 82°49' W
 Quarry Heights, Canal Zone, 8°57' N, 79°
 34' W
 Red Tank, Canal Zone, 9°00' N, 79°36' W
 Río Chagres, Canal Zone, 9°08' N, 79°41' W
 Río Chucunaque, Darién, 8°23' N, 77°49' W
 Río Indio, Canal Zone, 9°15' N, 79°59' W
 Río Paya (Boca del Río Paya), Darién, 7°
 55' N, 77°31' W
 San Miguel Island (Isla del Rey), Panamá,
 8°23' N, 78°56' W
 Santa Fé, Veraguas, 8°31' N, 81°04' W
 Tacarcuna, Darién, 8°05' N, 77°17' W
 Talé, Chiriquí, 8°15' N, 81°41' W