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Alfred Lunt Gardner<br>Louisiana State University and Agricultural \& Mechanical College

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# THE SYSTEMATICS OF THE GENUS DIDELPHIS <br> (MARSUPTALIA:DIDETPHIDAE) IN NORTH AND MIDDIE AMERICA 

## A Dissertation

# Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Doctor of Philosophy 

in
The Department of Zoology and Physiology
by
Alfred Lunt Gardner
B.S., The University of Arizona, 1962
M.S., The University of Arizona, 1965 August, 1970

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#### Abstract

Opossums of the genus Didelphis, the largest New World marsupials living today, occur from southern Canada to central Argentina. Karyological data indicate that American marsupials have either 14, 18, or 22 chromosomes. Four genera represented by six species, including the three species of the genus Didelphis, have 22 chromosomes. Five of the six 22-chromosomed species have nearly identical autosomes consisting of three pairs of large and seven pairs of medium-sized acrocentric chromosomes. Didelphis virginiana, the only Nearctic member of the genus, is a striking exception, since its autosomes consist of three pairs of large and three pairs of medium-sized subtelocentrics, and four pairs of medium-sized acrocentrics. Differences between the karyotypes of D. Virginiana and D. marsupialis are analyzed. A number of features, primarily of cranial morphology and color pattern, determined by studying specimens of known karyotype, serve to distinguish D. Virginiana and D. marsupialis. D. Virginiana is found from southern Ontario to southwestern Nicaragua, and D. marsuplalis occurs in South and Central America northward to Tamaulipas in eastern México. They are sympatric at lower elevations in eastern México and Central America. Mexican and Central American populations


of D. marsupialis are assigned to D. m. caucae. Four subspecies of D. virginiana are recognized: D. V. virginlana, found in the United States and southern Canada with introduced populations established in the western Unjted States; D. V. pigra occurs along the Gulf Coast from Texas to South Carolina; D. V. californica is found from southern Texas and Sonora, México, to southwestern Nicaraça; D. V. yucatanensis is restricted to the Yucatán Peninsula.

An evaluation of the morphological, ecological, and distributional characteristics of both species, along with features of the fossil record and the distinctive karyotype of D. virginiang suggests allopatric speciation for the latter promoted by structural chromosomal rearrangements in a D. marsupialis isolate during the Pleistocene in western México.

Members of the genus Didelphis, although the largest Recent American marsupials, are small to medium-sized mammals, attaining a total length barely in excess of a meter, and may weigh up to five and one-half kilograms.

These opossums 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 welldeveloped marsupium in females. They are known from Pliocene deposits of South Anerica and now occur from central Argentina north to southern Canada. Their elevational range extends from sea level on both the Atlantic and Pacific coasts to over 3,000 meters in the mountains of México and South America. Ecologically, they are usually associated with molst forests or woodlands near water in a wide variety of tropical, subtropical, and temperate habitats and climates. These habitats include the temperate Pine-Oak Forest, Prairle and Mesquite Grassland, and Chaparral of southern Canada, the United States and the Mexican Plateau, and the subtropical and tropscal Cloud Forest, Rain Forest, Tropical Evergreen and Tropical Deciduous Forest,

Savanna, Thorn Forest, and Tropical Scrub of Mexico and of Central and South Anerica.

Representatives of the genus Didelphis were the first marsupials known to Europeans. Vicente Yañez Penzón brought a female opossum (probably D. marsupialis) to Spain from what is now Brazil in 1500, over a hundred years before the discovery of the rich marsupial fauna of Australia.

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 Ricen animals is indistinguishable from karyotypes for D. paraguayensis ( $=$ D. albiventris), D. aurita ( $=$ D. marsupialis aurita Wied, 1826), Lutreolina crassioaudata Desmarest, 1804, and Philander opossum (Linnaeus, 1758) reported by Biggers, et al., 1965, Dreyfus and Campos, 1941, and Saez, 1931 and 1938. This information indicates greater chromosomal variation within a single species than is known to exist between several species in three distinct genera. The primary purpose of this study was to examine D. marsupialis to explore the taxonomic, cytogenetic, and evolutionary implications of the two very different chromosomal patterns in Didelohis.

Linnaev.s' genus Didelphis (1758:54) was intricately composite and included all of the then known American marsupials. Marsupialis, the first species Linnaeus listed under this genus, was also composite and included all the large opossums. Thomas (1888:316) destgnated D. marsupialis Linnaeus as the type species and (p. 323) restricted marsupialis to include only two forins, marsupialis vax. typica, and marsupialis var. azarae. Subsequent attempts to fix the identity of D. marsupialis Linnaeus (restricted) resulted in conflictins opinions and confusion, even to rejecting the name Didelphs 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's memoir (1704:1565-1575) on the anatomy of opossums based on aninals definitely known to have come from Virginia. Thomas (1901:144-145) pointed out that Linnaeus' primary reference for marsupialis was Philander Seb. Mus., I p. 64, t. 39., and that the animal depicted on Seba's plate xxxix is clearly a Didelphis and probably came from Guiana as did most of Seba's South American animals. Rehn ( $1.901: 147-149$ ), passing over Linnaeus' reference to Seba, decided that the reference to Hernandez should be given priority over the reference to Tyson and he thus retained Didelphis virginiana Kerr, 1792, for the

Virginia opossum, and applied marsupialis to Mexican Didelphis. Rehn's treatment was followed by Allen (1901) when he made the first serious attempts at reviewing 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. pruinosa Wagner, 1843, to be junior synonyms of D. californica Bernett, 1833, which name he referred to $\underline{D}$. marsupialis; described as new $\underline{D}$. 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). The following year (2902) Allen, in his paper exemining the variation within South Anerican Didelphis, reviewed the nomenclature of the genus. Here he accepted I'homas earlier conclusions and cited Seba as the primary reference for D. marsupialis Linnaeus (restricted), thereby shiftine the type locality of marsupialis from, ". . . the region about the city of México." (1901:1.69) to northeastern South America. In this same publication, Allen resurrected Oken's names for the large opossums of North and South America, applying D. parasuayensis to the white-eared South American species and D. mesamericana to the Mexican populations, and recognized two groups within Didelphis
(102:256-257). 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. richnondi in Nicaragua; D. marsupialis with seven subspecies in Panama and South America of which only the names $D$. marsupialis caucae Allen, 1900 ( $=\underline{D}$. 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 under 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) decided that there were only two species in the genus, Didelphis azerae Temminck, 1825 (later rejected by Hershkovitz, 1969:54, as being composite in favor of D . albiventris), restricted to South America, and D. marsupialis, varying from the tropical zone D. M. Mersupialis of South America, Panamá, and Costa Rica to the temperate zone D. M. Virginiana of the United States and Canada.

Hershkovitz ostensibly recognized californica (mesamericana Oken, 1916, being rejected as unavailable under current rules of zoological nomenclature) as representing transitional variation between the subspecies marsupialis and Virginiana. Hall and Kelson (1952:323324; 1959:5-9), 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 employed californica for the populations Allen listed under D. 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 the North American Continent from southern Canada to the southwestern border of Nicaragua and Costa Rica. D. marsupialis is a tropical zone species whose range extends from southern Tamaulipas, Mexico to the northern border of Argentina. A third species, D. albiventris, is a subtropical and temperate zone species restricted to South America.

Studying animals of known karyotype, I have been able to find a number of distinctive nonchromosomal features useful in distinguishing virginiana and marsupialis. These features include differences in 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 covers the ranges of nine heretofore recognized subspecies of $D$. marsupialis (sensu Hall and Kelson, 1959). I have given very little attention to the Canadian and United States populations of D. Virginiana with the exception of the Gulf Coast subspecies D. V. pigra, and the Rio Grande population of southern Texas.

## Specimens

The number of specimens examined exceeds 2,800. Of these, 1,752 are from Mexico and Central America. The majority of the approximately 1,000 additional specimens represent D. Virginiana from the United States. A smaller number represent South American D. marsupialis and D. albiventris, examined but not tabulated. All specinens examined are in the institutional collections listed below and are indicated by their appropriate initials in the list of specimens examined in Appendix $A$.
Amnh Anericen Museun of Natural History

CAS California Academy of Sciences
IB Instituto de Biologia, Universided Nacional Autónoma de México

KU University of Kanses, Museum of Natural History

LaCM Los Angeles Ccunty Museum
LsUMZ Lovisiana State University, Museun of Zoology
MCZ Harvard, Museum of Comparative Zoojogy
MSB University of New Mexico, Museum of Southwestern Biology

MSC MCNeese State College
MVZ Univereity of Calliominat Berkeley, Museum of vertebrate Zoology
TCWC Texas A 2 U Uiversitys Texas Cooperative Wildiffe Collections

UA University of Arjzona

UCLA University of California at Los Angeles
UMMZ University of Michigan, Museum of Zoology USNM United States National Museum

## Measurements

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

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

Condylobasal lensth. .-.The distance, in the mldilne of the skull, from the anterior surface of the premaxillary bones to a line connecting the postexior margins of the condyles.

Palatal lensth. - The distance, in the midventral line of the skuil, 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.

Interoxbital 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 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.

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

Breadth across molaxs.--The greatest distance between the outer margins of the third upper molars ( $M^{3}-M^{3}$ ).

Length of maxillary tooth row. --The greatest distance from the anterior face of the upper canine to the posterior face of the last upper molar ( $M^{4}$ ).

Length of upper molar series. --The distance between the anterior face of the first upper molar ( $\mathrm{M}^{\frac{1}{1}}$ ) and the posterior face of the last upper molar ( $\mathrm{M}^{4}$ ).

Lensth of mandible.--The length of one ramus of the lower jaw measured from the anteriormost point (excluding incisors) to the posteriornost surface of the mandibular condyle.

Length of lower molar series.--The distance between the anterlor face of the first lower molar ( $\mathrm{M}_{\mathbf{i}}$ ) and the posterior face of the last lower molar ( $M_{4}$ ).

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

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

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

Height of sagittal crest. -. The greatest helght of the sagittal crest measured from the top of the brain case.

All measurements have been segregated on the bases of age class and sex of the individual. Measurements were entered on IBM code sheets, transferred to IBM cards, and computer analyzed.

## Chromosome Preparations

The animals used for chromosomal analysis were collected in steel traps, live traps, or by hand. Jive opossums were injected interperitoneally with a 0.025 per cent solution of Velban (vinblastine sulfate, Eli Lilly Co.). Individuals weighing 50 to 200 granis received a 0.5 cc injection, whereas those between 200 grams and 1 1/2 pounds received 1.0.cc, and those over $11 / 2$ pounds but under 4 pounds received 2.0 cc . No animals heavier than 4 pounds were treated. After a two-hour minimum incubation period, the opossums were killed and slides were prepared using dividing bone marrow cells for chromosomal analysis, following the techniques described by Patton (1967).

Chromosomal material was prepared in the laboratory from Louisianian and Texan D. Virginiana. Additional material was collected under field conditions from D. virginiana in México and from D. marsupialis in México, Costa Rica, and Perú. For comparative purposes, slides were also prepared from D. albiventris in Peru.

Slides were immersed in a five per cent buffered Giemsa solution ( $\mathrm{pH} \pm 7.2$ ) for eight to ten minutes or until the chromosomes were evenly stained. After staining, the slides were rinsed in a bath of water, followed by two baths of acetone, and drled under a lamp for at least 12 hours. Cover glasses were affixed with Permount. The warm dry slides were dipped into a xylol bath before mounting to facilitate spreading of the mounting medium, settling of the cover glass, and drying. This method proved to be the most satisfactory, since there was a minimum of moisture contamination under the cover slip--a problem in humid climates. A few slides were stained in the field for on-the-spot evaluation of technique and examination of chromosomes. The dried mounted slides were scanned under a microscope, and certain metaphases were marked and later photographed. Pictures of individual chromosomes were cut from photographs and arranged according to size in $\underline{D}$. marsupialis and D. albiventris, or on the bases of morphology and size in D. virgindana. Negatives of selected metaphases were projected in a photographic enlarger on writing paper, and the chromosome images were
outlined in pencil and measured to determine relative chromosome 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 specinens 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. Since this aging method requires the skull, "skin only" specimens were not assigned to any particular age class. Animals designated "Immature" belong to the youngest age class and were young of varlable stages of growth, all still lacking the first upper molars. All remaining individuals were classed according to the following criteria: Age l.--First upper molars, as well as first and sometimes second lower molars, are in position for wear. Age 2.--Second upper molars, as well as second and sometimes third lower molars, are in position. Age 3.-Third upper molars are in position and the permanent premolars are erupting. Age 4.--The permanent premolars and the fourth lower molars are in position. Age 5.--All teeth have erupted, but the last upper molar shows very little wear regardless of the amount of wear on the other teeth. Age 6.--The fourth upper molar shows moderate to excessive wear.

The sequence of tooth eruption proceeds rapidly until attalnment of the fourth age class, then seems to lag until the positioning of the last upper molar.

Only those individuals in age classes 4 and older were utilized in the computer analysis of cranial measurements. Animals as young as age 4 were used because many females

In this class were noted with pouch young, therefore were sexually mature. A few sexually precocious females assigned to age 3 were pregnant or were noted with pouch young; however, measurements of animals in this age class were not considered in the computer analysis.

## VARIATION

## Georraphic Variation

Seasonal variation.--Primarily, any seasonal variation is expressed in length and density of the fur-mthe pelage being longer, thicker, and of higher fur quality in late fall and winter than during other tirnes of the year. The differences are most pronounced in populations from the United States and at higher elevations in Mexico. Populations from northem latitudes and higher elevations also exinibit seasonal variation in breeding activity through the absence of young individuals during the winter and early spring (see Reynolds, 1.945 , regarding some United States populations). Most Mexican and Central American opossums from lower elevations and more southerly latitudes do not demonstrate seascmal variation in fur quality and reproductive activity, probably because of the milder climates in these regions.

Dichromatism.--Two color phases occur in the majority of populations of all three species of Didelphis. The color phases gray or black are expressed through the color of long guard hair. The daxk color phase is uncommon to rare in most United States populations but increases in frequency along the Gulf Coast and in southern Texas. The black color phase is cominon in Latin American populations (see Table 1). The Eray phase is predominant in most

Table 1,--Percentage of regional population samples of D. Virginiana and D. marsupialis in the gray (G) or black (B) color phase.

|  | D. Virsiniane |  |  | D. marsupialis |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | (N) | G | B | (N) | G | B |
| Teras (except southern portion). | (73) | 85 | 15 |  |  |  |
| Southern Texas and northeastern Mexico (Tamaulipas, Coahuila, and Nueva Leon). | (89) | 46 | 54 |  |  |  |
| Eastern México (San Luis Potosi and Veracruz). | (32) | 78 | 22 | (47) | 48 | 52 |
| Northwestern México (Sonora, Sinaloa, Chihuahua, and Durango). | (65.) | 42 | 58 |  |  |  |
| Western México (Nayarit, Jalisco, Colima, and Michcacān). | (72) | 56 | 44 |  |  |  |
| Mexican Highlands (Hidalgo, México, Districto Federal, Puebla, and Morelos). | (44) | 96 | 04 |  |  |  |
| Southern Mexico (Guerrero and Oaxaca). | (77) | 74 | 26 |  |  |  |
| México east of the Isthmus of Tehuantepec (Tabasco, Campeche, Quintena Roo, Yucatán, and Chiepas). | (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, Panamã). |  |  |  | (201) | 53 | 47 |

Mexican and Central American populations of D. Virginiana, with its greatest frequency at upper elevations in the Mexican highlands. According to Allen (1901:172), the black 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 include all of the animals examined by Allen, have the dark phase in a ratio approximating one to one of the gray phase. Moreover, this ratio still may not be characteristic of the population, having been biased in favor of dark phase individuals because of the composition of Allen's sample. All of Allen's antmals were collected before the turn of the century by workers who were undoubtedly familiar with the very light-colored opossums of the eastern United States. I suggest that these workers were more likely to make museum specimens of the odd or more unusual individuals (i.e., black phase) in preference to the more familiar gray phase. My own collecting experience has convinced me that a series of animals, particularly as common as opossums, yet as troublesome to prepare properly as are Didelphis specimens, often contain a higher percentage of individuals with an unusual color phase, color pattern, or structural anomaly. On the basis of specimens examined, one-half to about two-thirds of the individuals in D. marsupialis populations exhibit the dark phase.

Length of extremities. --D. Virginiana shows geographic variation 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 in absolute and relative length southward, averaging 73 per cent along the Gulf Coast to southern Texas, where it reaches an average of 82 per cent. This relative length of the tall is maintained throughout Mexican and Central American populations except in northwestern México (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 wellknown ecological principle that the length of extremities tends to be shorter in colder climatic zones than in warmer zones. In contrast to this generality, populations from the Mexican highlands at elevations up to 3,000 meters along the Transvolcanic Axis and near Mexico City have the tail slightly longer (ca. 85 per cent) than do adjacent populations at lower elevations. The greater tail length in northwestern Mexican populations (ca. 93 per cent) 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 D. marsupialis from northern Veracruz to Panamá. No geographic variation in tail length is discernible in 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, D. Virginiana in the central and northern United States is characterized by light 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. Animals from populations in the southeastern United States and along the Gulf Coast are characterized by generally darker color, almost all white head except for darker facial markings, flesh colored tips of the ears reduced or absent, the white of the forereet restricted to the toes, the white of the hind feet restricted to the terminal phalanges or absent from one or both feet, and the black basal portion of the naked tail longer (up to 20 per cent of the bare tail 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 all-black, feet all-black, and the black pigmented base covering between 25 and 50 per cent of the naked tail. Nearly all other Mexican and Central American
D. Virginiana have a dark head with an all-white cheek, 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 fourfifths of the bare 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 clear white cheek; the reduction or loss of light 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-phased animals and an increase in tail length are associated with these character shifts. The only geographic variation in color pattern noted. in D. 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 bare portion of the tail in marsupialis from México through Honduras. A few Nicaraguan animals have up to one-half of the tail black, and populations south of the range of virginiana, in Costa Rica and Panamá, commonly have half or more of the tail black.

## Nongeographic Variation

The skulls of Didelphis exhibit an unusual amount of individual variation, much of it dependent upon the age and
sex of the individual. Allen (1901:152-159) dwelt at length on a number of features subject to individual variation. The two lists Allen compiled of large skulls of Didelphis particularly warrant comment. The first list covers 21 of the largest male skulls from a series of about 200 from such diverse areas as New Jersey, Florida, and localities in western and southern México. His second list includes 12 of the largest female skulls from the same series, again from equally diverse and widely separated geographic areas, this time including Nicaragua. Allen's purpose in presenting this information was primorily to demonstrate sexual dimorphism in size. Secondarily, he points out that large (and old) opossums come from several widely separated localities and suggests that the factor these regions share is some kind of protective environment allowing individuals to reach old age and thus attain large size. I was able to examine these specimens and found that, with a single exception on each list, all the animals are D. Virginiana. The two exceptions, a male from Frontera, Tabasco, México, and a female from Greytown, Nicaracua (the type of D. richmond1), are both D. marsupialis.

During the course of gathering data for this study, I made the following observations: (1) differences in staull size between the sexes usually does not become pronounced until about age class four; (2) skulls with low, poorly developed cranial crests that were assigned to age classes four, rive, and six 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; (3) those skulls with broken or excessively worn teeth, yet on the basis of tooth eruption belonging 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 the numerous exceptions when skulls of obviously old males were the same size or smaller than skulls of averagesized females, nor did he explain the occasional female skull that has the size and configuration of the skull of an adult male.

Ontogenetic variation in skull development is very pronounced. It is well known that the skull and the postcranial skeleton of opossums increase in size throughout the Iife 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 most significant of all environmental factors is diet. An extreme example of the effect of diet is provided by the skulls of two male D. marsupialis from El Salvador with unusually worn teeth despite the fact that both were young (age class two) when collected. Label information for the two, MVZ 130305 and 130306, gives their stomach contents as "seeds" and "coffee beans," respectively-hardily optimum foods.

In an attempt to explain at least some of the variation 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 while utilizing marginal food sources. Diets deficient in certain nutrients are reflected in a slower growth rate and smaller size independent of age and sex. Marginal foods with abrasive quallties accelerate attrition of the teeth, thereby eventually affecting the longevity of the animal. Size differences between sexes becomes accentuated following the attainment of reproductive maturity (age class four in females). This accentuation suggests that the nutritional load placed on pregnant and lactating females diverts energy sources that would otherwise contribute to increased
growth. The instances where male-sized females have been observed could be examples of either the availability of an unusually good food source or the reduction of reproduction rate due to a variety of factors from less breeding activity to complete sterility. These remarks are presented in an attempt to explain the amount of morphological variation observed that is considered to be relatively independent of genetic influences.

## CHROMOSOMES

American marsupials (Didelphidae) are separable, on the basis of diploid numbers, into the 14 -chromosome, the 18-chromosome, and the 22-chromosome groups. Mexmosa, Metachirus, and Caluxomys (recarded by Reig, 1965, as one of the three surviving genera of the otherwise extinct Microbiotheriinae), comprise the 14 -chromosome group. The 11 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 marsupial.s known to have 18 chromosomes. Their karyotype (Rejg, pers. comm.) differs from that of the 14 -chromosome group by having four additional pairs of medium-sized uniarmed 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 uniarmed elements like the karyotype described below for D. maxsupialis except that I. crassicaudata has a mediumsized metacentric X-chromosome. The distinctive and unjque chromosomal pattern characterizing the seventh species of the group, D. virginiana, is described in a later section.

## Karyotype Analysis

Photoidiograms of the three species of Didelphis are shown in $\mathrm{F}^{2}$ gure 1. The number of individuals analyzed, their provenance, sex, chromosome numbers, and fundamental numbers (number of autosomal arms), as well as the morphological types of chromosomes for each species are summarized in Table 2. The karyotype descriptions are as follows:

Didelphis marsupialis. --The diploid number is 22 and the fundanental number is 20. The three pairs of large, and the seven pairs of medium-sized, autosomes are all acrocentric chromosomes. 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 is identical to that just described for D. marsupialis except that the Y-chromosome is minute.

Didelphis Virginiana. --The diploid number is 22 and the furdamental number is 32 . The autosomes are three paj.rs of large-sized subtelocentrics, three pairs of medium-sized subtelocentrics, and four pairs of mediumsized acrocentric chromosomes. The X is a smaller, medium-sized submetacentric, and the $Y$ is a small acrocentric. The metaphase chromosomes are analyzed in Table 3.

Figure I. -- Photoidiogram of the karyotypes of three species of Didelphis.
D. albiventris, E slope Cordillera Carpish, Departamento de Huãnuco, Perí, LSUMZ 14009; D. marsupialis, ca. 13 km . N Huixtia, Chiapas, Nexico, Lsumzll912; ${ }^{2}$. Virginiana, Edinbuxg, Texas, LSUMZ 13393.
(1) Didelphis albiventris, Cordillera Carpish, Depto. Huánuco, Perú.

(2) Didelphis morsupialis, $13 \mathrm{~km} . \mathrm{N}$ Huixtla, Chiapas, México.

(3) Didelphis virginiana, Edinburg, Hidalgo Co., Texas.


Table 2.--Somatic chromosome numbers and morphological types for the three species of Didelphis.

|  | Sex |  | Chromosomes* |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | 2 n | Autosomes |  | X | Y | FN |
|  | O | 9 |  | ST | A |  |  |  |
| Didelphis albiventris |  |  |  |  |  |  |  |  |
| Didelphis marsupialis |  |  |  |  |  |  |  |  |
| Mexico | 3 | 4 | 22 | -- | 10 | A | A | 20 |
| Costa Rica | 1 | 2 | 22 | -- | 10 | A | A | 20 |
| Perú | 5 | 2 | 22 | -- | 10 | A | A | 20 |
| Didelphis virciniana |  |  |  |  |  |  |  |  |
| Texas | 2 | $\cdots$ | 22 | 6 | 4 | ST | A | 32 |
| México | 6 | 3 | 22 | 6 | 4 | ST | A | 32 |

* Autosome numbers refer to numbers of homologous pairs, $S T=$ subtelocentric, $A=a c r o c e n t r i c, ~ F N=f u n d a m e n t a l$ number.

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Table 3.--Analysis of mean chromosome length for 2l metaphases from a female D. Virginiana (LSUMZ 15107) from El Salto, San Luis Potosi, Méxíco.
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| Chromosome | Short Arm (s) | Lons Arrn (J.) | Arm Ratio | Chromosome Lengeth |
| :---: | :---: | :---: | :---: | :---: |
|  | Mean** \% TCL | Mean** \% TCL | ( $1 / \mathrm{s}$ ) | \% TCL |
| 1 | $7.67 \quad 1.18$ | 39.296 .05 | 5.12 | 7.24 |
| 2 | 7.141 .10 | $37.52 \quad 5.78$ | 5.25 | 6.88 |
| 3 | 7.241 .11 | $36.00 \quad 5.55$ | 4.97 | 6.66 |
| 4 | 6.671 .02 | $34.57 \quad 5.33$ | 5.18 | 6.35 |
| 5 | $6.67 \quad 1.02$ | $33.57 \quad 5.17$ | 5.03 | 6.20 |
| 6 | 6.761 .04 | 31.954 .92 | 4.73 | 5.96 |
| 7 | 7.001 .07 | 27.574 .25 | 3.94 | 5.33 |
| 8 | 6.571 .01 | 26.624 .10 | 4.05 | 5.11 |
| 9 | $7.00 \quad 1.07$ | $25.62 \quad 3.95$ | 3.66 | 5.03 |
| 10 | 6.761 .04 | $24.90 \quad 3.84$ | 3.68 | 4.88 |
| 11 | $6.67 \quad 1.02$ | $24.57 \quad 3.79$ | 3.68 | 4.81 |
| 12 | $6.33 \quad 0.97$ | 23.903 .68 | 3.78 | 4.66 |
| 13* | 6.33 - | 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 | 8.481 .30 | $12.95 \quad 2.00$ | 1.53 | 3.30 |
| X | 7.811 .20 | 11.81 1.82 | 1.52 | 3.02 |

## * Acrocentric chromosomes.

** Expressed in measurement units.

## Comparison of Karyotypes

A comparison of the chromosomes of D. Virginiana with those of $\underline{D}$. marsupialis suggests that the six pairs of biarmed autosomes of virginiana arose through a sexies of pericentric inversions, since there is a difference in fundamental number without a corresponding change in diploid number. However, the short arms of the autosomes of D. Virsiniana are so short that they could represent accumulations of extraneous material on the chromosomes. Also the submetacentric X-chromosome of D. Virginiana is similar to the metacentric $X$ of Lutreolina crassicaudata which Reig (pers. comm.) 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 formation. of an isochromosome, then the long arms of the autosomes and X -chromosome of D. Virginiana should approximate the lengths of the chromosomes of $D$. marsupialis.

The chromosome lengths of D. Virginiana and D. marsuplalis are compared with each other (see Fig. 2) and with a modified chromosomal complement of $\underline{D}$. Virginiana (biarmed chromosomes represented by the long arms only) in Table 4. The average chromosome length is the ranking critexion used in making these comparisons, since it is the only method applicable to the all-uniarmed chromosomes of $D$. marsupialis. The mean length in measurement units for each chromosome is also expressed as a percentage of

Figure 2.--A comparison of the chromosome lengths of Didelphis marsupialis (average of 23 metaphases) with the chromosomes of D. Virginiana (average of 21 metaphases).

The meen length of each chromosome is expressed as a percentage of the total diploid complement length. Autosomes are arranged by size. Centromere position is indicated for biarmed chromosones.


Table 4. --Comparison of the chromosome lengths of D. Virginiana (v), D. marsupialis (m), and a modified chromosomal complement of D. virginiana (1). Mean expressed in measurement units for 21 metaphases from a female D. Virginiana from El Salto, San Luis Potosí, México (LSUMZ 15107), and 23 metaphases from a female D. marsupialis from Fortin, Veracruz, México (ISUMZ 15104). Mean chromosome Iengths are aiso expressed as a percentage of the total diploid complement length (\% TCL).

| Chromosome | D. |  | virginiana (1) |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $n=21$ |  | $n=23$ |  | modiried$n=21$ |  | Difference Difference |  |
|  | Mean* | \% TCL | Mean* | \% TCL | Mean* | \% TCL | ( $\mathrm{v}-\mathrm{m}$ ) | (1-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 |
|  | 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 |

[^0]the total diploid complement length ( $\%$ TCL). The values for the modified chromosomal complement of D. 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 4) were calculated for comparison of the normal complement of D. marsupialis with the normal complements of D. virginiana and the modified complement of $D$. Virginiana.

A breakdown of the difference values for chromosome lengths in the D. Virginiana versus D. marsupialis comparison shows that 15 chromosomes differ by less than 0.20 and 8 chromosomes differ by less than 0.06 . Values for the modified D. Virginiana versus the normal D. marsupialis comparison reveal greater differences between chromosome lengths since 15 of the 20 autosomes differ by more than 0.20. These findings support the hypothesis that the blarmed autosomes of D. 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. 2). However, since a minimum of two breaks had to occur in each chromosome for each pericentric inversion, a large number of chromosomal fractures probably took place in the evolution of the $\underline{D}$. Virgingana karyotype. Multiple breaks would allow for extensive chromosomal rearrangements and would explain the $s i x$ pairs of subtelocentric autosomes by a
series of pericentric inversions and the larger
submetacentric $X$-chromosomes through one or more unequal translocations--probably with the larger autosomes, since they are comparatively shorter in D. virginiana.

## CHARACTERS OF TAXONOMIC VALUE

Chromosomal features provided the primary characters of taxonomic significance utilized in this study. Subsequent examination of individuals of known karyotype revealed a number of other features useful for distinguishing between 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 the 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 posterjor margin, all of which he applied to characterize species and subspecies of Didelphis. However, $I$ have found that Allen's characters are of limited value except for characterizing some populations of D. 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 specfmens in collections.

## Cranial Characters

Nasal-lacrimel region. --The relationship of the lateral margin of the nasal bones with the medial border of the lacrimal bones, and of both with the maxillo-frontal
suture, is useful for distinguishing D. virginiana from D. marsupialis. The lateralmost extent of each nasal in virginiana, where intercepted by the maxillo-frontal suture, is in line with, or a ilttle anterior to, the point where the same suture meets the lacrimal (Fig. 3 A ; Fig. 4 C and D ; Fig. 6 B ). 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 (Fig. 3B; Fig. 4 A and B; Fig. 7 B).

The nasal-lacrimal features are variable, particularly in virginiane, where these characters will occasionally seem marsupialis-like, but in such cases the dorsal lacrimal-frontal suture will usually be bowed medially (Fig. 4 D). Contact between the nasals and lacrimals, seen in only one deformed marsupialis skull, is a common feature of virginiana (Fig. 4 E ).

Nasal bones. --Typtcally, D. marsupialis has narrow nasals that terminate posteriorly in an acute angle. The nasals of $\underline{D}$. Virginiena 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.

Lacrimal-jugal region.--The configuration of the posterior extension of the lacrimal bone that forms the

Figure 3.--Dorsal views of the frontal-nasal region of a skull of Didelphis virginiana ( $A$ ) and a skull of $D$. marsupialis (B). X 2.6.
D. Virginiana (A), 2 mi. S Grosse Tete, Iberville Parish, Louisiana, LSUMZ 6067, and D. marsupialis (B), 1 km . W Fortín, Veracruz, México, LSUMZ 15104.


Figure 4.--Dorsal views of two skulls of Didelphis marsupialis ( $A$ and $B$ ) and three skulis of D. Virginiana ( $C, D$, and $E$ ). $X 0.64$
D. marsupialis: (A) 1 km . W Fortín, Veracruz, Mexico, LSUMZ $15104 ;(B)$ Xilitia, San Luis Potosí, México, LSUMZ 2742. D. Virciniana: (C) 2 mi. S Grosse Tete, Iberville Parish, Louisjana Lsumz 6067; (D) 1 mi . E reapa, Tabasco, México, ISUMZ 7314; (E) Bledos, San Luis Potosí, México, L.SUMZ 4763.


Figure 5.--Lateral views of the orbital region of skulls from Didelphis virginiana ( $A$ and $B$ ) and $D$. marsupialis (C and D) comparing the widths of the palatine (P). X 2.0
D. Virginiana: (A) $1 \mathrm{mi} . E$ Teapa, Tabasco, México, ISUMZ 14009; (B) Bledos, San Luis Potosí, Néxico, ISUMZ 4763. D. marsupialis: (C) 1 km . W Fortín, Veracruz, México $27 \mathrm{ISUMZ} 15104 ;(\mathrm{D}) \mathrm{Xilitla} ,\mathrm{San} \mathrm{Luis} \mathrm{Potosí}, \mathrm{México}$,
LSUMZ 42 .


Figure 6. --Three views of a skull of Dideiphis virginiana from Edinburg, Hidalgo County, Texas; ISUMZ 13393.
D. Viroiniana: (A) dorsal view, $x$ 0.8; (B) dorsal view of frontal-nasal region, $X 2.3$; (C) lateral view of orbital region ( $P=$ palatine ), $X 2.3$.

$\begin{aligned} \text { Figure 7. } & \text { Three views of a skull of Didelphis marsupialis } \\ & \begin{array}{l}\text { from } 1 \mathrm{~km} . ~ E ~ F o r t i n, ~ V e r a c r u z, ~ M e x i c o, ~ L S U M Z ~\end{array} \\ & 15104 .\end{aligned}$


lower anterior margin of the orbit, and its relationship to the underlying jugal, is one of the few cranial characters that will virtually always serve to separate D. Virginiana from D. marsupialis. The lacrimal of virginiana recedes from the outer margin of the jugal before terminating, usually in a rounded point (Fig. 3 A ; Fig. $4 \mathrm{C}, \mathrm{D}$, and E; Fig. 6 B ). Also, in virginiana, the lacrimal appears to be set down into a shallow depression in the jugal (Fig. 5 A 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 (Fig. 3 B; Fig. 4 A and B; Fig. 7 B ), and the lacrimal usually appears to lie on top of, instead of down into, the jugal (Fig. 5 C 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 (Fig. 5 A and B ; Fig. 6 C ), whereas it is always narrow in marsupialis (Fig. 5 C and D; Fig. 7 C), sometimes becoming a narrow point or occasionally absent entirely.

## External Characters

Color pattern. --Perhaps the most distinctive and easily observed external character that can be used to separate D. virginiana and D. 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 that extends from the ear through the eye. Dark-phase 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 light yellow to a deep buffy orange and much of the hair is tipped with dark brown or black, thereby imparting a dusky overall appearance. The lighter 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) called adventitious stainine, 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 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, which are conspicuous in whole animals but difficult to appreciate in prepared specimens, involve the relative distribution of the guard hair and the length of the furred base of the tail. D. marsupialis often has a "razorback" appearance because the guard hair tends to be concentrated along the midine, whereas in virginiana, the guard hair is more or less evenly distributed over the dorsum. The furred base of the tail of adults is more extensive in marsupialis than in virginiana.

## Behavior

Individuals of D. marsupialis display an elaborate series of protracted movement patterns and sounds when confronted in a stressful situation. More pronounced in males than in females, the movement pattern consists of turning the head from side to side to such an extent that the weight is shifted alternately from one fron foot to the other. The lateral movements of the head and foreparts of the body are interrupted at irregular intervals by forward lunges. Throughout this display, the mouth is open and the opossum hisses and growls or, at times, makes a garbled attempt at both simultaneously. This stereotyped bluffing behavior may be continued for several minutes and is remarkably like the reactions of Philander opossum under similar circumstances in intensity and duration.

The bluffing response by $D$. Virginiana to a stressful situation is similar to that of $D$. marsupialis, but is not
as extreme in that there is much less movement of the body, and the growling, hissing, and lunging usually is not as prolonged.

I have seen examples of "playing possum" by individuals of D. virginiana when they were cornered or when caught in a trap. However, I have never seen this behavior in D. marsupialis. Individuals caught in steel traps are always active when approached, whereas $\underline{D}$. 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 would do littie more than growl and move their bodies from side to side. I was not able to catch a marsupialis in this manner, but those who have caught Didelphis this way in areas where D. Virginiana does not occur (south of Nicaragua) have told me that the result is an active, biting, aggressive opossum quite unlike the more docile D. Virginiana they were accustomed to from the United States.

Another behavioral trait, tail coiling, was observed in D. marsupialis, but not seen in D. vireiniana. In a stressful situation, D. marsupialis coils the tail, sometimes drawing it up under the body. Under similar circumstances, D. Virginiana does not coill the tail. This response to stress is another trait shared by D. marsupialis and Philander opossum.

## 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 Mexico.

## Origin and Dyspersal Pattern

Clemens (1968) does not regard Didelphis as an archetypal marsupial. Instead, on the basis of the derived nature of several morphological characters, particularly features of dentition, he considers Didelphis to be a relatively late evolutionary product of a South American radiation from an Alphadon-like ancestor. Clemens ${ }^{\circ}$ statement (1968:16) that after the establishment of a Panananian land bridge between North and South America in the Pliocene, ". . . some groups of South American marsupials dispersed northward into Central and North Americal is in accord with Simpson's
views (1965) on the origin and dispersal of northern mammals with South American affinities. The postPleistocene 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 judeed to date back three to four thousand years, while the most northern records of occurence 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 Figure 8 and is presented in greater detail for D. marsupialis and D. Virginiana in Figures 9 and 10 , which are based on specimens examined. Distributional patterns susgest that Pleistocene and Recent records for Didelphis in the United States represent D. Virginiana. The southern Iimits for D. Virginiana coincide with the southern extent of the northern highlands of Middle America and are near the southern end of the seasonally arid Tropleal Deciduous Forests of the Pacific slope and coastal plajn of México

Figure 8.--Map showing the combined distribution of Didelphis marsupialis and D. Virsiniana in North and Central America.

Subspecies of D. Virginiana: (1) D. V. Vireiniana including introduced populations; (2) D. V. plere;
(3) D. V. californica; (4) D. V. yucatanerisis.

and Central America. The fact that D. virginiana does not also occur in the mountains of Costa Rica and western Panamá argues against the hypothesis that Virginiana dispersed northward from South America to occupy its present range. Their 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, then 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 D. Virginiana to occupy successfiully an extremely broad array of ecological situations, clearly indicate a North American origin for the species.

The other species, D. marsupialis, is a typical Neotropical opossum that reaches the northernmost limits of its range in the isolated remnants of the humid montane and wet tropical forests of eastern San Luts Potosi and Tamaulipas, México. Throughout its range, D. marsupiajis is associated with warm, humid, tropical forest habitats at moderate and lower elevations (usually below 4,000 feet in México and Central America). The present distribution of
D. marsupialis (Fig. 9) almost exactly coincides with that of another typical tropical marsupial, philander opossum.

Hershkovitz (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 Hershkovitz's alternatives (1969:17).

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

The Speciation of Didelphis virginiana
The northern distributional limits of D. marsupjalis, 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 Elaciation sugeests 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 speciation of $D$. Virginiana from a marsupialis progenitor in North or Central America seems highly unlikely. Herein lies the probable significance of the unusual karyotype of $D$. Virginiane. I believe that $\underline{D}$. Virginiana achieved reproductive isolation from 1 ts progenitor, marsuplalis, through a series of chromosomal rearrangements, a method called "quantum evolution" by Simpson (1961) and "saltational speciation" by Levis (1966). This evolutionary scheme is quite urlike 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 $\underline{D}$. Virginiana and D. 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 chromosome 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, since the oldest groups have the lowest chromosome 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 since 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 didel.phid karyotypes suggests that eithex the frequency of inversions and translocations is very low or the selective pressures against the establishment of altered chromosome patterns is very great. Undoubtedly, the circumstances leading to the establishment of the distinctive and unique karyotype of D . virginiana were unusual.

These conditions probably enforced the isolation of a small inbreeding population of $\underline{D}$. 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, cites evidence supporting the idea that an additional consequence of inbreeding is extensive chromosome breakage, a prerequisite for deriving a virginia karyotype from the marsupialis karyotype.

The prime essential under these conditions is the ability to produce offspring and not the ability to compete with normal individuals. Competition does become 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 chromosome pattern in $\underline{D}$. virciniana was the establishment of reproductive isolation from its parental species, D. marsupialis. If hybridization occurs after renewed contact between the two populations, then secondary barriers reducing or. eliminating
hybridization could be expected to develop. However, it
is equally possible that the number of rearrangements established in the chromosomes of D. virginiana precluded hybridization with $\underline{D}$. marsupialis without the necessity or intensifying the barriers to intexspecific reproduction.

Geographic Origin of Didelphis virginiana Cooling Pleistocene climates at the onset of each glacial stage caused D. 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 $D$. 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 D. 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 virsiniana 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. Furthermore, 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, 1956) would have prevented the dispersal of D. marsupialis into the southeastern United States. However, a number of well preserved fossils of Didelphis from

Pleistocene fissure fillings have been collected in Florida. These specimens are part of the Frick collection in the Department of Vertebrate Paleontology, The American Museum of Natural History. Although, unfortunately, I have not been able to examine them, I would assume that these fossils are D. virginiana and represent a late Pleistocene fauna.

In its ecological tolerances, D. Virginiana differs from D. marsupialis primarily in its ability to inhabit cold and arsd habitats. The survival of an otherwise tropical opossum in western Mexico 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 were the elevational depression of temperate habitats, perhaps as much as 1,000 meters, during glacial stages. Two additional climatic shifts profoundly affected biotic communties. 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 D. Virginians from a Pleistocene isolate of D. 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 D. 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 D. virginiana and aided in selecting for individuals with broad ecological tolerances.

Exactly when during the Pleistocene D. Virginiana evolved is unknown. Didelphis fossil material of Sangamon interglacial age from the United states suggests that Virginiana differentiated sometime earlier, perhaps during the Illinoian glacial age.
D. Virginiana has been able to expand its range until now it occupies a variety of habitats, including the cool arid Mexican Platieau, 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 sympatrically with D. marsupialis in the hot tropical lowlands of eastern and southern México and Central America to southwestern Nicaragua.

## Genus Didelphis Linnaeus

Didelphis Linnaeus, 1758 , Syst. Nat., ed. 10, p. 54. Type, Didelphis marsupialis Linnaeus, 1758, by selection, Thomas, 1888, Cat. Marsup. Monotr. British Mus., p. 323. Placed on Official List of Generic Names, International Commission on Zoological Nomenclature, Opinion 91, Stiles, 1926, Smithsonian Misc. Coll., 73:337.

Didelphys Schreber, 1778, Saugth., 3:536, p1. 145.
Sarigua Muirhead, 1819, Brewster's Amer. Ed. Edinburgh Encycl., 12(pt. 2):505 (part).

Micoureus Lesson, 1842, Nouv. Tabl. Regn. Anim., Mamm., p. 186 (part).

Leucodelphis Ihering, 1914, Rev. Mus. Paulista, 9:347.

## Didelphis marsupialis Limaeus

Didelphis marsupialis Linnaeus, 1758, Syst. Nat., ed. 10, p. 54.

Didelphis karkinophega Zimmermann, 1780, Geogr. Gesch. Thiere, 2:266.

Didelphis cancrivora Gmelin, 1788, Syst. Nat., 1:108. Did [elphis] austro-americana Allen, 1902, Bull. Amer. Mus. Nat. Hist., 16:251 (ex Oken, 1816).

Did [elphis] mes-americana Allen, 1902, Buli. Amer. Mus. Nat. Hist., 16:251 (ex Oken, 1816).

Didelphis richmondi Allen, 1901, Bull. Amer. Mus. Nat. H1st., 14:175.

Type.--Philander, maximus, orientalis Seba, 1734, Thesaurus, 1:64, pl. 36, by primary designation, Linnaeus, 1758, Syst. Nat., ed. 10, p. 54.

## Didelphis marsupialis caucae Allen

Didelphis aurita Allen, 1897, Bull. Amer. Mus. Nat. Hist., 9:43 (nec Wied, 1826).

Didelphis karkinophaga, Bangs, 1900, Proc. New England Zool. Club, I:89.

Didelphis karkinophasa caucae Allen, 1900, Bull. Amer. Mus. Nat. Hist., 13:192.

Didelphis karkinophaga colombica Allen, 1900, Bull. Amex.
Mus. Nat. Hist., 13:93.
Didelphis marsupialis tabascensis Allen, 1901, Bull. Amer. Mus. Nat. Hist., 14:173.

Didejphis rjchmondi Allen, 1901, Bull. Amer. Mus. Nat. Hist., 14:175.

Didelphis marsurialis battyi Thomas, 1902, Novit.
Zool. 9:137.
Didelphis maxsupislis colombica Allen, 1902, Bull. Amer.
Mus. Nat. Hist., 16:257.
Didelphis marsupialis caucae Allen, 1902, Bull. Amer.
Mus. Nat. Hist., 16:257.

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

Type.--Adult female (skin with skull), AMNH I4192, collected by J. H. Batty.

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

Rance.--From central Tamaulipas in eastern México at elevations generally under 4,500 feet, through eastern San Luis Potosí, Veracruz, eastern Puebla and Oaxaca to the Isthmus of Tehuantepec, thence southward from coast to coast through México ana Central America to northern and western Colombia, western Ecuador, and northwestern Perú. The distribution of D. marsupialis caucae, as

Figure 9.-. Map showing the distribution of Didelphis maxsupialis in Mexico and Central America as determined from specimens examined.

determined from specimens examined, is indicated by the map in Fig. 9.

Characters.--Body size large; tail long (usually longer than head and body); color pattern varlable with head and body usually dark except for lighter-colored base of rostral vibrissae and cheek (light yellow to orangebuff); ears, lower legs, and feet black; proximal portion of tail black (up to 50 per cent of bare tall in southern populations); dichromatic; skull long and narrow, with nasals usually pointed posteriorly. The characters used to separate this species from D. 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 $D$. 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, sexual, ontogenetic, and dietary influences requires 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 $D$. virsiniang. J. A. Allen, the first to attempt a revision of the senus, was confused regarding the morphological identity of
D. marsupialis (sensu stricto) as exemplified by his description of $\underline{D}$. yucatanensis (1901:178). I found that the type (USNM 108299) is a D. Virginiana, yet the two paratypes (USNM 108298 and 108300) from the type locality (Chichén Itzá, Yucatán) are both D. 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 $\underline{D}$. marsupialis tabascensis are D. virginiana, and all his D. richmondi are clearly D. marsupialis.

Hall and Dalquest (1963:195) claimed that all the specimens they included under D. ․ . 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. caucae (tabascensis as understood by Hall and Dalquest).

Measurements.--See Appendix B.

Specimens examined.--See Appendix A.

## Didelphis virginiana virsiniana Kerr

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

Didelphis virginiana Kerr, 1792, An. King., p. 193.
D [1delphis] pilosissima Link, 1795, Beytrage zur Naturgeschichte, p. 67.

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

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

Didelphys marsupialis var. typica Thomas, 1888, Cat. Marsup. Monotr. British Mus., p. 323 (part).
Did [elphis] boreo-americana Allen, 1902, Bull. Amer. Mus. Nat. Hist., 16:252 (ex Oken, 1816).
[Didelphis marsupialis] virsiniana, Hershkovitz, 1951, Fieldiana--Zool., Chicago Nat. Hist. Mus., 31:550. Type.--Based on "Virginian Opossum" of Pernant, 1781, Hist. Quadrupeds, p. 301, pl. 34.

Type locality.--Virginia.

Ranse. -~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.

Characters.--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 tall 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, Oxegon, and Washington are successfully established and expanding their range. Introduced opossums in Arizona apparently have dijed out, and the status of the populations in New Mexico and Idaho is unknown. Miller (1899) and Seton (1926) 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.

Measurements.--See Appendix B.
Specimens examined.--See Appendix A.

## Didelphis virginiana pigra Bangs

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

Type.--Adult female (skin with skull), MCZ 3500, collected 31 January 1896 by 0. Bangs.

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

Range. --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.

Characters.--Like D. V. Virginiana except for longer tail (usually exceeding 70 per cent of head and body) and generally darker color overall; head light colored 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, light 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 $\underline{D}$. V. Virginiana.

Remarks.--This weakly differentiated subspecies intergrades with the lighter-colored and shorter-tailed northern subspecies, Virginiana, and the much darker Texan and Mexican subspecies, californica, to the west. D. 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 $\underline{D}$. $V$. californica).

Measurements.--See Appendix B.

Specimens examined.--See Appendix A.

Didelphis virginiana californica Bennett
Didelphis Californica Bennett, 1833, Proc. Zool. Soc. London, p. 40.

Didelphis breviceps Bennett, 1833, Proc. Zool. Soc. London, p. 40.

Didelphis pruinosa Wagner, 1843, Suppl. Schreber's Saug., 3:40.

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

Didelphis marsupialis Allen, 1901, Bull. Amer. Mus. Nat. Hist., 14:166 (not of Linnaeus, 1758).

Didelphis marsupialis texensis Allen, 1901, Bull. Amer. Mus. Nat. Hist., 14:172.

Didelphis marsupialis tabascensis Allen, 1901, Bull.
Amer. Mus. Nat. Hist., 14:173 (part).
Did [elohis] mes-americana Allen, 1902, Bull. Amer. Mus. Nat. Hist., 16:251 (ex Oken, 1816).

Didelphis mes-americana texensis Allen, 1902, Bull. Amer. Mus. Nat. Hist., 16:256.
Didelphis mes-americana tabascensis Allen, 1902, Bull.
Amer. Mus. Nat. Hist., 16:257.
Didelphis yucatanensis Bangs, 1903, Bull. Mus. Comp. Zool., 39:157 (not of Allen, 1901).
Didelphis marsupialis californica Hershkovitz, 1951, Fieldiana--Zool., Chicago Mus. Nat. Hist., 31:548.

Type.--Skull, (sex?), British Museum (Natural History) 55.12.26.190, collected by D. Douglas.

Type locality. --"That part of California which adjoins to Mexico" (see Remarks).

Range. --From Axansas 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 EI Salvador, and through central and western Nicaragua to the southwestern border of Nicaragua. To be expected in northwestern Costa Rica.

The distribution of $D$. $V$. californica, as determined by specimens examined, is outlined by the map in Fig. 10.

Characters.--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 light 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 northeastern Mexico and the Rio Grande Valley of Texas have irregularly white-tipped ears); extensive black pigmentation on tail (usually more than 30 per cent, and sonetimes more than 50 per cent of bare tail); dichromatic, with dark phase common; Jong, broad skulls in adults with narrow nasals usually terminating posteriorly in a rounded or truncated point; postorbital processes not unusually prominent.

Figure 10.--Map showing the distributions of Didelphis virginiana californica and D. v. yucatanensis as determined from specimens examined.


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 Edward Hill of the Mammal Section of the British Museum (Natural History) compared the skulls of Bennett's types of D. californica and D. breviceps with several detailed photographs of D. marsupialis and D. Virginiana, accompanied by descriptions that I sent to h 1 m , and concluded that both californica and breviceps are referable to virginiana. Information on the label of the type, written by Oldfield Thomas, states that it was "taken from one of the types of D. californica Benn. D. Z. S. 1833, p. 40." (fide J. E. Hill, pers. comm.). J. A. Allen (1902:256; footnote), mentioned having examined Bennett's types in the British Museum (Natural History) and said, "A skull . of one of the two specimens on which $\underline{D}$. 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 types, and Hershkovitz (1951:550) restricted the type locality to
that state. Bennett (1833) named five species in addition to D. californica and D. breviceps and assumed that they all came from the same region.

Obviously, Sonora was selected for the type locality because of its proximity to California; however, the point should be kept in mind that these specimens reported by Bennett were collected prior to 1833 (and prior to the Gadsden Purchase), shortly after Mexican Independence from Spain during a time when travel in México consisted of short journeys between presidios and when northern regions including present-day California were still largely unexplored and unmapped. The specimens of Didelphis were supposedly collected by Douglas "on his journey across Mexico," (Allen, 1901:169). Apparently, Douglas was on his way between the Pacific coast of North America and England when he traversed México. Guy Musser (pers. comm.) recently examined the type of Sciurus nigrescens Bennett, 1833, from the same collection, and believes that the squirrel came from somewhere in the State of Puebla--a long way from either Sonora or California. Therefore, I think that, although the type of californica may actually have come from Sonora, the probability is greater that it came from elsewhere in México and that Dourlas' collection contained animals from a number of widely separated localities in that country.

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. Y. 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 color phase (see Geographic Variation : Dichromatism) and the more pronounced head markings to distinguish his D. marsupialis texensis from D. Virginiana, and he relied on the configuration of the nasals for distinguishing D. ㅍ. texensis from his D. ․․ marsupialis. However, with the exception of the relative color phase frequencies, these characters are found in all populations of Latin American virginiana.

Didelphis mesembrinus (Hall and Kelson, 1952:322) is a nomen nudum used with reference to the common Mexican opossum, and was intended to read mesamericana.

Measurements.--See Appendix B.

Specimens examined.--See Appendix A.

## Didelphis virginiana yucatanensis Allen

Didelphis yucatanensis Allen, 1901, Bull. Amer. Mus. Nat. Hist., 14:178.

Didelphis yucatanensis cozumelae Merriam, 1901, Proc. Biol. Soc. Washington, 14:101. Didelphis marsupialis yucatanensis, Goldman and Moore, 1946, Jour. Mamm., 26:360.

Didelphis marsupialis californica, Hershkovitz, 1951, Fieldiana--Zool., Chicago Mus. Nat. Hist., 5:324. Didelphis marsupialis cozumelae, Hall and Kelson, 1952, Univ. Kansas Publs., Mus. Nat. Hist., 5:324.

Type.--Adult male (skin with skull), USNM 108299, collected 1 February 1901 by E. W. Nelson and E. A. Goldman.

Type locality.--Chichén Itzá, Yucatán, México.
Rance. - - 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 by the map in Fig. 10.

Characters.--size small to meáium, tail over 80 per cent of head and body length; color as in D. V. californica with from 40 to 60 per cent of bace tail black; skull small with prominent postorbital processes.

Remarks.--Three of the ten 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 three marsupielis (USNM 108297, 1.08298, and 108300) are those with tail ratios (with head and body) exceeding 100 per cent (Allen, 1901:178). I hesitate to recogntze a subspecies of any Didelphis represented by so ren specimens on the
basis of size; and were it not for the greater developnent of the postorbital processes characterizing the majority of the specimens assigned herein to yucatanensis, I would not separate this subspecies from californica.

The nomen nudum Didelphis nelsoní Allen, 1901, probably was intended to apply to this subspecies.

Measurements.--See Appendix B.

Specimens examined.--See Appendix A.

## SUMMARY AND CONCLUSIONS

When J. A. Allen (1902) published his second revisionary study of the genus Djdelphis, 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 Micuel, Panamá. However, considerable confusion existed regarding the true identities of the named species and subspecies of pidelphis, due in part to the great amount of individual variation exhibitec by these opossums. Hershkovitz (1951), in an attempt to resolve some of the taxoromic problems surrounding members of the genus, recognized only two species of Didelphis. One of these, D. albiventris, is a temperate zone species restricted to South Anerica. The other species he called $\underline{D}$. marsupialis and gove its range as from southern Canada to northern Argentina.

In North America he recognized D. marsupielis virginiana, and said that it intergraded with the nominate form, marsupialis, of Costa Rica, Panamá, and South Aneiica through a series of Mexican and northern Central American populations to which he applied the name californica. Hall and Kelson (1952 and 1959) considered Hershkovitz' action to be extreme and while following his lead in recognizing a single species, 1 . marsupialis, in North and Central America, chose to recognize eleven subspecies as occurring
north of Colombia, South America. I became interested in Didelphis after finding that an analysis of chromosomal material prepared from Costa Rican animals 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. Often, several distinct species in different genera are characterized by the same karyotype. The karyotype of the Costa Rican Didelphis is like the karyotypes of six species in four genera including $D$. albiventris from South America. It consists of 22 acrocentric chromosomes with three pairs of large and seven pairs of medjum-sized autosomes, a small X-chromosome, a minute $y$-chromosome, and a fundamental number of 20. Although Didelphis from the United States also have 22 chromosomes, they have three pairs of large-sized and three pairs of medium-sized subtelocentrics, 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, since American opossums are conservative regarding karyotypic variation.

The examination of other chromosomal material collected from opossurs in Louisiana, Texas, México, and Perú confirmed the existence of two very different karyotypes
in North and Central American 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 for separating these two kinds of opossum by gross morphology. Then I examined over 2,800 museum specimens of Didelphis in order to determine the distribution of the two kinds in North and Central Amexica, and record variation within and between populations. As a result, I recognize D. Virginiana as being distinct from D. marsupialis and ranging 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. D. marsupialis is widely distributea throughout the lowlands of South and Central Anerica, as far north as Tamaulipas in eastern México, usually occurring in tropical forests at elevations below 4,500 feet.

An analysis of the different karyotypes suggests that the karyotype of D . virginiana was derived from a D . marsupialis karyotype 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 Didelphis
remains until the Sangamon Interglacial Stage over two million years after the establishment of a land connection between the two continents. An examination of the distributions and ecological affinities of D. Virginiana and D. marsupialis supports Hershkovitz's (1969) hypothesis that Didelphis was probably in Middle America before the closing of the Panamanian seaway during the Pliocene.

The present distribution of D. Virginiana, with its ability to utilize a broad array of ecological situations, its fossil record, and its unique karyotype, suggests that Virginiana differentiated in México from a D. 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 D. marsupialis could be expected to show decreased vigor, increased frequency of abnormal development (includinf chromosomal breakage), and a tendency toward a greater tolerance of severe climates. An increased frequency of chromosomal breakage would help explain the evolution of the D. VIrginiana karyotype.

On this basis, I am advancing the hypothesis that $D$. Virciniana speciated from $D$. marsupialis primarily as the result of a number of chromosomal reaxrangements 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 $D$. Virginiana that is accumulating from studies of its morphology, reproductive physiology, cytogenetics, cellular physiology, and biochemistry be reevaluated in the light of the probable evolutionary history of the species. Also, data derived from such studies on D. Virginiana should not be interpreted as characterizing other marsupials.

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

## APPENDIX A

Localities in the following lists of specimens examined are arranged from north to south and from west to east within each political unit. Museum numbexs are included for specimens from localities in southern Texas and Latin America. Each point on the distribution maps (Figs. 9 and 10) represents one or more localities. None of the localities has been assigned identifying numbers nor is a gazeteer provided. Instead, I refer the reader to the following reports in which adequate descriptions are given for most of the localities. These references are: Allen, 1906 (Sinaloa and Jalisco); Alvarez, 1963 (Tamaulipas); Burt, 1938 (Sonora); Burt and Stirton, 1961 (El Salvador); Dalquest, 1953 (San Luis Potosi); Davis, 1944 (eastern and central México); Duellman, 1960 (Isthmus of Tehuantepec) and 1961 (Michoacán); Fairchild and Handley, 1966 (Fanamá); Goldman, 1951 (general for México and Guatemala); Goodwin, 1942 (Honduras), 1.946 (Costa Rica), and 1969 (Oaxaca); Griscom, 1932 (Guatemala); Hall and Dalquest, 1963 (Veracruz); Hardy and McDiarmid, 1969 (Sinaloa); Hooper, 1952 (México and Central America); Monroe, 1968 (Honduras); Schaldach, 1963 (Colima and adjacent parts of Jalisco); Stewart, 1951, 1954, and 1963 (Guatemala); Villa, 1949 (southwestern Chiapas).

## Didelphis marsupialis caucae

Specimens examined.--613. MÉXICO: Tamaulipas:
Ejido Santa Isabel, 2 km . W Pan American Highway, 1 (skin with skuil), KU 57524. San Luis Potosí: El Salto, Río Naranjo, 3 ( 2 skins with skulls, 1 skull), AMNH 176700, 176702, LSUMZ 4773; Rancho Sabinal, 1 (skull), LSUMZ 7853; ca. $2 \mathrm{~km} . \mathrm{W}$ Xilitia, 2 (skins with skulls), LSUMZ 15102, 15103; Xilitla, 3 (2 skins with skulls, l skull), LSUMZ 2742-2744; Río Axtla, $3 \mathrm{~km} . \mathrm{W}$ Axtla, 1 (skin with skull), KU 19048; $3 \mathrm{~km} . \mathrm{N}$ Tamazunchale, 1 (skin with skull), KU 19049. Veracruz: 6.5 km . NNW E1 Higo, 1 (skin with skull), IB 10773; Hacienda Tamiahua, Cabo Rojo, 2 (skulls), KU 82834, 82835; 17 km . NW Tuxpan, 2 (skins with skulls), KU 82836, 82837; 9 km . NW Tuxpan, 1 (skin with skull), KU 82838; Tuxpan, l (skull), KU $82839 ; 5 \mathrm{~km} . \mathrm{S}$ Tihuatlán, 2 (skulls), KU 23395, 23397; Papantla, 2 (skins with skulls), USNM 93043, 93044; 9 km. E Papantla, 1 (skull), KU 23398; $9 \mathrm{~km} . \mathrm{NW}$ Nautla, 1 (skull), KU 23399; 3 km . SW San Marcos, 2 (skulls), KU 23400, 23401; 4 km . W Tlapacoyan, 1 (skull), KU 23402; 1/2 mi. NW Las Minas, 1 (skin with skull), USNM 329399; 1 mi. NE Las Minas, 1 (skull), USNM 329398; $5 \mathrm{~km} . \mathrm{N}$ Jalapa, 2 (l skin with skull, 1 skin with lower jaws), TCWC 1925, 1926; $2 \mathrm{~km} . \mathrm{W} \mathrm{Jico}$,1 (skin with skuli), KU 19054; Mirador, 5 (skins with skulls), USNM 58687-58691; $24 \mathrm{mf}$. . S Veracruz, 4 (skins with skulls), AMNH 203557-203559, 20356l; Boca del Rfo, l (skin with skuil), TCWC 2748; 4 km . WNW Fortín, 3 (skins with skulls),

KU 17683-17685; Río Metlác, 1 km . W Fortín, 2 (skins with skulls), ISUMZ 15104, 15105; Potrero Viejo, 1 (skull), KU 32048; 3 km . SE Orizaba, 3 (skins with skulls), KU 19055-19057; 15 km . ESE San Juan de la Punta, 2 (skins with skulls), KU 19060, 19061; Rio Blanco, $20 \mathrm{~km} . \mathrm{W}$ Piedras Negras, 2 (skins with skulls), KU 10951, 10962; 15 mi. N San Andrés Tuxtla, 2 (skins with skulls), AMNH 172154, 172168; San Andrés Tuxtla, l (skin with skull), AMNH 172165; 3 km . E San Andrés Tuxtla, 4 (skulls), KU 23404-23406, 24001 ; 15 km . NE Catemaco, 4 (skulls), IB 7923-7925, 7932; Catemaco, 3 (2 skins with skulls, 1 skull), AMNH 172151, USNM 65543, 65957; Lake Catemaco, 3 (2 skins with skulls, 1 skin), AMNH 172169, 172174, 172176; Agua Dulce, 1 (skin with skull), USNM 271103; 60 km . ESE Jesús Carranza, 1 (skull), KU 23410; 20 km . E Jesús Carranza (Boca del Río Chalchijapa), 2 (skulls), KU 23407, 23408. Puebla:. Metlaltoyuca, 1 (skin with skull), USNM 92979. Oaxaca: $10 \mathrm{~km} . \mathrm{S}$ Yetla, 1 (skin with skull), KU 99528; 8 mi. S Veracruz (sic), 2 (skins with skulls), AMNH 1721.52, 172155; Santo Domingo (Mts. near), 1 (skin with skull), USNM 73321; $1 \mathrm{~km} . \mathrm{N}$ Cerro Baul, Ranch Carlos Minné, 37 km . NW (by road) Riza de Oro (Chiapas), l (skin with skull), CAS 14634; Tapanatepec, 1 (skull), IB 2475; "Oaxaca" (general designation), 1 (skin with skull), AMNH 26597. Tabasco: 15 km . NW (sic) Alvaro Obregón, 1 (skin), KU 19064; Frontera, 2 (skins with skulls), USNM 100507, 100508; La Venta, 1 (skin with skull), USNM 271104; $15 \mathrm{mi} . W, 6 \mathrm{mi}$.

N Villa Hermosa, 1 (skull), KU 66270; 6 mi. S Cardenas, 3 (2 skins, with skulls, 1 skull), $K U$ 66271-66273; 10 mi . E, $19 \mathrm{mi} . \mathrm{N}$ Macuspana, 1 (skull), KU 66274 ; $4 \mathrm{mi} . \mathrm{N}, 2 \mathrm{mi} . \mathrm{E}$ Macuspana, 1 (skull), KU 66275; 5 mi . SE Macuspana, 2 (1 skin with skull, 1 skull), KU 66276, 66277; Río Puyacaterıgo, 15 km . E Teapa, 1 (skin with skull), IB $6958 ; 6.5 \mathrm{~km}$. NE Teapa, l (skin), IB 8089; Teapa, 6 ( 4 skins with skulls, 2 skulls), IB 7561, 7563, USNM 100510-100513; 1 mi. E Teapa, 2 (skins with skulls), LSUMZ 7312, 8094; "Tabasco" (general designation), 1 (skin with skull), USNM 10196/38687. Campeche: Apazote, near Yahaltuma, l (skin with skull), USNM 108297; 7.5 km . W Escárcega, l (skin with skull), KU 91449. Yucatán: Chichén Itzá, 2 (skins with skulls), USNM 108298, 108300. Chiapas: 16 mi. NW Palenque, 1 (skin with skull), TCWC 16282; ca. $5 \mathrm{~km} . \mathrm{S}$ Solusuchiapa, 1 (skin with skull), ISUMZ 11913; 2 mi. E El Real, 1 (skull), KU 66278; 3 mi. SSE Soyaló, 1 (skull), TCWC 8273; Tuxtla, 4 (skins with skulls), USNM 76205-76208; 4 mi . NE Chiapa de Corzo, 1 (skin with skeleton), TCWC 8272; $5 \mathrm{mi} . ~ S ~ C h i a p a, ~$ 1 (skull), AMNH 172173; $20 \mathrm{mi} . W$ Comitán, 1 (skin with skull), AMNH 172156; 18 mi . E Zapaluta, l (skin with skull), TCWC 827l; 25 mj. SE Comitán, l (skin with skull), AMNH 172166; 24 mi. SSE ZapaIuta ( 5 mi. W Hwy. 190), 2 (skins with skulls), TCWC 8933, 8934; $16 \mathrm{mi} . \mathrm{N}$ Chiapas-Guatemala border (sic), 1 (skin with skull), AMNH 172162; $3 \mathrm{~km} . E$ Risa de Oro, 1 (skin with skuli), ISUMZ 11911; Cerca Finca Prusia, 1 (skin with skull), IB 7; Paval, $20 \mathrm{~km} . \mathrm{NE}$

Mapastepec, l (skin with skull), IB 9; Finca La Esperanza, $45 \mathrm{~km} . \mathrm{N}$ Huixtla, 1 (skin with skull), IB 10; Finca Germania, 24 km . NE Huixtla, 1 (skin with skull), IB 11; Río Huixtla, ca. 13 km . N Huixtla, 1 (skin with skull), LSUMZ 11912. BRITISH HONDURAS: Cayo: Central Farm, 1 (skin), USNM 360463. GUATEMALA: E1 Petén: Toocoq, 15 km. SE La Libertad, 1 (skull), KU 81962. Alta Verapaz: Chinajá, 1 (skin with skull), KU 81964; Chimoxan, 3 (skins with skulls), AMNH 79097-79099. Suchitepequez: Finca Selache, 3 (skins with skulls), AMNH 68520, 68521, 68542. Santa Rosa: Astillero, 4 (skins with skulls), KU 6459664599. "Guatemala" (general designation), 2 (skins with skulls), USNM 61214, 61215. HONDURAS: Gracias a Dios: Patuca, 1 (skull), USNM 36065; Patuca River, 1 (skin with skull), USNM 21012/36060. Atlantida: 7 mi. W Ia Ceiba, 1 (skin), TCWC 14511. Cortés: 2 mi. W San Pedro Sula, 1 (skin with skull), TCWC 11088; Las Ventanas, near Lake Yojoa, 1 (skin with skull), AMNH 126138. Santa Bárbara: $7 \mathrm{~km} . \mathrm{N}$ Santa Bárbara, 1 (skull), TCWC 18551; Santa Bárbara, 1 (skin with skull), AMNH 123289. Copán: Copán, 1 (skin with skull), TCWC 18550. Lempira: Las Flores, Gracias, 23 (22 skins with skulls, 1 skin), AMNH 128975, 128977128990, 128992, 128993, 129693-129696, 129699, 129700. Octopeque: 1 km . NW Nuevo Octopeque, 1 (skin with skull), TCWC 18011. Districto Central: Tegucigalpa, l (skin with skull), AMNH 126761. Francisco Morazán: El Zapote, 7 km . S Sabana Grande, I (skin with skull), AMNH 126763.

EL SALVADOR: Chalatenango: San José del Sacare, 1 (skin with skull), MVZ 130277. Cuscatlán: Colima, l (skin with skull), MVZ 130278. Morazán: N slope Mt. Cacaguatique, 1 (skin with skull), MVZ 98151; 3/4 mi. NE Divisadero, 1 (skin with skull), MVZ 130280; Carolina Mine, $4 \mathrm{~km} . \mathrm{W}$ Divisadero, 1 (skin with skull), MVZ 130284; Monte Cristo Mine, 1 l/2 mi. W Divisadero, 2 (skins with skulls), MVZ 98149, 130282; 1 mi. W Divisadero, l (skin with skull), MVZ 130281. San Miguel: Mt. Cacaguatique, 6 (skins with skulls), MVZ 130304-130309; Volcán de San Miguel, 2 (skins with skulis), MVZ 130314, 130315; SW edge Lake Olomega, 2 (skins with skulls), MVZ 98153, 98157. Sonsonate: Hacienda Chilata, 6 ( 4 skins with skulls, 2 skulls), MVZ 98158-98161, 130315, 130316. Ahuachapan: Barra de Santiago, I (skin with skuli), MVZ 130273. Libertad: $10 \mathrm{mi} . \mathrm{W}$ La Libertad, 1 (skeletọ), TCWC 6620. Usulutản: Puerto del Triunfo, 6 (skins with skulls), MVZ 130317-130322. NICARAGUA: Comarca de Cabo: Río Coco, 1 (skin with skull), AMNH 29256. Nueva Segovia: $41 / 2 \mathrm{~km} . \mathrm{N}, 2 \mathrm{~km}$. E Jalapa, 11 (l skin with skull, 3 skulls, 7 in alcohol), KU 110604-110613, 110617. Jinotega: 2 km . E Yali, 1 (skin with skull), KU 105880; Hacienda La Trampa, 16 km . E, $51 / 2 \mathrm{~km}$. N Jinotega, 3 (skulls), KU 99422, 99424, USNM 338812. Mataçalpa: Finca Tepeyac, $101 / 2 \mathrm{~km} . \mathrm{N}, 9 \mathrm{~km} . E$ Matagalpa, 46 ( 15 skins with skulls, 31 skulls), KU 104518-104522, 104524-104.532, 104555104573, 104575, USNM 337527-337529, 337532-337534, 337538, 337540, 337542-337545; Santa Marra de Ostuma, l (skin with
skull), KU 105881; Lavala (=Savala), 4 (skins with skulls), AMNH 28324, 28327, 28961, 29323. Chinandega: Hacienda San Isidro, $10 \mathrm{~km} . \mathrm{S}$ Chinandega, 3 (l skin with skull, 2 skulls), KU 104545, 104547, 104551; San Antonio, 3 (skulls), KU 105883, 105884, 114460. Managua: Hacienda Azacualpa, 5 km. N, $2 \mathrm{~km} . \mathrm{W}$ Villa El Carmen, 3 (skulls), KU 108218-108220; 3 mi. SW Managua, I (skin with skull), KU 70184. Boaco: Santa Rosa, $17 \mathrm{~km} . \mathrm{N}, 15 \mathrm{~km} . \mathrm{E}$ Boaco, 1 (skull), KU 110629. Chontales: $1 \mathrm{~km} . \mathrm{N}, 21 / 2 \mathrm{~km} . \mathrm{W}$ Villa Somoza, 1 (skull), KU 110648. Granada: Hacienda Mecatepe, $2 \mathrm{~km} . \mathrm{N}, 111 / 2 \mathrm{~km} . \mathrm{E}$ Nandaime, 1 (skull), KU 108144; La Calera, $3 \mathrm{~km} . \mathrm{S}, 5 \mathrm{~km} . \mathrm{W}$ Nandaime, 1 (skull), kU 108145. Carazo: $3 \mathrm{~km} . \mathrm{N}, 4 \mathrm{~km} . \mathrm{W}$ Diriamba, 2 (skulls), KU 110649, 114463. Zelaya: Bonanza, 10 (skulls), KU 96362, 96363, 99397-99403, 99405; Kurinwas River $1252 \mathrm{~N}, 8403 \mathrm{~W}, 1$ (skin with skull), USNM 392858; El Recreo, 32 ( 8 skins with skulls, 8 skulls, 16 in alcohol), KU 104419-104426, 110631-110647, 114462, USNM 337655-337659; Río Escondido, 50 mi . from Bluefields, 1 (skin with skull), USNM 36486/48855. Río San Juan: La Esperanza, $5 \mathrm{~km} . \mathrm{S}$, $31 / 2 \mathrm{~km} . E$ San Carlos, 14 (skulls), KU 108221-108230, USNM 361208, 361210, 361211, 361213; Toro Rapids, 1 (skin with lower jaws), AMNH 136926; Greytown, 4 (skins with skulls), USNM $33134 / 45138,33135 / 45139,33137 / 45141,45140$. "Nicaragua" (general designation), 3 ( 2 skins with skulls, 1 skull), AMNH 136947, USNM 337539, 337546. COSTA RICA: Limón: Cariari, l (skull), LsumZ 12635; Pandora, 2 (1 skin, I in alcohol), LACM 26028, USNM 284466; Talamanca, 2 (I
skin with skull, 1 skull), USNM 12210/14210, 14213.
Alajuela: Alajuela, 1 (skull), ANNH 177084. Cartago: Santa Teresa, Peralta, 1 (skin with skull), AMNH 140336; $5 \mathrm{~km} \cdot \mathrm{SE}$ Turrialba, l (skin with skull), KU 26921; IICA, Turrialba, 4 (skins with skulls), LSUMZ 9336, USNM 284467284469; Cartago, l (skull), KU 26929. San José: Finca Lornessa, 2 km . NW Santa Ana, 2 (skins with skulls), LSUMZ 14458, 14459; Santa. Ana, 1 (skin with skull), LSUMZ 12632; San José, 10 ( 6 skins with skulls, l skin with skull inside, 1 skin, 2 skulls), AMNH 3654, 3675, 10095, USNM 9070/38861, 9071/37941, 9072/38855, 9073/38862, 9074/37942, 9075/38863, 15969; San Pedro, Montes de Oca, 1 (skin with skull), AMNH 139250; Universidad de Costa Rica, San Pedro, l (skin with skull), LSUMZ 11433; Hatillo, 2 (in alcohol), LACM 24539, 24540; San Isidro del General, 10 ( 9 skins with skulls, 1 in alcohol.), AMNH 139240-139248, LACM 25797. Puntarenas: Monteverde, 1 (in alcohol), LACM 26241; Pozo Azul, l (skin), AMNH 19204; Geronimo Pirris, 3 (skins with skulls), AMNH 124819, USNM 250318, 250480; Finca Ligia, Parrita, l (skin), LaCM 26680; 4 mi. NE Palmar, l (skull), TCWC 10577; Palmar, 6 ( 5 skins with skulls, 1 skull), AMNH 139305-139310; 9 mi. ENE Puerto Golfito, 1 (skeleton), TCWC 10585; Camp Seattle, Osa Peninsula, 1 (skin with skull), LACM 23989. "Costa Rica" (general designation), 4 (skins with skulls), USNM 8808/37940, 61199, 105272, 256466. PANAMA: Bocas del Toro: Nievecita Farm, l (skull), USNM 291145; Boca del Draso, 3 (2 skins with skulls, I skull), USNM 315089-315091;

Almirante, 14 (skins with skulls), USNM 315075-315088. Colón: Porto Bello, 1 (skin with skull), USNM 171486; Colón, 1 (skin with skull), USNM 296196. Canal Zone: Fort Sherman, 2 (skins with skulls), USNM 296197, 296351; Mojinga Swamp, 1 (skin with skull), USNM 301149; Río Indio, near Gatún, 4 (skins with skulls), USNM 170899-170902; Fort Davis, 4 (skins with skulls), USNM 296348-296350, 302328; Gatún, 9 (8 skins with skulls, l skull), AMNH 36705-36709, USNM 171058, 171224, 171235, 171734; Lion Hill, 2 (skins with skulls), USNM 172735, 172736; Barro Colorado, 3 (1 skin with lower jaw, 2 skulls), USNM 256175, 256176, 257316; Juan Mina Station, Río Chágres, 1 (skin), AMNH 164492; Río Chágres, l (skin with skull), AmNH 147758; Camp Piña, 9 (skins with skulls), UA 5285, USNM 301148, 301383-301387, 302461, 302464; Río Mandinga, 2 mi. W Gamboa, l (skin with skull), USNM 296199; Madden Road, 2 (skins with skulls), USNM 301147, 301150; Empire, 3 (skins with skulls), USNM 178724, 179552, 179553; Red Tank, 1 (skin with skull), USNM 301388; Curundu, 2 (skins with skulls), USNM 297882, 297883; Fort Clayton, 6 (skins with skulls), USNM 296198, 296347, 296352-296354, 301146; Corozal, 1 (skin with skull), UA 7297; Ancón, 1 (skin with skull), USNM 171984; Quarry Heights, 1 (skin with skull), USNM 303289; Fort Kobbe, 3 (skins with skulls), USNM 296346, 297881, 298705. San Blas: Mandinga, 1 (skin with skull), USNM 305163; Armila, 4 (3 skins with skulls, 1 skin), USNM 335041-335044. Chiriquí: Cerro Punta, 5 (skins with skulls), USNM 314191-314194,

322488; Palo Santo, l (skin with skull), USNM 291102; Boquete, 2 ( 1 skin with skull, 1 skin), AMNH 18916, 27023; Boquerón, 27 ( 13 skins with skulls, 9 skins, 5 skulls), AMNH 18917, 18918, 18921, 27024-27041, 27682, 29669-29673; l. mi. SW Progreso, 8 (skins with skulls), USNM 362353362360; 2 mi . E Concepción, 1 (skin with skull), TCWC 10578; Bambito, 1 (skin with skull), USNM 314195; 2 mi. NE Talé, l (skin), USNM 331076; Guabala, l (skin), USNM 331074; 1 mi. S Guabala, 2 (1 skin wịth skull, 1 skin), USNM 331072, 331073. Veraguas: Santa Fé, Río Santa María, 2 (skins with skulls), USNM 304731, 304732; Isla Coiba, 3 (2 skins with skulls, 1 skin), AMNH 18922, 27021, 27022. Coclé: El Valle, 1 (skull), MVZ 118730. Panamá: 6 mi . E El Valle (Prov. Coclé), 1 (skin with skull), USNM 304730; La Zumbadora, 30 (skins with skulls), UA 7298, USNM 302454302460, 302462, 302463, 302658-302664, 303086-303088, 305162, 305164,305165 , 306455-306460; San Miguel Island, 1 (skin with skull), MCZ 8439. Darién: Río Chucunaque, 2 (1 skin with skull, 1 skull), USNM 306461, 306462; E1 Real, 3 (skins with skulls), AMNH 37568, 37627, USNM 309334; Tacarcuna, 1 (skin with skull), USNM 309334; Capetí, 1 (skin with skull), AMNH 38181; Cituro, 2 (skins with skulls), AmNH 38172, 38173; Boca de Río Paya, 2 (skins with skuils), USNM 306463, 306464; Mount Pirre, near head of Río Limón, .1 (skin with skull), USNM 179052; Cana, 8 (skins with skulls), USNM 179050, 179051, 179058, 179165, 179913-179915, 180732; Jaqué, jct. Río Jaqué and Río Imamada, 3 (skins with skulils),

USNM 362350-352352; 8 mi. E Jaqué, l (skin with skull), USNM 362349. Los Santos: Guánico, 10 (skins with skulls), USNM 298704, 322979-322987; Cerro Hoya, 1 (skin with skull), USNM 322978. "Panamá" (general designation), 2 (skulls), AMNH 63358s USNM 33175.

Didelphis Virginiana virginiana
Specimens examined.--819 UNITED STATES. Wisconsin: Walworth County: 7 1/2 mi. NW Elkhorn, 1 AMNH. Michigan: Branch County: Coldwater, 2 AMNH. New York: Oswego County: Hastings, 1 AMNH. Onondaga County: Jamesville, 1 USNM. Schoharie County: Schoharie, 2. AMNH. Steuben County: $3 \mathrm{mi} . \mathrm{SE}$ Bath, 1 KU . Oranse County: Ft. Montgomery, 3 AMNH; Highland Falls, 2 USNM; West Point, 3 USNM; "Orange County" (general designation), 1 USNM. Westchester County: Golden's Bridge, 1 AMNH; Mamaroneck, 1 AMNH; Montrose, 1 AMNH; Mt. Kisco, 2 AMNH; Peekskill, l AMNH; Poundridge, 1 AMNH; South Salem, 2 AMNH; Yorktown Heights, 3 AMNH; "Westchester County" (general designation),

2 AMNH. Rockland County: South Nyack, 1 AMNH. Queens County: Richmond Hill, Staten Island, 1 AMNH. New York County: Wash Market, New York, 1 AMNH. Richmond County: Whitlock, "Staten Island," I AMNH. Surrolk County: Holtsville, 1 AMNH; Miller's Place, Long Island, 3 AMNH; Setauket, Long Island, I AMNH; Smithtown, Long Island, I AMNH; "Long Island," I AMNH; Manorville, 1 AMNH; 2 mi. S Mastic, 1 AMNH; Montank Point, 2 USNM. South Dakota: Douslas County: Bennings, l USNM. Towa: Plymouth County:
$11 / 2 \mathrm{mi} . \mathrm{N}, 11 / 2 \mathrm{mi} . \mathrm{W}$ Kingsley, 1 KU . Pottawatomie County: $7 \mathrm{mi} . \mathrm{E}$ Oakland, 1 KU . Mahaska County: $1 \mathrm{l} / 2 \mathrm{mi}$. $\mathrm{s}, 2 \mathrm{l} / 2 \mathrm{mi}$. E New Sharon, $4 \mathrm{KU} ; 3 \mathrm{l} / 2 \mathrm{mi}$. N Oskaloosa, 1 KU ; Oskaloosa, $2 \mathrm{KU} ; 6 \mathrm{mi} . \mathrm{S}$ Oskaloosa, 1 KU . Keokuk County: $8 \mathrm{mi} . W$ Sigourney, 1 KU . Fremont County: 10 mi . E Hamburg, 1 KU. Nebraska: Brown County: Ainsworth, 1 AMNH; K. McConnell Ranch, 1 AMNH; 5 mi. N Pine Grove, Long Pine Creek, 1 AMNH. Rock County: 3 ml . S Bassett, Skull Creek, 2 AMNH; Skull Creek, Johnson Ranch, 2 AMNH. Scott's Bluff County: 3 mi . N McGrew, I KU. Madison County: Elthorn River, 2 mi. E Norfolk, 1 KU . Stanton County: Elkhorn River, 7 mi. E, 1 mi. $S$ Norfolk (Kadison County), 1 KU. Cumming County: Beemer, 1 USNM, Butler County: 3 mi. S Bellwood, l KU; $4 \mathrm{mi} . \mathrm{S}, 4 \mathrm{mi} . \mathrm{W}$ David City, 1 KU ; 4 mi. ERising City, 2 KU . Adams County: Hastings, 1 KU . Gage County: $1 \mathrm{mi} . \mathrm{W}, 1 \mathrm{mi} . S$ Barnston, $1 \mathrm{KU} ; 2 \mathrm{mi} . \mathrm{S}$, 1/2 mi. E Barnston, 3 KU . Webster County: Bladen, 3 AMNH. Richardson County: $2 \mathrm{mi} . \mathrm{S}, 4 \mathrm{mi}$. E Rulo, $1 \mathrm{KU} ; 4 \mathrm{mi}$. E Barada, 15 KU . Kansas: Cheyenne County: 1 mi. N St. Francis, 1 KU ; Republican River, 16 mi . SW St. Francis, 1 KU. Marshall County: 1 mi. S , 9 mi. W Frankfort, 1 KU . Nemaha County: Sabetha, 6 KU . Doniphan County: Geary, 1 KU; "Doniphan County" (general designation), 2 KU. Clay Courty: 6 mi. SW Clay Center, 2 KU . Riley County: Manhattan, 3 AMNH; "Riley County" (general designation), 1 KU. Jackson County: $10 \mathrm{l} / 2 \mathrm{mi}$. WSW Holton, $1 \mathrm{KU} ; 4 \mathrm{mi} . \mathrm{SW}$ Muscotah, 1 KU . Atchison County: 5 mi . SW Effingham, 1 KU .

Leavenworth County: Fort Leavenworth, I KU, 1 USNM. Wyandotte County: Kansas City, 1 KU . Trego County: Wakeeney, 7 KU ; "Trego County" (general designation), 1 KU . Wabaunsee County: 3 mi . NE Maple Hill, I KU. Shawnee County: Richland, 2 KU . Douglas County: $21 / 2 \mathrm{mi} . \mathrm{N}$ Baldwin, $1 \mathrm{KU} ; \mathrm{Clinton}$,7 KU ; neax Lawrence, $1 \mathrm{KU} ; 1 \mathrm{ml} . \mathrm{N}$ Lawrence, 1 KU ; Lawrence, 2 AMNH, $16 \mathrm{KU} ; 21 / 2 \mathrm{mi} . \mathrm{W}$ Lawrence, $1 \mathrm{KU} ; 2 \mathrm{mi} . S E$ Lawrence, $1 \mathrm{KU} ; 4 \mathrm{mi} \mathrm{SE}$ Lawrence, I KU; 7 mi . SW Lawrence, $23 \mathrm{KU} ; 71 / 2 \mathrm{mi}$. SW Lawrence, 31 $\mathrm{KU} ; 8 \mathrm{mi} . \mathrm{SW}$ Lawrence, $4 \mathrm{KU} ; 10 \mathrm{mi} . \mathrm{SW}$ Lawrence, $1 \mathrm{KU} ; 11$ mi. SV Lawrence, 3 KU ; Highway 10 between Lawrence and Eudora, 1 KU ; Sibley, 1 KU ; Washington Creek, $1 \mathrm{KU} ;$ "Douglas County" (general designation), 48 KU . Johnson County: Gardner, $1 \mathrm{KU} ; 15 \mathrm{mi} . E$ Lawrence (Douglas County), 1 KU . Franklin County: $S$ of Ottawa, 1 KU . Miami County: 1 mi . N, I mi. E La Cygne, 1 KU . Anderson County: $4 \mathrm{mi} . \mathrm{S}$ Garnett, $2 \mathrm{KU} ; 6 \mathrm{mi} . \mathrm{S}$. Garnett, 5 KU . Stafford County: Little Salt Marsh, 3 KU . Reno County: $2 \mathrm{mi} . \mathrm{N}, 2 \mathrm{mi} . \mathrm{E}$ Hutchinson, $2 \mathrm{KU} ; 3 \mathrm{mi} . \mathrm{N}_{3} 5 \mathrm{I} / 2 \mathrm{mi}$. E Hutchinson, 1 KU . Greenwood County: Hamilton, 2 AMNH, $2 \mathrm{KU} ; 1 / 2 \mathrm{mi} . \mathrm{E}$ Hamilton, I $\mathrm{KU} ; 3 / 4 \mathrm{mi}$. E Hamilton, 1 AMNH; $8 \mathrm{mi} . \mathrm{SW}$ Toronto, $6 \mathrm{KU} ; \mathrm{S}$ of Toronto, 2 KU ; "Greenwood County" (general designation), 3 KU . Harvey County: "Harvey County" (general designation), 1 KU. Woodson County: "Woodson County" (general designation), 1 KU . Allen County: I mi. N, 1 mi. W Neosho Bridge, Humboldt, 1 KU . Kiowa County: 5 mi . $N$ Belvidere, 1 AMNH. Elk County: Longton,

I KU. Seward County: 1 mi. E Arkalon, 1 KU. Meade County: $14 \mathrm{mi} . \mathrm{SW}$ Meade, 1 KU . Barber County: $3 \mathrm{mj} . \mathrm{N}, ~ \mathrm{I} \mathrm{Mi.E}$ Sharon, 1 KU. Cowley County: Winfield, 1 USNM. Chautauqua County: Cedar Vale, 5 USNM. Labette County: $10 \mathrm{mi} . \mathrm{SW}$ Oswego, 3 KU . Cherokee County: 8 mi . SW Columbus, 3 KU ; 9 mi. SW Columbus, $1 \mathrm{KU} ; 10 \mathrm{mi} . \mathrm{SW}$ Columbus, 1 KU. "Eastern Kansas," 58 KU. Missouri: Jackson County: 2 mi . E, 1/2 mi. N 86 and Greenwood Street, Kansas City, $1 \mathrm{KU} ;$ ca. 9 mi . S Swope Park, Kansas City, l TCWC. Pettis County: Sedalia, 2 USNM. Cass County: $2 \mathrm{mi} . E, 7 \mathrm{mi} . \mathrm{S}$ Harrisonville, 1 KU . Barton County: Golden City, 1 USNM. McDonald County: Noel, 1 KU. Stone County: Marble Cave, 1 USNM. Howell County: West Plains, 1 USNM. Illinois: Cook County: "Cook County" (general designation), 1 KU . Hancock County: Warsaw, 2 USNM. Coles County: near Ashmore, 1 KU . Madison County: Wood River, 1 AMNH. St. Clair County: Belleville, I USNM. Alexander County: Olive Branch, 1 USNM. Indiana: Porter County: Chesterton, 1 USNM. Wells County: "Wells County" (general designation), 5 USNM, Howard County: Russiaville, 1 USNM. Grant County: "Grant County" (general designation), I USNM. Jay County: Salamonia, 3 AMNH. Knox County: Bicknell, 7 USNM. Lawrence County: Mitchell, 1 USNM. Jackson County: Freetomn, 1 USNM. Pike County: Stenaal, 1 USNM. Ohio: Ashtabula County: Mechanicsville, 1 KU . Cuyahoga County: Shaker Heights, 1 KU . Portage County: Gaxretsville, 4 AMNH. Wayne County: Wooster, 4 USNM. Varren County: Fort Arcient, 1 AMNH. Athens County:

7 mi. SE Athens, 2 USNM. Hamilton County: near Cincinnati,
1 USNM. "Ohio," (general designation), l AMNH.
Pennsylvania: Crawford County: near Hartstown, 1 KU.
Bucks County: Morrisville, 1 USNM. Cumberland County:
Carlisle, 6 USNM. Somerset County: Markleton, l USNM. Chester County: "Chester County" (general designation),

2 USNM. New Jersey: Morris County: Boonton, 3 AMNH. Essex County: Irvington, 1 USNM; Upper Montclair, 2 AMNH. Union County: Elizabeth, 1 AMNH, 1 USNM. West Virginia: Monongalia County: Wadestown, 1 KU . Tucker County: near Davis, Blackwater Falls State Park, 1 AMNH. Cabell County: 3 mi . E Huntington, 1 USNM; $36 / 10 \mathrm{ml}$. E Huntington, 1 USNM. Maryland: Plummers Island, 2 USNM. Montgomery County: Bethesda, 2 USNM; Boyds, 1 USNM; Cabin John, 3 USNM; "Montgomery County" (general designation), 3 USNM. Howard County: Long Comer, 2 USNM. Prince Georges County: Beltsville, 2 USNM; Bladensburg, 1 USNM; Branchville, 4 USNM; Greenbelt, 2 USNM; Laurel, 36 USNM. Anne Arunde? County: Patuxent Research Lodge, 1 USNM. Charles County: Indian Head, 1 AMNH; Newport, 2 USNM. "Maryland," (general designation), 2 USNM. Washington, D. C.: Bennings, 12 USNM; Chain Bridge, 1 USNM; Cleveland, I USNM; Cleveland Park, 5 USNM; Rock Creek, l USNM; Washington Market, 1 USNM; "Washington D. C." (general designation), 3 USNM. Virginia: Clarke County: "Clarke County" (general designation, 1 USNM. Fairfax County: Bush Hill, 2 USNM; Dunn Loring, 1 USNM; Mt. Vernon, 2 USNM. (Ind. City): Falls Church, 1 USNM.

Arlington County: Arlington, 1 USNM. (Ind. City): Alexandria, 1 USNM. Albemarle County: Covesville, 1 AMNH. Powhatan County: Pilkinton, l USNM; Butterwood Creek, Powhatan, I USNM. Chesterfield County: Chesterfield, l USNM; Skinquarter Creek, 1 USNM. Dickenson County: 5 mi . $S$ Haysi, 1 USNM. (Ind. City): Newport News, 1 AMNH. Norfolk County: Dismal Swamp, 1 USNM. Rockbridge County: Blackburg, 7 USNM. Nelson County: "Nelson County" (general designation), 2 USNM. Warwick County (sic), 2 USNM. Kentucky: Madison County: Berea, 1 USNM; Round Hill, 2 USNM. Trigg County: Canton, I USNM. Oklahoma: Grant County: $15 \mathrm{mi} . S$ Enid, 1 TCWC. Tulsa County: Red Fork, 2 USNM. Dewey County: 10 mi . NW Canton, 1 KU . Custer County: Weatherford, 1 KU ; $1.25 \mathrm{mi} . \mathrm{W}$ Weatherford, 1 KU . Oklahoma County: Oklahoma City, l USNM. Pottawatomie County: Little R., 7 mi . SE Tecumseh, I KU. Washita County: $3 \mathrm{mi} . E, 9 \mathrm{mi} . S$ Weatherford (Custer County), 1 KU . Cleveland County: Norman, $1 \mathrm{KU} ; 3 \mathrm{mi} . \mathrm{S}$ Norman on S . Canadian River, J. KU; 3 mi . SE Norman on S. Canadian River, 1 KU. Pittsburg County: Hartshorne, 7 USNM; Savanna (Ind. Terr.), 1 USNM. Latimer County: Red Oak 3, USNM. Caddo County: Fort Cobb, 3 USNM. Comanche County: Fort Sill Game Refuge, I USNM; Mt. Scott, 15 USNM; Wichita Mts. Refuge, 6 USNM; Wichita National Forest, 1 KU. Carter County: $4 \mathrm{mi} . \mathrm{S}, 1 / 2 \mathrm{mi}$. E Ardmore, 1 KU . Arkansas: Washington County: Fayetteville, 2 USNM; 2 mi . SW Winslow, 1 KJ ; near Winslow, 1 KU . Arkansas County: Stuttgart, 1

USNM. Tennessee: Tennessee River (general designation), 1 USNM. Montsomery County: Clarksville, 3 USNM. Sumner County: Hockland, 1 USNM. Houston County: Danville, 1 USNM. Grainser County: Thorn Hill, 2 USNM. Carter County: Roan Mountain, 1 USNM. Benton County: Big Sandy, I USNM. Sevier County: $21 / 2 \mathrm{mi}$. NW Pigeon Forge, 2 AMNH. Giles County: Frankewing, 1 USNM. North Carolina: Mitchell County: Roan Mountain, 2 USNM. Haywood County: Cataloochee Ranch, 1 USNM. Wake County: Apex, 1 USNM; Raleigh, 4 USNM. Dare County: Hatteras, 4 AMNH; Stumpy Point, I USNM. Transylvania County: Pisgah National Forest, 12 USNM. Cabarrus County: Concord, 1 USNM. Harnett County: Liliington, 4 AMNH . Craven County: 5 mi . SE Van Bern, 1 USNM. South Carolina: Pickens County: Easley, $6 \mathrm{mi} . \mathrm{N}$ Wolf Creek, 1 USNM; Walhalla, 2 USNM. Charleston County: Christ Church Parish, 1 USNM. Sumter County: Rembert, 2 LSUMZ; $3 \mathrm{mi} . \operatorname{Sembert,~} 1$ LSUMZ. Georgia: Dooly County: Flint River, Vienna, 1 USNM. Talbot County: 2 mi. S Geneva, 2 USNM; $11 / 2$ mi. W Jackson City, 2 KU . Alabama: Colbert County: $10 \mathrm{mi} . \mathrm{N}$ Leighton, 1 USNM; Leighton, 1 USNM. Cullman County: Ardell, 4 USNM. Tallảega County: Sylacuga, 4 USNM. Mississippi: Lee County: 1 mi . W Tupelo, 1 Lsumz. Bolivar County: 5 mi . E Hushpuckana, 1 LSUMZ; Lobdell, 2 USNM. Noxubee County: "Noxubee County" (general designation), 1 USNM. Sharkey County: Washington, 1 USNM. Louisiana: Bossier Parish: 2 mi . NE Red Point, 1 LSUMZ; West Carroll Parish: $11 / 4 \mathrm{mi}$.

W Oak Grove, 1 LSUMZ. Lincoln Parish: Hico, 1 LSUMZ. Ouachita Parish: Monroe, 1 LSUMZ. Bienville Parish: 0.5 mi. N Arcadia, 1 LSUMZ. Texas: Potter County: $8 \mathrm{mi} . \mathrm{N}$ Amarillo, I TCWC. Wichita County: Midwestern Farm, 1 KU ; 3.mi. SE Iowa Park, I KU. Cooke County: Gainsville, 3 USNM. Archer County: 13 mi . NE Maybelle, 1 KU . Tarrant County: 3 mi . E Keller, 1 TCWC. Palo Pinto County: Brazos, 3 USNM. Henderson County: 6 mi. NW Athens, 1 TCWC. E1 Paso County: El Paso, 1 USNM. Hill County: $4 \mathrm{mi} . \mathrm{n}$ Blums, I KU. Limestone County: I mi. N Navasota River, 4 mi. NE Groesbeck, 1 TCWC. Menard County: Menard, 2 USNM. Burnet County: "Burnet County" (general designation), l USNM. Brazos County: 4 mi. W Bryan, 1 TCWC; 2 mi. NW Bryan, 1 TCWC; Bryan, 1 TCWC; 2 mi. N College Station, 1 TCWC: 7 mi. W College Station, l TCWC; 5 mi . W College Station, 1 TCWC; $3 / 4 \mathrm{mi}$. W College Station, 1 TCWC College Station; 5 TCWC; 5 ml . SW College Station, 2 TCWC. Walker County: 7 ml . WNW Huntsville, 1 TCWC; 17 mi . SW Huntsville, 3 TCWC. Trinity County: 1.3 m . E Trinity, 1 TCWC. Kimble County: 4 mi . NE Junction, $1 \mathrm{TCWC} ; 10 \mathrm{mi}$. NE Junction, 1 USNM. Mason County: Mason, 6 USNM. Burleson County: 6 mi. E Caldwell, 1 TCWC. Washington County: $111 / 2 \mathrm{mi}$. SW Brenham, 2 TCWC; $10 \mathrm{mi} . W$ Brenham, 2 TCWC. Kerr County: 20 mi . W Mountain Hone, $3 \mathrm{TCWC} ; 20 \mathrm{mi}$. W Hunt, 2 TCWC; 40 mi. W Kerrville, 2 TCWC; Ingram, 2 USNM; 2 mi. V Kerrville, 1 TCWC; Kerrville, 1 USNM. Kendall County: Waring (S. side

Guadalupe River), 2 USNM. Medina County: Rio Medina, 7 mi. N Castroville, 3 KU ; Rio Medina, 4 mi . N Castroville, 1 KU . Bexar County: San Antonio, 7 AMNH; $10 \mathrm{mi} . S$ San Antonio, 1 AMNH; $15 \mathrm{mi} . S$ San Antonio, 1 AMNH; $18 \mathrm{mi} . \mathrm{S}$ San Antonio, 1. AMNH; "Bexar County" (general designation), 1 AMNH. Karnes County: Runge, 1 USNM. Atascosa County: Benton, 8 KU. "West Texas," 1 USNM. Idaho: Lemhi County: $2 \mathrm{mi} . W$ Salmon, I USNM. Oregon: Umatilla County: Pilot Rock, I USNM. California: Riverside County: 1 mi. S Riverside, 2 KU . Los Angeles County: Culver City, 1 USNM. Arizona: Pima County: Fort Lowell Road (Tucson), 1 UA. New Mexico: Valencia County: Belen, I MSE.

## Didelohis virginiana pigra Specimens examined.--287 UNTIAD STATES. South

 Carolina: Beaufort County: Hilton Head Island, I USNM; "Beaufort County" (general designation), 3 USNM. Georgia: Chatham County: "Chatham County" (General designation), 1 USNM. Líbeyty County: Riceboro, Le Conte Plantation, 1 USNM; "liberty County" (general designation), 1 USNM. Dougherty County: Pretoria, 1 USNM. Tift County: Tifton, 1 USNM. Glynn County: St. Simon Island. 2 USNM. Thomas County: Thomasvilles 15 AMNH; Boston, 7 AMNH: Metcalfe, 9 AMNH: "Thomas County" (general designation), 22 AMNH. Charlton County: Big Water (Okefenokec Swamp), I USNMg Fioyds Island (Okefenokee Swamp), 3 AMNH. Berrien County: Nashville, 2 USNM. Alabame: Conecuh County: Castleberry,2 USNM. Baldwin County: Bon Secour, 1 USNM. Mobile County: Mobile, 1 AMNH. Mississippi: Forrest County: 2 mi . NE Petel, 1 LSUMZ. Hancock County: Bay St. Louis, 3 USNM. Harrison County: Pass Christian, 9 AMNH; Mississippi City, 1 LSUMZ. "Gulf Coast," 4 AMNH. "Southern part," 2 AMNH. Louisiana: Natchitoches Parish: Cypress, 1 LSUMZ; Kisatchie, 4 IsUMZ; Natchitoches, 1 LSUMZ; Vowells Mill, 1 LSUMZ; Provencal, 4 LSUMZ. Sabine Parjsh: 2 mi. NW Toro, 1 LSUMZ. Rapides Parish: $15 \mathrm{ml}, \mathrm{S}, 4 \mathrm{mi} . \mathrm{NE}$ Alexandria, Forest Hill, 1 LsumZ. Avoyelles Parish: Hwy. Belledeaux, 3.5 mi . on Hessmer, 4 LSUMZ; 10 mi . N Marksville, 1 LSUMZ. Beauregard Parish: 6 mi. S Sugartown, I ISUMZ. St. Landry Parish: 3 mi . $S$ Palmetto, 1 LSUMZ. Pointe Coupee Parish: Fordache, I LSUMZ; Lakeland, I Lsumz. W. Feliciana Parish: 8 mi . NE St. Francisville, 1 LSUMZ; Cornor, 1 LSUMZ. E. Feliciana Parlsh: Jackson, 1 AMNH, 2 LSUMZ. St. Helena Parish: $2 \mathrm{mi} . \mathrm{S}$ Greensburg, 1 ISUMZ. Tangipahoa Parish: Loranger, 1 LSUMZ; $11 / 4 \mathrm{mi}$. W ponchatoula, I ISUMZ. Washington Parish: $21 / 10 \mathrm{mi} . \mathrm{N}_{\mathrm{g}} 32 / 1.0 \mathrm{mi}$. W Varnado, 1 LSUMZ; $5 \mathrm{mi} . W$ Varnado, 1 LSUMZ; $11 / 2 \mathrm{mi} . W$ Varnado, 1 LSUMZ; 1 mi. E Varnado, 1 LSUMZ; Bogalusa, 1 LSUMZ. West Baton Rouge Parish: ca. 1 mi . $S$ Port Allen, 1 LSUNZ. Eest Baton Rouge Parish: Zachary, 1 LSUMZ; 7 mi. SW Zachary, 1 LSUMZ; $1 / 2 \mathrm{mi} . W$ LSU Campus, Baton Rouge, 1 USNM; $31 / 4 \mathrm{mi}$. NE University (Baton Rouge), 1 IsUMZ; Baton Rouge, $1 \rightarrow$ LSUNZ; $1 / 2 \mathrm{mi} . W$ University (Baton Rouge), 1 Insumz; University, $1 / 2$ mi. W Bellview Subaivision (Baton Rouge), 2 LSUMZ; ISU

Campus (Baton Rouge), 4 LSUMZ; 7 mi. E University, I LSUMZ;
1 mi. $S$ IsU Campus (Baton Roure), 2 LSUMZ; $2 \mathrm{mi}$.S LSU
Union, 1 LSUMZ; 4 mi . ESE University (Baton Rouge), 1
IsSUMZ; 2 mi. $\mathrm{S}, 6 \mathrm{mi} . \mathrm{E}$ University, 1 LSUMZ; 3 mi. S
University, 1 LSUMZ; $3.3 \mathrm{mi} . \operatorname{SE}$ LSU, 1 LSUMZ; $4 \mathrm{mi.S}$
LSU Campus, 1 LSUMZ; $4 \mathrm{~J} / 2 \mathrm{mi} . S$ University, 1 LSUMZ;
5 mi . S University, 1 LSUMZ; 5 mi . ESE Baton Rouge, I ISUMZ;
9 mi. S University on River Road, 1 LSUMZ; $12 \mathrm{mi} . \mathrm{S}$
University, 1 LSUMZ; Kleinpeter, 1 LSUMZ; 12 ml . S ISU
Campus, Baton Rouge, 1 USNM; 1 mi. W Pride, 1 LSUMZ.
Iivingston Parish: $4 \mathrm{mi} . \mathrm{N}$ Denham'Springs, 1 LSUMZ;
3 mi. S Denham Springs, 1 LsUMZ. St. Tamrany Parish: 16
mi. E Hammond, 1 LSUMZ; Salt Bayou, 2 LSUMZ; $3 / 10 \mathrm{ml}. \mathrm{S}$, $2 / 10 \mathrm{mi}$. E Pearl River, 1 LSUMZ. Calcasieu Parish: Vinton,

1 LSUMZ; Sulphur, 1 ISUMZ; $11 / 2 \mathrm{mi}$. E Sulphur, 1 LSUMZ;
Lake Charles, 1 AMNH, 1 LSUMZ; Iowa Station, I USNM;
"Calcasieu Parish" (general designation), I USNM. Lafayette
Parish: Lafayetie, 1 USNM. Iberville Parish: $2 \mathrm{mi} . \mathrm{S}$ Grosse Tete, 1 ISUMZ. Ascension Parish: 3 mi. $S E$

Donaldsonville, 1 ISUMZ; $31 / 4 \mathrm{mi} . S$ Gonzales, 1 LSUMZ; 1 mi. S Burnside, 1 LSUMZ; 2 mi. SE Burnside, I LSUMZ;

Sorrento, 1 LSUMZ; $3 / 4 \mathrm{mi}$. E Sorrento, 1 LSUMZ. Cameron Parish: Cameron, 2 LSUMZ. Vermilion Parish: $20 \mathrm{mi} . \mathrm{SW}$ Abbeville, l USNM. St. Charles Parish: Bommet Carre Spillway, I LSUMZ. Orleans Parish: 1500 blk. Robert E. Lee (New Orleans), 1 LsumZ. St. Mary Pardsh: Morgan City, 3 USNM. Lafourche Parish: 5 mi. NE Mathews, 1 LSUMZ.

Terrebonne Parish: 1/2 mi. W Schriever, 1 ISUMZ; Grand Caillou, 1 LSUMZ; Houma, 2 USNM. Texas: Hardin County: 7 mi. NE Sour Lake, 4 USNM; 9 mi. NE Sour Lake, 1 USNM. Liberty County: Liberty, 1 USNM; Tarkington, 2 USNM. Austin County: 5 ml . N Bellville, 1 TCWC. Harris County: 2 1/2 mi. N Hockley, 3 TCWC; 4 mi. N Huffman, l TCWC. Colorado County: 3 mi. NW Altair, 1 TCWC; 6 mi . N Eagle Lake, 1 TCWC. Galveston County: Dickinson Bayou, opposite Galveston, 1 USNM; Virginia Point, 1 USNM. Iavaca County: Maddox Ranch, 15 mi. $S$ Hallettsville, 1 TCWC; l/2 mi. W Sweet Home, 1 TCWC. DeWitt County': $10 \mathrm{ml} . W$ Cuero, 1 TCWC. Victoria County: 2 mi . NE Victoria, 1 ISUMZ. Matagorda County: Matagorda, 2 USNM; Deming Station, 3 USNM; "Matagorda County" (general designation), 1 USNM. Brazoria County: Velasco, I USNM. Calhoun County: Port Lavaca, 1 USNM: ${ }^{\prime}$ Connorsport, 1 USNM. Florida: Jackson County: 4 mi. W Marianna, $1 \mathrm{KU} ; 5 \mathrm{mi} . \mathrm{N}$ Sneads, 2 AMNH. Liberty County: Torreya State Park, 1 AMNH. Leon County: vicinity Tallahassee, 1 AMNH; 10 mi . SE Tallahassee, St. Mark's River, 2 AMNH. Franklin County: Carrabelle, 1 USNM. Alachua County: Gainesville, 2 AMNH. Marion County: Ocala, Lynne Planking Sta., 1 USNM; Lake Bryant, Ocala National Forest, l USNM. Citrus County: l mi. SW Homosassa Springs, 1 AMNH. Brevard County: Florida: St. John's River, 1 AMNH. Hillsborough County: St. Petersburg, 1 AMNH; Ruskin, 3 KU ; Lake Harney, 3 USNM. Pinellas County: 4 mi. S Indian Rocks, 1 KU . Polk County: Sawgrass Island,

6 USNM. Osceola County: Kenansville, 1 USNM. Indian River County: Sebastian, 1 USNM. DeSoto County: Kissimmee River, 5 USNM; Fort Kissimmee ( 3 mi . N Orange Hammock), 2 USNM. Charlotte County: $10 \mathrm{mi} . \mathrm{S}$ Punta Gorda, 1 KU . Colliex County: Little Marco (West Coast), 1 AMNH; 10 mi . N Everglades, 1 USNM. Hendry County: 1 mi. E Denaud, 1 KU . Dade County: $5 \mathrm{mi} . \mathrm{S}$ Miami, 1 AMNH; Homestead, 2 USNM. Monroe County: Key West, 1 USNM; Big Pine Key, 2 USNM; Key Largo, 1 USNM. (County not known): Lake Kissimmee River, 1 USNM; Fort Gardner, Kissimmee River, 2 USNM; Iake Kissimmee, 1 USNM; Lake Hatchineha', 1 USNM. "Florida," 1 AMNH.

## Didelphis virginiana californica

Specimens examined. -869 UNITED STATES: Texas:
Wiilacy County: County line Rd. between Willacy and Cameron Counties, 2 mi. E Sebastian, 1 (skin with skull), UA 17586. Val Verde County: Del Rio, 4 ( 3 skins with skulls, 1 skull) USNM 18341/25222, 18342/25223, 126881, 127586; Devil's River (under Amistad Reservoir), 1 (skin with skull), USNM 117533. Nueces County: Corpus Christi, 7 ( 3 skins with skulls, 2 skins, 2 skulls), AMNH 1021, 3519, 3520, USNM 31415/43280, 99907, 99908, 116956; Nueces River, 1 (skin with skull), USNM 31.909/43770; Nueces Bay, 3 (1 skin with skull, 1 skull, 1 Jaw), USNM 31908/43769, 43547, 43805; $11 \mathrm{m1}$. SE Corpus Christi, 1 (skin with skull), TCWC 779. Maverjek County: Eagle Fass, I (skin with skull), USNM 24358/31764. Kinney

County: Fort Clark, 11 (10 skins with skulls, 1 skull), USNM 63130-63135, 143135-143139; Mouth of Sycamore Creek, 1 (skin with skull), USNM 24359/31765. Jim Wells County: Alice, 1 (skin with skull), USNM 31414/43279. Hidalgo County: Edinberg, 1 (skin with skull), LSUMZ 13393; ca. 6 mi. S Mission, 1 (skin with skull), ISUMZ 15161. Dimmit County: Catarina, 2 (skins with skulls), TCWC 4472, 20838; San Rogue Creek, 8 mi . E Catarina, 1 (skin with skull), TCWC 6571. Aransas County: Rockport, 3 (skins With skulls AMNH 7274/5878, 7275/5879, 14826. Cameron County: "Washington County," 1 (skull), USNM 7495; "Washington County," Long Point, 1 (skull), USNM 7740; 16 mi . SE Brownsville (toward mouth of Rio Grande), 1 (skin with skull)y USNM $14909 / 38852$; Brownsville, 12 ( 8 skins with skulls, 1 sking 3 skulls), AMNH 3286/2565, 182979, KU 36-38, UCLA 11571, USNM 29791/41871, 32691/44614, 33131/45135, 33132/45136, 41820, 45137; "Cameron County" (general designationl, 2 (skulls), UCLA 11575, 11576; "Lower Rio Grande," 1 (skull), USNM 1171. MEXICO: Sonora: Oputo, 1 (skin), USNM 251115; Ures, 1 (skin with skull), UCLA 51069; Hermosillo, 1 (skin with skull), USNM 33705/45740; I mi. E Soyopa, I (skin with skull), UA 265; I mi. S El Novillo, east bank Río Yaqui, 1 (skull), MSB 19055; Canoa, Río Mayo, 4 (skins with skulls), MVZ 8526l-85264; Tesia, 1 (skin with skull), UCLA $16946 ; 1 / 2 \mathrm{mi} . \mathrm{N}$ La Aduana, 1 (skull), MSB 9356; "Alamos region," 1 (skin with skull), MSC 902. Chyhuahua: near Batopilas, 1 (skin with skull),

USNM 96224. Coahuila: La Gacha, 1 (skull), KU 67277; 1/2 mi. S Sabinas, 1 (skin with skull), KU 34543; Monclova, 1 (skull), KU 34890; 1 mi. SW San Pedro de Las Colonias, 1 (skull), KU 40194; 1 mi. N San Lorenzo, l (skull), KU 40195. Nuevo León: near Golondrinas, 1 (skull), USNM 33033; El Obispado, Monterrey, 1 (skin with skull), IB 1193; Monterrey, 5 ( 4 skins with skulls, 1 skull), IB 1239, USNM 25558/32951, 25559/32952, 25560/32953, 25735/33135; Aguaje del Lobo, $10 \mathrm{mi} . S$ Monterrey, 1 (skin with skull), MVZ 91164; Hacienda La Barranca, Rio San Juan, 1 (skin with skull), KU 100195; Hacienda Vargas, Río San Juan, 2 (sxins with skulls), KU 100196, 100197; Ranch Chapotal, Río San Juan, 1 (skin with skull), KU 100198; 20 km . NW Montemorelos, 1 (skin with skull), TCWC 2749. Tamaulipas: Matamoros, 4 (1 skin with skull, 3 skulls), USNM 138/1121, 1401, 1402, 1404; El Mulato, 5 ( 4 skins with skulls, l skull), UMMZ 61548-61551, 61562; San Fernando, I (skin with skull), KU 88267; Villa Mainero, 2 (l skin with skull, 1 skull), KU 88265, 88266; $36 \mathrm{~km} . \mathrm{N}, 10 \mathrm{~km} . \mathrm{W}$ Ciudad Victoria ( $1 \mathrm{~km} . \mathrm{E}$ El Barretal on Río Purificación), 2 (skins with skulls), AMNH 146770, KU $36938 ; 12 \mathrm{~km} . \mathrm{N}, 4 \mathrm{~km}$. W Ciudad Victoria (near Laredo-Ciudad México Highway), 1 (skin with skull), KU 36939; Victoria, 1 (skull), USNM 119995; 3 mi. N Soto la Marina, 1 (skin with skull), KU 54914; Sierra de Tamaulipas, $10 \mathrm{mi} . \mathrm{W}, 2 \mathrm{mi} . \mathrm{S}$ Piedra, 7 (2 skins with skulls, 5 skulls), KU 54915-54921; 4 mi. N Jaumave, 1 (skull), KU 54922; Altamira, 5 (4 skins with skulls, 1
skull), USNM 92962-92964, 94092, 95962. Sinaloa: Sierra de Choix, 50 mi. NE Choix, 1 (skin with skull), USNM 96225; 3 mi. NE San Miguel, 1 (skin with skull), KU 84943; Culiacan, l (skin with skull), USNM 96820; $3 \mathrm{mi} . \mathrm{N}$ El Dorado, 1 (skin with skull), KU 75183; 6 mi. SW (sic) Mazatlán, AMNH 146986; near Mazatlán ( $=9$ mi. SE Mazatlán), 2 (skins with skulls), USNM 96821, 96822; Copala, 7 (skins with skulls), LACM 8809-8813, 8963, 8964; 1 km. E Santa Lucia, 1 (skin with skull), KU 67278; 1 km. NE Santa Lucia, 7 ( 5 skins with skull; 2 skulls), KU 93973-93979; El Batel, $70 \mathrm{~km} . \mathrm{NE}$ Mazatlán, $2(s k i n s ~ w i t h ~ s k u l l s), ~ M V Z ~ 106114, ~ 106115 ; ~ ; ~$ Rosario, 1 (skin with skull), USNM 91170; Escuinapa, 47 ( 30 skins with skulls, 9 skins, 8 skulls), AMNH 24033-$24045,24715,24717-24730,24821-24826,24862-24870$, 25947, 25948, USNM 98077; "Sinaloa" (general designation), 1 (skin with skull), UA 9058. Durango: Chacala, l (skin with skull), USNM 96819. Zacatecas: San Juan Capistrano, 1 (skin with skull), USNM 90988; $8 \mathrm{mi} . \mathrm{S}$ Moyahua, 1 (skin with skull), CAS 13136. San Luis Potosí: El Salto, Río Naranjo, 3 (skins with skulls), AMNH 176701, LSUMZ 2741, 15107; ca. 5 km . W (by road) El Naranjo, l (skin with skull), LSUMZ 15106; 19 km. SW Ebano, 1 (skull), LSUMZ 4774; Bledos, 12 (skulls), LSUMZ 4761-4772; Hacienda Capulín, 1 (skull), ISUMZ 4684. Nayarit: Acaponeta, 1 (skin with skull), USNM 91169; $5 \mathrm{mi} . ~ S S W$ Rosa Morada, 1 (skull), KU 64450; Crucero de Solquipa, ca. 8 mi. E (by road) San Blas, 1 (skin with skull), LSUMZ ll902; 9 km. E San Blas, l (skin
with skull), IB 5719; Alticama (sic), 1 (skull), KU 36366; 1/2 mi. N Alticama (sic), 2 (skuils), KU 36364, 36365; Tepic, 1 (skin with skuil), USNM $88143 ; 8$ mi. SSW Las Varas, 1 (skin with skull), KU 64451. Jalisco: $5 \mathrm{mi} . \mathrm{NE}$ Huejuguilla, 1 (skull), KU 109467; Chinampas, 1 (skull), KU 112030; San Sebastian, 1 (skin with skull), USNM 88142; 4 mi. NNE Puerto Vallarta, 3 (skins with skulls), KU 6445264454; 1 mi. WNW Tequila, 1 (in alcohol), KU 36921; Etzatlán, 11 (skins with skulls), USNM 34501/46586-34511/ 46595; 3 mi. N Guadalajara, 1 (skull), KU 30817; Guadalajara, 6 (skins with skulls), ANNH 16625-16630; 2 mi. SW Tapatitlán, 3 (in alcohol), KU 63135-63137; $2.5 \mathrm{mi} . \mathrm{E}$ Tepatitlán, 3 (1 skin with skull, 2 skulls), KU 62302-62304; Ameca, 2 (skulls), USNM 87059, 87060; 3 mi. ENE Santa Cruz de las Flores, 1 (skull), KU 30818; 19 mi. SW Guadalajara, 2 (skins with skulls), KU 36362, $36363 ; 5 \mathrm{mi}$. SW Arandas, 1 (skin with skull), KU 62305; Huascato, 1 (skin with skull), AMNH 115621; Ocatlán, l (skin with skull), USNM 120098; 1 mi. S Ocotlán, 1 (skull), kU 30820; Atemajac, 2 (skins with skulls), USNM $34338 / 46429,34339 / 46430 ; 2.5 \mathrm{mi}$. NNE Autlán, 1 (skull), KU 30819 ; $8 \mathrm{mi} . \mathrm{S}$ Purifaction (sic), I (skull), KU 33316; $2 \mathrm{mi} . \mathrm{N}$ Ciudad Guzmán, 4 (skulls), KU 30821, 36367-36369; Zapotlán, 1 (skin with skull), USNM 33517/ 45562; Estancia, 6 (skins with skulis), AMNH 25181-25183, 25185-25187; Las Canoas, 1 (skin with skull), AMNH 26017; Los Masos, 4 ( 2 skins with skulls, 2 skins), AMNH 2724327246; Río Santa María, 2 (skins with skulls), AMNH 25184,

25188; "Wakenakili" (sic), I (skin with skull), AMNH 25852; La Mesa María de León, 1 (skull), KU 107131. Guanajuato: Celaya, 2 (1 skin with skull, 1 skull), USNM 78428, 78481. Queretaro: Jalpan, 1 (skin with skull), USNM 81449. Hidalgo: Tasquillo, 3 ( 2 skins with skulls, 1 skull), IB 12, TCWC 2750, 2751; Ixmiquiltán (sic), l (skin with skull), USNM 81726; Pachuca, 4 (2 skins with skulls, 2 skulls), USNM 26418/33831, 26419/33832, 51865, 52699; Real del Monte, 1 (skin with skull), USNM 26420/33833; Tulancingo, 2 (1 skin with skull, 1 skull), USNM 55581, 55582. Veracruz: 6.5 km . NNW El Higo, l (skin with skull), IB 10775; 1 km . NNE EI Higo, 1 (skin with skull), IB 10774; Tuxpan, l (skull), KU 82840; $121 / 2 \mathrm{mi} . \mathrm{N}$ Tihuatlán, 1 (skull), KU 88268; $5 \mathrm{~km} . \mathrm{S} \mathrm{Tihuatlán}$,4 (skulls), KU 2339223394, 23396; $4 \mathrm{~km} . W$ Tlapacoyan, 1 (skull), KU 23403; Las Vigas, 1 (skin with skull), USNM 54280; 2 km . E Perote, 1 (skin with skull), KU 19050; $5 \mathrm{~km} . \mathrm{N}$ Jalapa, 2 (skins with skulls), KU 19052, 19053; Jico, 1 (skin with skull), USNM 54989; Mirador, l (skull), USNM 58692; $24 \mathrm{mi}$. S Veracruz, 1 (skin with skull), AMNH 203560; Río Atoyac, 8 km. NW Potrero, 2 (l skin with skull, 1 skull), KU 17686, 17688; Orizaba, 10 (3 skins with skulls, 7 skulls), USNM $7846 / 38853,58159 \cdots 58165,58415,58416 ; 7 \mathrm{~km}$. SE San Juan de la Punta, 2 (skins with skulls), KU 19058, 19059;
 (skin with skull), AMNH 172164; Río Blanco, $20 \mathrm{~km} . W$ Piedras Negras, 4 (2 skins with skulls, 2 skulls), KU 17687-17690,

19063； 15 mi．N San Andrés Tuxtla， 3 （skins with skulls）， AMNH 1721．57－172159；Tapalapan，Sierra San Andrés Tuxtla，l （skin with skull），MVZ $121179 ; 15 \mathrm{~km}$ ．NE Catemaco， 2 （skeletons），IB 7922，7933；Catemaco， 2 （l skin with skull， 1 skull），IB 7930，USNM 65956；Lake Catemaco， 2 （1 skin with skull， 1 skull），AMNH 172167,$172174 ; 1 \mathrm{~km}$ ．E Catemaco， 1 （skeleton），IB 7926； 1 km 。 S Catemaco，l（skull），IB 7949； Coatzacoalcos，l（skin with skull），KU 66269；Pasa Nueva （see Hall and Dalquest，1963：184）， 2 （skins with skulls）， AMiNH 17175，17176；Minatitlán，l（skin with skull），USNM 78123； 20 km ．ENE Jesús Carranza， 1 （skulı），KU 32049； 25 km．SE Jesús Carranza， 2 （skulls），KU 32050，32051； 34 km． SE Jesús Carranza， 1 （skull），KU 23409．Colima：Colima， 7 （1 skin with skull， 6 skulles），USNM 23269／45274，45294－ 45298,$45300 ; 4 \mathrm{mi} . S W C o l i m a, ~(s k i n ~ w i t h ~ s k u l l), ~ K U ~$ 39458；Hacienda Magdalena， 8 （7 skins with skulls， 1 skull）， AMNH 1．71912－171918，USNM 45299； 5 km ．NE Santiago，l（skin with skull），KU 87660；Manzanillo， 9 （skins with skulls）， USNM $32635 / 44558-32640 / 44562,32645 / 44568,32646 / 44569$ ， 33226／45231；Armeria， 8 （ 5 skins with skulls， 3 skulls）， USNM 33264／45269－33268／45273，45291－45293；＂Colima＂（general designation）， 1 （skin），USNM 7022．Michoacán：Hacienda EI Molino，Negrete，l（skin with skull），USNM 20443／35673； Querendaro， 4 （ 3 skins with skulls， 1 skuil），USNM 35526／ 47810－35528／47812，50832；Jiquilpan，1（skin with skull）， KU 62306； 1 km ．S Tzintzuntzan， 1 （skull），IB 7921； $3 \mathrm{mi} . N$ Pátzcuaro， 1 （skin with skull），MVZ 100063； 2 mi．W

Pátzcuaro, 2 (skins with skulls), MVZ 100064, 100065; Pátzcuaro, 1 (skin with skull), USNM 34911/47176; $5 \mathrm{mi} . \mathrm{S}$ Pátzcuaro, 1 (skin with skull), MVZ 100066; La Salada, 2 (skins with skulls), USNM 126166, 126167; 2 mi. N Nueva Italia, 2 (skulls), KU 39459, 39460; near La Huacana, 1 (skull), USNM 126688; $13 / 4$ mi. S Tacambaro, l (skin with skull), MVZ 100074; 1 mi. E, 6 mi. S Tacambaro, 1 (skin with skull), MVZ 100067. México: San Cayetano, 2 (1 skin, 1 skull), IB 1312, 7072; Teotihuacan (cave near Pyramid of the Sun), 1 (skull), IB 7456; Salazar, 1 (skin with skull), USNM 36169/48513; Amecameca, l (skin with skull), USNM 51506. Districto Federal: Bosque de Chapultepec, Ciudad México, 3 (skins with skulls), IB 5, 437, KU 27979; Pedregal de San Ancel, Ciudad México, 3 (skins with skulls), IB 137, 795, 8736; Tlapan, 4 (3 skins with skulls, I skull), KU 66268, USNM 50062-50064. Morelos: Joya de Atexcapa, Lagunas de Zempoala, I (skin with skull), IB 1344; Cerro Cuautepet1, Lagunas de Zempoala, 3 (2 skins with skulls, 1 skin), IB 1967-1969; Cerro Zempoala, l (skin with skull), IB 9758; Cuernavaca, I (skin with skull), USNM 20921/36033; Xiutepec, 1 (skull), IB 7069; Yautepec, 2 (1 skin with skull, 1 skull), USNM 51124, 51125; Las Estacas, 1 (skin with skull), IB 6; Alpuyeca, 3 (skins with skulls), TCWC 4502-4504; Tequisquitengo, 7 (skins with skulls), AMNH 143565-143571. Puebla: Metlaltoyuca, l (skin with skull), USNM 92978; Huachinango (sic), 1 (skin with skuil), USNM 93042; Río Otlati, 15 km .

NW San Martin, 1 (skin with skull), TCWC 2753; San Martin, 2 (1 skin with skull, 1 skull); USNM 55579, 55580; Atlixco, 2 (skins with skulls), USNM 55320, 55321; Chalchicomula, I (skin with skull), USNM 53489; 4 mi. W Matamoros, 1 (skin with skull), KU 62307. Guerrero: El Limón, 1 (skin with skull), USNM 126715; Los Sabinos, 17 km . E Teloloapan, 1 (skin with skull), IB 6473; Buena Vista de Cuellar, 1 (skull), KU 66267; Ahuehuepa, I (skull), IB 7070; I mi. NW Omilteme, 1 (skin with skull), USNM 329397; Acahuizotla, 3 (skins with skulls), TCWC 4964, 4965, 5161; Agua de Obispo, 2 (I skin with skull, 1 skull), KU 99527, TCWC 5392 ; Río Aguacatillo, 30 km . N Acapulco, 1 (skin with skull), TCWC 2752; Acapulco, 6 (skins with skulls), USNM 70616-70620, 70657. Oaxaca: Tuxtepec, 5 (3 skins with skulls, 1 skin, 1 skull), USNM 65423, 65424, 65542, 65954, 65955; Reyes, 3 (skins with skulls), USNM 69590-69592; Cuicatlán, 5 (I skin with skull, 4 skulls), IB 7068, KU 32022, USNM 69798-69800; Vista Hermosa, 1 (skin with skull), KU 99529; Oaxaca, 1 (skin with skull), USNM 68196; 3 mi . ESE Oaxaca, 2 (skulls), $K U 68617$ s 68618; 15 mi. SW Oaxaca, 1 (skujl), KU 54345; Juchitan, 1 (skin with skull), USNM 9374/8660; La Ventosa, 2 (skins with skulls), ANNH 148964, 148965; Santa María de1 Mar, 4 (skins with skulls), AMNH 145179-145181, 145629; San Mateo del Mar, 1 (skull), USNM 73708; San Dionisio, Buena Vista, 1 (skin with skull), AMNH 145951; Guichicovi, 1 (skin with skull), USNM $73491 ;$ La GIoria (Santa María Chimalapa), 1 (skin with skull),

AMNH 145639; Tenango, 3 (skins with skulls), AMNH 148966148968; San Antonio, 5 (skins with skulls), AMNH 145641, 145955, 145957-145959; Potrero Gueladu, 1 (skin with skull), AMNH 145178; Guiengola, 1 (skin with skull), AMNH 145630; Salazar, 8 (skins with skulls), AMNH 143468, 143469, 145182, 145631-145634, 145953; La Presa, 2 (skins with skulis), AMNH 145635, 145636; Mixtequilla, 7 (skins with skuils), AMNH 143920-143926; Cerro de Mixtequilla, 2 (skins with skulls), AMNH 145175, 145176; Las Cuevas, 3 (skins with skulls), AMNH 143470, 145952, 145954; Las Tejas, 2 (skins with skulls), AMNH 145637, 145638; Las Pilas (between Cajon de Piedra and Tehuantepec), l (skin with skull), AMNH 145177; Tehuantepec, 3 (skins with skulls), AMNH 145628, USNM 73490, 73492; Cerro del Tigre, 1 (skin with skull), amnh 145956; Boca del Río (Tehuantepec), 12•(skins with skulls), AMNH 148952-148963; "Districto de Tehuantepec," 1 (skin with skull), AMNH 143974; Gueladu ( 9 mi. E Jalapa de Diaz), 1 (skin with skull), AMNH 148951; Jamaica Junction, km. 212 on Puerto Escondido Rd., l (skull), CAS 14309; Sinai ( $=10 \mathrm{~km}$. E Nopala), 1 (skin with skull), CAS 14939; Chacalapa, 1 (skull), KU 62308; 3 km . SW Colonia Rudolfo Figuroa, 1 (skull), CAS 14633; Tapanatepec, 2 (1 skin with skull, 1 skin), AMNH 176703, IB 2475. Tabasco: La Venta, l (skin with skull); uSNM 271102; Teapa, l (skin with skull), USNM 100509; 1 mi. E Teapa, 1 (skull), LSUMZ 7314. Chiapas: ca. 5 km . S Solusuchiapa, 3 (skins with skulls), LSUMZ 11906-11908; Tumbala, 4 (skins with skulls),

USNM 76211-76214; Pueblo Nuevo Solistahuacán, I (skin with skull), AMNH 172153; Yajalon, I (skin with skull), USNM 76210; El Real, 34 km . NE Altimirano, 1 (skin with skull), TCWC 8931; Yaxoquintela, 37 km . NE Altimirano, 1 (skin with skull), TCWC 8932; Ocuilapa, l (skin with skull), USNM 76203; Ocozocuautla, 1 (skin with skull), USNM 76202; Tuxtla, 1 (skin with skull), USNM 76204; San Cristóbal, 2 (skins with skulls), AMNH 172160, USNM 76209; 4 mi . S La Trinitaria, 1 (skin with skull), TCWC 8248; Valley of Comitán (=Hda. Juncana, ca. 22 mi. SE Comitán), l (skin with skull), USNM 76716; San José, 28 mi . ESE Comitán, 2 (skulls), MVZ 113484, 113485; San Bartolomé, 2 (1 skin With skull, 1 skull), USNM 133187, 133206; $14 \mathrm{~km} . \mathrm{NE}$ Tonalá, 1 (skull), IB 7931; $6 \mathrm{mi} . N W$ Tonalá, 1 (skull), KU 68619; Finca Ocuilapa, 10 km . SE Tonalá, 3 (skins with skulls), LSUNZ 11903-11905; Cerca Finca Prusia, I (skin with skull), IB 8; Huehuetán, 4 (1 skin with skull, 3 skulls), USNM 77687, 77688, 77875, 78001. Campeche: 1 km. SW Puerto Real, Isla del Carmen, 1 (skin with skull), KU 91450; Apazote, near Yahaltuma, 1 (skin with skull), USNM 108296; La Tuxpena, 2 (skins with skulls), USNM 181261, 181262; $65 \mathrm{~km} . \mathrm{S}, 128 \mathrm{~km} . E$ Escárcega, 1 (skuli), KU 93806. GUATEMALA: E1 Petén: Chuntuqui, 4 (skeletons), USNM 244907-244910; Libertad, 5 (skeletons), USNM 244911244914; 251161. E1 Quiche: 1 mi. NE Nebaj, 1 (skin with skul1), KU 64594. Huehuetenango: Nenton, 1 (skin with skull), USNM 76717; Jacaltenango, 3 (skins with skulls),

USNM 76713-76715; Barillas, $231 \mathrm{~km} .(b y$ road) N Quetzaltenango, 2 (l skin with skull, 1 skull), LACM (DRP 1276, 1386); El Benado (Sic), Río Ixcan, 16 km . E Barillas, 1 (skull), LACM (DRP 1309). Alta Verapaz: Chinaja, 2 (skulls), KU 81963, 81967. Escuintla: Finca Valles Lirios, Escuintla, 1 (skin with skull), USNM 275678. Santa Rosa: $5 \mathrm{mi} . S$ Chiquimulilla, 1 (skin with skull), KU 64595. "Guatemala" (general designation), 3 (skins with skulls), USNM 61211-61213. EL SALVADOR: Chalatenango: Los Esesmiles, 3 (skins with skulls), MVZ 130274-130276. Morazán: N slope Mt. Cacaguatique, 1 (skin with skull), MVZ 981.52; 2 mi. N Divisadero, l (skin with skulj), MVZ 130283; Divisadero, 2 (l skin with skull, l skin), MVZ 98150, 130279. San Salvador: San Salvador, I (skull), USNM 238705. San Miguel: Río San Miguel, 3 (skins with skulls), MVZ 130310-130312; Lake Olomega, 6 (skins with skulls), MVZ 130298-130303; SW edge Lake Olomega, 3 (skins with skulls), MVZ 98154-98156. HONDURAS: Atlantida: 7 mi. W La Ceiba, 1 (skin with skull), ICWC 14510; Yaruca, 1 (skin with skull), MCZ 10611; Lacetilla, 1 (skull), TCWC 11090. Cortéz: Chernelicón (sic), l (skin with skull), USNM 148'748; La Limon (sic), 1 (skin with skull), TCWC 11089; El Jaral, Lake Yojoa, l (skin with skull), AMNH 126139. Santa. Bárbara: $7 \mathrm{~km} . \mathrm{N}$ Santa Barbara, 1 (skull), TCWC 18552; Santa Bárbara, 2 (skins with skulls), AMNH 123284, 123285. Francisco Morazén: El Caliche Cedros, 2 (skins with skulls), AMNH 127565, 127566. Lempira:

Las Flores, Gracias, 6 ( 3 skins with skulls, 3 skulls), AMNH 128974, 128976, 128988, 129691, 129692, 129697. La Paz: Muin Intibuca, l (skin with skull), AMNH 126191; El Manteado, Intibuca, l (skin with skull), AMNH 126193; El Horno Intibuca, 2 (skins with skulls), AMNH 126190, 126192. Districto Central: Las Flores Archaga, 8 (skins with skulls), AMNH 126140, 126141, 126189, 126194, 1284.75128478; Tegucigalpa, 2 (skins with skulls), AMNH 123286, 126762. "Honduras" (general designation), 1 (skin), USNM 19463. NICARAGUA: Jinotega: Hacienda La Trampa, 16 km . E, $51 / 2 \mathrm{~km} . \mathrm{N}$ Jinotega, 23 (skulls), KU 99405-99421, 99423, 99425-99429. Comarca de Cabo: Rio Coco, 2 (1 skin with skull, 1 skin), AMNH 29255, 29272. Nueva Segovia: Jalapa, 1 (skin and skull), AMNH 29254; $11 / 2 \mathrm{~km} . \mathrm{N}, 1$ km . E Jalapa, 3 (skulls), KU 110614-110616. Chinandega: $61 / 2 \mathrm{~km} . \mathrm{N}, 1 \mathrm{~km} . E \operatorname{Cosiguina,~} 1$ (skull), KU 114458; E1 Paraiso, $1 \mathrm{~km} . \mathrm{N}$ Cosiguina, 1 (skull), KU 114459; Hacienda San Isidro, 10 km .5 Chinandega, 23 ( 7 skins with skulls, 16 skulls), KU 104533, 104534, 104536-104540, 104542-104544, 104546, 104548-104550, 104552-104554, USNM 337521-337526; San Antonio, ll (2 skins with skulls, 2 skulls, 7 in alcohol), KU 97319-97329. León: Hacienda Las Colinas, 4 km . WNW Puerto Momotombo, 13 ( 8 skins with skulls, 1 skin, 4 skulls), KU 104327-104330, 104350, UA 2505-2508, USNM 334582-334584, 337654. Matagalpa: Finca Tepeyac, $101 / 2 \mathrm{~km} . \mathrm{N}, 9 \mathrm{~km}$. E Matagalpa, 4 (skins with skulls), KU 104523, USNM 337530, 337531, 337541; Santa

María de Ostuma, 11 (1 skull, 10 in alcohol), KU 110618110628; Matagalpa, 7 ( 6 skins with skulls, l skin), AMNH 28405, 28406, 28962, 29251-29253, 29257; Lavala (=Savala), 2 (l skin with skull, 1 skull), AMNH 28408, 28410; 2 mi. SE Dario, l (skin with skull), TCWC 10579. Managua: Hacienda Corpus Christi, Chiltepec (sic), 16 (skins with skulls), UA 2499 , USNM $332423-332427,332429-332434,334578-$ 334581; 5 km . N Sabana Grande, 1 (skin with skuil), KU 97330; $1 \mathrm{~km} . \mathrm{N}$ Sabana Grande, 1 (skull), KU 114461; $3 \mathrm{mi} . ~ S W$ Managua, 11 ( 7 skins with skulls, 4 skulls), KU 70180-70183, 70185-70191; $5 \mathrm{mi} . ~ S W ~ M a n a g u a, ~ l(s k i n ~ w i t h ~ s k u l l), ~ K U ~$ 70192; 10 ml . SW Managua, 1 (skull), KU 70193; Hacienda Azacualpa, $5 \mathrm{~km} . \mathrm{N}, 2 \mathrm{~km} . W$ Villa El Carmen, 6 (skulls), KU 108213-108215, 108217, USNM 361205, 361206. Carazo: 3 km . N, $4 \mathrm{~km} . \mathrm{W}$ Diriamba, 1 (skull), KU 110650. Granada: Hacienda Mecatepe, $2 \mathrm{~km} . \mathrm{N}, 11 \mathrm{l} / 2 \mathrm{~km}$. E Nandaime, 10 (skulls), KU 108133-108140, 108142, 108143; La Calera, 3 km . s, $5 \mathrm{~km} . \mathrm{W}$ Nandaime, 1 (skull), KU 108146. Boaco: $8 \mathrm{~km} . \mathrm{N}$, $12 \mathrm{~km} . \mathrm{E}$ Boaco, 1 (skull), KU 110630. Chontales: Peña Blanca, 1 (skin), AMNH 29782; Villa Somoza, 1 (skull), KU 104427. Rivas: Finca Amayo, $13 \mathrm{~km} . \mathrm{s}, 14 \mathrm{~km}$. E Rivas, 31 ( 5 skins with skulls, 2 skins, 12 skulls, 12 in alcohol), KU 97331, 97333-97344, 104652-104666, 105651, USNM 337846, 337848; Sapoa, 1 (skull), KU 105882. Río San Juan: La Esperanza, $5 \mathrm{kra} .5,31 / 2 \mathrm{~km}$. E San Carlos, $1 .($ skull), USNM 361209. (Departamento unknown), Aloa, Lake Jiloa, l (skin with skull), ANNH 177021. "Nicaragua" (general designation), 2 (skuils), USNM 253502, 332428.

## Didelphis virginiana yucatanensis

Specimens examined. $--43 \mathrm{MEXICO}:$ Campeche: Campeche, 1 (skin with skull), USNM 100531; Champotón, 1 (skin with skull), KU 91447; 5 kms .5 Champotón, 1 (skin with skull), KU 91448. Yucatán: Mérida, 6 (skins with skulls), AMNH 30524, USNM 11422/37937, 11423/37938, 11424/37475, 11425/ 37939, 11850/38854; Izamal, 1 (skin with skull), USNM 172068; Chichén Itzá, 8 (skins with skulls), AMNH 30524 , 91172, 91174, 91176, 91177, 91180, MCZ 12370, USNM 108299; ca. I km. E Chichén Itzá, 2 (I skin with skull, l skull), LSUMZ 11909, 11910; "Yucatán Peninsula" (general designation), 1 (skin), MCZ 12301. Quintena Roo: Pueblo Nuevo X-can, 2 (1 skin with skull, 1 skull), KU 91438 , 91439; 3.5 km . N San Miguel, Isla Cozumel, 10 (2 skins with skulls, 2 skulls, 6 in alcohol), KU 91428-91437; Cozumel Island, 6 (skins with skulls), USNM 108494-108499; 4 km . NNE Felipe Carrillo Puerto, 1 (skin with skull), KU 91446; Xcopen, 1 (skin with skull), MCZ 13200. BRITISH HONDURAS: Corozal: Corozal, 2 (skins with skulls), AMNH 146585, 146586.

Didelphis virginiana (Not Assigned to Subspecies)
Specimens examined. --6 UNTTED STATES: Mississippi: "Mississippi" (general designation), 3 AMNH, 1 USNM. Iouisiana: "Louisiana" (general desienation), I AMNH, I USNM. Texas: (County not knowrl): Coleto Creek, 1. USNM; Lomita Ranch, 1 USNM.

## APPENDIX B

Cranial measurements from selected samples of Didelphis marsupialis and Didelphis Virginiana are presented in the following tables. Measurements are described under Material and Methods. The sample size $(n)$, mean, range, standard deviation (Sd), and coefficient of variation (CV) are given for each variable.

Eech sample includes specimens from several
localities, usually representing large geographic areas; however, from within the same physiographic region. Ages 4, 5, and 6 have been grouped together, although each sex is treated separately.


| variable | n | mean | range | Sd | CV |  | 33000000 |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Greatest length of skull | 14 | 114.59 | 101．80－124．90 | 7.20 | 6.29 |  |  |  |
| Condylobasal length | 14 | 110.75 | 98．85－119．95 | 6.56 | 5.92 |  |  |  |
| Palatal length | 14 | 64.88 | 58．70－69．95 | 3.47 | 5.25 |  |  |  |
| Zygomatic breadth | 14 | 59.50 | 51．95－67．40 | 4.66 | 7.82 |  |  |  |
| Interorbital constriction | 14 | 21.72 | 18．60－25．35 | 1.69 | 7.79 |  |  |  |
| Postorbital constriction | 14 | 11.43 | 10．50－12．20 | ． 44 | 3.89 |  |  |  |
| Breadth of brain case | 14 | 20.82 | 18．10－24．75 | 1.88 | 9.04 |  |  |  |
| Breadth of palatal shelf | 12 | 30.40 | 28．70－31．65 | ． 84 | 2.78 |  |  | － 1 |
| Breadth across canines | 14 | 29.66 | 26．00－33．70 | 2.18 | 7.36 |  |  | － |
| Breadth across molars | 14 | 17.04 | 16．50－18．15 | ． 52 | 3.07 |  |  | $\bigcirc$ |
| Length of maxillary tooth row | 12 | 45.40 | 42．95－48．40 | 1.76 | 3.88 |  |  | － |
| Length of upper molar series | 11 | 20.31 | 19．40－21．35 | ． 56 | 2.76 |  | 呂 | ${ }_{0}$ |
| Length of mandible | 13 | 92.06 | 81．60－99．50 | 5.91 | 6.42 |  |  | O in |
| Length of lower molar series | 13 | 22.26 | 20．50－23．60 | ． 92 | 4.11 |  | \％ 0 | 0 星 |
| Greatest breadth of nasals | 13 | 29.10 | 26．50－33．65 | 2.26 | 7.78 |  | \％88 | $\bigcirc$ |
| Breadth of rostrum across jugals | 14 | 15.35 | 13．20－ 17.45 | 1.33 | 8.67 |  |  | －贸 |
| Breadth of rostrum across frontals | 13 | 18.19 | 16．20－21．40 | 1.83 | 10.07 |  | $\checkmark$－1 | － |
| variable | $n$ | mean | range | Sd | CV | － |  | $\stackrel{\square}{4}$ |
| Greatest length of skull | 8 | 99.81 | 93．40－107．65 | 5.80 | 5.81 |  |  |  |
| Condylobasal length | 8 | 98.16 | 92．05－104．55 | 5.47 | 5.58 |  |  | 先 |
| Palatal length | 8 | 60.13 | 57．80－63．10 | 2.37 | 3.95 |  |  |  |
| Zygomatic breadth | 7 | 49.14 | 44．35－54．90 | 3.90 | 7.94 |  |  | $\bigcirc$ |
| Interorbital constriction | 8 | 18.76 | 16．75－21．30 | 1.41 | 7.53 |  |  | － |
| Postorbital constriction | 8 | 11.84 | 10．90－12．20 | ． 44 | 3.74 |  |  | －3 |
| Breadth of brain case | 8 | 17.18 | 16．25－18．50 | ． 70 | 4.08 |  | 5 | ${ }^{\sim}$ |
| Breadth of palatal shelf | 8 | 30.06 | 29．00－31．20 | ． 73 | 2.44 |  | $\cdots$ | ${ }_{0}$ |
| Breadth across canines | 7 | 26.56 | 24．80－28．90 | 1.66 | 6.26 |  | ${ }^{\circ}{ }^{\circ}$ | $\stackrel{+}{+}$ |
| Breadth across molars | 7 | 16.09 | 13．40－17．60 | 1.38 | 8.56 |  | \％ | \％ |
| Length of maxillary tooth row | 8 | 42.22 | 39．75－43．40 | 1.15 | 2.72 |  | ${ }^{\circ}$ | ${ }^{\circ}$ |
| Lengith of upper molar series | 7 | 20.46 | 19．10－21．60 | ． 73 | 3.59 |  |  |  |
| Length of mandible | 8 | 80.93 | 75．40－87．50 | 5.01 | 6.19 |  | $\bigcirc$ | O |
| Length of lower molar series | 8 | 22.44 | 21．15－23．10 | ． 71 | 3.17 |  |  |  |
| Greatest breadth of nasals | 8 | 25.84 | 24．75－28．40 | 1.21 | 4.68 |  |  |  |
| Breadth of rostrum across jugals | 8 | 13.33 | 12．30－14．90 | ． 87 | 6.56 |  |  |  |
| Breadth of rostrum across frontals | 7 | 15.66 | 14．55－17．85 | 1.21 | 7.74 |  |  |  |




| variable | n | mean | range | Sd | CV |
| :---: | :---: | :---: | :---: | :---: | :---: |
| createst length of skull | 17 | 109.68 | 97.80-123.00 | 7.32 | 6.68 |
| Condylobasal length | 16 | 106.04 | 95.50-118.40 | 6.79 | 6.40 |
| Palatal length | 17 | 64.46 | 59.70-70.00 | 3.60 | 5.59 |
| Zymomatic breadth | 16 | 57.37 | 50.70-67.00 | 5.05 | 8.80 |
| Interorbital constriction | 17 | 21.19 | 18.45-25.50 | 1.76 | 8.30 |
| Posiorbital constriction | 17 | 11.34 | 10.80-12.15 | . 38 | 3.33 |
| Breaith of brain case | 17 | 19.42 | 17.35-21.40 | 1.11 | 5.72 |
| Breadth oi palatal shelf | 16 | 30.33 | 28.75-31.80 | . 97 | 3.21 |
| Breadth across canines | 17 | 27.72 | 25.20-31.80 | 1.77 | 6.38 |
| Breadth across molars | 14 | 16.81 | 15.55-18.30 | . 86 | 5.12 |
| Lensth of maxillary tooth row | 15 | 45.32 | 43.55-47.20 | 1.43 | 3.16 |
| Lensth of upper molar series | 15 | 20.63 | 19.70-22.40 | . 6.80 | 3.89 |
| Length of mandible | 17 | 88.47 | 78.90-100.30 | 6.01 | 6.80 |
| Length of lower molar series | 16 | 22.40 | 21.00-23.80 | . 82 | 3.66 |
| Greatest breadth of nasals | 17 | 27.22 | 23.60-32.10 | 2.16 | 7.94 |
| Breadth of rostrum across jugals | 17 | 15.13 | 12.80-18.30 | 1.36 | 9.02 |
| Breadth of rostrum across frontals | 17 | 17.59 | 15.20-21.55 | 1.53 | 8.72 |
| variable | n | mean | range | Sd | CV |
| Greatest length of skull | 18 | 101.14 | 91.40-115.10 | 6.77 | 6.69 |
| Condylcbasal Iength | 17 | 98.78 | 89.25-110.95 | 6.53 | 6.61 |
| Palatal length | 18 | 61.51 | 56.35-67.60 | 3.91 | 6.36 |
| Zygomatic breadth | 17 | 48.43 | 41.65-56.15 | 3.62 | 7.47 |
| Intercrbital constriction | 18 | 18.88 | 17.00-21.30 | 1.28 | 6.78 |
| Postorbital constriction | 18 | 11.66 | 10.95-12.40 | . 45 | 3.84 |
| Breadth of brain case | 15 | 17.24 | 14.55-19.85 | 1.49 | 8.62 |
| Breadth of palatal shelf | 16 | 29.47 | 28.35-30.90 | . 93 | 3.18 |
| Breadth across canines | 18 | 25.49 | 22.30-30.30 | 1.75 | 6.88 |
| Breadth across molars | 16 | 16.94 | 14.95-19.25 | 1.04 | 6.14 |
| Length of maxillary tooth row | 15 | 42.17 | 38.95-45.40 | 1.82 | 4.32 |
| Length of upper molar series | 14 | 19.78 | 18.40-20.50 | . 65 | 3.27 |
| Length of mandible | 18 | 81.68 | 72.80-94.00 | 5.82 | 7.12 |
| Lensth of lower molar series | 15 | 21.74 | 20.45-23.80 | . 91 | 4.17 |
| Greatest breadth of nasals | 15 | 25.75 | 23.35-28.40 | 1.60 | 6.20 |
| Breadtin of rostrum across jugals | 15 | 13.80 | 12.20-15.50 | 1.15 | 8.35 |



| variable | n | mean | range | Sd | CV |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Greatest Iength of skull | 16 | 121.34 | 108.30-132.30 | 10.13 | 8.35 |  |
| Condylobasal length | 12 | 115.27 | 102.50-127.65 | 8.77 | 7.60 |  |
| Palatal length | 16 | 67.85 | 54.50-75.10 | 5.99 | 9.18 |  |
| Zygomatic breadth | 15 | 64.98 | 53.80-71.60 | 5.96 | 9.18 |  |
| Interorbital constriction | 16 | 24.22 | 19.70-28.40 | 2.89 | 11.94 |  |
| Postorbital constriction | 16 | 11.60 | 9.90-13.40 | . 76 | 6.56 |  |
| Breadth of brain case | 16 | 22.59 | 18.15-26.50 | 2.17 | 9.59 |  |
| Breadth of palatal shelf | 16 | 33.82 | 31.20-36.10 | 1.26 | 3.73 | S |
| Breadth across canines | 14 | 32.33 | 28.30-35.95 | 2.52 | 7.78 |  |
| Breadth across molars | 14 | 18.44 | 16.15-20.15 | 1.02 | 5.54 | 8 |
| Length of maxillary tooth row | 10 | 50.19 | 47.20-51.90 | 1.51 | 3.02 |  |
| Iength of upper molar series | 10 | 22.60 | 20.80-23.75 | -.93 | 4.12 |  |
| Length of mandible | 16 | 97.74 | 84.10-107.75 | 7.93 | 8.11 |  |
| Length of lower molar series | 16 | 24.23 | 23.40-25.20 | . 65 | 2.69 |  |
| Greatest breadth of nasals | 15 | 32.97 | 27.50-38.10 | 3.84 | 11.64 |  |
| Breajth of rostrum across jugals | 15 | 19.87 | 15.70-23.65 | 2.62 | 13.17 |  |
| Breadth of rostrum across frontals | 15 | 20.72 | 16.15-24.45 | 2.73 | 13.18 |  |
| variable | n | mean | 16.1 | Sd | $\underline{\mathrm{CV}}$ |  |
| Greatest length of skull | 10 | 110.31 | 90.85-116.80 | 7.52 | 6.81 |  |
| Condylobasal length | 10 | 108.14 | 90.60-113.80 | 6.74 | 6.23 |  |
| Palatal lensth | 10 | 65.37 | 60.30-68.60 | 2.12 | 3.24 |  |
| Zygomatic breadth | 9 | 58.39 | 54.90-61.40 | 2.78 | 4.75 |  |
| Interorbital constriction | 10 | 20.54 | 16.80-22.65 | 1.66 | 8.05 |  |
| Postorbital constriction | 10 | 12.00 | 11.30-12.50 | . 40 | 3.36 |  |
| Breadth of brain case | 10 | 19.35 | 16.80- 20.50 | 1.20 | 6.19 | 0 |
| Breadth of palatal shelf | 10 | 32.57 | 30.50-34.90 | 1.35 | 4.14 |  |
| Breadth across canines | 10 | 30.82 | 25.20-34.20 | 2.40 | 7.79 |  |
| Breadth across molars | 10 | 18.36 | 16.35-19.80 | 1.06 | 5.76 | 0 |
| Length of maxillary tooth row | 9 | 45.48 | 44.05-48.05 | 1.30 | 2.86 |  |
| Length of upper molar series | 9 | 21.46 | 21.25-21.95 | . 52 | 2.41 |  |
| Length of mandible | 9 | 89.62 | $74.80-95.30$ | 6.33 | 7.07 |  |
| Length of lower molar series | 8 | 23.45 | 22.80-24.15 | . 44 | 1.87 |  |
| Greatest breadth of nasals | 10 | 29.78 | 24.40-35.50 | 3.03 | 10.18 |  |
| Breadth of rostrum across jugals | 10 | 17.54 | 14.60-20.00 | 1.58 | 9.03 |  |
| Breadth of rostrum across frontals | 10 | 18.33 | 14.85-20.10 | 1.52 | 8.30 |  |

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| variable | n | mean | range | Sd | CV |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Greatest length of skull | 12 | 101.16 | 89．90－115．30 | 6.51 | 6.43 |  | 畀 |  |
| Condylobesal Iength | 10 | 97.57 | 87．40－113．10 | 7.23 | 7.41 |  | － |  |
| Palatal length | 12 | 57.57 | 52．00－66．05 | 3.96 | 6.87 |  | 8 |  |
| Zygomatic breadth | 11 | 53.49 | 45．90－63．50 | 4.75 | 8.87 |  | ． |  |
| Interorbital constriction | 13 | 18.42 | 15．80－24．15 | 2.20 | 11.92 |  |  |  |
| Fostorbital constriction | 13 | 10．47 | 9．75－11．20 | ． 48 | 4.55 |  |  |  |
| Ereadth of brain case | 12 | 18．91 | 17．20－23．90 | 2.01 | 10.65 |  | 50\％ | $\square$ |
| Breadth of palatal shelf | 11 | 28.34 | 22．90－31．10 | 2.14 | 7.54 | 3 | ＋ |  |
| Breadth across canines | 12 | 27．47 | $23.60-32.55$ | 2.32 | 8.46 | io |  | 0 |
| Ereadth across molars | 11 | 16.30 | 14．80－17．60 | ． 77 | 4.69 | 0 | ¢ | $\stackrel{\sim}{\sim}$ |
| Iength of maxillary tooth row | 20 | 40.40 | 37．60－43．10 | 1.52 | 3.75 | O | 100 | P |
| Iengtin of upper molar series | 10 | 18.69 | 17．85－19．25 | ． 49 | 2.64 |  | $\bigcirc$ | $1{ }^{1}$ |
| Lensth or mandibie | 13 | 80.47 | 12．95－92．90 | 5.93 | 7.37 |  | － |  |
| Lensth of Iower molar series | 13 | 20.94 | 19．30－21．80 | ． 86 | 4.10 |  | ¢ ${ }_{5}$ | $\stackrel{4}{4}$ |
| Greatest breadith of nasals | 13 | 26.51 | 21．75－33．00 | 2.94 | 11.09 |  | 员号 | ${ }^{\text {H }}$ |
| Ereadth of rostrum across jugals | 12 | 1.4 .53 | 12．65－17．60 | 1.44 | 9.93 |  |  | S |
| Breadth of rostrum across frontals | 13 | 15.95 | 14．35－19．70 | 1.54 | 9.68 |  | $\begin{aligned} & 40 \\ & 0 \end{aligned}$ | 号 |
| variable | 17 | mear | ranke | Sd | CV |  | 岛茄 | \％ |
| Greatest leneth or skull | 8 | 91.79 | 77．85－108．90 | 8.87 | 9.67 |  | 家 | 0 |
| Condylobasal length | 8 | 89．61 | 77．10－104．60 | 7.76 | 8.66 |  |  |  |
| Palatal length | $\bigcirc$ | 53.92 | 47．30－62．00 | 4.05 | 7.51 |  | N |  |
| Zysometic breadth | 8 | 40.19 | 38．20－60．60 | 17.52 | 43.61 |  | $\text { 昌 }{ }^{\circ} \text { ■ }$ |  |
| Interorbital constriction | 9 | 16.52 | 13．60－20．70 | 1.85 | 11.18 |  | $\stackrel{\oplus}{\bullet}$ | ＋ |
| Postorbital constriction | 9 | 10.59 | 10．05－11．10 | ． 35 | 3.26 | ${ }^{12}$ | $\stackrel{\square}{5}$ | \％ |
| Breadth of brain case | 9 | 16.09 | 13．90－18．00 | 1.31 | 8.16 | 㸓 | \％\％ | 8 |
| Breadth of palatal shelf | 8 | 26.14 | 21．60－29．50 | 2.88 | 11.00 | $\stackrel{\sim}{\circ}$ | ¢\％ |  |
| Breadth across canines | 8 | 24.51 | 20．95－30．40 | 3.03 | 12.38 | 0 |  | as |
| Breadth across molars | 9 | 15.58 | 14．20－17．55 | 1.07 | 6.88 | $\square$ |  |  |
| Length of maxillary tooth row | 7 | 38.61 | 37．20－43．90 | 2.39 | 6.18 |  |  |  |
| Length of upper molar series | 7 | 18.53 | 17．90－19．30 | ． 55 | 2.96 |  |  |  |
| Length of mandible | 9 | 73.18 | 62．35－86．95 | 6.77 | 9.25 |  | 5\％ |  |
| Length of lower molar series | 9 | 20.37 | 19．00－22．00 | ． 82 | 4.03 |  |  |  |
| Greatest breadth of nasals | 9 | 23.28 | 20．00－27．10 | 1.98 | 8.48 |  | 5 |  |
| Breadth of rostrum across jugals | 8 | 13.08 | 10．15－16．70 | 1.88 | 14.40 |  |  |  |
| Breadth of rostrum across frontals | 8 | 14.28 | 11．00－18．00 | 1.94 | 13.56 |  |  |  |

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Alfred Lunt Gardner was born in Salem, Massachusetts on November 10, 1937. He attended Danvers H1gh School, Danvers, Massachusetts and Tucson Senior High School, Tucson, Arizona where he graduated in June 1955. He attended the University of Arizona from 1955 to 1959 and from 1961 to 1962, when he received the Bachelor of Science degree in Wildilfe Management. He entered the University of Arizona Graduate School in September of 1963 and received the Master of Science degree in Zoology in June 1965. In September of that year he entered Louisiana State University Graduate School, and is now a candidate for the Doctor of Philosophy degree in Vertebrate Zoology.

## EXAMINATION AND THESIS REPORT

Candidate: Alfred Lint Gardner

Major Field: Vertebrate Zoology

Title of Thesis: The systematics of the genus Didelphis (Marsupialia:Didelphidae) in North and Middle America

Approved:


EXAMINING COMMITTEE:


Date of Examination:


[^0]:    * Measurement units.

