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Didelphis virginiana.

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Didelphis virginiana Kerr, 1792

Virginia Opossum

Didelphis virginiana Kerr, 1792:193, Type locality, Virginia.

CONTEXT AND CONTENT. Order Marsupialia, Superfamily Didelphoidea, Family Didelphidae, Subfamily Didelphinae. The most recent review of the systematics of the genus *Didelphis* (Gardner, 1973) recognizes three species *D. virginiana*, *D. marsupialis*, and *D. albiventris*, the latter two being restricted to Middle and South America. *D. virginiana* is comprised of four subspecies:

D. v. virginiana Kerr, 1792, see above.
D. v. pigra Bangs, 1898:172, Type locality, Oak Lodge, on east Peninsula opposite Micco, Brevard Co., Florida.
D. v. californica Bennett, 1833:40, Type locality, "That part of California which adjoins to Mexico."
D. v. yucatanensis Allen, 1901:178, Type locality, Chichen-Itza, Yucatan, Mexico.

DIAGNOSIS. White cheek hairs bordered above and behind by darker colored fur; guard hairs more or less evenly distributed over dorsum; tail less than 93% of head and body length; interceptions of nasal and lacrimal with maxillo-frontal suture nearly opposite (figure 1); nasal relatively broad (average 15 to 16 mm), terminating in a rounded or truncated angle; lacrimal recedes from outer margin of jugal before terminating, usually in a rounded point; dorsal extension of the orbital portion of the palatine usually broad (narrow or absent in *D. marsupialis*; see Gardner (1973) for detailed photographs of skull characters); death feigning behavior well developed, tail coiling behavior when stressed absent; chromosome number 22, consisting of three pairs of large and three pairs of medium-sized subtelocentrics, four pairs of medium-sized acrocentrics, and sex chromosomes; fundamental number 32.

GENERAL CHARACTERS. More extensive descriptions of inter- and intraspecific variation in the *Didelphis* group are given in Gardner (1973); statistical analyses also are given.

DISTRIBUTION. The range of the four currently recognized subspecies of *D. virginiana* is mapped in Figure 2. *D. v. virginiana* has expanded its range northward and westward within the past century (Hamilton, 1958; Hoffmann and Jones, 1970) and has been introduced widely in areas of the western United States. The southern limits of the present distribution correspond to the southernmost extent of the northern highlands of Middle America and are near the southern end of the seasonally arid Tropical Deciduous Forests of the Pacific slope and coastal plain of Mexico and Central America (Gardner, 1973).

FOSSIL RECORD. *Didelphis* remains were recovered from the Pliocene of South America, but do not appear in North America until the Sangamon interglacial stage of the Pleistocene (Hibbard *et al.*, 1965). The latter remains probably are of *D. virginiana* and post-Wisconsin remains from archeological sites (Guilday, 1958) indicate that as recently as 1400 to 1600 AD the northern range limits were northern West Virginia and northern Ohio. The present distribution is farther north (figure 2).

FORM. *Didelphis* is robust and relatively heavy bodied; adult males average 2.8 kg and adult females 1.9 kg (Hamilton, 1958).

Pelage and skin coloration in *Didelphis* vary markedly from region to region (Allen, 1901; Gardner, 1973). In northern populations, a relatively thick underfur, which is whitish basally and occasionally tipped with black, is overlain by a thin covering of pale guard hairs, giving the animal a gray, grizzled appearance. Southern populations have sparser underfur and show a greater proportion of black guard hairs; consequently they are darker. The digits and margins of the pinnae are typically pale in northern populations and dark in southern areas. Pigmentation of the basal part of the tail rarely extends beyond the haired part in northern populations, but may extend as much as one-half to two-thirds the tail length in those from the southern part of the range of the species. The chest area of males often is stained, suggesting the presence of skin glands, the function of which needs to be studied. Sweat glands, if present, are apparently nonfunctional (Higgenbotham and Koon, 1955). Enders (1937) provided an account of the *panniculus carnosus* and the development of the pouch, and a description of the mammary glands was given by Hartman (1921). Teats are usually 13, but may range from nine to 17 (Hamilton, 1958). The skull is primitive, characterized by a small brain case, a strong sagittal crest, and an inflected angular process. The adult dentition is i 5/4, c 1/1, p 3/3, m 4/4, total 50. Petrides (1949) used the

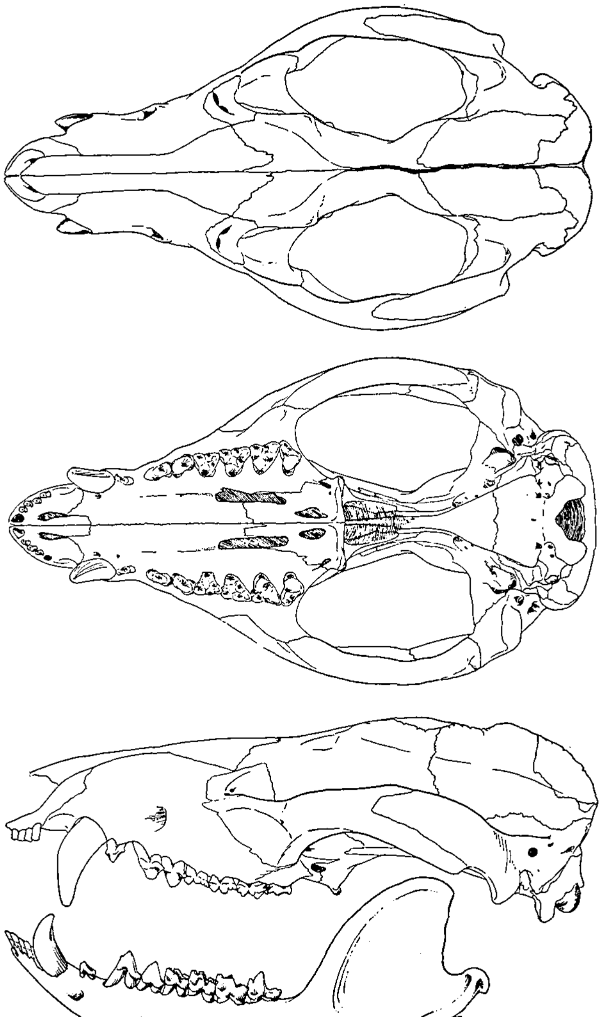

FIGURE 1. Views of the skull of *Didelphis virginiana virginiana* (KU 3780, male, from Hall and Kelson, 1959:6, courtesy of The Ronald Press, Inc., New York).

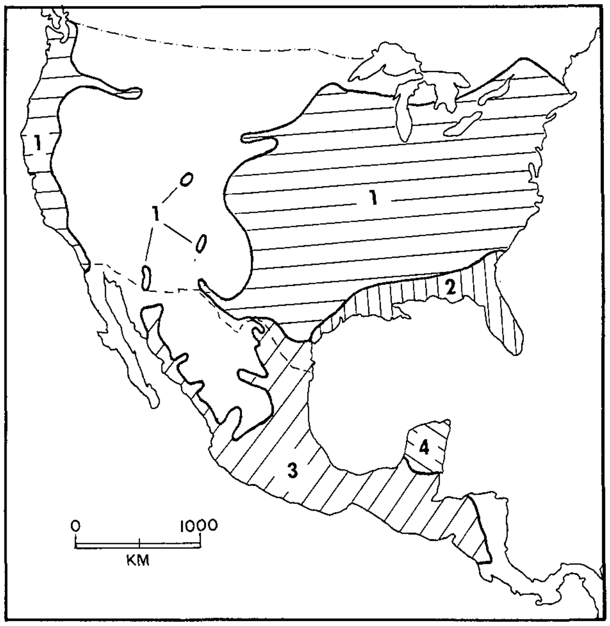

FIGURE 2. Distribution of the subspecies of *Didelphis virginiana*: 1, *D. v. virginiana*; 2, *D. v. pigra*; 3, *D. v. californica*; 4, *D. v. yucatanensis*. Redrawn from Gardner (1973).

tooth formula as a criterion of age, as follows: at 3 months, i 5/2, c 1/1, p 2/2, m 0/0; at 4 months, i 5/4, c 1/1, p 3/3, m 1/2; at 5 to 8 months, i 5/4, c 1/1, p 3/3, m 2/3; and at 7 to 11 months, i 5/4, c 1/1, p 3/3, m 3/4. Nesslinger (1956) studied the development of ossification centers in the entire skeleton, and the pectoral and pelvic girdles were treated by Cheng (1955) and Elftman (1929), respectively. Skeletal proportions in *Didelphis* are apparently characterized by a considerable degree of variability (Lowrance, 1949). Vertebral numbers are relatively fixed—7 cervical, 13 thoracic, 6 lumbar, 2 sacral, and 26 to 29 caudal. Digits bear claws, except the opposable hallux of the pes. Friction ridges are present on the plantar surfaces of the forefeet and the hind feet and the tail is prehensile. Hiiemae and Jenkins (1969) studied the masticatory muscles of the head. The heart and its vessels were described by Wade and Neely (1949), and the lymphatic system by Azzali and DiDio (1965). Accounts of the forebrain, midbrain, and hind brain were given by Loo (1930), Tsai (1925), and Voris and Hoerr (1932), respectively. Riese (1945) described the condition of the brain in neonates. The opossum brain is primitive in structure and is unusual in that a corpus callosum is lacking.

Descriptive anatomy of the male and female reproductive systems was reported by Chase (1939) and Hill and Fraser (1925), respectively. The pendulant scrotum lies anterior to the hemipenis, and the uterus is of the didelph type, with two lateral vaginae that receive sperm, and a median vagina, which serves as the birth canal. The respiratory and digestive systems have not been examined in detail, and aside from works on the thymus (Kingsbury, 1940), Cowper's and Bartholin's glands (Rubin, 1943, 1944), the prostate (Martan and Allen, 1965; Hruban *et al.*, 1965), and the pituitary (Wheeler, 1943), little has been done on the endocrine system of *Didelphis*. In overall view, the anatomy of the opossum is primitive and generalized, and it is thought to bear close resemblance to ancestral mammalian stocks (Colbert, 1969).

FUNCTION. Several studies concerned with thermoregulation in adult and pouch young opossums have been conducted. Body temperatures of 35.0, 35.2, and 35.5°C were reported by Higgenbotham and Koon (1955), Morrison and Petajan (1962), and McManus (1969), respectively. *Didelphis* can maintain body temperature at ambient temperatures lower than 0°C, although in the northern parts of its range extensive frostbite of the extremities may result (Wiseman and Hendrickson, 1950; Hamilton, 1958; McManus, 1969). Behaviorally, the opossum depends heavily on saliva spreading for temperature control under heat stress, a feature apparently shared by many marsupials (Robinson, 1954; Robinson and Morrison, 1957). Evaporative heat loss at high temperatures is facilitated by sparsely haired extremities, particularly the tail. Vasoconstriction, piloerection, shivering, and behavioral avoidance of low temperature are the most important thermoregulatory devices at low temperatures. A detailed study of the ontogeny of thermoregulation (Morrison and Petajan, 1962; Petajan and Morrison, 1962) showed that, prior to day 55, no signs of temperature regulation were evident in pouch young. By day 95, just before weaning, however, young opossums were able to maintain deep body temperature when exposed to ambient temperatures as low as 5°C for up to 2 hr. Basal metabolic rate in *Didelphis* is among the lowest recorded for mammals (0.15 ml O_2/g of body weight/hr for a 3.5 kg individual). The lower critical temperature is near 25°C and metabolism increases to 0.5 ml O_2/g/hr at 0°C (Brocke, 1970).

Electrocardiographic studies of the opossum (Nardone *et al.*, 1955; Wilber, 1955; Francq, 1970) indicated that the normal heart rate is near 200 beats per min. Wilber (1955) gave the following standard cardiographic values for an opossum under light nembutal anesthesia: rate 200/min.; P-R .08 s; QRS .02 to .03 s; OR –1.1 to 3.2 mv; Q-T .14 s; T –.1 to .25 mv; T .06 to .08 s; $P < .01$ to .05 mv; R-R .32. Heart rate was correlated directly with colonic temperature.

A study of gas transport by the blood of the opossum (Scott 1938) revealed that oxygen capacity was 15% of blood volume and 40% of cell volume, corpuscles made up 36% of blood volume, and there were 5 million red cells per mm^3 (all values are averages). Saturation of venous blood varied from 11 to 42%, whereas arterial blood of one specimen was found to be 93% saturated. Arterial blood was from 38 to 49% carbon dioxide by volume and venous blood from 50 to 60%. Scott indicated that the O_2 and CO_2 dissociation curves of the opossum were comparable to those of placental mammals. Rink and Miller (1967) observed that pouch young were among the most resistant of mammals to asphyxia, and Parmelee *et al.* (1960) could detect no growth abnormalities or deleterious effects on pouch young kept with the female under abnormally high oxygen concentrations (50 to 60%), although Patz *et al.* (1953) found that adults died in atmospheres of 70% O_2.

Wound healing in neonate opossums was investigated by Block (1960) and Mizell and Isaacs (1970). Newborn young prove susceptible to infection prior to day 6, but between days 6 and 10 hemopoietic centers develop and provide a supply of leucocytes adequate to combat induced infection. Regeneration of excised limbs occurs and acceptance of xenoplastic and homoplastic transplants is tolerated by neonates. Opossum fetuses have also been grown in culture for short periods of time (New and Mizell, 1972).

An electrophysiological study of taste reception in the opossum (Tamar, 1961) revealed *Didelphis* to be similar to bats and carnivores, having a generally low taste sensitivity. Opossums are able to make simple visual discriminations of black and white objects under test conditions (James, 1960) and, surprisingly, also appear to have a limited capacity for color perception (Friedman, 1967).

ONTOGENY AND REPRODUCTION. Development and reproduction of *Didelphis* have been studied intensively. Major works include a classic series of papers by Hartman (1920, 1921, 1923*a*, 1923*b*, 1924, 1928) and monographs on the embryology (McCrady, 1938) and reproduction (Reynolds, 1952) of the opossum. Postnatal growth was studied by Petrides (1949) and the development of ossification in *Didelphis* was investigated by Nesslinger (1956). Correlation between behavioral development and degree of myelinization in the nervous system was demonstrated by Langworthy (1925, 1928).

The mating season in *Didelphis* is long and extends from January or February to June or July in areas of the United States that have been studied; these include: California (Reynolds, 1952), Florida and Georgia (McKeever, 1958), Illinois (Holmes and Sanderson, 1965), Iowa (Wiseman and Hendrickson, 1950), Maryland (Llewellyn and Dale, 1964), Missouri (Reynolds, 1945), New York (Hamilton, 1958), and Texas (Hartman, 1923; Lay, 1942). Peak periods of reproduction appear to occur from late January through late March and from mid-May to early July (Hamilton, 1958).

During copulation, insemination of both uteri takes place in *Didelphis*, but Hartman indicated that ovulation may be delayed for as long as 4 days *post coitum*. An average of 11 ova (0.75 mm in diameter) is released from each ovary (record 43 total ova) and fertilization occurs within the Fallopian tubules. Passage to the uterus requires about 24 hours, during which time albumen and a shell membrane are added. First cleavage occurs in the uterus and because a morula stage is lacking in *Didelphis*, a blastula is formed by the 16-cell stage.

Endoderm differentiation begins at the 50-cell stage and by day 6 following ovulation the mesoderm forms and the primitive streak stage is attained. Actual placenta formation is not present, although the embryo is encompassed by the folds of the uterine wall. Intimate contact between the chorion and blood vessels of the uterine mucosa provides for transport of nutrients from mother to young. Parturition occurs approximately 12.5 to 13 days after copulation and has been described by Hartman (1920) and Reynolds (1952). Because females typically possess 13 teats, a high percentage of the neonates cannot be accommodated; in addition, it is rare to find all teats occupied. Thus, although births of 18 and 21 young have been observed (Hartman, 1923), the average litter size is between 6.8 (Lay, 1942) and 8.9 (Reynolds, 1952). Two litters per year appears to be the rule, but occasionally a third may be produced.

The young are quite altricial at birth. Average birth weight and crown-rump length are 0.16 g and 14 mm, respectively. Hamilton (1958) reported a sex ratio of 51.7% males, 48.3% females. From birth to the period days 50 to 65 the young remain fixed to the nipple, which lengthens and enlarges within the mouth, making detachment unlikely. However, there are *some indications that mortality may occur while in the pouch* (Sanderson, 1961). The period from conception to release of the nipple is roughly comparable to the gestation period of a placental mammal of equivalent size. The young continue to suckle until weaning, which occurs between days 95 and 105 after parturition. Prior to weaning, however, the young may eat solid food. Females apparently breed in the first season following birth, regardless of whether weaning occurred in spring or summer.

Reynolds (1952) found the estrous cycle to average 29.5 days (range 22 to 38) and reported that the period of receptivity is not longer than 36 hours. Receptivity apparently terminates with copulation (McManus, 1967). Because gestation is shorter than the estrous cycle, nonfertilization or loss of the young at parturition does not interrupt the following estrus, and Reynolds (1952) suggested that if fewer than three young reached the pouch, the female removed them and mated again *at the next estrous. Such behavior would insure maximum* fecundity.

Hartman (1923) suggested that the opossum may live to at least 7 years, whereas Petrides (1949) computed an average life expectancy of 1.33 years with a 4.8-year turnover in the population. Llewellyn and Dale (1964) felt that Hartman's figure was too high, and that even Petride's estimate was slightly high.

ECOLOGY. Numerous ecological investigations of opossums have been conducted in various parts of the United States: Florida and Georgia (McKeever, 1958), Illinois (Holmes and Sanderson, 1965; Sanderson, 1961; Stieglitz and Klimstra, 1962; Verts, 1963), Iowa (Wiseman and Hendrickson, 1950), Kansas (Fitch and Sandidge, 1953; Fitch and Shirer, 1970), Maryland (Llewellyn and Dale, 1964), Michigan (Taube, 1947), Missouri (Reynolds, 1945), New York (Hamilton, 1953, 1958), Texas (Lay, 1942) and Wisconsin (Long and Copes, 1968).

Didelphis virginiana utilizes a wide variety of habitats, ranging from areas of relative aridity (Hock, 1952; Sands, 1960) to much more mesic environments. It is typically found, however, in the wetter areas of its distribution, particularly near streams and swamps. Estimates of the home range size of the opossum vary widely, mostly because of the difficulty of adequate sampling and because of the transient nature of the movements of opossum. In a Texas population, Lay (1942) found that a sample of 29 individuals captured three or more times had an average home range of 11.5 acres (4.65 ha), ranging from one-third (0.12 ha) to 58 acres (23.47 ha). Using radiotracing methods in Kansas, Fitch and Shirer (1970) determined the mean radius of activity from the nest site to be 620 m. Llewellyn and Dale (1964) noted that ranges were typically elongate rather than circular, often following water courses; the average home range length for a sample of 25 opossums was 0.98 km. Populations are heavily weighted toward young of the year; Petrides (1949) found an Ohio population consisting of 75% young. Mortality during the first year is apparently quite high and population turnover is rapid. Although opossums commonly inhabit burrows of other animals, Lay (1942) felt that populations of the opossum were not limited by lack of nest sites. Similarly, few predators seem to take opossums with regularity. Fitch and Shirer (1970) suggested that avian predators may be a source of mortality for young of the year.

Food habits of the opossum have been studied extensively (Dexter, 1951; Hamilton, 1953, 1958; Lay, 1942; McManus, 1970; Reynolds, 1945; Stieglitz and Klimstra, 1962; Taube, 1947) and all studies indicate highly opportunistic dietary patterns. The bulk consists of animal foods, chiefly insects and carrion, but considerable amounts of plant material are accepted, particularly fruits and grains in season. It is probable that the relatively unrestricted diet has been one of the main factors contributing to the current success of the species.

The parasites and diseases of the opossum were reviewed by Barr (1963) and Potkay (1970), and have also been treated by Hamilton (1958) and Reynolds (1945). Compared to other furbearers, *Didelphis* appears to be relatively free of arthropod ectoparasites, but sustains a rather high incidence of endoparasites, particularly the stomach nematode, *Physaloptera turgida* and the trematode, *Echinostonia revolutum. Didelphis* is a reservoir host for several important communicable diseases (Barr, 1963).

The opossum is of moderate economic importance. It is hunted and sometimes eaten in the southeastern United States (Hartman, 1952), and the pelt is an abundant, although low quality item in the fur industry. Hamilton (1958) has reviewed the economic relations of *Didelphis* in detail. Moore and Bodian (1940) noted the potential of opossum pouch young as experimental materials, and Wiedorn (1954) suggested the suitability of adults in psychological experimentation.

BEHAVIOR. The general behavior of the opossum was studied by McManus (1970), and Francq (1969) has reviewed the behavior associated with death feigning. Reproductive behavior was treated extensively by Reynolds (1952), and a considerable number of other reports on opossum behavior have appeared, but the latter are mostly anecdotal in nature.

The opossum employs terrestrial, arboreal, and aquatic patterns of locomotion. On the ground, movement is of a primitive, plantigrade-quadrupedal type termed metherptic (Magne de la Croix, 1936). A detailed cineradiographic analysis of limb posture and locomotion was reported by Jenkins (1971). *Estimates of maximum running speeds range from 7.1* km/hr (Layne and Benton, 1954) to 7.4 km/hr (McManus, 1970). Foraging above ground is facilitated by use of the prehensile tail, opposable hallux, and friction ridges on the palmar and plantar surfaces, but arboreal locomotion is typically slow, and often clumsy. Underwater swimming was observed as an escape mechanism (Moore, 1955), and Doutt (1954) concluded that the opossum is a strong, if slow swimmer. Two swimming patterns are used; one involves essentially the same limb movements as in terrestrial locomotion and the other resembles a pacing gait, wherein the limbs on one side move in synchrony and alternate with those of the other side. In both types the tail performs sculling movements. Maximum swimming speed is about 1.1 km/hr and distances of at least 100 m can be covered with relative ease (McManus, 1970).

Extensive use is made of the hind foot during grooming. The four digits exclusive of the hallux are held rigid and are used to comb parasites and particulate material from the fur. Opossums wash the face with the forefeet, licking them in a catlike fashion. In females, particular attention is given to the marsupium, which is licked extensively, particularly if pouch young are present.

Nest building was described by Pray (1921), Smith (1941), and Layne (1951). Litter is grasped in the mouth, passed under the thorax, and placed on the tail, which is drawn forward between the hindlegs. The tail encircles and transports the litter and thus frees the limbs for locomotion. This method is adaptive for the construction of arboreal nests.

The vocal repertoire consists chiefly of the hiss, growl, and screech, which are given in agonistic encounters and which represent, in that order, a spectrum of intensity (McManus 1970). A fourth sound, the "metallic click" described by Hartman (1923), is uttered in a variety of situations including mating (Reynolds, 1952; McManus, 1967), aggressive encounters between adults, and by females in the presence of young (McManus, 1970). The significance of this vocalization is not known.

Defensive behavior is highly developed in the opossum and has been studied by James (1937), Wiedorn (1954), Francq (1969), and McManus (1970). Bluff or intimidation displays are most commonly seen; these consist of hisses, growls, and screeches, baring of the teeth, and occasionally the extrusion of a greenish secretion of varying consistency from two anal glands located to either side of the vent. In the face of strong threatening stimuli, catatonia or death feigning may occur.

FIGURE 3. Karyotype of *Didelphis virginiana* (Louisiana State Univ. 13393, male from Edinburg, Hidalgo County, Texas, courtesy of A. Gardner).

While feigning death, opossums become immobile, usually with the mouth open, and lie with a ventral flexion of the body and tail. Sensitivity to tactile stimulation is much reduced, although the animals do respond weakly to sudden, low-pitched sounds. Catatonia might be brief, lasting less than a minute, or as long as 2 to 6 hr (Wiedorn, 1954). Using EKG techniques, Francq (1970) was unable to distinguish between catatonic heart activity and that during the active state.

A study of general activity throughout the year (McManus, 1971) showed *Didelphis* to be almost exclusively nocturnal with a broadly unimodal pattern of activity. Activity begins at or soon after dusk and continues until dawn. Maximum activity occurs between 2300 and 0200 and in spring and summer as many as 80% of a group of caged individuals were active during this interval. Activity is markedly depressed in late autumn and winter (for example, maximum activity in winter was 17%), particularly under conditions of reduced ambient temperature, but hibernation does not occur. Despite large absolute seasonal differences in the level of general activity, the relative time devoted to specific behaviors is fairly stable throughout the year.

Social behavior is poorly developed and with the exception of mating, most encounters between adults are agonistic. Although Reynolds (1952) was able to keep groups of females in a large enclosure, males cannot be confined without continual fighting and death of the weakest (McManus, 1970). Aggressive behavior between males and females is similar and consists of aggressive vocalizations, displays of bared teeth, and frequent physical contacts. In males, a "dance" is sometimes given (Reynolds, 1952). With the hind quarters depressed and the forelimbs extended, the tail is lashed back and forth. Clicks usually precede and follow this display, but the dance itself is silent. Catatonia may occur in the weaker of a fighting pair. When housed as bisexual pairs, the male frequently attempts to nuzzle the genital area of the female, but if she is not in estrous these advances are invariably met with aggressive displays from the female. Conspecific inhibition of aggression is well developed in the male and the attacks of the female are never returned.

When the female comes into heat, copulation occurs soon afterward (McManus, 1967). The male straddles the female, clasping her hind legs with his hind feet and her nape with his jaws. The pair topple to one side and insertion of the penis occurs within 2 minutes. The male maintains his grasp of the female for the duration of the coupling, which may last for up to 20 minutes. At its termination, the female resumes her aggressive attitude and any further advances of the male are resisted.

Not much maternal behavior is exhibited in *Didelphis*. Prior to detachment from the nipples the female licks the pouch and joeys, but afterwards the young groom themselves. Captive females never defended the young and made no attempts to retrieve young removed from the nest. No play behavior was seen in young prior to or after weaning.

GENETICS. The chromosomes of *Didelphis virginiana* (Shaver, 1962; Biggers *et al.*, 1965; Gardner, 1973) are mentioned in the diagnosis (see figure 3).

REMARKS. Two previous revisions of the genus *Didelphis* (Hershkovitz, 1951; Hall and Kelson, 1959) included *D. virginiana* as a subspecies of *D. marsupialis*. Gardner's (1973) study revealed distintive karyotypic and morphological differences between *D. virginiana* and *D. marsupialis*. Sympatric populations of the two, which occur in southern Mexico and Central America, differed significantly ($P < .05$) in 17 skull characters. Gardner proposed that *D. virginiana* was derived from a *D. marsupialis* isolate during the Pleistocene in western Mexico. The separation involved a structural chromosomal rearrangement, probably caused by a series of pericentric inversions.

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Addendum: Since this manuscript was submitted, additional information on the resting rate of metabolism (Lustick and Lustick, 1972) and on diel fluctuations in body temperature (Dills and Manganiello, 1973) in *D. virginiana* has been published.

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