Philander opossum. By Iván Castro-Arellano, Heliot Zarza, and Rodrigo A. Medellín

Philander Brisson, 1762

Didelphis Linnaeus, 1758:54 (part).
Didelphys Schreber, 1777:532 (part, invalid emendation of *Didelphis* Linnaeus).
Philander Tiedemann, 1808:426. Included *Philander virginianus* Tiedemann, 1808 (= *Didelphis opossum* Linnaeus, 1758).
Sarigua Muirhead, 1819:429 (part).
Philander Gray, 1843:101 (part, based on *Philander* Brisson, 1762, not *Philander* Tiedemann).
Metachirus Burmeister, 1854:135 (part, as a subgenus of *Didelphis* Linnaeus).
Gamba Liais, 1872:329 (part).
Metachirops Matschie, 1916:262. Type species *Didelphis quica* Temminck, 1824, by original designation (p. 268).
Holothylax Cabrera, 1919:47. Type species *Didelphis opossum* Linnaeus, 1758, by original designation.
Metacherius Sanderson, 1949:787. Incorrect subsequent spelling of *Metachirus* Burmeister.

CONTEXT AND CONTENT. Order Didelphimorphia, family Didelphidae, subfamily Didelphinae, genus *Philander*. The systematics of the genus is controversial. Based on mtDNA, Patton and Da Silva (1997) suggested the genus comprises four species: *P. andersoni*, *P. frenata*, *P. mcilhennyi*, and *P. opossum*, but other authors (Gardner, 1993; Hershkovitz, 1997) recognized only two species, *P. andersoni* and *P. opossum*; Hershkovitz (1997) included *P. mcilhennyi*, as a subspecies of *P. andersoni*. Here, we restrict the number of species to three: *P. andersoni*, *P. mcilhennyi*, and *P. opossum*. In spite of its highly divergent cyt-b sequence we retain the form *frenata* as a subspecies of *P. opossum*, because of the immense geographic distance between the sample localities tested by Patton and Da Silva (1997). However, the classification is not definitive because all geographic and taxonomic forms have not been thoroughly studied.

Didelphids are very conservative in their chromosomal complements and form three distinct groups with diploid numbers of 14, 18, or 22. The clade with 2n = 22 includes the large opossums *Chironectes*, *Didelphis*, *Lutreolina*, and *Philander* (Reig et al., 1977). This group showed high relatedness, not only in their karyotype but also using cladistic analysis with several morphologic characters (Reig et al., 1987). Moreover, data from mtDNA cytochrome b gene sequences (Patton et al., 1996) and DNA–DNA hybridization data (Kirsh et al., 1993) indicate that *Didelphis* and *Philander* are strong sister taxa. The relationships between these two taxa are so close that *Philander* has been classified as a subgenus of *Didelphis* (Pine, 1973).

The following key to species of *Philander* is based on information from Gardner and Patton (1972), Hershkovitz (1997), Hutterer et al. (1995), and Patton and Da Silva (1997):

1 Upperparts uniformly grayish brown, a blackish middorsal stripe absent or poorly defined; tail either entirely brown or bicolored with distal three-fifths of tail more or less unpigmented . . . . *P. opossum*
Upperparts either uniformly dark gray or with well-defined blackish middorsal stripe with long, coarse, and erectile hairs; tail usually bicolored with proximal one-half to four-fifths brown or blackish and the rest unpigmented 2

2 Dorsum with a well-marked black median dorsal stripe, 3–4 cm wide; dorsal guard hairs short (ca. 10 mm) and soft; creamy to grayish colored venter; furred portion of tail ca. 18% of its total length; pale cream spot at the medial base of ear present . . . . *P. andersoni*
Dorsum uniformly black without a middorsal black stripe; dorsal guard hairs long (ca. 18 mm) and coarse; dark gray-colored venter; furred portion of tail >23% of its total length; no pale cream spot at the medial base of ear . . . . *P. mcilhennyi*

Philander opossum Linnaeus, 1758
Gray Four-eyed Opossum

[*Didelphis*] *opossum* Linnaeus, 1758:55. Type locality "America," restricted to Suriname by Allen (1900:195); further restricted to Paramaribo, Suriname, by Matschie (1916:268).
Didelphis opposum Brongniart, 1792:115. Incorrect emendation of *D. opossum* Linnaeus.
Philander virginianus Tiedemann, 1808:426. Type locality "Virginien, Mexiko, Peru u. s. w.;" a new name for *D. opossum* Linnaeus (Hershkovitz, 1949).
S [*arigua*]. *opossum*: Muirhead, 1819:429. New name combination.
D [*idelphys*]. *opossum* Wagner, 1843:44. Incorrect emendation of *D. opossum* Linnaeus.
[*Didelphys* ([*Metachirus*])] *opossum*: Burmeister, 1856:69. New name combination.
Gamba opossum: Liais, 1872:329. New name combination.
Metachirus fuscogriseus pallidus Allen, 1901:215. Type locality "Orizaba, Veracruz, Mexico."
[*Didelphis* (*Metachirops*)] *pallidus*: Matschie, 1916:268. New name combination.
[*Didelphis* (*Metachirops*)] *opossum*: Matschie, 1916:268. New name combination.
Didelphis austro-americana Thomas, 1923:604. Type locality "Suriname"; preoccupied by *Didelphis austroamericana* J. A. Allen, 1902:251 (= *D. marsupialis* Linnaeus, 1758); both names based on *Didelphis austro-americana* Oken, 1816.
Metachirops opossum pallidus Miller, 1924:7. New name combination.
Metachirops opossum Tate, 1939:161. New name combination.
Philander opossum Gilmore, 1941:316. New name combination; based on *Philander* Brisson, 1762, not *Philander* Tiedemann, 1808.
Philander opossum pallidus Dalquest, 1950:2. New name combination.

CONTEXT AND CONTENT. Context as above. Hershkovitz (1997) listed seven subspecies but Patton and Da Silva (1997) recognized six. The extent and composition of each subspecies dif-

Fig. 1. *Philander opossum* from Chajul, Chiapas, Mexico. Photograph by R. A. Medellín.

fers between these two authors. Pérez-Hernández (1989) suggested the presence of a subspecies from the Orinoco Delta, Venezuela, but did not name it. A second unnamed subspecies may occur in northern Colombia (Allen, 1916; Hershkovitz, 1997). Based on these works, seven subspecies can be defined for South America and an additional one for Mexico and Central America:

P. o. azaricus (Thomas, 1923:604). Type locality "Sapucay, Paraguarí, Paraguay."

P. o. canus (Osgood, 1913:96). Type locality "Moyobamba, [San Martin], Peru" (*crucialis* Thomas is a synonym).

P. o. frenatus (Olfers, 1818:204). Type locality "Sudamerica," restricted to Bahia, Brasil, by Wagner (1843:44; *D. quica* Temminck is a synonym).

P. o. fuscogriseus (Allen, 1900:194). Type locality "Central America," restricted to Greytown, Nicaragua, by Allen (1911:247).

P. o. melanurus (Thomas, 1899:285). Type locality "Paramba, Rio Mira, N. Ecuador," (*melantho* Thomas is a synonym).

P. o. opossum (Linnaeus, 1758:55). See above (*virginianus* Tiedemann is a synonym).

P. o. subsp. nov. I. Pérez-Hernández, 1989:373.

P. o. subsp. nov. II. Allen, 1916:201.

DIAGNOSIS. *Philander opossum* (Fig. 1) can be differentiated from other species of the genus as follows: *P. opossum* has a white chin with a darker upper labia, a whitish belly and feet, a small tail, short and soft hair, and a nearly uniform grayish brown dorsum. This contrasts with the almost entirely black color and long, coarse, dorsal pelage of *P. mcilhennyi* (Hershkovitz, 1997; Hutterer et al., 1995). Also, *P. mcilhennyi* is larger (>280 mm, head and body) and has a more extensively (>26%) furred basal portion of tail than sympatric populations of *P. opossum*. However, size and proportion relations are not maintained if *P. mcilhennyi* is compared to all populations of *P. opossum* (Gardner and Patton, 1972; Hershkovitz, 1997; Patton and Da Silva, 1997). Shorter lacrimal bones in *P. opossum* contrast with anteriorly expanded lacrimals in *P. mcilhennyi* (Patton and Da Silva, 1997). The uniform grayish brown coat of *P. opossum* distinguishes it from *P. andersoni*, which has a well-defined black, median, dorsal stripe (Patton and Da Silva, 1997).

The closest generic relative of *P. opossum* is *Didelphis*, which is substantially larger, with a head and body length between 325 and 500 mm. Also, the shaggy pelage of *Didelphis* has long white-tipped guard and wool hairs. *Didelphis* has a whitish face and gray, black, or reddish upperparts with faint or no whitish spots above the eyes. Skull of *Didelphis* is broader with frontal and maxillary sinuses more inflated and a higher, bladelike sagittal crest (Hershkovitz, 1997; Nowak, 1991).

Philander opossum can be differentiated from *Metachirus nudicaudatus* by smaller, more widely separated, and cream-colored spots above the eye in *Metachirus*. Usually *Philander* is less brownish in contrast to brown dorsal coat of *M. nudicaudatus*. Also, *M. nudicaudatus* has a more pointed snout and longer legs than *P. opossum* (Medellín et al., 1992; Nowak, 1991). Tail of *M. nudicaudatus* is longer (>330 mm), gradually changing from dark to pale color, in contrast to the entirely brown or dark tail of *P. opossum*. Female *Metachirus* lack a pouch.

In contrast to *Chironectes minimus*, *P. opossum* does not have broad black bands across the back, nor palmated feet. Skull of *Chironectes* is heavier and broader with a braincase width ca. 35% of condylobasal length in contrast to <30% on *Philander*. Also, angle between sagittal and frontal planes is greater, nasals are shorter, zygomatic breadth is greater, and palate is wider in *Chironectes* (Hershkovitz, 1997).

GENERAL CHARACTERS. The gray four-eyed opossum is variable in external color and pattern of coat. Individual hairs are light-colored at the base, turn darker, and end in silvery tips, the overall effect being a uniform grayish brown coat (Allen, 1900; Patton and Da Silva, 1997). Upperparts and color pattern of tail vary geographically: animals from Mexico are pale gray; those from Central America are dark gray; and those from coastal Colombia and north Ecuador are dark gray to blackish with a dark brown to black tail sometimes with a whitish tip. Animals in coastal Venezuela, Guyana, Suriname, French Guiana, and the eastern Amazon basin of Brazil are uniformly pale gray to buffy brown. Specimens from western Amazonian and eastern Peru have the gray color typical of the species. Animals from the Paraná basin, eastern Bolivia,

and southwestern Brazil are pale gray and the form present in coastal regions of eastern and southeastern Brazil is dark gray with a darker middorsum but without the distinct stripe (Emmons and Feer, 1990; Hershkovitz, 1997; Patton and Da Silva, 1997). Underparts are yellowish-white to orange and chest is pale gray. Female has a pouch, stained orange if she has had young. Scrotum of males is black (Emmons and Feer, 1990; Pérez-Hernández et al., 1994).

Face is dusky, almost black in some individuals, with black around eyes and across crown. Dark face contrasts with white supraorbital spots, and a chin and cheeks that are creamy white. Ears are large and naked, rims are black, and a pale spot is present on forehead at medial base of ears. Nose, lips, toes, and a region above chin are pink. A distinct median black band runs along top of head (Allen, 1900; Emmons and Feer, 1990; Redford and Eisenberg, 1992).

Fur is short, loose, and soft (Allen, 1900). Body is slim and usually lean. Head is large with an elongate, conical rostrum (Nowak, 1991). Tail is cylindriform, slender, tapered, slightly prehensile, scaly, and almost bare except for basal 50–60 mm, which is densely furred. In general, tail color is uniformly brown or dark, but in some populations it is bicolored with dark proximal part usually contrasting sharply with a white tip (Gardner and Patton, 1972; Hershkovitz, 1997).

Ranges of external and cranial measurements (in mm) of adults of both sexes are as follows (sample size in parentheses): length of head and body, 200–331 (329); length of tail, 195–355 (322); length of hind foot, 29–52 (315); length of ear, 18–43 (216); condylobasal length, 60–82.1 (395); zygomatic breadth, 28–43.7 (372); braincase width, 18–24 (370); and palatal length, 34.1–50.2 (381). Skull is narrow and slender (Fig. 2). Bony palate has four fenestrae. Sagittal and occipital crests are well developed in adults. Auditory bullae are small. Adult body mass ranges from 200 to 674 g, but in captivity may reach 1,500 g (Allen, 1900; Collins, 1973; Eisenberg, 1989; Fonseca and Kierulff, 1989; Goodwin, 1969; Hall, 1981; Hall and Dalquest, 1963; Hershkovitz, 1997; Redford and Eisenberg, 1992).

DISTRIBUTION. *Philander opossum* is Neotropical and ranges from east-central Mexico to northeastern Argentina (Fig. 3). In Mexico it occurs in south-central part of Tamaulipas and throughout coastal plain of the Gulf of Mexico, including eastern San Luis Potosí, northern and eastern Hidalgo, Puebla, Veracruz, northeastern Oaxaca, Chiapas, and all the Yucatan Peninsula. In Central America it is present in all countries (Hall, 1981; Jones et al., 1974). In northern South America its range occupies lowlands of northern and southern Venezuela, Guyana, Suriname, French Guiana, and from northern Colombia to northern Peru west of the Andes. East of this mountain range it is present in almost all the Amazon basin except for the high basin area in eastern Colombia. *P. opossum* is also absent from extreme eastern Brazil. It has been reported in the Paraná River basin and eastern Paraguay, reaching its southernmost distribution in the Chaco region and in Formosa and Misiones provinces, Argentina (Eisenberg, 1989; Emmons and Feer, 1990; Handley, 1976; Pérez-Hernández et al., 1994). The gray four-eyed opossum is generally found from sea level to 1,650 m (Hall and Dalquest, 1963).

FOSSIL RECORD. Early Pliocene remains of *Philander* occur in beds of Montehermosan age in Buenos Aires Province, Argentina. The genus is represented by a single tooth, which was made the type of *P. entrerrianus* (Reig, 1957). Minimum radiometric age for the Montehermosan at Corral Quemada is 3.59×10^6 years ago (Marshall, 1981). Fossils of *P. opossum* occur in cave deposits of late Pleistocene–Holocene from Lagoa Santa, Minas Gerais, Brazil (Winge, 1893).

FORM AND FUNCTION. Under ultraviolet light, pelage is fluorescent: purple on basal part of dorsal pelage and rose, pink, lavender, or purple with two lateral yellow spots on ventrum. Males may have more purple fluorescence (Pine et al., 1985). Pelage in young is fine, thin, and gradually replaced by coarser and thicker pelage of adults. Molt patterns have not been determined (Hershkovitz, 1997).

Usual mammary formula for the gray four-eyed opossum is 3–1–3 = 7, with two symmetrical rows of three mammae arranged on either side of a medial teat. Only five mammae were found in in-

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Philander opossum* from Chajul, Chiapas, Mexico (male, Instituto de Biología, Universidad Nacional Autónoma de México 22185). Greatest length of skull is 69.1 mm.

dividuals from Panama (Enders, 1935). All mammae are concealed within the marsupium (Hershkovitz, 1997).

Dental formula is i 5/4, c 1/1, p 3/3, m 4/4, total 50. Denture is complete at 1 year of age (Atramentowicz, 1986). *P. opossum* has looser attachments of vertebrae and longer neural spines than *Didelphis*, thus *Philander* is more agile (Hall, 1981). Both fore- and hind-feet are modified for grasping, because pollex and hallux are opposable. Skull is elongate with a mean condylobasal length of 67 mm; dorsal surface is nearly flat between muzzle and braincase; nasals are long, >40% of greatest skull length; tips of premaxillary bones are rounded. Hershkovitz (1997) has extensive, detailed descriptions of skull and teeth.

Mean cranial volume is 3.72 ± 0.41 ml (*SD*), which is among the largest for Didelphidae. An intrafamilial comparison of encephalization quotients shows that *P. opossum* is unusual because it has a high encephalization quotient value and is strongly terrestrial (Eisenberg and Wilson, 1981). The gray four-eyed opossum, compared to other didelphids, has relatively underdeveloped masseter and temporalis muscles, an elongated skull with canines and molars relatively close together, and, thus, a narrow rostral and buccal area. The elongated rostrum may be associated with predation on small vertebrates (Medellín, 1991).

Hemoglobin and hematocrit values are higher at highest alti-

tudes and lower in pouch young than in adults (Hershkovitz, 1997). Body temperature of a young female from Barro Colorado, Panama was 35.4°C at an ambient temperature of 26.1°C (Enders and Davis, 1936).

Age can be estimated by number of molars and their degree of wear. Young at weaning do not have molars. Molars emerge successively from M1 to M4. Appearance of M4 is followed by replacement of P3, the only deciduous tooth in marsupials. At this point dentition is complete and wear on molars is predictable and related to age (Atramentowicz, 1986). Age of pouch young can be accurately estimated using the equation t = (log$_e$HB − 3.01)/0.024 where t = estimated age in days and HB = head and body length in millimeters (D'Andrea et al., 1994).

ONTOGENY AND REPRODUCTION. *Philander opossum* breeds throughout the year in some areas, but breeds seasonally in others (Hunsaker and Shupe, 1977). In general, reproductive activity increases during the rainy season (Fleck and Harder, 1995; Fleming, 1972) and has been reported at the end of the rainy season from December through January (Fleming, 1973). Reproduction seems to be interrupted only when a female cannot meet increased nutritional requirements due to rearing of young (Julien-Laferrière and Atramentowicz, 1990). In mature forest *P. opossum* breeds all year, but fewer births occur in secondary forest during the period of low fruit availability from July through August (Fleck and Harder, 1995).

Reproductive activity of *P. opossum* varies temporally across its range. Gray four-eyed opossums reproduce throughout the year in Veracruz, Mexico (Hall and Dalquest, 1963); from February to June in Lacandona, Chiapas, Mexico (Medellín, 1992); from February to October in Nicaragua (Biggers, 1966; Collins, 1973); and from February to November in Panama with copulations observed in late January (Fleming, 1973), and pouch-gravid females observed from April through July (Enders, 1935). *P. opossum* is reproductively active from May to October in Colombia and from January through April in Surinam (Collins, 1973; Husson, 1978). Three pouch-gravid females were collected from September to October in Venezuela (Collins, 1973). Pouch-gravid females were collected throughout the year in Peru with a higher proportion of females nursing young in the wet season (Fleck and Harder, 1995). Reproductive activity occurred throughout the year in French Guiana but decreased at the end of the rainy season (Julien-Laferrière and Atramentowicz, 1990). *P. opossum* reproduces from September to February in Minas Gerais, Brazil (Fonseca and Kierulff, 1989); from August through February in Rio de Janeiro, Brazil; and from August through February in Misiones, Argentina (Redford and Eisenberg, 1992).

Females usually have seven mammae, and maximum number of pouch young matches number of mammae (Enders, 1935; Hershkovitz, 1997). Thus number of young per litter in *P. opossum* varies from one to seven, but litter size averages four or five young (Collins, 1973; Fleck and Harder, 1995) and varies with latitude (Fleming, 1973). Recorded litter sizes for *P. opossum* include the following: from five to seven young in Veracruz, Mexico (Davis, 1944); six nursing young in Campeche, Mexico (Jones et al., 1974); an average of five young in Chiapas, Mexico (Medellín, 1992); from five to seven young in Guatemala and Nicaragua (Handley, 1950); from three to five young in El Salvador (Felten, 1958); a mean of 4.6 young in Costa Rica and Panama (Fleming, 1973; Goodwin, 1946); from two to three young in Surinam (Husson, 1978); a mean of 4.2 young in French Guiana (Atramentowicz, 1986); a mean of 4.5 young in southeastern Brazil; and from four to six young in northeastern Argentina (Redford and Eisenberg, 1992).

Female age or mass at parturition has great influence on survival of pouch young. Death of pouch young is more frequent in females <11 months and >17 months (Gentile et al., 1995; Julien-Laferrière and Atramentowicz, 1990). The nidicolous period lasts 8–15 days. Birth to weaning lasts ca. 68–75 days in *P. opossum* (Charles-Dominique, 1983). Pouch young have been measured from ca. 35 to 107 mm (head and body); the last value was for a captive female (Phillips and Jones, 1969).

Mass of newborns is estimated at 9 g and that of young at weaning at 50–75 g (Hershkovitz, 1997). In captivity, young at weaning weigh 100–200 g and weigh 673–800 g after 1 year (Collins, 1973). Maximum life span is 3 years 6 months in captivity (Hunsaker, 1977), but, based on dental wear, Atramentowicz (1986) estimated that longevity in the field does not exceed 2.5 years.
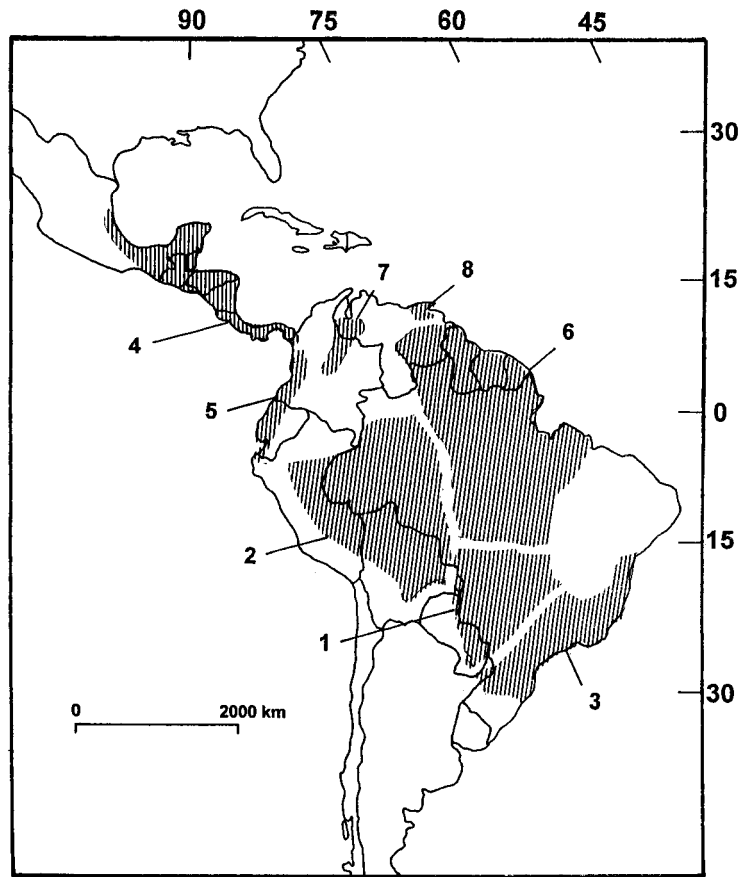
FIG. 3.   Distribution of *Philander opossum* in Central and South America: 1, *P. o. azaricus*; 2, *P. o. canus*; 3, *P. o. frenatus*; 4, *P. o. fuscogriseus*; 5, *P. o. melanurus*; 6, *P. o. opossum*; 7, *P. o.* subsp. nov. I; and 8, *P. o.* subsp. nov. II.

Males are sexually mature at a body length of 230 mm or after 7 months, and probably are sexually active throughout the year (Charles-Dominique, 1983; Fleming, 1973). In the breeding season males have a pale yellowish patch on sides of lower abdomen anterior to thighs. Males also have abdominal or sternal gland activity (Allen, 1901; Fonseca and Kierulff, 1989). Spermatozoa of *P. opossum* are similar to those of *Didelphis*, and pairing of spermatozoa in epididymides occurs (Biggers and De Lamater, 1965). Testes vary seasonally with respect to size but not mass or spermatogenesis (Biggers, 1966; Fleming, 1973).

Females are sexually mature at 6–7 months of age (Hershkovitz, 1997). In captivity, vaginal smears suggest that the first estrus occurs at 15 months of age (Collins, 1973). *P. opossum* is polyestrous. Females can produce two or more litters per season, but young from a third litter are mostly aborted while in the pouch (Fleming, 1973; Gentile et al., 1995; Hershkovitz, 1997). Ovarian cycling is inhibited during lactation but not during gestation (Charles-Dominique et al., 1981).

ECOLOGY. *Philander opossum* normally inhabits tropical evergreen forests and secondary growth forests but also invades croplands (Charles-Dominique, 1983; Eisenberg, 1989; Handley, 1976). Of 46 specimens collected in Venezuela, 98% were on the ground and 2% were on logs. All were captured in streams or moist areas with 91% in evergreen forests and 9% in openings such as orchards, cropfields, and yards (Handley, 1976). *P. opossum* is mainly associated with streams and other moist areas such as swamps (Alvarez, 1963; Atramentowicz, 1986; Hershkovitz, 1997; Jones et al., 1974; Villa-R., 1949). In Veracruz, Mexico, *P. opossum* was mainly found near rivers and streams, but was also recorded in a sugar cane field and on a hillside far from water (Hall and Dalquest, 1963).

Philander opossum has been reported as primarily carnivorous (Emmons and Feer, 1990; Hunsaker, 1977; Streilein, 1982), omnivorous (Hall and Dalquest, 1963; Hershkovitz, 1997), and frugivorous–insectivorous (Atramentowicz, 1986). Reported food items include sweet-lemons, jobo plums (*Spondias*), fruit of the chicozapote (*Manilkara sapota*—Hall and Dalquest, 1963), corn (Kuns and Tashian, 1954), nectar, frogs (Eisenberg, 1989), pulp of *Corozo oleifera* nuts, spiny rats (*Proechimys semispinosus*—Fleming, 1972), other small mammals, birds and their eggs, reptiles, amphibians, insects, crustaceans, snails, earthworms (Pérez-Hernandez et al., 1994), and carrion (roadkills—Davis, 1944). In Chiapas, Mexico, during a year-long study at Montes Azules Biosphere Reserve, 24 food items were identified in 99 scats. The three most important food items were beetles from the family Scarabaeidae (74% mean occurrence), crustaceans (67%), and seeds of *Cecropia obtusifolia* (60%). Other important food items were seeds of *Piper* and cockroaches (Blattidae). The only vertebrates in the diet were birds, which occurred in 3% of scats. Diet was seasonal with plant matter more frequent during the wet season and insects dominant during the dry season (Clemente, 1994). Fruits from 44 species were identified in the diet at two sites in French Guiana by direct observation and stomach contents analysis; consumption of nectar from flowers of the Balanoporaceae was also recorded (Atramentowicz, 1988). Of 44 fruit species, a high proportion (77%) consisted of fruits <5 cm in diameter. Common traits of these fruits included a fleshy pulp, a high content of water, a high concentration of sugars or lipids, and a poor total nitrogen content. Nineteen (43%) fruits had seeds <1 cm in size that could be disseminated. These 19 seeds were mainly from pioneer taxa such as *Cecropia*, *Vismia*, and Melastomaceae (Atramentowicz, 1988).

In captivity, Enders (1935:410) reported that *P. opossum* "are more carnivorous than any of the other opossums. They ate meat of all kinds including ant-eater, carcasses of rodents, grasshoppers, and eggs in preference to any kind of fruit, although they did eat banana, papaya, pineapple and figs." Field collectors have used flesh as bait to capture *P. opossum*. The gray four-eyed opossum may steal rodents and other small mammals from live-traps (Alvarez, 1963; Hall and Dalquest, 1963). One individual fed on live bats caught in a mist net (Fleming, 1972) and another fed from garbage cans at the edge of a village (Julien-Laferrière et al., 1989).

Philander opossum and *D. marsupialis* are important in dispersal of *Cecropia* because both deposit seeds in high-quality germination sites (open sites in secondary growth) compared to arboreal frugivores, such as *Ateles, Bassariscus,* and *Potos,* which are restricted to primary forest. However, gray four-eyed opossums disperse fewer seeds over shorter distances compared to *D. marsupialis* in the same habitat (Medellín, 1994).

Sex ratio of *P. opossum* populations varies geographically. In Lacandona, Mexico, overall sex ratio was 1.75:1. Sex ratio was 1.19:1 in pouch young. Thirty-eight percent of females produced more males than females and 44% of the litters were male-biased (Medellín, 1992). In Nicaragua and Panama all litters had a 1:1 sex ratio or a very close figure (Fleming, 1972, 1973; Phillips and Jones, 1969). In French Guiana females were slightly more abundant, with a sex ratio of males to females of 1.28:1 (Atramentowicz, 1986) and in Brazil a litter with four females and one male was found (Fonseca and Kierulff, 1989).

Although the gray four-eyed opossum is widely distributed and fairly common, information on its population density and dynamics is relatively scarce. In Montes Azules Biosphere Reserve in Chiapas, Mexico, average density was estimated as 0.48 individuals/ha with an average biomass of 176 g/ha. Highest density was recorded in October and density was lowest in April. Both sexes moved an average of 47.1 m between captures (SD 36.7, $n = 90$) and greatest movement was 117 m by an adult male (Medellín, 1992).

In the Panama Canal Zone population levels were similar in two different biomes: second-growth tropical forest and mature moist tropical forest. Highest densities occurred in the dry season in both sites and were 0.65/ha and 0.55/ha, respectively. Population density of *P. opossum* was lower than that of sympatric *D. marsupialis.* Males and females moved an average of 60–73 m between successive capture sites and longest recorded movements were from 108 to 125 m (Fleming, 1972).

An average of 137 individuals/km² was estimated for a secondary forest site in French Guiana; monthly averages ranged from 85 to 180 individuals/km². Biomass of *P. opossum* was 55.8 kg/km². Adult population showed a high mobility; 97% of adult population changed, with 20.3% of new adults arriving to the area and a 13.4% recapture of individuals marked in the pouch. Fewer than 17% of individuals stayed in the study area for >200 days (Atramentowicz, 1986). In a primary forest in French Guiana, a lower average density of 17 individuals/km² was estimated; biomass was calculated as 7 kg/km² (Julien-Laferrière, 1991). At Cacao, French Guiana, *P. opossum* was caught more frequently at the village periphery when compared to the village interior and nearby forest. Two radio-collared individuals living near the village had smaller home ranges than one individual in the forest (Julien-Laferrière et al., 1989).

Predators of *P. opossum* are the boa *Corallus enhydris* (Eisenberg, 1989), the crotalid *Lachesis muta* (Atramentowicz, 1986), and possibly *D. marsupialis* (Wilson, 1970). Ocelots (*Leopardus pardalis*) and other felids such as the eyra cat (*Herpailurus yaguarondi*) are potential predators, as well as the tayra (*Eira barbara*), the grison (*Galictis vittata*), foxes (e.g., *Urocyon cinereoargenteus*), and large owls (e.g., *Tyto alba*—Atramentowicz, 1986; Hershkovitz, 1997).

Many arboviruses occur naturally in the gray four-eyed opossum, including acara, eastern equine encephalitis, ilheus, itaporanga, itaqui (rare in marsupials), Mucambo, pacui, piry, St. Louis encephalitis, turlock, Venezuelan equine encephalitis, vesicular stomatitis (Indiana and New Jersey strains), and yellow fever (Hunsaker, 1977). Parasitic protozoans found in this marsupial were *Babesia brasiliensis, Sarcocystis garnhami, Trypanosoma cruzi,* and *Trypanosoma rangei*–like. Also, the fungus *Histoplasma capsulatum* was detected in this opossum (Hershkovitz, 1997). Round worms (Nematoda) from this didelphid include *Cruzia tentaculata, Globocephalus marsupialis, Viannaia barusi, V. conspicua, V. minispicula, V. skrjabini, V. tenorai,* and *V. vianniai* (Hershkovitz, 1997; Hunsaker, 1977). Platyhelminthes (flatworms) hosted by gray four-eyed opossums were flukes (Trematoda) *Amphimeruse ruparupu, Duboisiella proloba, Paragonimus amazonicus, Plagiorchis didelphidis,* and *Zonorchis allentoshi* as well as tapeworms (Cestoda) *Linnistowia iheringi, Oochoristica braziliensis,* and *Sparganum reptans* (Hershkovitz, 1997; Hunsaker, 1977).

Ectoparasites recorded from *P. opossum* include lice (Mallophaga) *Gliricolla porcelli, Gryopus ovalis,* and *Trimenophon hispidus*; fleas (Siphonaptera) *Adoratopsylla intermedia, A. antiquo-rum, Ctenocephaloides felis, Neotyplocercus rosenbergi, Polygenis roberti, P. klagesi, Rhopalopsyllus australis, R. cacicus, R. lutzi, Tritopsylla intermedia,* and *Xenopsylla cheopsis*; mites, ticks, and chiggers (Acarina) *Amblyomma auricularium, A. geayi, Androlaelaps fahrenholzi, Archemyobia pectinata, Crotiscus disdentatus, Euschoengastia nunezi, Eutrombicula alfreddugesi, E. goeldii, E. tropita, Haemolaelaps glasgowi, Ixodes lasallei, I. luciae, I. venezuelensis, Ornithonyssus wernecki, Pseudoschoengastia bulbifera, Trombicula dunni, T. keenani, Tur apicalis,* and *T. uniscutatus* (Hershkovitz, 1997; Hunsaker, 1977).

Additional parasitic genera recorded for this marsupial are numerous, including (Arthropoda: Acarina) *Ctenocephalides, Gigantolaelaps, Heterothrombidium, Intercutestrix, Leeuwenhoekia, Microthrombidium, Neotyphloceras, Pentastoma, Porocephalus, Shongastia,* and *Trimenopon*; (Insecta: Siphonaptera) *Pulex*; (Acantocephala) *Echinorhynchus* and *Hamanniella*; (Nematoda) *Aspidodera, Capillaria, Cortiamosoides, Gnatosthoma, Gongylonemoides, Macielia, Oxysoma, Philostrongylus, Physaloptera, Skrjabinofilaria, Subulura, Travassostrongylus,* and *Trichuris*; (Protozoa) *Besnoitia* and *Haemogregarina*; and (Trematoda) *Brachylaemus, Maritrema, Opistorchis, Phaneropsolus, Platynosomum,* and *Podospathalium* (Collins, 1973).

Philander opossum, as well as other forest-dwelling marsupials, serves as a reservoir for *Trypanosoma cruzi*: 5% of 85 individuals from 19 different localities in French Guiana harbored trypanosomes. An even higher infection level occurred at Cacao, French Guiana: 2 of 5 individuals (40%) in nearby forest sites and 4 of 31 (13%) individuals in settlement surroundings tested positive for *T. cruzi* (Julien-Laferrière et al., 1989). Although *P. opossum* is not eaten by the Mayan Lacandon in Chiapas (March, 1987), it is hunted for food in other parts of Mexico (Medellín, pers. obs.) and was eaten by Creoles and Indians of Guyana (Hershkovitz, 1997).

BEHAVIOR. Feigning death, as exhibited by *Didelphis virginiana,* is not known in *P. opossum.* Instead, the gray four-eyed opossum threatens by opening the mouth wide, hissing loudly, and fighting savagely (Hershkovitz, 1997; Nowak, 1991). Some consider *P. opossum* to be the fiercest fighter of the opossums (Enders, 1935; Goldman, 1920). The gray four-eyed opossum is generally nocturnal but is active during the day in Surinam (Nowak, 1991). Mainly terrestrial, *P. opossum* can also climb and swim well. Upon release from a trap, 93% and 94% of animals in Brazil (Fonseca and Kierulff, 1989) and Peru (Fleck and Harder, 1995), respectively, used terrestrial escape routes. *P. opossum* is somewhat scansorial and uses the ground and middle vegetation levels while foraging (Charles-Dominique et al., 1981; Handley, 1976). This opossum is agile and quick, and appears more alert than most other didelphids (Eisenberg and Wilson, 1981; Emmons and Feer, 1990; Nowak, 1991). Generally solitary, adults have minimal contact apart from mating. *P. opossum* is not territorial and overlap among ranges of neighboring adults is broad (Charles-Dominique, 1983; Emmons and Feer, 1990; Redford and Eisenberg, 1992). Home range depends on availability of resources and the gray four-eyed opossum seems to be nomadic with large variation in home range (Hunsaker, 1977). From the data of Fleming (1972), Hunsaker (1977) calculated home range size as 0.34 ha in the Panama Canal Zone.

Nests of dry leaves are built in hollow trees, tree forks, fallen logs, and in ground burrows. In Peru, nests were found in cultivated banana and swamp palm trees (*Mauritia flexuosa*—Fleck and Harder, 1995). In Veracruz, Mexico, two gray four-eyed opossum nests were found in roofs of palms of abandoned houses (Hall and Dalquest, 1963). Nests are globular with a diameter of ca. 30 cm (Emmons and Feer, 1990; Enders, 1935).

The gray four-eyed opossum sleeps rolled up into a ball, and although eyes are not visible, supraocular spots give the appearance of an awake animal with open eyes (Hershkovitz, 1997). Clicks, chirps, and hisses, such as those noted for *Caluromys* and *Marmosa,* are used by *P. opossum* (Redford and Eisenberg, 1992). On the ground, the usual locomotor pattern is a measured walking gait, whereas *P. opossum* uses a trot when running. Leaps or bounds are only used for rapid escape (Hershkovitz, 1997). *P. opossum* grooms in the same fashion as *Didelphis,* but for longer periods of time (Hunsaker, 1977). It washes its face mouselike using its hands, and the rest of the body is groomed using the tongue in a catlike manner (Hershkovitz, 1997).

GENETICS. The gray four-eyed opossum has a diploid chromosome number of 22 (Biggers et al., 1965; Reig et al., 1977). Karyotype consists of 10 pairs of uniarmed autosomes with terminal centromeres, an acrocentric X, and a minute Y chromosome. No intraspecific geographic variation has been reported and this species shares an identical karyotype with *Chironectes minimus, D. albiventris, D. marsupialis,* and *P. andersoni* (Reig et al., 1977). Average variation of haplotypes of mtDNA cytochrome b sequences within local populations and among geographic localities for the subspecies *P. o. canus* and *P. o. opossum* was minimal, 0.15% and 1.34%, respectively (Patton and Da Silva, 1997).

REMARKS. *Philander opossum* is called the gray four-eyed opossum in English, however, because of its wide distribution and relatively high abundance it has many colloquial names including tlacuache cuatro ojos, ratón tlacuache gigante (México—Alvarez del Toro, 1977), zorrito de árbol (México—Villa-R., 1949), ooch (Mayan Lacandon—March, 1987), uc c'o (Mayan Tzeltal—Hunn, 1977), cayopolin (Honduras—Reid, 1997), zorro de cuatro ojos (Costa Rica), fo-ai awari (Surinam), cucha gris de cuatro ojos (Colombia), zorro (Ecuador), pericote (Peru), mucura-de-cuatro-olhos (Brazil), carachupa (Bolivia), chucha mantequera (Paraguay), comadreja gris de cuatro ojos, Guaiki (Argentina), and mbicuré (Guarani—Emmons and Feer, 1990).

The generic name *Philander* is derived from the primary vernacular name, 'Philander, opassum, sive Carigueja' used by Seba (1734). Assigning this species to the genus *Philander* has been disputed. Hershkovitz (1949) established the name *Philander* Tiedemann and pointed out that *Philander virginianus* Tiedemann was a replacement name for *Didelphis opossum* Linnaeus. Pine (1973) and Husson (1978) argued against use of this name and preferred *Metachirops* Matschie. Hershkovitz (1976, 1981) and Gardner (1981, 1993) rejected this change. However, the International Commission on Zoological Nomenclature (1998) determined that *Philander* Brisson, 1762 had priority for this generic name; therefore, *Philander* Tiedemann, 1808 became a junior synonym and homonym.

We thank A. Gardner, J. Patton, and T. Friedrich for their help in obtaining some references; thanks also to A. Hernández from the Laboratorio de Microcine, Facultad de Ciencias, Universidad Nacional Autónoma de México, for the skull photographs. Information for the distribution map was kindly provided by J. Patton and information for generic and specific synonyms was kindly enhanced by comments of Dr. Alfred Gardner who greatly clarified this part. This paper is dedicated to Don Miguel Alvarez del Toro whose early work raised awareness of the importance of conservation of the southern part of Mexico and its unique fauna.

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