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Composition of the Family Didelphidae Gray, 1821
(Didelphidae: Marsupialia), with a Review of
the Morphology and Behavior of the Included
Four-Eyed Pouched Opossums of the
Genus *Phlogothraupis* Tiedemann, 1848

Philip Hershkovitz

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Zoology

NEW SERIES, NO. 86

Composition of the Family Didelphidae Gray, 1821 (Didelphoidea: Marsupialia), with a Review of the Morphology and Behavior of the Included Four-Eyed Pouched Opossums of the Genus *Philander* Tiedemann, 1808

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Composition of the Family Didelphidae Gray, 1821 (Didelphoidea: Marsupialia), with a Review of the Morphology and Behavior of the Included Four-Eyed Pouched Opossums of the Genus *Philander* Tiedemann, 1808

Philip Hershkovitz†

Abstract

The generic content of the family Didelphidae as currently conceived consists of *Didelphis*, *Philander*, *Chironectes*, and *Lutreolina*. It is shown that most defining characters of the Didelphidae determined from those of the genus *Didelphis* are highly derived and not shared by *Chironectes* or *Lutreolina*. Accordingly, the family content was restricted to *Didelphis* and the genus *Philander*, which is smaller and less derived than *Didelphis*. The genus *Didelphis* had previously undergone a partial taxonomic revision. A complete revision of the genus *Philander* now follows. Two species of the genus have been recognized. Comparisons were made with outgroups *Chironectes* and *Lutreolina*. Habits of *Philander*, insofar as known, are described. The more primitive genus *Metachirus*, which is sometimes regarded as a didelphid, is being treated separately.

Introduction

The four-eyed pouched opossums, genus *Philander* Tiedemann, 1808, most nearly related to the larger opossums of the genus *Didelphis* Linnaeus, 1758, are common throughout much of the neotropics from northern Argentina into Tamaulipas, México. About 20 Linnaean names have been proposed for four-eyed pouched opossums, but only two species are recognized here. The earliest known, *P. opossum* Linnaeus, 1758, with its geographic distribution nearly equal to that of the genus, is the smaller of the two and generally less darkly colored. *Philander andersoni* Osgood, mainly western Amazonian in distribution, contains two subspecies. One, *P. andersoni andersoni* Osgood, occurs in Perú and in the Territorio Federal Amazonas, Venezuela. The wide gap in distribution between the two countries may be for lack of collecting or the result of a climatic event. The blackish *P. andersoni mcilhennyi* Gardner and Patton is known only from the upper Río Purús basin in Amazonian Perú.

This report is the author's sixth on New World marsupial systematics and behavior. The series began in 1992 with a taxonomic revision of the gracile mouse opossum, genus *Gracilinanus* (Marmosidae) (Hershkovitz, 1992a). It was followed in the same year by a critical examination of the significance of ankle bones as phylogenetic indicators (Hershkovitz, 1992b). The description of a seemingly abnormal staggered third lower incisor, which proved to be the hallmark of all didelphimorphs since the earliest Cretaceous, if not late Jurassic, was published in 1995. In press is a taxonomic review and life history account of the relict Chilean mouse opossum *Dromiciops* (Microbiotheriidae). Also awaiting publication is another review, that of the brown four-eyed pouchless opossum, genus *Metachirus*. This taxon was used at first as an outgroup for the *Philander* opus. As work progressed, however, *Metachirus* took on greater importance and is being completed under its own title.

In preparation is a monograph of living New

World marsupials from which the above-mentioned articles have been partially derived and elaborated.

Abbreviations

The following abbreviations are used for the institutions where the specimens examined are preserved.

- AMNH = American Museum of Natural History, New York
BM(NH) = British Museum (Natural History), London
FMNH = Field Museum of Natural History, Chicago
MVZUC = Museum of Vertebrate Zoology, University of California, Berkeley
USNM = National Museum of Natural History, Washington, D.C.
USPMZ = Universidade de São Paulo Museu de Zoologia, São Paulo, Brasil
MPEG = Museu Paraense Emilio Goeldi, Belém, Brazil
UKMNH = University of Kansas Museum of Natural History, Lawrence
LSUMZ = Louisiana State University Museum of Zoology, Baton Rouge
MNRJ = Museu Nacional, Rio de Janeiro
RMNH = Rijksmuseum van Natuurlijke Historie, Leiden

Didelphidae: Taxonomic Status, The Genera

The family Didelphidae, erected by Gray, 1821, included all then-known American marsupials divided into the genera *Didelphis* Linnaeus and *Cheironectes* [sic] Illiger. It was not until late in the 20th century that critical attention was paid to higher systematic categories of living New World marsupials.

The early arrangement of the taxa persisted, nevertheless, as if all female marsupials were pouched and all individuals prehensile-tailed,

scansorial, and members of the genus *Didelphis*. Discovery of the first caenolestid by Tomes in 1863 added another dimension to the concept of American marsupials by directing attention to the existence of nonpouched, non-prehensile-tailed and terrestrial American marsupials. Notwithstanding, apart from accommodations made in catalogs for the increasing number of newly discovered taxa, no significant changes were made in the classifications. Recent catalogers (Cabrera, 1958; Hall & Kelson, 1959; Honecki et al., 1982; Gardner, 1993) recognized the three current orders of American marsupials, each with a single family, its content as found in the literature. The categories, with the numbers of their respective living genera and species in parentheses (ex Gardner, 1993), follow:

- Order Didelphimorphia
 - Family Didelphidae (15 genera, 63 species)
- Order Paucituberculata
 - Family Caenolestidae (3, 5)
- Order Microbiotheria
 - Family Microbiotheriidae (1, 1)

Research by Reig et al. (1977) on chromosomes of the Didelphidae resulted in significant advances. Three karyotypes were distinguished among living American marsupials. The largest diploid number of chromosomes was 22, possessed by four genera of American marsupials, namely *Didelphis* (three species), *Chironectes* (one), *Lutreolina* (one), and *Philander* (two). The other complements were $2n = 18$ in the short-tailed mouse opossum *Monodelphis* (three of about 15 species) and $2n = 14$ in *Caluromys* (three species), *Caluromysiops* (one), *Marmosa* (*sensu lato*; eight species of about 38, since rearranged into four genera), *Metachirus* (one), and *Dromiciops* (one). The $2n = 14$ karyotype is generally regarded as the primitive one. No reclassification of American marsupials was based on their cytogenetic constitution. In any case, Kirsch (1977) had already removed woolly opossums (*Caluromys*) from the Didelphidae and erected the family Caluromyidae for them. In 1992, Hershkovitz (1992a) established the family Marmosidae for most so-called mouse opossums previously known as *Marmosa* and raised *Glironia* to family rank. Four opossum

FIG. 1. Representatives of the four genera of large American marsupials usually referred to as the family Didelphidae, subfamily Didelphinae. Here only *Didelphis marsupialis* and *Philander opossum* are so classified. (Figures not to scale.)

Philander opossum
Linnaeus



Didelphis marsupialis Linnaeus



Chironectes minimus
Zimmermann



Lutreolina crassicaudata Thomas

genera were retained in Didelphidae because they are the largest and their karyotype is $2n = 22$. These four genera are *Didelphis*, *Chironectes*, *Philander* of Linnaeus, and *Lutreolina* Thomas, 1910 (Figs. 1–3).

Biochemical, chromosomal, and anatomical characters were considered by Reig et al. (1985) in an attempt to determine the phylogenetic relationships among didelphoid marsupials. The extinct forms they considered are outside the scope of this monograph, as are most of the included genera. The Didelphidae of concern here include the three subfamilies Herpetherinae, Caluromyinae, and Didelphinae. The latter was further subdivided into the tribes Didelphini, Metachirini, and Marmosini. Their tree (Reig et al., 1985, Fig. 2, p. 339) shows all American didelphoids and basic Australian forms emerging from Upper Cretaceous Microbiotheriidae, an improbability. It also shows didelphids arising in the Eocene and giving rise to the Marmosini with the primitive karyotype $2n = 14$ and pouchless reproductive system in the Oligocene–Miocene. This also seems unlikely. The pouchless and non-prehensile-tailed, terrestrial Metachirini with $2n = 14$ may have given rise to didelphids rather than the reverse as depicted.

Studies by Kirsch et al. (1993a) of DNA/DNA hybridization resulted in assignment of the five largest American genera (*Didelphis*, *Philander*, *Lutreolina*, *Chironectes*, and *Metachirus*) to the Didelphidae. Morphologically, as shown below, *Lutreolina* and *Chironectes* share few traits with each other and fewer with *Didelphis*, and the indicated position of *Metachirus* is even less tenable.

Patton et al. (1995 [1996]) regarded the systematic position of *Metachirus* to be somewhat equivocal:

While the brown four-eyed opossum *Metachirus* forms a sister taxon to the (*Didelphis* + *Philander*) clade in all trees, this relationship is not well supported. Bootstrap values for parsimony analyses are only 68 and 54 for DNA and amino acid sequences, respectively, and decay indices indicate that it would take only two or three additional steps to collapse the relationship between *Metachirus* and the other two genera. Similarly, confidence limits for this node are only 28% in the DNA neighbor-joining distance tree. The pouchless, primitively $2n = 14$ brown four-eyed opossum contrasts markedly with the pouched, derived $2n = 22$ *Didelphis* and *Philander* pair, although the three genera apparently do share similarities in bullar structure (Reig et al., 1987). Indeed, the total evidence Wagner tree presented by Reig et al. (1987, Fig. 59), based on 45 craniodental, cytological, sero-

logical, and soft anatomical characters, does place *Metachirus* in a sister relationship with *Didelphis* and *Philander*, in contrast to *Marmosa* and *Monodelphis*, as do DNA-DNA hybridization data (Kirsch et al., 1995; Lapointe and Kirsch, 1995). Nevertheless, placements of *Metachirus* either as the sister of (*Didelphis* + *Philander*), with the mouse opossum lineage, or outside of both clades are all equally likely based on an evaluation of these alternative topologies by the log-likelihood test of Kishino and Hasegawa (1989). As a consequence, perhaps *Metachirus* is best considered as a basal member of the (*Didelphis* + *Philander*) and ((*Marmosa* + *Micoureus*) + *Monodelphis*) clades. This is the same conclusion reached by Kirsch (1977) and Reig et al. (1987).

Returning to *Philander*, Patton et al. (1995 [1996]) do not explain why they dropped the prior name *Philander andersoni* Osgood, 1913, and consistently used instead its junior synonym, *P. mcilhennyi* Gardner and Patton, 1972, in all their discussions of marsupial relationships.

A Morphological Test

The four genera of large American marsupials have consistently been regarded as forming a natural assemblage within the family Didelphidae. This can be tested by the 30 morphological characters outlined below. *Philander* shares most characters with *Didelphis*. *Chironectes* and *Lutreolina*, however, have diverged widely from the preceding two genera and from a hypothetical common ancestor of all four. Two of the few shared characters (large size and $2n = 22$) may have evolved independently; other characters that may appear trivial are diagnostic nevertheless. An appraisal of the evolutionary stage of each character is shown in parentheses.

1. Largest of living New World marsupials (derived)

The four genera including the largest living New World opossums (Fig. 1) range in size from the smallest, *Philander*, through *Chironectes* and *Lutreolina*, to the largest, *Didelphis*. Size may have evolved independently in each genus, and its phylogenetic significance in the present context is dubious.

2. Karyotype $2n = 22$ (derived)

The same karyotype evolved independently in unrelated *Marmosa canescens* from a $2n = 14$ karyotype (Engstrom & Gardner, 1988, p. 231). It also occurs in

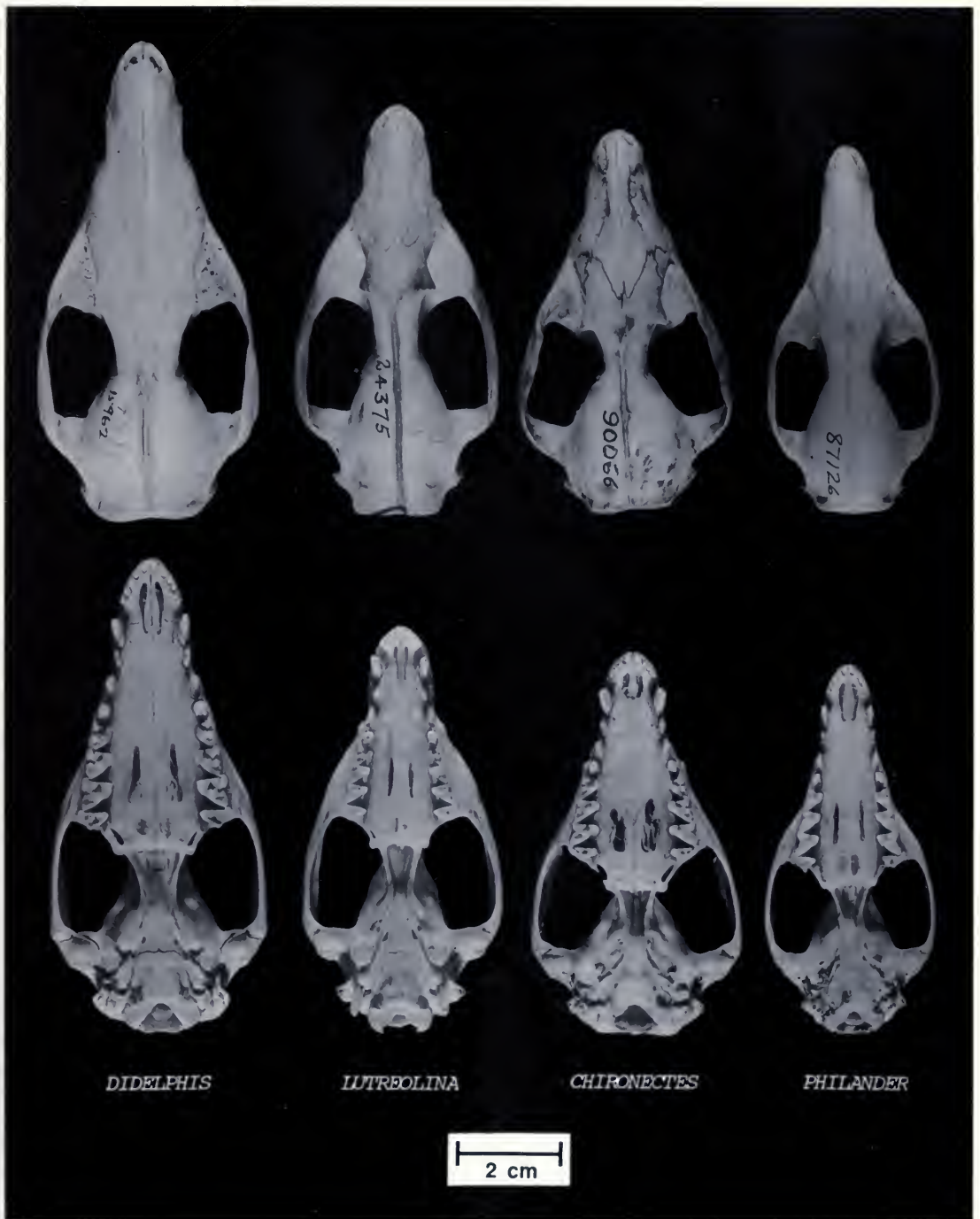


FIG. 2. Dorsal and ventral aspects of skulls of four large American marsupials (shown in order of decreasing size from left to right).

- Australian Macropodidae and Potoroidae. The phylogenetic significance of the same chromosome number in *Chironectes* and *Lutreolina* may be misleading. A different karyotypic pattern in *Didelphis virginiana* does not alter the fact that this species and *D. marsupialis* are very nearly alike and most intimately related.
3. Tail as long as or longer than head and body combined (incipiently derived)
Excludes *Lutreolina*
 4. Tail fully prehensile (derived)
Excludes *Lutreolina* and *Chironectes*
 5. Tail terete (plesiomorphic)
Excludes *Lutreolina* and *Chironectes*
 6. Tail base not notably thickened (plesiomorphic)
Excludes *Lutreolina* (muscle, not fat)
 7. Tail thinly pilose, the scales fully exposed dorsally (plesiomorphic)
Excludes *Lutreolina*
 8. Complete marsupium present in females, absent in males (derived)
Excludes *Lutreolina* and *Chironectes*
 9. Thumb and first toe fully opposable (derived)
Excludes *Lutreolina*
 10. Pedal digits partially or not webbed (incipiently derived)
Excludes *Chironectes*
 11. Crown color pattern whitish above eyes, brownish between (derived)
Excludes *Chironectes* and *Lutreolina*
 12. Ears large, roundish, leaflike, and when laid forward extending midway or more to outer canthus of eye (possibly derived)
Excludes *Lutreolina* and *Chironectes*
 13. Manual unguis sharp and protruding (plesiomorphic)
Excludes *Chironectes*
 14. Paired posteromedian palatal vacuities present (plesiomorphic)
Excludes *Chironectes*
 15. Premaxillary symphysis angular (plesiomorphic)
Excludes *Lutreolina* and *Chironectes*
 16. Depression at proximal end of temporal ridges (?)
Excludes *Lutreolina* and *Chironectes*
 17. Interorbital region not notably constricted (derived?)
Excludes *Lutreolina*
 18. Supraorbital processes rudimentary (incipiently derived)
Excludes *Lutreolina* and *Chironectes*
 19. Spread of zygomatic arches comparatively narrow (plesiomorphic)
Excludes *Chironectes*
 20. Lacrymal foramina facial (derived)
Excludes *Lutreolina* and *Chironectes*
 21. Nasals behind convergent to a single point or with slight spread between points (plesiomorphic?)
Excludes *Lutreolina* and *Chironectes*
 22. Maxillary sheath for insertion of lower canine shallow (plesiomorphic)
Excludes *Lutreolina* and *Chironectes*
 23. Occipital condyles projecting behind vertical plane of supraorbital bone (plesiomorphic)
Excludes *Chironectes*
 24. Incisive foramina long, narrow, and tapered (plesiomorphic)
Excludes *Chironectes*
 25. Foramen magnum ovate (?)
Excludes *Lutreolina*
 26. Ventral mandibular plane between canine and incisors horizontal (plesiomorphic)
Excludes *Lutreolina* and *Chironectes* (?)
 27. Upper incisors 2-5 with little or no deflection inward and upward (plesiomorphic?)
Excludes *Lutreolina* and *Chironectes*
 28. P² nearly as long as P³ (plesiomorphic?)
Excludes *Lutreolina*
 29. Lower incisors not overlapping (staggered i₃ not included) (plesiomorphic)
Excludes *Lutreolina* and *Chironectes*
 30. Locomotion terrestrial-scansorial (derived)
Excludes *Lutreolina* and *Chironectes*
- Taking into account other characters mentioned beyond, comparisons reveal *Didelphis* as a shaggy, oversized "*Philander*." The otter-like *Chironectes*, distinguished mainly by its nonprehensile, naked tail, with both sexes pouched, and the terrestrial weasel-like *Lutreolina*, with its nonprehensile, completely hairy tail and nonopposable first digit, have radiated far from didelphoid roots. Lacking affinities with each other of didelphid grade, *Chironectes* and *Lutreolina* are each treated as a type of a distinct subfamily. The new arrangement follows:
- Superfamily Didelphoidea
 Family Didelphidae Gray, 1821
 Subfamily Didelphinae
 Genus *Philander* Tiedemann, 1808
Philander opossum Linnaeus, 1758
Philander andersoni Osgood, 1913



Chironectes minimus Zimmerman

FIG. 3. *Chironectes minimus* Zimmerman. Plantar and dorsal surfaces of fully webbed right hindfoot.

Genus *Didelphis* Linnaeus, 1758

Didelphis marsupialis Linnaeus, 1758 (*aurita* Wied-Neuwied a synonym)

Didelphis albiventris Lund, 1840

Didelphis virginiana Kerr, 1792

Subfamily Chironectinae (new)

Genus *Chironectes* Illiger, 1811

Chironectes minimus Zimmerman, 1780

Subfamily Lutreolinae (new)

Genus *Lutreolina* Thomas, 1910

Lutreolina crassicaudata Desmarest, 1804

northernmost species, *D. virginiana*, occurs in North and Middle America; the more southern *D. marsupialis*, in México and Middle and South America; and *D. albiventris*, in South America. The North American representatives of *D. virginiana* and *D. marsupialis* have been taxonomically revised by Gardner (1973).

Distinctive characters of the family and subfamilies are explicit in each of the 30 characters described above. Detailed accounts of *Chironectes* and *Lutreolina* await formal taxonomic revision such as given below for *Philander*. *Didelphis* is highly derived. Its roots in the past are unknown. The animal that evolved a prehensile tail, opposable first digit, complete marsupium in stages, and other derived characters is far removed in time from *Didelphis*. It is most unlikely

Didelphis is the best known and most widely distributed genus of American marsupials. Its

that the genus *Didelphis* existed as such in the Early Tertiary or even Late Tertiary. To refer to a staggered-lower-incisored *Didelphis* as the stock from which the Early Paleocene Bolivian microbiothere *Pucadelphys andinus* Marshall and de Muizon (1988) could be derived is anachronistic and morphologically perverted.

A taxonomic revision of *Philander*, the remaining genus of the Didelphinae, follows. Comparisons are made with *Didelphis*, *Chironectes*, and *Lutreolina*. Except for an occasional reference here, *Metachirus* is dealt with in a separate paper that is in preparation.

Genus *Philander* Tiedemann (Four-Eyed Pouched Opossums)

Philander Brisson, 1762:13, 207–214—name from non-Linnaean work and not available. Gilmore, 1941:316—*Metachirops* Matschie antedated; characters; distribution; yellow fever susceptibility. Hopwood, 1947:533—names from Brisson not valid; *Philander* Gronovius non-Linnaean and not available.

Philander Tiedemann, 1808:426—included species *P. virginianus* Tiedemann [= *D. opossum* Linnaeus], *P. murinus* [= *Marmosa murina*], *P. brachyurus* [= *Monodelphis brachyura*]. Hershkovitz, 1949:11—type *P. virginianus* Tiedemann = *Didelphis opossum* Linnaeus; *Philander* Brisson, 1762, and *Philander* Gronovius, 1763, not valid. Hildebrand, 1961:239—comparative body proportions. Peronidini and Peronidini, 1965:381, Fig. 7 (metaphase chromosomes), Fig. 8 (karyogram)—chromosome complement $2n = 22$. Enders, 1966:195—breeding season; habits. Biggers, 1966:251—male external genitalia; spermatozoan types; temperature regulation. Enders and Enders, 1969:431, Pl. 1 (uterus with 5 fetuses), Pls. 2–6 (uterus section)—placenta; fetal membranes; fetal size at birth. Hayman and Martin, 1969:192—chromosomes ($2n = 22$); chromosome phylogeny. Collins, 1973:69—care and maintenance in captivity; reproduction; growth and development; diet; parasites. Tyndale-Biscoe, 1973:25, 38, 40, 61, 65, 189, 192, 230—biology. Pine, 1973:391—not the four-eyed pouched opossum. Hershkovitz, 1976:295—history, nomenclature. McNab, 1978:115—comparative bioenergetics (*P. opossum*). Husson, 1978:27—treated as synonym of *Didelphis* Linnaeus by designation of the Virginia opossum as lectotype of type species *P. virginianus* Tiedemann. Landsmeer, 1979:337, Figs. 1, 4, 11, 12 (cheiridia, extensor assemblies)—digital extensor muscles; claw retraction. Hersh-

kovitz, 1981:943—*Philander* valid generic name; type *P. virginianus* Tiedemann = *Didelphis opossum* Linnaeus. Gardner, 1981:447—*Philander* valid; Husson opinion rejected. Rodger, 1982:270—testis and excurrent ducts; paired spermatozoa. Jenkins and Knutson, 1983—type specimens in British Museum (Natural History). Pérez-Hernández, 1985:53, 65—generic characters. Pérez-Hernández et al., 1986:14—dental morphology and diet. Gardner (in Wilson & Reeder, eds.), 1993:22—synonymy; species (*P. opossum*, *P. andersoni*) distribution.

Metachirops Matschie, 1916:262, 267, 268—included species *pallidus* Allen, *fuscogriseus* Allen, *griseescens* Allen, *melanurus* Thomas, *opossum* Linnaeus, *canus* Osgood, *andersoni* Osgood, *quica* Temminck (designated type), *frenata* Lichtenstein; taxonomy. Miranda Ribeiro, 1936:340—characters. Krumbiegel, 1941:199—review. Pine, 1973:391—valid generic name for four-eyed pouched opossum; *Philander* regarded a synonym of *Didelphis*. *Holothylax* Cabrera, 1919:47—type *Didelphis opossum* Linnaeus by original designation.

Metachirus Burmeister, 1854:135—subgenus of *Didelphis* [sic] Linnaeus, part, *D. quica* Temminck only. Burmeister, 1856:68—part, *M. opossum* Linnaeus only. Thomas, 1888:329—part, *D. opossum* Linnaeus only. Sonntag, 1924:743—comparative tongue anatomy (*M. opossum*). Hill and Fraser, 1925:196, Pl. 1, Fig. 3 (urogenital organs), Pl. 4, Figs. 15–17 (vagina)—female urogenital system. Boardman, 1952:848—hair tracts (*M. opossum*). Lyne, 1959:84—vibrissae (*M. opossum*).

Metacheirus [sic] Sanderson, 1949:787—misspelling of *Metachirus*, in combination with *M. opossum*.

TYPE SPECIES—*Philander virginianus* Tiedemann = *Didelphis opossum* Linnaeus.

Key to the Species (see also Fig. 4)

- Dorsum uniformly dark or grayish, blackish mid-dorsal stripe absent or poorly defined *P. opossum* (p. 33)
- Dorsum with well-defined blackish middorsal stripe or band *P. andersoni* (p. 33)

DISTRIBUTION—Figure 5. Tropical and subtropical forests including second growth, in South and Middle America, from Misiones and Chaco in Argentina, and in Paraguay east of the Río Paraguay, northward into eastern Brasil as far as Bahia on the southeast, west from the Río Tocantins–Araguaia into Bolivia, and Perú north into Ecuador, Colombia, Venezuela, the Guianan countries, Panamá, Costa Rica, Nicaragua, Honduras, Salvador, Guatemala, Belize, and in México, the state of

FIG. 4. Pigmentation of dorsum. A, *Philander opossum*; B, *P. andersoni andersoni*; C, *P. andersoni mcilhennyi*.

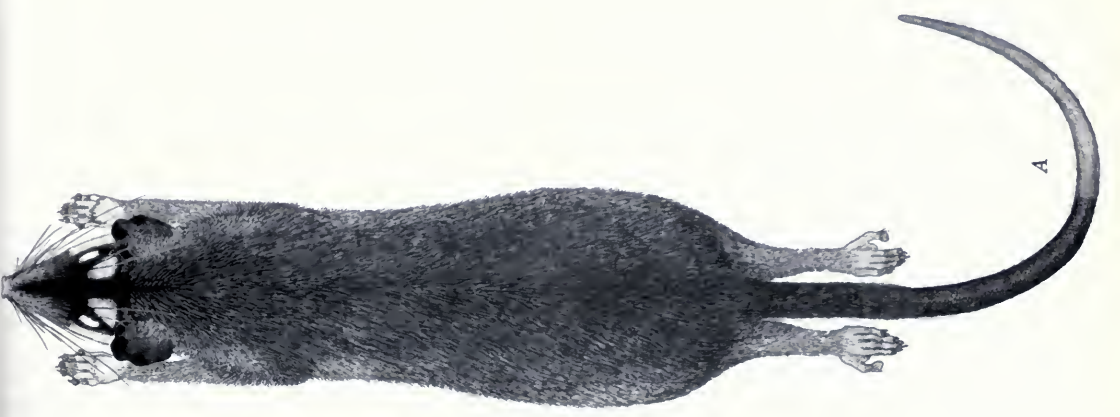
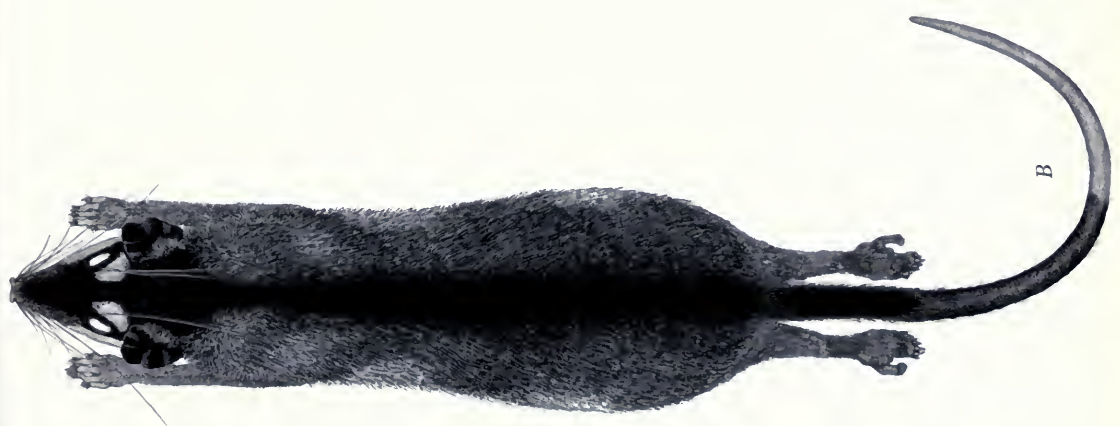




FIG. 5. Distribution of subspecies of *Philander opossum* (a–g), *P. andersoni* (h), and *P. andersoni mcilhennyi* (i) in South America and Middle America (part inset).

Tamaulipas on the Atlantic versant, Oaxaca on the Pacific; altitudinal range from sea level to about 2000 m above.

Philander is unknown in the Caribbean islands, the Caribbean coast of Venezuela and Colombia, and the inland highlands (tepui) of Venezuela. The genus has not been recorded from the Sierra Nevada de Santa Marta and the northwestern lowlands in Colombia. Spotty records from the Brazilian Amazonas suggest that *Philander* may be present throughout the basin east of the Río Negro and east of the Río Tocantins–Araguaia. Although *Philander* is generally absent from the drier parts of the *cerrado* of central Brasil, it does occur in

the gallery forests. The habitats are described in greater detail in the species and subspecies accounts.

Nomenclature

Tiedemann (1808, p. 426) included three nominal didelphid species in his *Philander*. The first of these is “*Virginische opossum, P[hilander]. virginianus (Did. opossum L[innaeus])*” and is based on bibliographical references to figures of opossums by Buffon (1763) and Schreber (1739–1810) and anatomical accounts by Tyson (1698)

and Cowper (1704). His diagnosis, "Korper rothlich braun. Ueber jedem Augen ein gelblich weiser flecken. Schwanz so lang als der Leib. 1 Fuss und 3 Zoll lang ohne den Schwanz," is of a four-eyed opossum, and Tiedemann's use of *Didelphis opossum* Linnaeus in apposition definitely restricts the name to the pouched four-eyed species. The other two species are "*P. murinus* (*Did. murina* L.)," a *Marmosa*, and "*P. brachyurus* (*Did. brachyuros* Penn.)," a *Monodelphis*.

Philander Tiedemann derives ultimately from Seba's (1734) vernacular names, "*Philander, opossum s. Carigueja*," cited by Linnaeus (1758) in his description of *D[idelphis]. opossum*. *Philander virginianus*, a substitute name for *D. opossum* Linnaeus, is type by subsequent designation (Hershkovitz, 1949, p. 11).

Didelphis philander Linnaeus, 1758, designated type by Thomas (1888, p. 336), was not included in the original erection of the genus *Philander* and hence is not valid as type.

Pine (1973, p. 391) and Husson (1978, p. 27) argued against the use of *Philander* Tiedemann for the four-eyed pouched opossum and elected *Metachirops* Matschie, a junior synonym, instead. The arguments of both authors were discussed and rejected by Hershkovitz (1976; 1981) and by Gardner (1981, p. 44), who summarized and laid the dispute to rest.

External Characters and Comparisons

BODY SIZE AND FORM—Species of the genus *Philander* average smaller than those of *Didelphis*, *Lutreolina*, and *Chironectes* but larger than all other living didelphoids. Average combined head and body length is about 281 mm (slightly less in females than males); condylobasal length of skull, an indicator of body size, is about 72 mm. Trunk is elongate; muzzle long and slender; eyes large; ears conspicuous. *Philander andersoni* averages slightly larger than *P. opossum*, and geographically peripheral races of each species average larger than more central ones.

MEASUREMENTS—Table 1.

GROWTH—Body mass increases after full eruption of all molars. Largest individuals of a series or subspecies, however, are not necessarily oldest and may include individuals classified as subadult on the basis of dental eruption or wear and suture closure. Males may not be larger than females at birth but evidently outgrow females to maturity.

Adult wild-caught animals that had been maintained in cages and fed without stint in the now defunct Rockefeller Laboratories in Rio de Janeiro became extremely large in body mass and cranial length. Dental size, however, fixed at complete eruption, remains the reliable indicator of "normal" body size.

BASIC COLORATION (Fig. 4)—Trunk dark grayish or buffy agouti with or without a blackish middorsal stripe or band; face dark brown or blackish with contrasting supraorbital spot, rhinarial tip usually unpigmented; tail dark brown or with underside slightly paler, terminal half less pigmented or unpigmented.

The *Philander* color pattern of a dark, modified agouti coat, dark brown to buffy head, dark brown tail and ears, could give rise to all colors and color combinations present in didelphoids, including *Didelphis*, *Lutreolina*, and *Chironectes*. A dark brown eye ring is characteristic of nearly all didelphoids, and supraorbital spots such as those of *Philander* expand into temporal bands in *Chironectes* and the whitish face of many *Didelphis*. The more or less pigmented ears and tails of didelphoids derive from fully pigmented ones. The saturate, bleached, or whitish cover hairs evolved from agouti cover hairs. Blackish (melanistic), grayish, orange, or reddish phases, whitish guard hairs and wool hairs, can be derived from the basic color pattern of *P. opossum*. Coloration of body and limbs, tail, and ears of *Lutreolina* and the brindled body coloration of *Chironectes* can also be derived from a primitive *Philander* model. The saturate, pheomelanin facial pattern of *Lutreolina*, without markings, however, is rare among didelphoids. The nearest common ancestral facial pattern of both *Lutreolina* and *Philander* must have been nearly uniformly modified agouti.

COLOR PHASES—A "gray" or grayish brown phase and a "brown," orange-brown, or orange phase occur in both species of *Philander*. In the gray phase, the subterminal or pheomelanin bands of the cover hairs of dorsum and sides are bleached to pale buff or nearly colorless. The general effect is a grayish brown appearance. In the brown phase, the subterminal bands are more densely pigmented, giving the animal an ochraceous or orange appearance. Hairs of underparts in gray-phase individuals are usually bicolor with the dark eumelanin bases showing through. In brown-phase individuals, the ventral hairs are usually or predominantly pheomelanin to roots.

The color term "brown," used by Musttrangi

TABLE 1. Summary of measurements of subspecies of *Philander opossum* and subspecies of *P. andersoni*. Measurement means (extremes in parentheses) and number of specimens.

	Head and Body	Tail	Hind Foot	Ear
<i>Philander opossum opossum</i> Linnaeus				
♂♂	285 (250–320) 56	290 (235–343) 55	43 (35–50) 55	36 (30–42) 21
♀♀	283 (245–298) 31	285 (245–350) 31	40 (35–43) 25	32 (30–41) 10
♂♂♀♀	281 (245–320) 87	288 (245–350) 86	42 (35–50) 81	35 (30–42) 32
<i>Philander opossum quica</i> Temminck				
♂♂	260 (200–300) 67	292 (195–355) 63	40 (29–48) 64	34 (22–42) 44
♀♀	255 (220–330) 57	279 (220–310) 55	38 (32–46) 53	33 (22–43) 46
♂♂♀♀	258 (200–330) 124	291 (195–355) 118	39 (29–48) 117	34 (22–43) 90
<i>Philander opossum melanurus</i> Thomas				
♂♂	272 (258–296) 7	264 (250–276) 7	40 (37–43) 7	29 (27–35) 7
♀♀	284, 282	270, 229	35, 37	18, 32
♂♂♀♀	274 (258–296) 9	261 (229–276) 9	39 (35–43) 9	28 (18–35) 9
<i>Philander opossum fuscogriseus</i> J. A. Allen				
♂♂	281 (214–308) 73	289 (240–335) 73	45 (37–52) 72	36 (32–40) 57
♀♀	276 (237–331) 36	284 (240–320) 36	42 (37–50) 36	37 (25–40) 28
♂♂♀♀	279 (214–331) 109	287 (240–335) 109	44 (37–52) 108	36 (25–40) 85
<i>Philander andersoni andersoni</i> Osgood				
♂♂	279 (243–380) 13	284 (255–315) 13	42 (35–48) 15	37 (30–45) 13
♀♀	266 (225–300) 14	282 (255–332) 14	41 (35–51) 14	36 (33–41) 12
♂♂♀♀	272 (225–380) 27	283 (255–332) 27	41 (35–51) 29	37 (30–45) 25
<i>Philander andersoni mcilhennyi</i> Gardner and Patton				
♂♂	299, 279	276, 313	43, 40	41, 35
♀♀	293 (290–298) 5	292 (279–305) 5	41 (36–44) 5	37 (35–42) 5
♂♂♀♀	292 (279–299) 7	292 (276–313) 7	41 (36–44) 7	38 (35–42) 7

(1994, p. 252) to describe a pale color phase of *Marmosops incanus* Lund (= *M. scapulatus* Burmeister), may be a tone of pheomelanin, or reddish. True melanin, or “blackish,” is actually brown. The female *Philander* I captured in the Parque Nacional do Caparaó was reported by Musturangi (1994, p. 253), who happened to see the prepared specimen while it was en route to Chicago for my study. She described it as of “a similar, pale coloration” as the *Marmosops incanus* of her report. The pheomelanin or erythristic color phase and the melanistic phase are rare mutants among mammals and birds generally (cf. Hershkovitz, 1968; 1970; 1977; 1992a).

PELAGE—Fur short in *P. opossum*, longer in *P. andersoni*, particularly in *P. andersoni mcilhennyi*, in which middorsal guard hairs are predominant. Downy wool hairs are preeminent in the aquatic *Chironectes*. *Didelphis* pelage is shaggy, the long guard hairs and wool hairs about equally conspicuous and almost entirely concealing the cover hairs. Pelage of *Lutreolina* is short with underfur, the silky guard hairs weak. A pelage like that of

P. opossum is common among didelphoids and could give rise to any of the more derived types.

MOLT—Changes in pelage with age or season cannot be accurately determined on the basis of material at hand. The few available large series of *Philander opossum*, such as the 85 specimens (AMNH) from Ilha Taiuna, Pará, Brasil, collected between 31 October and 11 November 1931, provide no definite information on seasonal molt and very little regarding ontogenetic change. Adults in both old and new pelage without visible molt line may occur at the same time in the same general area. The fine, thin juvenal pelage is gradually replaced by coarser, thicker adult pelage. Juvenal coloration is like that of adults.

LIMB BONES AND LOCOMOTION (Table 2)—Using condylobasal length as an indicator of overall body size, the cranial length ranges from about 29 mm in *Dromiciops gliroides* to about 112 mm in *Didelphis marsupialis*, a differential of about 85 mm. The hind limb is longer than the forelimb in all taxa, and the tibia about as long as, or usually longer than, the femur. In the forelimb, the radius

TABLE 1. *Extended.*

Condylobasal Length	Zygomatic Breadth	Preorbital Width	Postorbital Width	Braincase Width
73.0 (65.4–82.1) 75	38.3 (33.0–43.4) 73	14.1 (11.5–18.9) 59	8.8 (7.5–9.7) 74	21.2 (18.4–24.0) 72
69.7 (64.0–80.8) 39	34.5 (31.1–40.7) 34	13.1 (11.4–18.4) 23	8.7 (8.0–9.7) 34	19.9 (18.9–21.4) 35
71.9 (64.0–82.1) 114	37.0 (31.1–43.4) 107	13.8 (11.4–18.9) 82	8.8 (7.5–9.7) 108	20.8 (18.4–24.0) 107
66.4 (60.0–76.4) 78	35.5 (30.7–43.7) 75	12.6 (10.8–15.7) 36	8.4 (7.4–9.1) 77	20.2 (18.2–23.1) 71
62.8 (57.1–72.4) 76	31.1 (28.0–38.3) 67	11.6 (9.7–14.7) 42	8.4 (7.5–9.9) 67	19.7 (18.0–21.9) 67
64.6 (57.1–76.4) 154	33.4 (28.0–43.7) 142	12.1 (9.7–15.7) 78	8.4 (7.4–9.9) 144	20.0 (18.0–23.0) 138
69.6 (64.6–71.9) 8	36.6 (33.8–38.1) 8	13.2 (12.3–13.9) 6	9.2 (8.7–9.7) 8	21.5 (20.4–23.5) 8
64.1, 65.8	33.5, 34.2	—, 12.5	9.4, 8.4	20.9, 19.3
68.7 (64.1–71.9) 10	36.0 (33.5–38.1) 10	13.1 (12.3–13.9) 7	9.1 (8.4–9.7) 10	21.2 (19.3–23.5) 10
72.7 (61.9–81.5) 76	38.4 (32.2–43.0) 73	13.4 (10.9–15.7) 61	9.0 (8.3–9.5) 73	21.0 (19.1–23.5) 75
69.7 (60.0–80.5) 41	36.1 (30.7–43.1) 40	12.9 (11.5–16.6) 31	8.9 (8.0–9.4) 40	20.6 (18.7–23.6) 40
71.6 (60.0–81.5) 117	37.6 (30.7–43.1) 113	13.2 (10.9–16.6) 92	8.7 (8.0–9.5) 113	20.9 (18.7–23.6) 115
72.3 (66.7–76.5) 17	37.1 (32.3–39.9) 17	13.6 (11.8–16.2) 13	9.3 (8.0–9.4) 17	21.2 (19.6–22.6) 16
68.9 (64.6–81.2) 17	34.1 (30.8–40.0) 17	12.6 (10.4–14.0) 13	8.8 (8.0–10.1) 18	20.6 (19.3–23.9) 17
70.6 (64.6–81.2) 34	35.6 (30.8–40.0) 34	13.1 (10.4–16.2) 26	9.1 (8.0–10.1) 35	20.9 (19.3–23.9) 33
74.4, 73.1	37.6, 36.5	14.0, 13.5	9.0, 8.4	21.2, 20.8
71.8 (70.2–73.9) 4	35.8 (34.2–36.8) 4	13.7 (12.7–14.7) 4	9.0 (8.7–9.2) 4	20.7 (20.2–21.0) 4
72.5 (70.2–74.4) 6	36.2 (34.2–37.6) 6	13.7 (12.7–14.7) 6	8.9 (8.4–9.2) 6	20.8 (20.2–21.2) 6

is about as long as the humerus or shorter. In the semiaquatic *Chironectes* it averages less.

The hind limb is longer than the forelimb in the Marmosidae, with the greatest differential shown by the Patagonian *Lestodelphys halli*, apparently a leaper or springer. It is closely followed in limb-to-trunk proportions by the terrestrial *Metachirus nudicaudatus*. No American marsupial is a burrower. *Chironectes* is the only living American marsupial adapted for aquatic life, but all American marsupials are good swimmers and divers, except possibly the Marmosidae. All are habitual tree climbers, except *Lutreolina*, *Metachirus*, *Chironectes*, *Lestodelphys*, and *Monodelphis*, all of which probably can climb but have not been observed doing so.

The long hind limbs of *Philander* are well adapted for running and springing. The proportionately shorter limbs of *Didelphis*, especially the anterior, are better specialized for climbing. Animals of both genera progress with facility on the ground, *Philander* with moderate to rapid speed and *Didelphis* slowly and with a lumbering gait that does not exclude a swift sprint by a frightened animal. *Chi-*

ronectes is preeminently adapted for aquatic life, its long legs and palmate hind feet serving for propulsion through water, the gritty palms and digits of the front feet for seizing slippery prey and climbing slippery rocks and boulders in mountain streams. Limbs of *Lutreolina* are short and weasel-like and apparently better adapted for terrestrial locomotion than for climbing or swimming.

CHEIRIDIA (Fig. 6)—Hands and feet of *Philander* are modified for grasping, the pollex and hallux opposable, the latter inunguis; fifth hind toe much shorter than fourth, three middle digits subequal; toes not webbed. Manual and pedal claws of *Didelphis* stout, hallux inunguis, opposable; claws sharp, recurved; digits of *Lutreolina* as in *Didelphis* but claws blunt, little recurved. In *Chironectes* manual digits with short needle-like claws, hind feet with toes webbed, hallux inunguis (Fig. 3).

TAIL (Fig. 7)—Tail in *Philander* and *Didelphis* is cylindrical, tapered, prehensile, scaly, practically bare except for densely furred basal 3–9 cm; naked ventrally, the terminal portion plicate between vertebral joints to permit clasping, length

TABLE 1. *Extended.*

	Palatal Length	i-m ¹	m ¹⁻⁴
<i>Philander opossum opossum</i> Linnaeus			
♂♂	44.0 (40.3–49.6) 75	38.0 (34.9–41.5) 75	13.8 (12.8–14.9) 75
♀♀	41.9 (38.4–45.8) 35	36.8 (34.8–39.3) 35	13.7 (12.7–14.7) 36
♂♂♀♀	43.3 (38.4–49.6) 110	37.6 (34.8–41.5) 110	13.8 (12.7–14.9) 111
<i>Philander opossum quica</i> Temminck			
♂♂	38.3 (34.1–44.8) 75	34.4 (32.0–37.7) 78	12.7 (11.6–14.4) 80
♀♀	39.2 (35.1–44.6) 71	32.9 (30.5–38.0) 71	12.5 (11.2–14.5) 78
♂♂♀♀	38.7 (34.1–44.8) 146	34.2 (30.5–38.0) 147	12.6 (11.2–14.5) 158
<i>Philander opossum melanurus</i> Thomas			
♂♂	42.0 (38.6–43.1) 8	36.5 (34.7–37.5) 8	13.6 (13.3–14.0) 8
♀♀	38.8, 39.9	34.6, 34.8	13.0, 13.0
♂♂♀♀	41.4 (38.6–43.1) 10	36.2 (34.6–37.5) 10	13.5 (13.0–14.0) 10
<i>Philander opossum fuscogriseus</i> J. A. Allen			
♂♂	44.2 (37.9–50.2) 74	38.1 (34.3–41.8) 77	14.2 (11.7–15.6) 77
♀♀	42.5 (37.0–48.7) 41	36.9 (33.9–41.2) 42	13.9 (12.8–15.3) 42
♂♂♀♀	43.6 (37.0–50.2) 115	37.7 (33.9–41.8) 119	14.1 (11.7–15.6) 119
<i>Philander andersoni andersoni</i> Osgood			
♂♂	43.4 (39.7–48.9) 20	38.0 (35.2–43.3) 20	13.9 (12.0–16.0) 20
♀♀	42.0 (39.7–49.6) 18	36.9 (34.2–42.9) 18	13.8 (12.6–15.0) 18
♂♂♀♀	42.8 (39.7–49.6) 38	37.5 (34.2–43.3) 38	13.8 (12.0–16.0) 38
<i>Philander andersoni mcilhennyi</i> Gardner and Patton			
♂♂	45.1, 44.5	39.8, 38.4	15.3, 14.6
♀♀	43.5 (42.0–44.7) 4	38.1 (36.4–39.7) 4	14.4 (13.7–15.3) 5
♂♂♀♀	44.0 (42.0–45.1) 6	38.5 (36.4–39.8) 6	14.6 (13.7–15.3) 7

about equal to that of combined head and body; rhomboidal scales arranged spirally; the interscutular bristles usually 5 per scale (Fig. 8). The *Didelphis* tail is more strongly prehensile than that of *Philander*, and that of the aquatic *Chironectes* is hardly if at all prehensile, its flattened ventral surface serving as a rudder. The *Lutreolina* tail is the most densely hirsute of the group. Length slightly less than head and body combined and, as in *Philander*, may be nearly the primitive proportion for mammals generally. The tails are not fat storing, but that of terrestrial *Lutreolina* is notably thick at base, where the transitional vertebrae provide insertion for large muscle mass (Fig. 1). (More on locomotion in *Philander* on p. 75.)

TRANSITIONAL CAUDAL VERTEBRAE (Table 3)—Transitional vertebrae of the postcranial skeleton, usually 4 or 5 in American marsupials, sometimes 6 depending on interpretation, are present between the sacrum and typical caudal (coccyxial) vertebrae. Although well differentiated (Fig. 9), they are usually counted as caudal. The morphological characters of the transitional vertebrae, however, are well marked, with the first distinct

from the sacrum, and the 5th (or 6th) usually sharply differentiated from the succeeding caudal vertebra. Muscles of the transitional vertebrae move the tail in particular directions. The action of a specific muscle may be narrowly restricted, such as that controlling movements of the tail tip.

EXTERNAL EAR (Fig. 1)—The auricular lamina of *Philander* is large, rounded, leafy or membranous and plicate, entirely blackish or with base of middle portion to total unpigmented; length, when laid forward, reaching outer canthus of eye. External ears of *Didelphis* and *Chironectes* are similar. The *Lutreolina* auricular lamina is much smaller, less leafy, hairy, and hardly if at all plicate. Auricles of the group could have evolved from a type with lamina little expanded, bare, and perhaps slightly motile or plicate. Didelphoid auricles are comparable to those of many species of shrews, lemurs, and callitrichids (cf. Hershkovitz, 1977, pp. 102–106).

MARSUPIUM—A fully formed pouch characterizes sexually mature females of *Philander* and *Didelphis* and both sexes of the semiaquatic *Chironectes*. The pouch opens from the side in the first

TABLE 2. Ratios of forelimb and hind-limb lengths to trunk length in four large marsupials. Means (extremes in parentheses) and number of specimens.

Name	Greatest Skull Length	Radius		Humerus		Tibia		Femur		Trunk (thoracic + lumbar + sacral)		Radius + Humerus		Tibia + Femur	
		Mean	(Extremes)	Mean	(Extremes)	Mean	(Extremes)	Mean	(Extremes)	Mean	(Extremes)	Mean	(Extremes)	Mean	(Extremes)
<i>Philander opossum</i>	75.6 (71-85)	5	46.2 (44-50)	5	46.0 (44-51)	5	60.0 (57-61)	5	54.8 (54-62)	5	158.8 (134-182)	5	57.6 (55-62)	5	72.6 (69-81)
<i>Philander andersoni</i>	63, 70		40, 48		38, 43		56, 62		51, 54		134, 145		58, 63		80, 80
<i>Didelphis marsupialis</i>	105 (96-112)	4	63.5 (60-69)	4	66.5 (61-71)	4	82.5 (80-87)	4	80.5 (77-85)	4	241 (221-266)	4	53.9 (47-55)	4	67.6 (59-71)
<i>Didelphis albiventris</i>	87, 109		63.2 (54-71)	4	65.0 (55-73)	4	81.5 (70-91)	4	77.2 (68-90)	4	231 (197-259)	4	55.4 (52-58)	4	67.2 (65-72)
<i>Chironectes minimus</i>	73.1 (69-77)	9	51.1 (47-53)	9	47.3 (44-50)	9	64.0 (58-67)	9	58.2 (54-62)	9	153.3 (141-173)	9	64.1 (56-72)	9	78.5 (67-89)
<i>Lutreolina crassicaudatus</i>	70.1, 74.0		36.4, 41.1		45.3, 48.8		53.3, 57.4		51.6, 55.9		180, 205		45, 44		58, 55

two, posteriorly in the female of the third, and medially in the male, in which it seals the scrotum during aquatic submersion. In *Lutreolina* the rudiment of a pouch is formed by a longitudinal skin fold on each side of the abdominal milk gland field.

Marsupium and scrotum are not homologous. They may be derived, however, from different parts of the same anlage (Tyndale-Biscoe & Renfree, 1987, p. 121).

A pouch consists of a pair of recessed longitudinal skin folds, one on each side of the mid-abdominoinguinal region. The folds are united caudally but are separate anteriorly. Only in *Didelphis* does the inner margin of each lateral fold appose the other to form a flexible but completely closed waterproof pocket for shielding suckling young (cf. Enders, 1937, p. 25; 1966, p. 200).

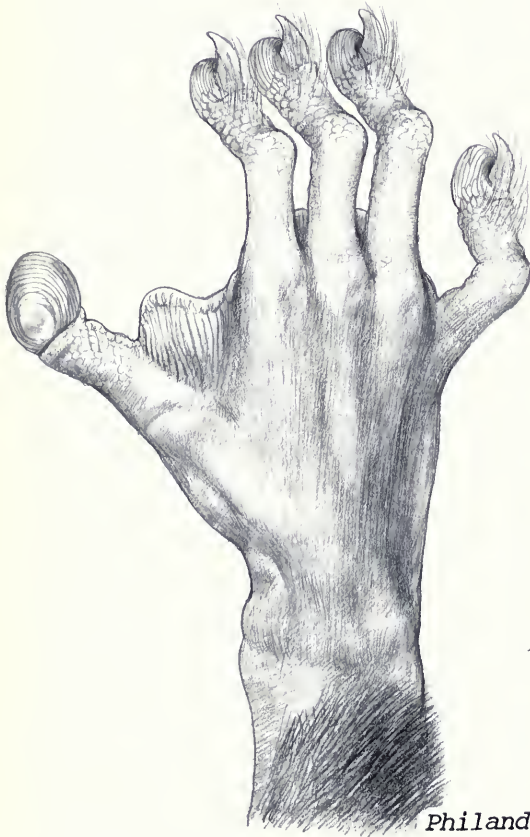
NIPPLES (Table 4)—The well-developed marsupium of *Philander* conceals two rows of nipples arranged symmetrically, one on each side of the ventrum, and a median row with but one teat, the total number odd. The usual number of nipples, often called teats or mammae, is 7. Enders (1935, p. 411) found only 5 in an unspecified number of live-trapped Panamanian opossums and a maximum of 5 pouch young. Miller (in J. A. Allen, 1916c, p. 589) reported from 5 to 8 pouch young, and Seba (1734, p. 57) affirmed that there are 6 and sometimes 8, or as many nipples as suckling young. These observations suggest that the prime mammary formula for *Philander opossum* is normally 3-1-3 = 7. The same holds for *Philander andersoni*. *Didelphis* usually has 11 or 13 teats. *Chironectes* has 5, *Lutreolina* 9 or 11. In pouchless didelphoids, the outer rows of teats may extend the length of abdomen and chest; the shorter median row is abdominal and has 1 to 5 teats. None are abdominal in the microbiotheriid *Dromiciops*.

Cranial Characters and Comparisons (Figs. 10-12; Table 5)

Skull elongate, mean condylobasal length about 67 mm in males, slightly shorter in females; dorsal surface nearly plane with little curvature between muzzle and braincase; occipital condyles turned slightly behind vertical plane of body of occipital bone; nasals long, posterior portions abruptly expanded at maxillofrontal suture then tapered to blunt points parted terminally, tips not extending anteriorly to vertical plane of first incisors; length of nasals more than 40% greatest



A



B

Philander opossum



skull length and 60% midline length from tips of nasals to lambdoidal crest; combined tips of premaxillary bones rounded, extending less than 1 mm beyond base of i^1 .

Distance from lacrymal foramen to anterior edge of glenoid fossa less than zygomatic breadth; supraorbital borders square or rounded, not ridged or overhanging; postorbital constriction narrower than preorbital constriction; well-defined postorbital processes short, bluntly pointed; temporal ridges uniting behind to form a low sagittal crest connected with a well-developed nuchal or lambdoidal crest; shallow pit or depression at junction of temporal ridges; cranial crests developed early in both sexes.

Palatal vault not markedly arched, its contour nearly flat; palatal extension behind transverse plane of last molars equal to combined length of last 2 or $2\frac{1}{2}$ molars; paired incisive foramina long, extending behind anterior plane of canines; paired maxillopalatal vacuities long, slitlike and extending from about the level of m^1 to that of m^3 ; paired postero-palatal vacuities usually present, short, ovate, extending from or behind plane of last molars to raised posterior palatal border; posterior choanae narrow, width measured across posterior base of pterygoid processes usually less than 10% of condylobasal length; tripartite auditory bulla, composed of tympanic wing of alisphenoid bone, separated from tympanic wing of petrous bone with ectotympanic bone suspended between, the components separate or touching but not fused (Hershkovitz, 1992a, Fig. 10, p. 25; Hershkovitz, in press).

COMPARISONS (Fig. 2)—Skull of *Didelphis* relatively broader, the frontal and maxillary sinuses more inflated, sagittal crest high, bladeliike. Skull of *Chironectes* heavier, broader, braincase width about 35% of condylobasal length (less than 30% in *Philander*); angle between sagittal and frontal planes greater, nasals relatively shorter, less tapered behind, the terminal points spread as in *Lutreolina*; zygomatic breadth greater, palate wider, the posterior vacuities rectangular, posteromedian vacuities usually absent; occipital condyles not projecting behind vertical plane of supraoccipital bone, their combined width about half that of palate between molars; turbinate bones enlarged and produced behind to nearly posterior border of palatal vacuities. *Lutreolina* braincase relatively lon-

ger than that of *Philander*, sagittal and nuchal crests heavier, postorbital region more elongate, braincase more deflected relative to palatal plane, frontal and maxillary sinuses more inflated, muzzle relatively shorter, nasals less than 38% greatest skull length and less than 55% midline length from nasal tips to lambdoidal crest.

In didelphoids generally, as growth continues after sexual maturity, crests enlarge and most cranial proportions shift.

Dental Characters and Comparisons (Table 6, Figs. 13–20)

The following dental formula for didelphids is the same for all living and known extinct didelphoids:

$$i \frac{1,2,3,4,5}{(1),2,3,4,5}, \quad c \frac{1}{1}, \quad p \frac{1,2,3}{1,2,3}, \quad m \frac{1,2,3,4}{1,2,3,4}$$

The same formula has persisted unchanged since no later than Early Cretaceous and likely Early Jurassic. Loss of i_1 , shown in parentheses, and the staggered or crowded position of i_3 (Figs. 12, 13, 14, 16), evidence of Mesozoic mandibular contraction, are didelphoid hallmarks. The metacone of m^{1-3} is consistently larger than the paracone. The size relationship between metacone and paracone in eutherians varies within families and sometimes individually.

According to Luckett (1993), the deciduous or primary teeth of incisors and canines are nonfunctional and vestigial. The functional incisors and canines are successional or second generation. The functional premolars are mixed: p_1 and p_2 are the unreplaced deciduous teeth; p_3 , the last tooth to erupt, succeeds a functional, fully molarized deciduous p_3 . This tooth is also the first to erupt. Molars are unreplaced primary teeth (Fig. 14).

The sequence of dental eruption revealed by didelphids at hand and by studies of prenatal and early postnatal *Didelphis virginiana* by McCrady (1938) and Berkovitz (1978) indicated the following (teeth enclosed by parentheses erupt at about the same time):

$$\frac{dp_3, p_2, i(2-4), i_5, i_1, (c, p_1), m_1, m_2, m_3, p_3, m_4}{dp_3, p_2, i(2-4), i_5, -, (c, p_1), m_1, m_2, m_3, p_3, m_4}$$

←

FIG. 6. Cheiridia of *Philander opossum*. A, Right hand, dorsal and plantar aspects; B, right foot, dorsal and plantar aspects.

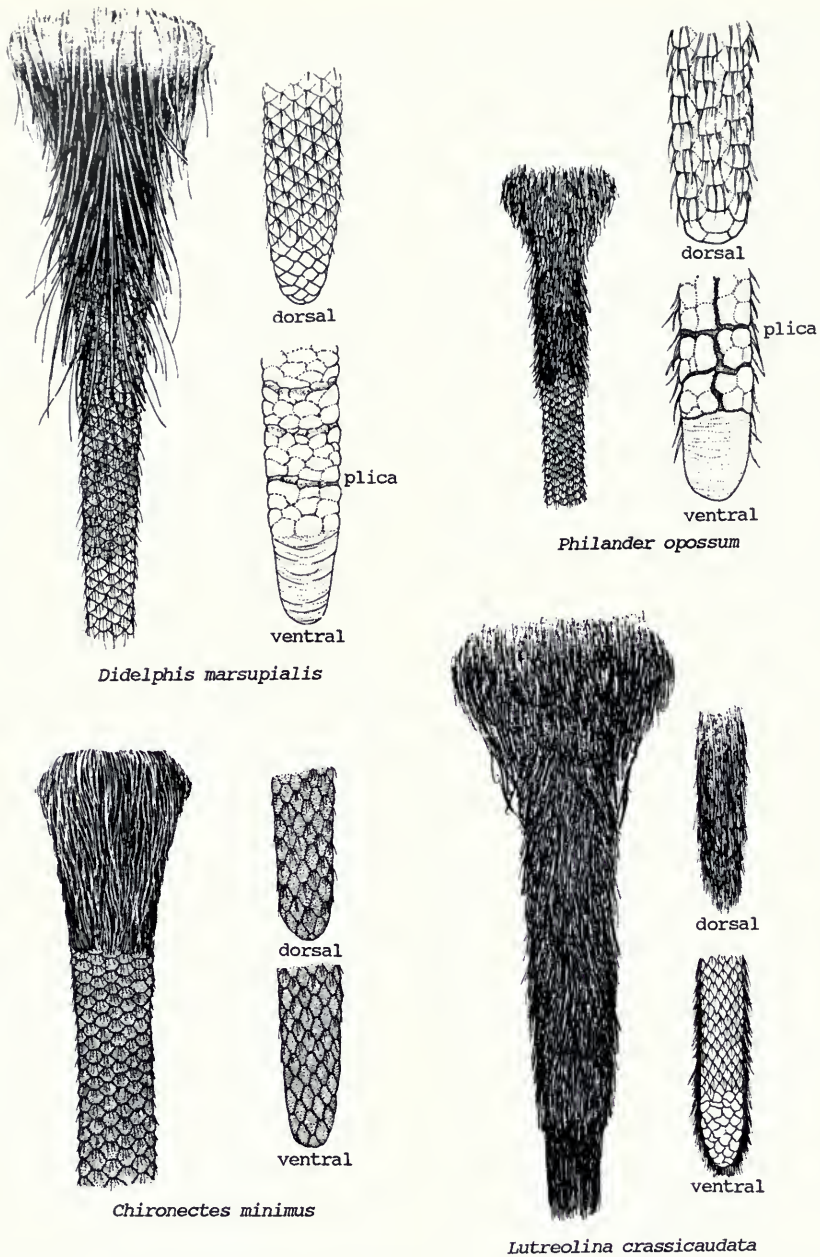


FIG. 7. Basal (dorsal) and terminal (dorsal and ventral) caudal segments of *Didelphis*, *Philander*, *Chironectes*, and *Lutreolina*. Plicas are cutaneous folds of prehensile tails.

Descriptions of Individual Teeth of *Philander*

UPPER INCISORS (Fig. 15)—Five in number, first (i^1) usually largest, sometimes as small as any of i^{2-5} ; i^1 most distinctive of series, subcylindroform,

orthodont or slightly prodont, the opposing pair convergent for about two-thirds their length, their pointed tips often divergent; unworn i^{2-5} uniformly premolariform (tridentate), crowns slightly to broadly overlapping except in old, worn teeth; i^2 from half to as high as i^1 , slightly less than that

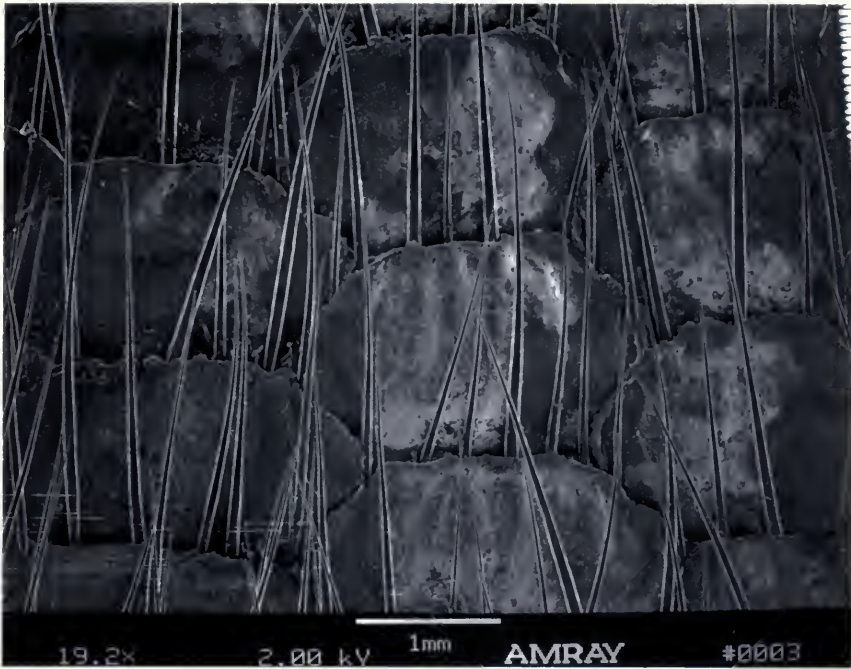


FIG. 8. Section of *Philander opossum* tail, ventral surface, showing spiral arrangement of scales and interscutular bristles, usually five per scale.

of $i^{3,4}$; a small diastema present between i^1 and i^2 ; mesiostyle (*a* or *A*) of i^{2-5} weak, distostyle (*b* or *E*) less defined or obsolete.

LOWER INCISORS—Four in number (2–5), the phylogenetic first lost; all uniform in structure but decreasing in size from numerical first (i_2) to last (i_5); all incisors markedly recumbent seen from lingual aspect; crowns usually well separated in adults but sometimes touching in young; each tooth with labial surface more or less spatulate, crown ovate, root cylindrical, tapered; lingual surface smooth, the median ridge or torus broadly sloping; occlusal groove often present on lingual surface; terminal styles obsolete; numerical sec-

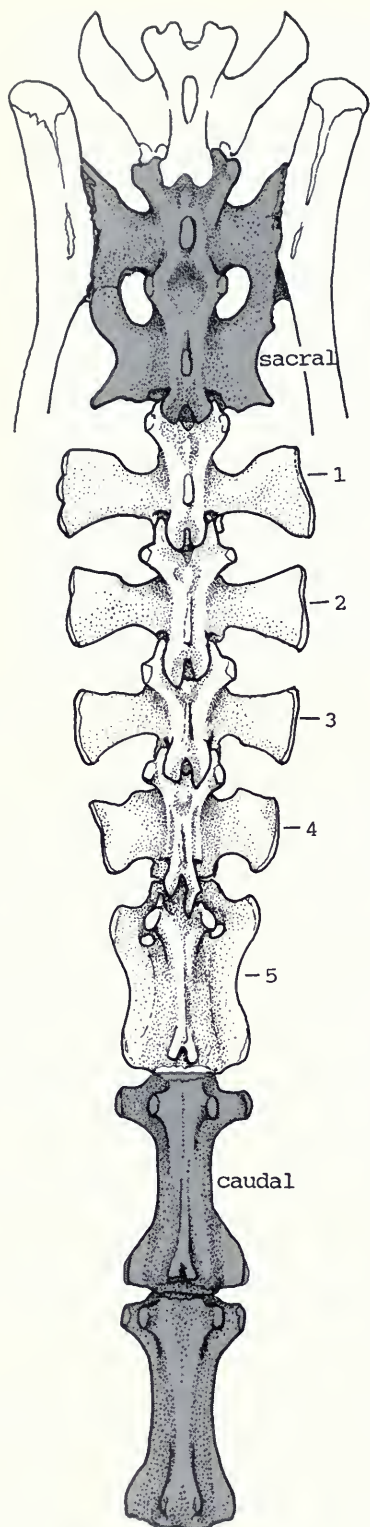
ond (phylogenetic i_3) staggered between i_2 and i_4 as in all didelphoids (Figs. 13, 14, 16).

REMARKS—Marsupial dental evolution appears to have been most manifest in the incisor field. The staggered i_3 marks divergence of the Didelphimorphia from the basic metatherian stock. Only microbiotheres, including *Pucadelphys andinus* Marshall and de Muizon, 1988 (Marshall et al., 1995), of the Early Paleocene of Bolivia are the known members of the unstaggered-incisor-toothed Microbiotheriomorphia (cf. Hershkovitz, 1992; 1995).

UPPER CANINE—Long, slender, smooth, recurved with axis directed slightly forward, its

TABLE 3. Vertebral count of largest American marsupials. Number of transitional vertebrae also included in count of caudal vertebrae as customary. Number of cervical vertebrae is consistently 7, of sacral, 2, in all marsupial taxa examined. Sample number in parentheses.

Taxon	Thoracic	Lumbar	Caudal	Transitional
<i>Philander opossum</i>	13 (5)	6 (2); 7 (3)	27; 28	4; 5 (3)
<i>Philander andersoni</i>	13 (2)	6 (2)	27; 31	4; 5
<i>Didelphis marsupialis</i>	13 (4)	6 (2); 7 (2)	31; 32 (2)	5 (3)
<i>Didelphis albiventris</i>	12 (2); 13 (2)	5; 6; 7	30 (2); 31	4; 5; 6
<i>Chironectes minimus</i>	13 (7); 14	6 (8)	27 (2); 28 (2); 29	4 (5); 5 (2)
<i>Lutreolina crassicaudata</i>	13 (2)	6; 8	11+ (2)	4; 5



Philander opossum
FMNH 60501

growth continuous past sexual maturity; cingulum and accessory conules absent; diastema between canine and last incisor approximately equal to or less than greatest diameter of canine.

LOWER CANINE—Shorter, weaker than upper, more or less recurved, its bulk about half that of upper; well differentiated from incisors, about twice their height, without diastema.

UPPER PREMOLARS—Teeth two-rooted, unicuspidate with well-developed ledgelike lingual and buccal cingula; first premolar about half or less the bulk of second, the diastema between approximately equal to crown length in old adults, about one-half to one-third crown length in young adults; middle premolar larger than last, often equal, infrequently smaller; unworn first premolar with terminal styles usually present and well defined; middle premolar with terminal styles poorly defined or absent except style *b* or *E*, the mesio-style (parastyle, *a* or *A*) less frequently present than the distostyle (*b* or *E*); eruption of replacement p^3 precedes that of m^4 , styles poorly differentiated or absent; FMNH 114685 with an incipient but well-defined metacone.

UPPER DECIDUOUS THIRD PREMOLAR (the only upper deciduous tooth) (Fig. 17)—Size about equal to that of m^4 , general outline and morphology as in m^1 , conules *A*, *B* often well developed, conule *C* larger than *B*, *D* greatly reduced or absent, *E* indicated.

LOWER PREMOLARS—Teeth two-rooted, unicuspidate with ledgelike lingual and buccal cingulids poorly defined, talonid basin simple; lower first premolar similar in size and shape to upper first and likewise separated by diastema from middle premolar, distostylid (*b* or *E*) more or less defined, mesiostylid (*a* or *A*) obsolete or absent; middle premolar as high or higher than incisors and nearly as high as canine, distostylid present, mesiostylid minuscule; last premolar like middle but smaller, buccal cingulum usually poorly defined, talonid basin slightly more developed; permanent p_3 erupts before m_4 .

LOWER DECIDUOUS THIRD PREMOLAR (the only lower deciduous tooth) (Fig. 17)—Like first per-

←

FIG. 9. Transitional caudal vertebrae 1-5 (untinted) of *Philander opossum* (FMNH 60501) between tinted sacral and first typical caudal (coccyxial) vertebrae. Transitional vertebra 5 differs notably from both the caudal behind and transitional 4 ahead.

TABLE 4. Nipple formulae of the largest didelphoids. Number of samples more than one shown in parentheses; specific names are those of cited source; formulae from Hershkovitz field notes are of captured animals, the prepared specimens preserved in FMNH or USNM; other preserved specimens in the museum collection are shown as FMNH.

Taxon	Prime Nipple Formulae [Functional formulae in brackets]	Source
DIDELPHIDAE		
Didelphini		
<i>Philander</i>		
<i>andersoni</i>	[2-1-2]	da Silva and Patton, pers. comm.
<i>andersoni</i>	[2-0-2]	da Silva and Patton, pers. comm.
<i>andersoni</i>	[3-0-3]	da Silva and Patton, pers. comm.
<i>andersoni</i>	3-1-3 = 7 (4)	da Silva and Patton, pers. comm.
<i>opossum</i>	3-1-3 = 7 (4)	Thomas, 1888
<i>opossum</i>	7	Osgood, 1921:75
<i>opossum</i>	3-1-3 = 7 (4)	Hershkovitz, field notes (FMNH)
<i>opossum</i>	3-1-3 = 7 (4)	da Silva and Patton, pers. comm.
<i>Didelphis</i>		
<i>albiventris</i>	5-1-5 = 11 (2)	Hershkovitz, field notes (USNM)
<i>albiventris</i>	[4-1-3 = 8] (2)	Hershkovitz, field notes (USNM)
<i>albiventris</i>	11 (2)	Carlsson, 1903:490
<i>albiventris</i>	5-1-5 = 11	Krieg, 1924:652, Fig. 1
<i>marsupialis</i>	5-1-5 = 11 (4)	Hershkovitz, field notes (USNM)
<i>marsupialis</i>	[4-1-4 = 9] (3)	Hershkovitz, field notes (USNM)
<i>marsupialis</i>	[10]	O'Connell, 1979:81
<i>virginiana</i>	13	Hartman, 1920:255
<i>virginiana</i>	13	McCrary, 1938:183
Lutreolininae		
<i>Lutreolina</i>		
<i>crassicaudata</i>	4-1-4 = 9	Thomas, 1888:335
<i>crassicaudata</i>	5-1-5 = 11	Krieg, 1924:652, Fig. c
<i>crassicaudata</i>	9	Osgood, 1921:75
<i>crassicaudata</i>	[7]-9	Creighton, 1984:24
Chironectinae		
<i>Chironectes</i>		
<i>minimus</i>	2-1-2 = 5	Hershkovitz, field notes (USNM)
<i>minimus</i>	5	Enders, 1966
<i>minimus</i>	[4] 5	Krieg, 1921
<i>minimus</i>	4 to 5	Mondolfi and Medira Padilla, 1958:155

manent molar (m_1) except one-fourth to one-third smaller.

UPPER MOLARS (m^{1-4}) (Figs. 17-20)—Crowns wider than long; second molar (m^2) longer and larger than first (m^1), slightly shorter to longer than third (m^3), fourth molar (m^4) about half bulk of third; mesiostyle and distostyle present in m^{1-4} , but distostyle may be obsolete or absent in m^4 ; trigon cusps of m^{1-3} with metacone largest, paracone smallest, of m^4 paracone largest, metacone smallest, often minute; stylocone (conule *B*) always large and prominent in m^{1-3} ; style (conule *C*) as large or larger than stylocone in m^1 , subequal or smaller in m^2 , subequal or usually smaller and often rudimentary or merely indicated in m^3 ; in m^4 buccal cusps small or rudimentary; accessory conules derived from buccal conules *B*,

D, from well defined to mere crenulations, or absent; crest of m^3 metacrista longest of molar series; paracrista connected with conule *B*.

LOWER MOLARS (m_{1-4})—Lingual cingulids and neocingulids absent; second or third molar largest, fourth smallest, largest cusp (paraconid or protoconid, 1) progressively larger than metaconid from m_1 to m_4 ; paraconid smaller than or subequal to metaconid, hypoconid larger than entoconid; mesiostylid (*a* or *A*) not certainly definable in every tooth, distostylid (*b* or *E*) well defined, its size increasing from first to last tooth, in m_4 often as high or higher than paraconid; postentoconid larger than distostylid, becoming larger than paraconid in following teeth.

VARIATION—Consistent dental differences between *Philander opossum* and *Philander ander-*

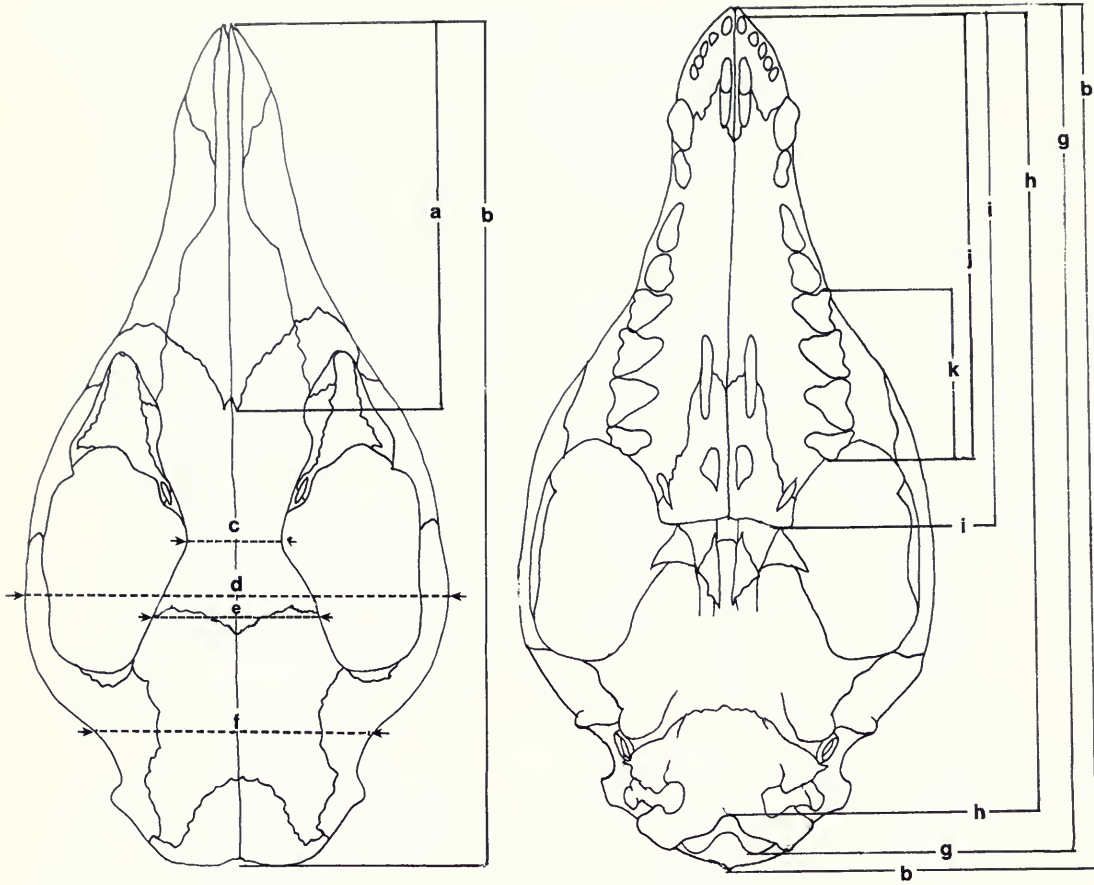


FIG. 10. *Philander opossum*, dorsal and ventral aspects, showing points of cranial measurements. a, nasals; b, greatest length of skull; c, least interorbital breadth or postorbital constriction; d, zygomatic breadth; e, postorbital width; f, braincase, greatest width; g, condylobasal length; h, basal length; i, palatal length; j, length upper tooth row (i^1 - m^4); k, length upper molar row (m^1 - 4).

soni have not been observed, but geographic differentiation does occur. In a comparison of "*Philander mcilhennyi*" from Balta, Perú, with sympatric *Philander opossum quica*, Gardner and Patton (1972, p. 3) noted a relatively deep indentation of the labial margin of m^3 present in the first species but not in the second. The indentation, or so-called "notch," is the angle or valley between conule C (stylar cone C) and adjacent conule B (Fig. 19).

In four specimens at hand of Balta *Philander andersoni mcilhennyi*, conule C of m^3 is well developed or molarized in three females but quite worn in the single male. In 8 adults of sympatric Balta *P. opossum quica*, I find conule C distinctly less developed in three females and rudimentary or virtually absent in 5 males. Examination of all available specimens from throughout the range of

the genus, however, reveals that variation from present to absent, or degree of molarization of conule C, is about the same for both species (Table 7).

Conule C, like any other derived excrescence of the buccal shelf, is firmly established, cusplike, and usually subequal to conule B in m^1 and m^2 . In m^3 , however, it varies geographically from a rudiment or anlage to a fair-sized cusp nearly equal in bulk to conule B (Fig. 19). Its molarization increases gradually from the most primitive and geographically central forms of *P. andersoni* and *P. opossum* to their most derived or geographically peripheral representatives.

COMPARISONS—Dentition of *Didelphis* is essentially like that of *Philander*. That of *Chironectes* is generally heavier, average transverse width of m^3 about 6 mm (4.5 in *Philander*), arcade of up-

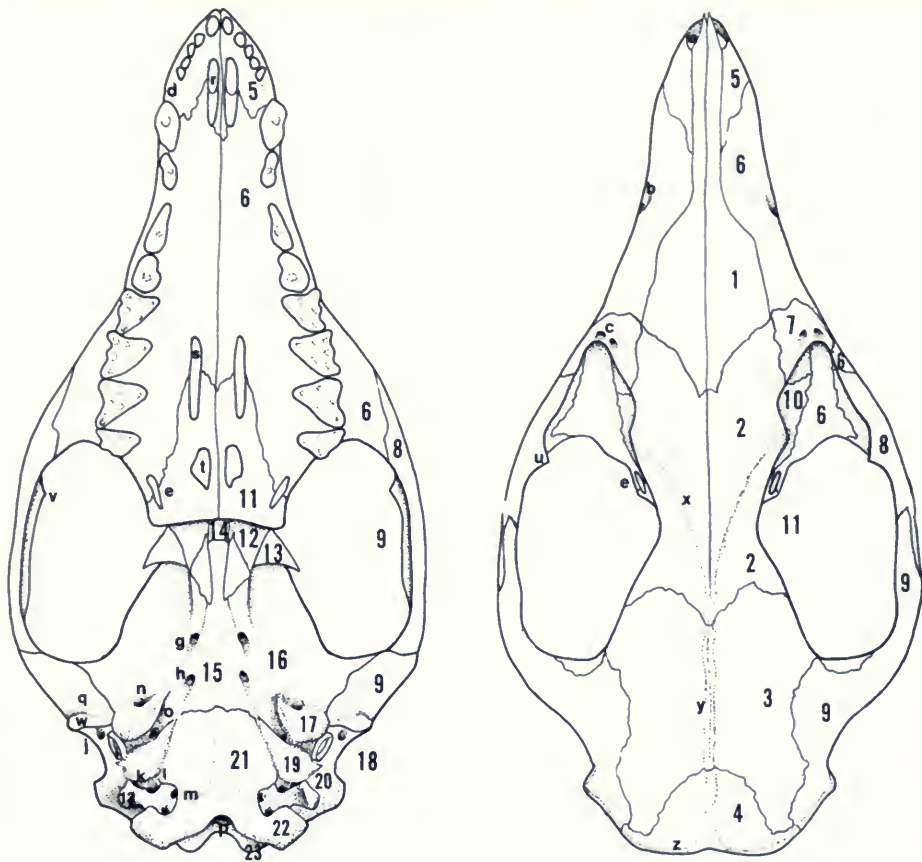


FIG. 11. Diagram of didelphid skull, ventral and dorsal aspects, showing topographic features. See Table 5 for explanation of symbols.

per and lower incisors more broadly curved with second lower (i_3) less abruptly staggered; unworn incisors of *Chironectes* triangular in lateral outline, but shape more nearly equilateral than obtuse; upper incisors of *Chironectes* and *Lutreolina* notably inflected inward and upward; first premolars less reduced, gap between first and middle premolars narrower in *Chironectes*, varying from less than half the crown length of anterior tooth to absent; molar crowns more hypsodont in *Chironectes* and *Lutreolina*, outline of occlusal surface more nearly square or rectangular than triangular, the outer posterior angle, particularly of m^3 , less produced.

Dental Abnormalities

Supernumeraries

Philander andersoni andersoni

AMNH 72017, adult ♀, Río Curaray, Loreto, Perú

Left supernumerary m^1 , slightly smaller than normal m^1 , rotated 180° with buccal shelf lingual.

Philander opossum fuscogriseus

AMNH 34373, adult ♂, Bagadó, Chocó, Colombia

Left supernumerary m^4 , fully erupted, slightly smaller than normal m^4 , otherwise similar.

Right supernumerary m^4 nearly fully erupted but impacted and rotated about 90° with buccal side anterior and overlapped by posterior portion of normal m^4 . Lower molars normal in number and form.

Philander opossum quica

LSUMZ 12009, adult ♀, Balta, Ucayali, Perú

Right supernumerary pm^1 , in diastema be-

TABLE 5. Explanation of cranial symbols 1-23 and a-z in Figures 11 and 12A.

Bones

1. Nasal
2. Frontal
3. Parietal
4. Supraoccipital
5. Premaxillary
6. Maxillary
7. Lacrymal
8. Jugal, zygomatic
9. Squamosal, temporal
10. Sphenoid (includes orbitosphenoid, alisphenoid, presphenoid, basisphenoid, pterygoid)
11. Palatine
12. Orbitosphenoid
13. Pterygoid process
14. Presphenoid
15. Basisphenoid
16. Alisphenoid
17. Alisphenoidal wing of auditory bulla
18. Ectotympanic
19. Periotic wing of auditory bulla
20. Mastoid (temporal)
21. Basioccipital
22. Occipital condyle
23. Exoccipital

Foramina, Fissures, Processes, Fossae, and Crests

- a. External nares
- b. Infraorbital foramen
- c. Lacrymal foramina or canals
- d. Canine fossa
- e. Posterolateral vacuity or foramen
- f. Sphenorbital fissure (concealed above 11)
- g. Foramen rotundum
- h. Foramen ovale
- i. Tympanic membrane and auditory meatus (see 18)
- j. Postglenoid foramen
- k. Stylomastoid foramen
- l. Jugular foramen
- m. Hypoglossal foramen and or condylar foramen
- n. Carotid foramen or canal
- o. Anterior lacerate foramen or petrotympanic fissure
- p. Foramen magnum
- q. Glenoid fossa
- r. Premaxillary or incisive foramen
- s. Maxillopalatine or mesolateral vacuity
- t. Posteromedial or palatine vacuity
- u. Ascending postorbital (zygomatic) process
- v. Ascending postorbital (zygomatic) process
- w. Postglenoid process
- x. Temporal ridge
- y. Sagittal crest
- z. Lambdoidal crest

tween normal first and second premolars, fully erupted, normal in appearance except rotated about 100° with posterior border linguad and slightly anteriad; heel with pronounced distostyloid (hypoconulid) as in left pm¹. "Normal" first premolar without

talonid presumably a result of crowding by developing supernumerary.

FMNH 114702, adult ♂, San Ramón, El Beni, Bolivia

Right supernumerary i₅, behind normal i₅, occludes with normal i⁵; normal i₅ occludes with i⁴ and so on to i₂, which bites into diastema between i¹ and i₂; position of i₁ more medial and anteriad compared to left homologue; jaw, teeth, and occlusion otherwise normal.

FMNH 114685, ♀

Left upper premolar with incipient but well-defined metacone.

Missing molar

Philander opossum opossum

USNM 393600, adult ♀, Utinga, Pará, Brasil
m⁴ missing; no sign of alveolus but arcade otherwise normal; m₄ normal; teeth moderately worn.

Sexual Dimorphism

Mature males with four molars fully erupted average larger than comparable females in body mass, skull length, and canine size. Postcanine teeth also average larger, but relative to skull length no larger than those of females or even smaller; the braincase is relatively narrower in males, cranial crests more developed, but the sagittal crest of old males is sometimes equaled by that of extremely large or old females.

Karyology

Descriptions of karyotypes of the present and supposed species of Didelphidae (Table 8) were first published in nearly 20 papers. All publications were critically reviewed, with new data added by Reig et al. (1977). The authors studied and described the chromosomes of 177 species of American marsupials representing nine genera and 22 species, including those considered in this report (Table 8). To avoid repetition and extralimital discussion, only Reig et al. (1977) is cited here for documentation.

The "standard" karyotype as understood by Reig et al. (1977) is present in all treated as didelphids with few minor exceptions. All listed in Table 8 share the diploid number of 22. The fundamental number is 20, except in *D. virginiana*.

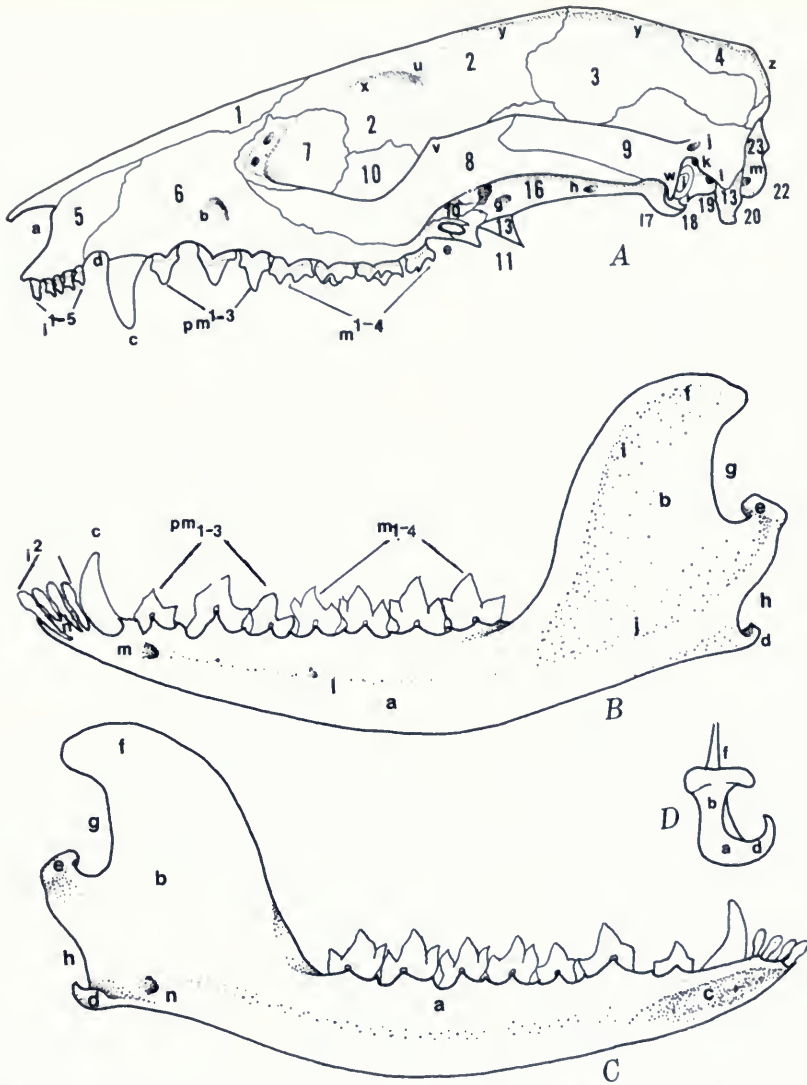


FIG. 12. A, Diagram of left side of *Philander opossum* skull; B, left mandible, buccal side; C, lingual side; D, posterior view. See Table 5 for names of cranial features and below for those of buccal and lingual sides of mandible: a, horizontal ramus; b, ascending ramus and masseteric fossa; c, symphysis; d, angular process; e, condyloid process; f, coronoid process; g, superior notch; h, inferior or lunate notch; i, superior masseteric line; j, inferior masseteric line; k, mylohyoid line (not shown); l, horizontal masseteric line; m, mental foramen; n, mandibular foramen.

where it is 32. Sex chromosomes are acrocentric in all but are metacentric in the X chromosome of *D. virginiana* and *L. crassicaudata*. It appears that the most variable complement among the four genera of Table 8 is *D. virginiana*.

Parasites

Captured marsupials are mostly parasitized by fleas, lice, and staphylinid beetles. These mobile

parasites usually leave a live caged animal shortly after capture and desert the host almost immediately at death.

The list of parasites is not exhaustive. It was compiled mainly as a source of reference for discussions on marsupial zoogeography. The taxonomic names used are those of the sources cited.

Viruses

Mucambo (Potkay, 1977; Pará, Brasil; Shope, 1967b (in Potkay, 1977, q.v.))

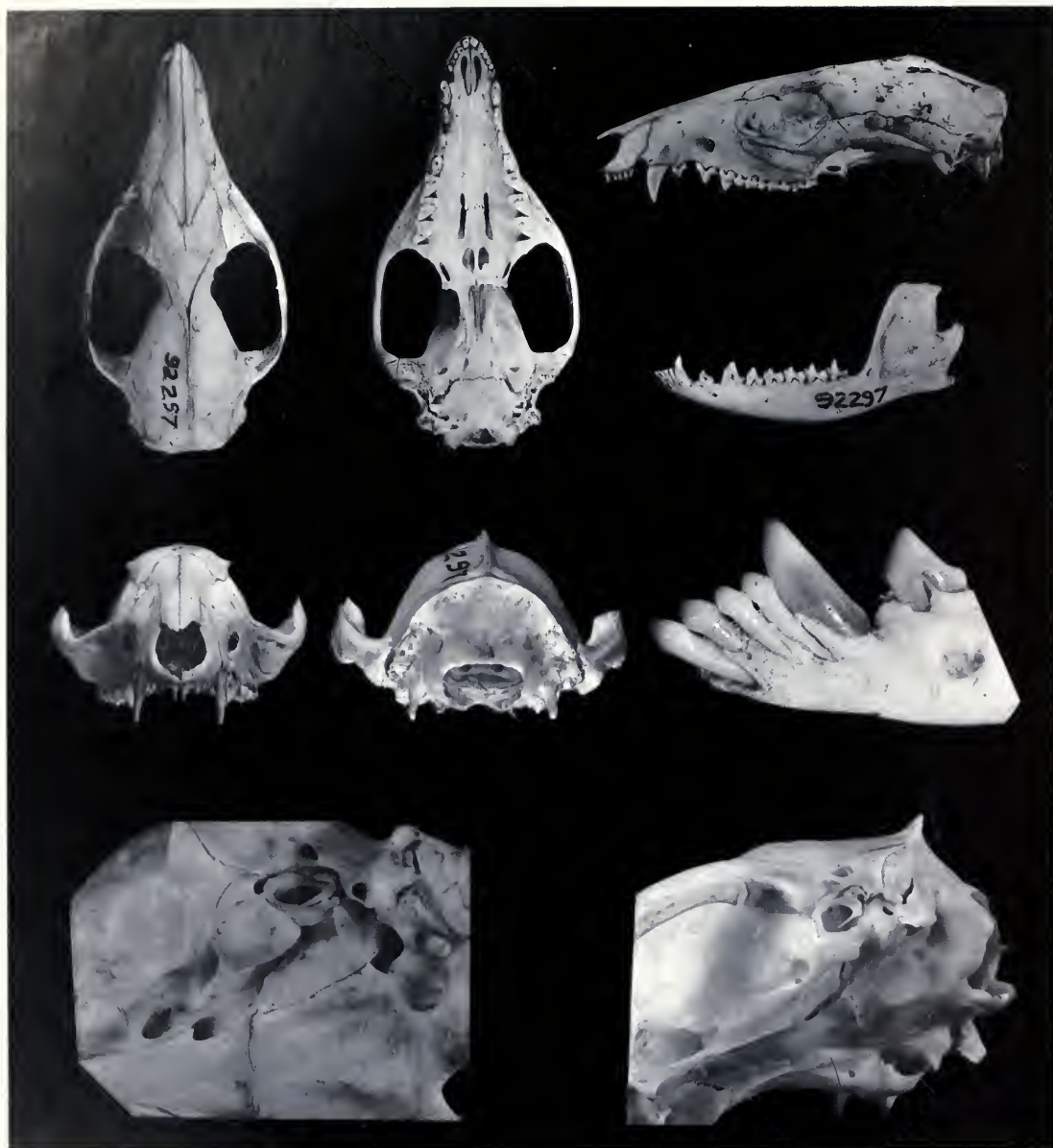


FIG. 13. Skull of *Philander opossum*. Upper row, dorsal, ventral, lateral aspects; middle row, anterior, posterior aspects and left lateral i_2 — pm_1 (note staggered i_3 with buttress); bottom row, two posterior portions of basicranium (see Figs. 11, 12 and Table 5 for identification of parts).

Venezuelan equine encephalitis (Almirante, Panamá; Grayson & Galindo, 1968, in Potkay, 1977)

Eastern equine encephalitis (Bahia, Brasil; Shope et al., 1966, in Potkay, 1977)

St. Louis encephalitis (Bahia, Brasil; Shope et al., 1966)

Group B (mosquito borne)

Ilheus (Bahia, Brasil; Laemmert, 1967)

Yellow fever (Bahia, Brasil; Laemmert et al., 1946)

Group C

Itaqui (Bahia, Brasil; Shope, 1967a)



FIG. 14. Upper and lower jaws with tooth rows of *Philander opossum*.

Capim Group

Acara (Bahia, Brasil; Belém Virus Laboratory, 1976c)

Mosquito-borne group

Turlock (Bahia, Brasil; Shope et al., 1966)

Phlebotomus-borne

Itaporanga (Bahia, Brasil; Trapp & Shope, 1967)

Vesicular stomatitis group

New Jersey strain (Panamá; Tesh et al., 1969)

Indiana strain (Panamá; Tesh et al., 1969)

Unknown vectors

Piry (Bahia, Brasil; Belém Virus Laboratory, 1967a)

Pacui (Bahia, Brasil; Belém Virus Laboratory, 1967b)

Oochoristica braziliensis (Colombia; Baer, 1927)

Sparganum reptans (Imperial Bureau of Agricultural Parasitology, 1933)

Protozoa

Babesia brasiliensis Regendanz and Kikuth (Brasil; Regendanz & Kikuth, 1928, p. 1567)

Sarcocystis garnhami (British Honduras; Lainson & Shaw, 1969)

Trypanosoma cruzi (Brasil; Wood & Wood, 1941; Costa Rica; Deane, 1961, 1964)

Trypanosoma rangeli-like (Pará, Brasil; Deane, 1964)

Fungus

Histoplasma capsulatum (Canal Zone, Panamá; Taylor & Shacklette, 1962)

Mallophaga (lice)

Gliricola porcelli (São Paulo, Brasil; Hopkins, 1949)

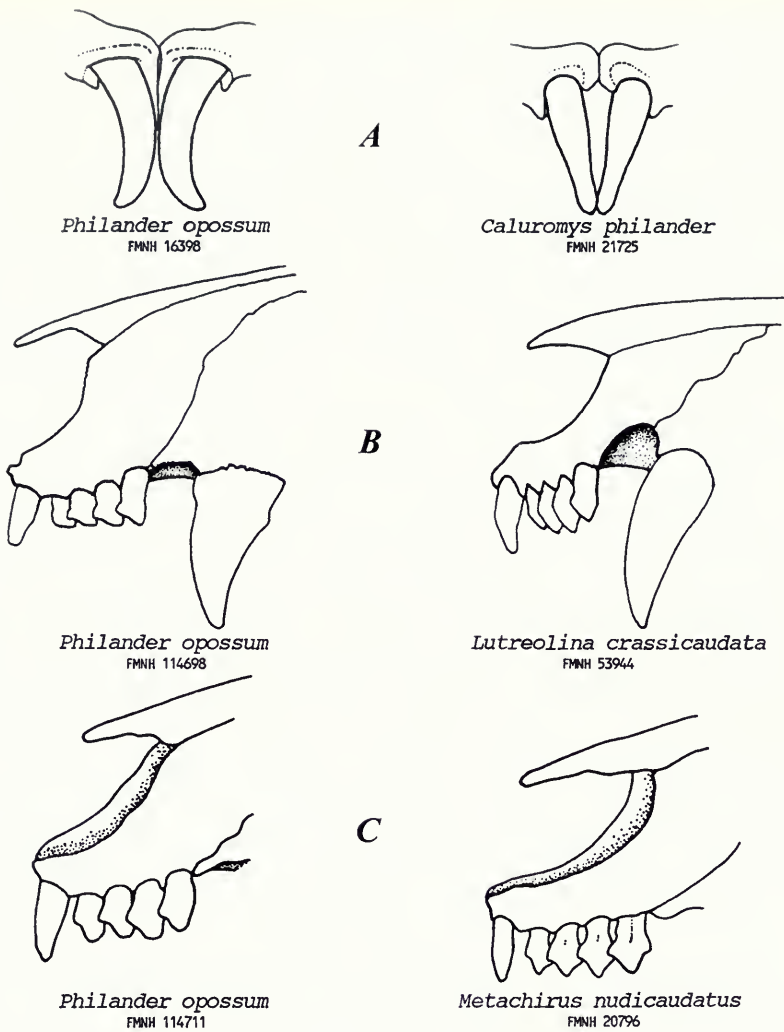


FIG. 15. Upper incisors and canine of *Philander opossum* compared with outgroups. **A**, *P. opossum* (FMNH 16398), i^{1-1} variably convergent proximally, divergent distally; *Caluromys philander* (FMNH 21725), i^{1-1} convergent to tip. **B**, *P. opossum* (FMNH 114698), premaxillary fossa for lower canine shallow, ventral margin of premaxillary bone nearly horizontal; *Lutreolina crassicaudata* (FMNH 53944), premaxillary fossa for lower canine deep, ventral margin upturned, premaxillary bone slender, inclined. **C**, *P. opossum* (FMNH 114711), outer margins of nares steep, incisive distostyles obsolete or absent; *Metachirus nudicaudatus* (FMNH 20796), outer margins of nares gently sloping, nasal tips produced forward, distostyles present, the incisors trident.

Gryopus ovalis (São Paulo, Brasil; Hopkins, 1949)

Trimenopon hispidium (São Paulo, Brasil; Hopkins, 1949)

Acarina (mites, ticks, chiggers)

Archemyobia pectinata Méndez (Panamá; Méndez, 1972, p. 615)

Amblyomma auricularium Conil (Panamá; Fairchild et al., 1966, pp. 191, 209)

Amblyomma geayi Neumann (Panamá; Fairchild et al., 1966, pp. 195, 209)

Amblyomma sp. (Panamá; Fairchild et al., 1966, pp. 209; Venezuela; Jones et al., 1972)

Androlaelaps fahrenheitsi Belese, 1911 (Venezuela; Furman, 1972)

The staggered marsupial incisor

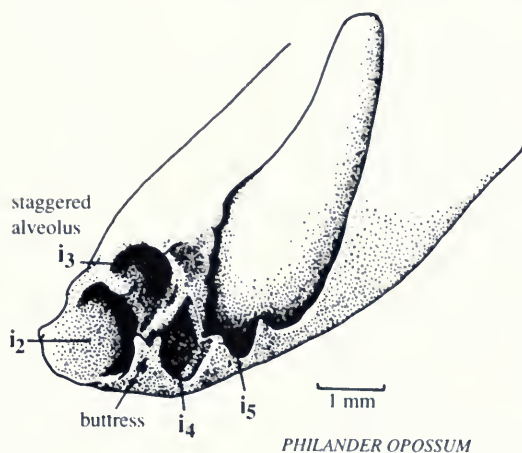


FIG. 16. Alveolus of staggered i_3 , and buttress, in *Philander opossum* (from Hershkovitz, 1982).

Crotiscus disdentatus Boshell and Kerr (Panamá; Brennan & Yunker, 1966, p. 260)

Pseudoschoengastia bulbifera Brennan (Panamá; Brennan & Yunker, 1966, p. 260)

Trombicula dummi Ewing (Panamá; Brennan & Yunker, 1966, p. 260)

Trombicula keenani Brennan and Yunker (Panamá; Brennan & Yunker, 1966, p. 260)

Eutrombicula alfreddugesi Oudemans, 1910 (Venezuela; Brennan & Reid, 1974; Panamá; Brennan & Yunker, 1966, p. 260)

Eutrombicula goeldii Oudemans, 1910 (Venezuela; Brennan & Reid, 1974; Panamá; Brennan & Yunker, 1966, p. 260)

Eutrombicula tropita Ewing, 1925 (Venezuela; Brennan & Reid, 1974)

Euschoengastia nunezi Hoffmann (Panamá; Brennan & Yunker, 1966, p. 260)

Ixodes lasallei Méndez and Ortíz, 1958 (Venezuela; Jones et al., 1972)

Ixodes luciae Senevet, 1940 (Venezuela; Jones et al., 1972)

Ixodes venezuelensis Kohls, 1953 (Venezuela; Jones et al., 1972)

Ixodes luciae Senevet (Panamá; Fairchild et al., 1966, p. 209)

Tur apicalis Furman and Tipton, 1961 (Venezuela; Furman, 1972)

Tur uniscutatus Turk (Panamá; Tipton et al., 1966, pp. 41, 42)

Ornithonyssus wernecki Fonseca (Panamá; Yunker & Radovsky, 1966, p. 92)

Haemolaelaps glasgowi Ewing (Panamá; Tipton et al., 1966, p. 34)

Nematoda

Aspidodera sp. (Venezuela; Guerrero, 1985)

Capillaria sp. (Venezuela; Guerrero, 1985)

Travassastrongylus sp. (Venezuela; Guerrero, 1985)

Moennigia sp. (Venezuela; Guerrero, 1985)

Strongyloides sp. (Venezuela; Guerrero, 1985)

Viannaia barusi Guerrero, 1983 (Venezuela; Guerrero, 1983)

Viannaia conspicua (Brasil; Imperial Bureau of Agricultural Parasitology, 1933, ex Potkay, 1977)

Rhopalia horridus (Angra dos Reis; Imperial Bureau of Agricultural Parasitology, 1933, ex Potkay, 1977)

Viannaia minispicula Guerrero, 1983 (Venezuela; Guerrero, 1983)

Viannaia skrjabini Lent and Freitas, 1937 (Venezuela; Guerrero, 1983)

Viannaia tenorai Guerrero, 1983 (Venezuela; Guerrero, 1983)

Viannaia vianniai Travassos, 1914 (Venezuela; Guerrero, 1983)

Cestoda

Linistowia iheringi (Brasil; Beveredge, 1982, p. 107)

Uniramia (Pterygota)

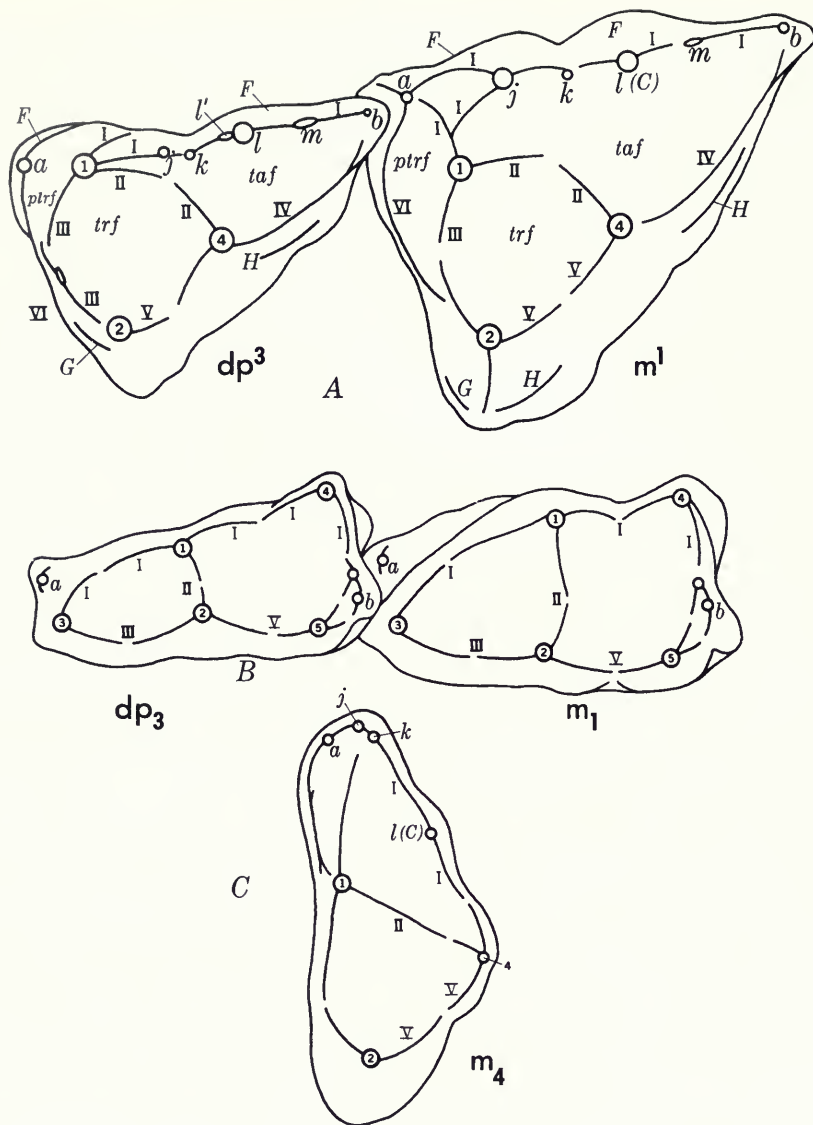


FIG. 17. Occlusal surface of deciduous premolar 3 and molars 1 and 4. **A**, Left dp_3 and m_1 of *Philander opossum* (FMNH 55411). **B**, Right dp_3 and m_1 of *P. opossum* (FMNH 66332). **C**, Left m_4 (composite FMNH 90086, 14015).

Coleoptera

Amblyopinus henseli (Serra dos Órgãos, Angra dos Reis, Brasil; Tijuca; SeEVERS, 1955, p. 247)

Siphonaptera (Fleas)

Adoratopsylla intermedia intermedia Wagner, 1901 (Venezuela; Tipton & Machado, 1972)

Adoratopsylla intermedia cophi Jordan (Panamá; Tipton & Méndez, 1966, p. 326; SW Colombia; Méndez, 1977, p. 166)

Adoratopsylla antiquorum cunhai Pinto (Brasil; Rio de Janeiro, Costa Lima & Hathaway, 1946, p. 228)

Ctenocephalides felis Jordan and Rothschild (cosmopolitan; Costa Lima & Hathaway, 1946, p. 213)

Xenopsylla cheopsis Rothschild (cosmopoli-

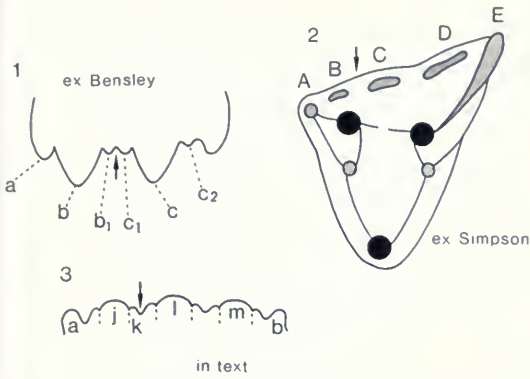


FIG. 18. Conules (stylar cusps, ectostyles, terminal styles) of m^3 . 1, buccal view from Bensley (1906, p. 6); 2, occlusal view from Simpson (1929, p. 119); 3, buccal view from Hershkovitz (1977, p. 287); arrow points to ectoflexus. See Tables 6–7 for explanation of symbols.

tan; Costa Lima & Hathaway, 1946, p. 228)

Polygenis roberti beebei I. Fox (Panamá; Tipton & Méndez, 1966, p. 326)

Polygenis klagesi klagesi Rothschild (Brasil: Pará, Amazonas, Colombia; Panamá; Venezuela; Costa Lima & Hathaway, 1946, p. 142)

Rhopalopsyllus australis tupinus Jordan and Rothschild (Panamá; Tipton & Méndez, 1966, p. 326)

Rhopalopsyllus cacicus saevus Jordan and Rothschild (Panamá; Tipton & Méndez, 1966, p. 326)

Rhopalopsyllus lutzi lutzi Baker (Argentina; Paraguay; Brasil: Goias, Minas Gerais; Costa Lima & Hathaway, 1946, p. 139)

Neotyplocercus rosenbergi Rothschild (Ecuador; Perú; Costa Lima & Hathaway, 1946, p. 229)

Tritopsylla intermedia intermedia Wagner (Brasil; Colombia; Ecuador; Paraguay; Central America; Costa Lima & Hathaway, 1946, p. 228)

Trematoda

Duboisiiella proloba Baer (Perú; Tantaleán et al., 1992) [*Bursotrema tetracotyloides* Szidat (Perú; Tantaleán et al., 1992)]

Zonorchis allentoshi Foster (Perú; Tantaleán et al., 1992)

Plagiorchis didelphidis Foster (Perú; Tantaleán et al., 1992)

Rhopalias caballeroi Kifune and Uyema (Perú; Tantaleán et al., 1992)

Rhopalias baculifer Braun (Perú; Tantaleán et al., 1992)

Paragonemus amazonicus Miyazaki, Grados, and Uyema (Perú; Tantaleán et al., 1992)

Rhopalias coronatus Rudolphi (Perú; Tantaleán et al., 1992)

Amphimeruse rurarupu Kifune and Uyema (Perú; Tantaleán et al., 1992)

Collins (1973, pp. 4, 74) listed the following genera of parasites of *Philander* without more information or regard for phylogenetic affinities. The list was culled from the "host catalog index card file of the Parasite Classification Index Catalogue of the United States Department of Agriculture's Parasite Control Center, Beltsville, Maryland."

Arthropoda

Adoratopsylla, flea

Amblyomma, tick

Ctenocephalides, flea

Crotiscus, chigger

Euschoengastia, chigger

Eutrombicula, chigger

Gigantolaelaps, louse

Gliricola,¹ louse

Gyropus,¹ louse

Haemolaelaps, mite

Heterothrombidium

Intercutestrix

Ixodes, tick

Leeuwenhoekia

Microthrombidium

Neothyphloceras, flea

Ornithonyssus, mite

Pentastoma (see *Porocephalus*)

Polygenis, flea

Porocephalus,

Pentastoma

Pseudoschongastia, chigger

Pulix, flea

Rhopalias

Rhopalopsyllus, flea

Schongastia

Trimenopon,¹ louse

Tritopsylla, flea

Trombicula, chigger

Tur, Acarina

Xenopsylla, flea

Acanthocephala

Echinorhynchus

Hamanniella

Cestoda

Oorchoristica

Sparganium

Nematoda

Aspidodera

Capillaria

Cortiamosoides

Cruzia

Globocephalus

Gnathostoma

Gongylonemoides

¹All refer to one captive individual and are certainly due to contamination," Werneck, in Hopkins, 1949, p. 439.

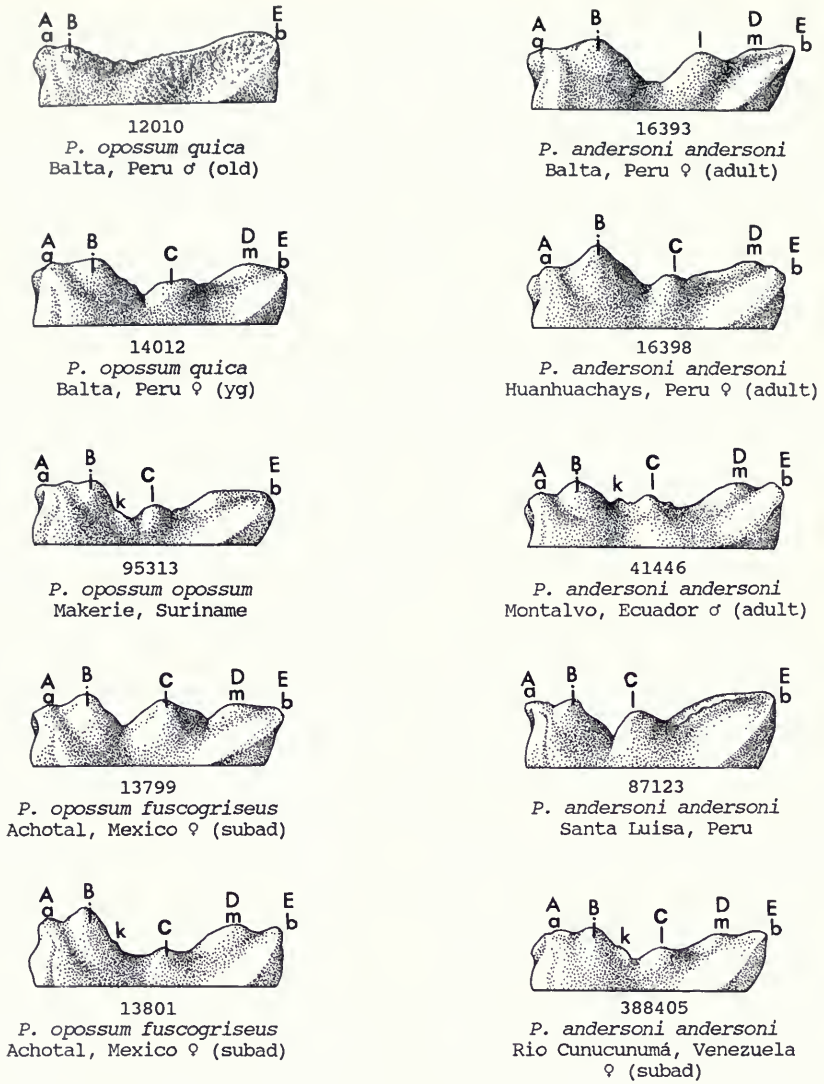


FIG. 19. (FNNH) Conules of third upper molar labial shelf of *Philander* species from various geographic localities. See Table 6 for explanation of symbols.

Macielia

Oxysoma

Philostrongylus

Physaloptera

Skrjabinofilaria

Subulura

Travassostrongylus

Trichuris

Viannaia

Protozoa

Besnoitia

Haemogregarina

Sarcocystis

Trypanosoma

Trematoda

Brachylaemus

Maritrema

Opisthorchis

Paragonimus

Phaneropsolus

Plagiorchis

Platynosomum

Podospathalum

Zonorchis

Species and Named and Unnamed Subspecies of *Philander opossum*

The taxonomic accounts are arranged in the following order.

1. *Philander opossum* Linnaeus
Philander opossum opossum Linnaeus
Philander opossum quica Temminck
Philander opossum frenatus Olfers
Philander opossum melanurus Thomas
Philander opossum subspecies nov. 1
Philander opossum subspecies nov. ?

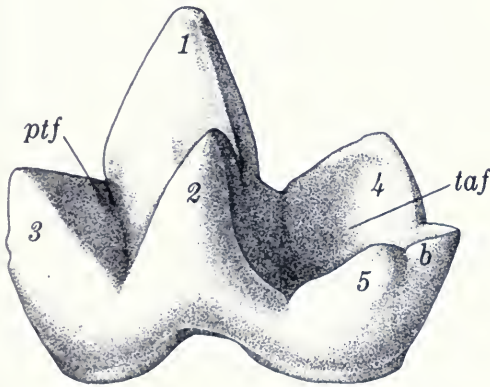
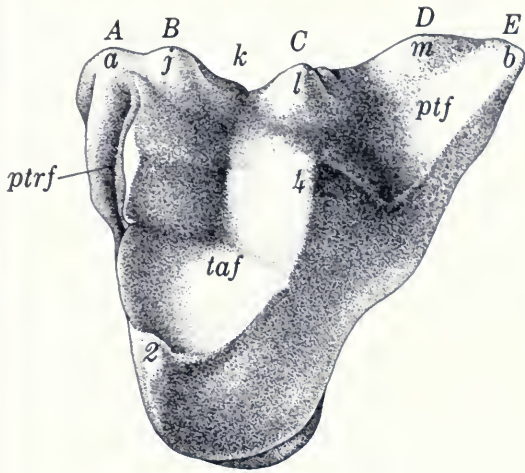


FIG. 20. Left upper third molar and right lower third molar of *Philander opossum*. See Table 6 for names of features.

Philander opossum fuscogriseus

J. A. Allen

2. *Philander andersoni* Osgood

Philander andersoni andersoni Osgood

Philander andersoni mcilhennyi

Gardner and Patton

Philander opossum Linnaeus

(Synonyms under subspecies heading)

DISTRIBUTION (Fig. 5)—Distribution as for the genus, except replaced by *P. andersoni* in Amazonian Colombia and Ecuador and contiguous

parts of Amazonian Perú, and in central Perú in the departments of Pasco, Junín, and Ayacucho. *Philander opossum* and *P. andersoni* are sympatric in the upper Río Purús and mid and lower Río Ucayali basins.

HISTORIC VARIATION—The nearest putative ancestor of *P. opossum* was perhaps slightly smaller than its living descendants and possibly grayish agouti, likely marked by pale brown superciliary spots. The warm, humid Late Pleistocene climate of the ancestral habitat east of the Andes supported a dense tropical forest that permitted spread of the four-eyed opossum around the northernmost projections of the Andes to the Pacific coast and Middle America. With the onset of the cooler, drier climate of Late Pleistocene or Early Recent, shrinkage and fragmentation of the forest resulted in isolated refuges surrounded by superceding or invading savannas (Prance, 1982). The isolated populations of *Philander* differentiated into the racial forms recognized here. The most widely distributed or largest portion of the erstwhile continuously distributed ancestral population is *P. opossum quica*.

An undescribed population (*P. opossum* subsp. nov. 1) of northeastern Venezuela (Fig. 5, f) is said to be very dark. The isolated *P. opossum melanurus* of coastal Ecuador is also dark. It remains to be seen if the ranges of *P. opossum melanurus* and *P. opossum fuscogriseus* meet on the west and between *P. opossum quica* and the undescribed *P. opossum* on the northeast.

The geographic range of the southeastward-spreading *P. andersoni* overlaps that of the westward-advancing *P. opossum quica*.

CRANIAL AND DENTAL CHARACTERS—Cranial and dental characters as for the genus, comparisons included.

COLORATION (Fig. 4)—Color pattern of head as for the genus; cheeks, chin, throat, neck, chest, belly, inner sides of limbs ochraceous to buffy or whitish; marsupial region brown, scrotum unpigmented or partially to completely pigmented; lateral line, if present, usually confined to pelvic region as a hip patch, less frequently as a shoulder stripe or patch, color buffy to ochraceous orange, often appearing olivaceous when pale hair bases show through; crown, midline of nape, and dorsum to basal hairy portion of tail brownish; middorsal band, if present, poorly to strongly defined, individual cover hairs agouti (banded), tip brown (eumelanin), buffy (pheomelanin) subterminally, followed proximally by a brown band merging into curly and distinctly thinner grayish

TABLE 6. Explanation of symbols used for marsupial dentition (Figs. 17–20).

Upper teeth		Lower teeth	
Cones ¹		Conids ¹	
1	Eocone (paracone)	1	Eoconid (protoconid)
2	Protocone	2	Metaconid
3	—	3	Paraconid
4	Metacone	4	Hypoconid
5	—	5	Entoconid
Conules and styles ²		Conulids and stylids ²	
<i>a</i> (A)	Mesiostyle- <i>a</i> (parastyle)	<i>a</i>	Mesiostylid (parastylid)
<i>b</i> (E)	Distostyle- <i>b</i> (metastyle; hypoconule)	<i>b</i>	Distostylid (hypoconulid)
<i>j</i> (B)	Ectostyle- <i>j</i>		
<i>k</i>	Ectostyle- <i>k</i>		
<i>l</i> (C)	Ectostyle- <i>l</i> (mesostyle)		
<i>m</i> (D)	Ectostyle- <i>m</i>		
Cristae ³		Cristids ³	
Cristae extend from—to or between cusps; reference cusps in parentheses are not elements of the indicated crista.		Cristids extend from—to or between cusps; reference cusps in parentheses are not elements of the indicated cristid.	
<i>I</i>	Eocrista [<i>l-a-j-k-l-m-b</i>]	<i>I</i>	Eocristid [<i>l-a-j-k-l-m-b</i>]
<i>II</i>	Centrocrista [<i>l-4</i>]	<i>II</i>	Centrocristid [<i>l-4</i>]
<i>III</i>	Epicrista [<i>l-2</i>]	<i>III</i>	Epicristid [<i>l-2</i>]
<i>IV</i>	Postmetacrista [<i>4-b</i>]	<i>IV</i>	Postmetacristid [<i>4-b</i>]
<i>V</i>	Plagiocrista (metaloph) [<i>2-4</i>]	<i>V</i>	Plagiocristid [<i>2-4</i>]
<i>VI</i>	Protoloph (protocrista; crested portion of cingulum (<i>G</i>))	<i>VI</i>	Protocristid (crested portion of cingulum <i>B</i>)
Basins or fossae		Basins or fossids	
<i>ptrf</i>	Pretrigon basin or fossa	<i>ptf</i>	“Trigonid” basin or fossid
<i>trf</i>	Trigon basin or fossa	—	—
<i>taf</i>	Talon basin or fossa	<i>taf</i>	Talonid basin or fossid
Upper and lower teeth			
Cingula and cingulids		Main enamel folds	
Primary		<i>ex</i> ectoflexus (between <i>l-4</i>)	
<i>F</i>	Buccal or external (buccal shelf)		
<i>G</i>	Anterolingual or anterior (primary lingual shelf)		
<i>H</i>	Posterolingual cingulum		

¹Most cones and conids are numbered in the order of their origin and development.

²Most conules, conulids, styles, and stylids are listed in the order of their position from buccal to lingual and anterior to posterior. Rare or infrequent elements of the tritubercular trigon are listed opportunistically toward the end. Supernumeraries or gemini of established cusps and cuspsids are not identified individually.

³Most cristae (-ids) are numbered in the order of their appearance or development in phylogeny, others are numbered opportunistically; all cristae (-ids) except *l-l* inclusive are modified parts of cingula (ids); homologies of the talonid cristids are not certain in every case.

bases; guard hairs uniformly brownish; shoulders, sides of body, inner sides of limbs contrastingly paler than dorsum, the subterminal bands of cover hairs paler than those of dorsum, the dark guard hairs fewer and shorter; metapodials brown above, digits usually contrastingly paler or unpigmented, plantar surface usually well pigmented and darker than upper surface; tail naked in appearance except for hairy base, color entirely brown or mottled to particolored from tip

to as much as distal three-fifths of tail more or less unpigmented; ears naked and wholly brown to nearly entirely unpigmented except for brownish borders.

DICHROMATISM—Gray and brown color phases described under the generic heading (p. 11) are present in *P. opossum*. In brown phase, the pheomelanin subterminal band of the cover hairs of dorsum and sides is saturate ochraceous or orange. The same band in the gray phase is bleached

TABLE 7. Molarization of conule C in m^3 . a = barely rudimentary; b = rudimentary conule not always well defined; c = low distinct conule; d = small cusp; e = cusp comparable to conule B in bulk. The tabulation is based on about 95 specimens in the Field Museum, plus about an equal number of borrowed specimens.

Locality	a-b	b-c	c-d	d-e
<i>Philander andersoni andersoni</i>				
Venezuela	8	8	4	-
Colombia	1	1	2	-
Ecuador	3	2	2	-
Perú (Andean)	2	-	-	-
Perú (Ucayali)	-	-	6	2
<i>Philander andersoni mcilhennyi</i>				
Perú (Ucayali)	-	-	8	2
<i>Philander opossum fuscogriseus</i>				
México	-	-	3	6
Guatemala	-	-	1	3
Honduras	-	-	-	1
Costa Rica	-	-	3	-
Panamá	-	-	1	1
Colombia	2	1	5	2
Ecuador	1	-	1	-
<i>Philander opossum melanurus</i>				
Ecuador	2	2	-	-
<i>Philander opossum opossum</i>				
Guianas	4	2	1	-
Brasil (Amazonian)	8	9	3	-
<i>Philander opossum quica</i>				
Eastern Brasil	4	2	1	-
Bolivia	12	7	3	-
Perú	7	10	2	-
Venezuela	2	5	8	-

to pale buff or nearly white. Old pelage with tips and subterminal bands of hairs eroded, appears brown in either color phase because of greater exposure of the dark bases. Hairs of underparts in gray phase are dominantly bicolor with terminal portions pheomelanic, basal portions eumelanic. In brown phase, the hairs are dominantly monochlor pheomelanic.

Sexual dichromatism, as seen in *P. andersoni*, is not evident in *P. opossum*.

Philander opossum opossum Linnaeus

Philander. Opossum [sic], sive *Carigueja*, Brasiliensis: mas., Seba, 1734:56, Pl. 36, Fig. 1 (male [Fig. 21])—description.

Philander. Americanus. sive Carigueja, cum catulus, saccum ventris intrantibus foemina, Seba, 1734:57, Pl. 36, Fig. 2 (female with pouch young [Fig. 21])—description.

Carigueja, junior, sive Opossum [sic], cum sacco aperto, Seba, 1734:57, Pl. 36, Fig. 3 (young female with open pouch)—description.

Sarigue, Buffon [and Daubenton], 1763:279, Pls. 45-50 (animals, anatomy)—part, anatomical description of male (Pl. 45) and female (Pl. 46) only.

Molucca opossum, Shaw, 1800:476, Pl. 108.

[*Didelphis*] *opossum*, Linnaeus, 1758:55.

Didelphis opossum, Cuvier, 1798:114—*le sarigue*. É. Geoffroy St. Hilaire 1803:141—characters; habits. Latreille, 1803:304—*sarigue ou opossum*. Desmarest, 1820:256—characters. Temminck, 1825:41—characters. Gray, 1843:101. Jentink, 1887:301—SURINAME; GUYANE FRANÇAISE: (*Cayenne*). Jentink, 1888:220—SURINAME. J. A. Allen, 1900:195—SURINAME: (type locality).

Didelphis opossum [sic], Brongniart, 1792:115—GUYANE FRANÇAISE: (*Cayenne*).

Didelphis opossum, Goldfuss, 1809:215. Waterhouse, 1841:90—part, GUYANA; SURINAME. Waterhouse, 1846:485—GUYANA. Thomas, 1888:329—part, GUYANA: *Demerara* (Better Hope); SURINAME. Lydekker, 1896:200—part, distribution; characters. Goeldi and Haggmann, 1904:100—BRASIL: *Pará*; local name, *mucurá chichica*.

TABLE 8. Karyotypes of largest American marsupials.

Taxon	2n	SM	A	X	Y	FN	N ♀, ♂	Source
<i>Philander opossum</i>	22	-	10	A	A	20	7, 9	Reig et al. (1977)
<i>Philander andersoni</i>	22	-	10	A	A	20	4, 3	Reig et al. (1977)
<i>Didelphis marsupialis</i>	22	-	10	A	A	20	19, 11	Reig et al. (1977)
<i>Didelphis albiventris</i>	22	-	10	A	A	20	3, 7	Reig et al. (1977)
<i>Didelphis virginiana</i>	22	6	4	M	A	32	10, 9	Reig et al. (1977)
<i>Chironectes minimus</i>	22	-	10	A	A	20	-, 1	Reig et al. (1977)
<i>Lutreolina crassicaudata</i>	22	-	10	M	A	20	1, 2	Reig et al. (1977, p. 199)

A = acrocentric; FN = fundamental number of autosomal arms; M = metacentric; SM = submetacentric; ST = subtelocentric; X = ♀ sex chromosome; Y = ♂ sex chromosome; 2n = diploid number of chromosomes; N ♀, ♂ = number of ♀ and ♂ samples.

TABLE 9. Measurements of *Philander opossum opossum* Linnaeus.

Locality	Head and Body	Tail	Hind Foot	Ear
<i>Philander opossum opossum</i>				
Guyana ♂♂				
All localities	-, 280, -, 312	-, 298, -, 330	-, 42, -, 41	-, 38, -,-
Guyana ♀♀				
All localities	254, 287, -, 270	266, 273, -, 264	-	-
Suriname ♂♂				
All localities	275 (250-305) 8	271 (254-310) 8	41 (40-42) 7	39, 39, 40
Suriname ♀♀				
Paramaribo	245, 277, 260	262, 264, 269	40, 40, 43	32, 36, 30
Guyane Française ♂♂				
Cayenne	272, 257	268, 276	42, 41	37, 34
Guyane Française ♀				
Cayenne	292	297	39	41
Brasil ♂♂				
Serra do Navio	302 (280-320) 4	315 (310-320) 3	44 (42-45) 4	35 (34-36) 4
Rio Amapari	260, 304	280, 300	42, 50	34, 42
Belém, Utinga	280, 270, 280	280, 290, 285	42, 42, 46	39, 41, 39
Capim	270, 280	290, 320	42, 42	36, 36
Baião	295, 280	295, 305	41, 42	-
Guamá	255	280	45	40
Tapareba	-	-	-	-
Cametá	290	300	35	-
Taiuna	290 (260-314) 24	289 (235-343) 24	45 (41-50) 24	-
Santarém Highway	270, 270, 280	300, 285, 310	41, 40, 44	30, 30, 32
Altamira	-	-	-	-
Rosarinho	285	285	35	-
Imperatriz	309	321	50	-
Baptista	-	-	-	-
Brasil ♀♀				
Serra do Navio	-	-	-	-
Rio Amapari	270	275	40	35
Murutucu	-, 280	-, 258	-, 35	-, 20
Belém, Utinga	-, 262, 290	-, 273, 275	-, 41, 41	-, 38, 40
Mocajuba	260	265	35	-
Baião	268 (252-284) 6	279 (274-290) 5	39.8 (39-40) 5	-
Tapareba	273	270	39	38
Cametá	290	350	-	-
Taiuna	275 (261-298) 11	298 (272-334) 11	42 (41-43) 9	-
Santarém Highway	255	290	40	30

D[idelphys]. opossum, Olfers, 1818:204—part, synonymy. Wagner, 1855:226—listed.

Sarigua opossum, Muirhead, 1830(1819):429—classification.

Metachirus opossum, Burmeister, 1856:69, Pl. 11, Fig. 1 (skull)—characters. Thomas, 1901b:153—GUYANA: *Rupununi* (Rupununi River; Kanuku Mts.). Thomas, 1910:188—GUYANA: *Demerara* (Supinaam River). Thomas, 1911:143—SURINAME: (type locality); Seba sole reference for *opossum* Linnaeus. Sonntag, 1924:743, Figs. 39c, 40i (tongue)—tongue anatomy. Boardman, 1952:848—hair tracts.

Metachirus opossum opossum, J. A. Allen, 1911:246—VENEZUELA: *Bolívar* (Río Yuruán).

Didelphys (Metachirus) opossum, Ménégau, 1902:496—GUYANE FRANÇAISE: (Ouanary River).

Gamba opossum, Liais, 1872:329—classification.

[*Metachirops*] *opossum*, Matschie, 1916:268—SU-

RINAME: *Paramaribo* (type locality); classification.

Metachirops opossum opossum, Krumbiegel, 1941:200—part, BRASIL: *Pará* (Ipitinga, Rio Acará; Peixe-Boi). Husson, 1978:24, Fig. 2c (front teeth), Pl. 1, Fig. 3 (hind foot), Pl. 5 (animal), Pl. 8 (skull)—SURINAME: *Nickerie* (Avanavero Falls, Kabalebo River; upper Nickerie River); *Paramaribo* (Paramaribo, various localities in and near town; Clevia; Lelydorp); *Suriname* (near Para River on road to Domburg, 10 km SE of Paramaribo); *Commewijne* (near Commewijne River); *Marowijne* (Albina); characters; habits; vernacular names. [*Holothylax opossum*] *opossum*, Cabrera, 1919:48—classification.

Metacherius [sic] *opossum*, Sanderson, 1949:787, Pl. 7, Fig. 1 (hand), Fig. 2 (foot)—part, SURINAME; local names, *fructu-awari*, *awari*.

Philander opossum, Gilmore, 1941:309—classifica-

TABLE 9. *Extended.*

Condylobasal Length	Zygomatic Breadth	Preorbital Width	Postorbital Width	Braincase Width
71.7 (68.4–75.4) 4	34.1, –, 34.6, 38.9	12.3, –, 12.9, –	9.1, –, 8.4, 8.5	20.3, 18.4, 22.5
66.0, –, 69.7, 70.3	31.4, –, 36.5, 36.0	–, –, 13.4, 12.5	–, –, 8.1, 8.5	19.6, –, 19.2, 19.6
70.6 (67.3–73.3) 7	36.9 (33.8–39.1) 6	12.8 (11.5–14.6) 7	8.4 (7.5–9.2) 7	20.7 (19.4–21.3) 7
69.3, –, –	35.7, –, –	12.8, –, –	8.0, –, –	20.8, –, –
69.5, 73.1	38.3, 38.5	13.4, 13.4	9.4, 8.8	20.6, 19.7
68.2	35.3	12.2	9.7	19.7
74.1 (69.7–82.1) 20	38.7 (35.3–43.4) 20	14.4 (12.5–15.3) 20	8.9 (8.2–9.5) 20	21.8 (20.5–22.9) 20
69.4, 77.1	34.5, 39.8	12.5, 18.9	8.6, 9.4	19.3, 21.7
68.2, 70.0, 74.6	34.7, 33.0, 38.7	12.4, –, 13.0	8.8, 8.5, 8.8	20.3, 19.7, 21.4
70.0, 74.9	33.0, 39.1	–, 13.3	8.5, 8.9	19.7, 22.1
73.2 (69.4–75.5) 4	37.3 (36.3–38.6) 4	–	8.7 (8.5–9.1) 4	21.9 (21.4–22.0) 4
75.1	37.2	–	9.0	20.9
69.8, 70.4	38.7, 37.1	16.1, 16.2	8.2, 8.0	–
72.1	39.4	17.6	9.2	21.7
74.2 (68.4–78.0) 20	39.5 (35.9–42.3) 20	14.2 (12.3–15.7) 19	8.8 (8.4–9.5) 20	20.9 (19.3–22.9) 20
70.4, 70.2, 73.3	35.3, 36.6, 39.3	12.9, –, –	8.9, 9.3, 9.7	20.7, 20.2, 21.4
72.5	35.7	–	9.0	21.5
65.4	35.0	–	8.5	21.3
79.0	43.0	–	8.9	24.0
72.9	34.5	–	8.8	19.3
75.7 (69.1–80.8) 4	–	–	–	–
75.5	39.0	18.4	9.0	20.4
69.7, 72.1	32.2, 36.2	–, 12.9	8.7, 9.0	19.5, 19.4
69.5, 70.9, 74.3	34.6, 35.1, 36.5	13.0, 12.4, 13.7	8.2, 8.5, 9.0	20.0, 20.0, 20.8
64.8	32.5	–	8.1	18.9
66.6 (64.0–69.2) 7	32.6 (31.3–34.0) 6	–	8.9 (8.3–9.2) 7	20.0 (19.3–20.8) 7
67.0	31.1	–	8.8	19.3
76.4	36.8	17.7	9.0	21.4
62.6 (65.4–75.5) 13	35.0 (32.1–40.7) 13	12.5 (11.4–13.7) 13	8.7 (8.1–9.1) 13	19.9 (19.2–21.4) 13
65.4	32.8	–	9.2	20.2

tion. Pine, 1973:51 (key), 56—BRASIL: *Pará* (Utinga, Belém). Miles et al., 1981a:331—BRASIL: *Pará* (Belém); tracking; habitat; comparison with *Metachirus nudicaudatus*. Miles et al., 1981b: 272—BRASIL: *Pará* (Belém); habitat; host of triatomine bugs vectors of *Trypanosoma cruzi*. Charles-Dominique et al., 1981:342—GUYANE FRANÇAISE: *Cayenne*; habitat; behavior, diet. Atramentowicz, 1986a:123 GUYANE FRANÇAISE: *Cayenne*; habits; reproduction. Charles-Dominique, 1983:395-422—GUYANE FRANÇAISE: *Cayenne*; habits, habitat; reproduction. Guerrero, 1985:41—VENEZUELA: parasites. Atramentowicz, 1988:47—GUYANE FRANÇAISE: *Cayenne* (frugivory).

Philander opossum opossum, Ávila-Pires, 1958:4—BRASIL: *Pará* (Utinga, Belém de Pará). Husson, 1978:5—SURINAME: local names, *fo-ai awari*, *vieroog-opossum*, *kaalstaart*. Carvalho, 1961:5—

BRASIL: *Rio Branco* (Poção, Caracarai; Poção, Boa Vista); habits; disagrees with Sanderson's reports. Carvalho, 1962:285—BRASIL: *Amapá* (Rio Amapari, Macapá; Rio Maracá, Mazagão; Rio Branco, Rio Maracá, Mazagão); local name, *mucura xixica*. Pine, 1973:56—BRASIL: *Pará* (Belém; Utinga); characters. Pérez-Hernández, 1989: 373—VENEZUELA: *Bolívar* (El Palmar; San Martín de Turumbarin; Chalunani).

Philander o[pposum], *opossum*, Carvalho and Toche-ton, 1969:217—BRASIL: *Pará* (Utinga, Belém; Sapucajuba, Belém; km 94 Belém—Brasília); local name, *mucura xixica*.

P[hilander], *virginianus* Tiedemann, 1808:427—replacement name for *D. opossum* Linnaeus.

Didelphis austro-americana Thomas, 1923:604—name ex Oken 1816:1148—a non-Linnaean work; synonym of *D. opossum* Linnaeus.

TABLE 9. *Extended.*

Locality	Palatal Length	i-m ⁴	m ¹⁻⁴
<i>Philander opossum opossum</i>			
Guyana ♂♂			
All localities	43.1 (41.6–44.1) 4	38.0 (36.9–38.8) 4	14.1 (13.6–14.5) 4
Guyana ♀♀			
All localities	40.7, –, 43.0, 43.7	36.5, –, 37.8, 38.8	14.0, –, 14.0, 14.7
Suriname ♂♂			
All localities	43.0 (41.8–43.8) 7	37.4 (36.5–38.1) 7	13.8 (13.4–14.4) 7
Suriname ♀♀			
Paramaribo	43.1, –, –	37.9, –, –	14.0, 14.0, –
Guyane Française ♂♂			
Cayenne	41.8, 45.8	36.9, 39.2	13.9, 14.2
Guyane Française ♀			
Cayenne	41.0	36.1	14.0
Brasil ♂♂			
Serra do Navio	45.1 (41.7–49.6) 20	38.9 (36.8–40.3) 20	14.1 (13.6–14.9) 20
Rio Amapari	42.1, 46.2	36.7, 39.8	14.0, 14.0
Belém, Utinga	42.3, 41.3, 44.2	36.7, 36.0, 38.8	13.4, 13.6, 13.7
Capim	41.3, 42.9	36.0, 37.6	13.6, 13.3
Baião	44.0 (41.6–46.7) 4	38.5 (37.0–41.5) 4	13.9 (13.0–14.1) 4
Guamá	44.4	38.2	14.0
Tapareba	40.8, 40.3	35.8, 37.7	13.7, 13.8
Cametá	42.6	37.7	14.5
Taiuna	44.3 (42.0–46.4) 20	38.2 (37.2–40.5) 20	13.4 (12.8–14.3) 20
Santarém Highway	41.8, 42.4, 43.9	36.8, 37.2, 38.4	13.6, 13.4, 14.3
Altamira	44.0	37.7	13.7
Rosarinho	40.3	34.9	14.1
Imperatriz	47.8	40.9	14.1
Baptista	44.9	37.7	13.1
Brasil ♀♀			
Serra do Navio	–	–	14.0
Rio Amapari	45.7	38.6	13.8
Murutucu	43.6, 43.3	36.9, 37.6	12.9, 13.7
Belém, Utinga	42.0, 42.3, 44.7	37.3, 36.5, 38.3	14.0, 13.5, 13.6
Mocajuba	38.4	34.8	13.4
Baião	40.7 (38.4–42.9) 7	36.0 (35.1–36.9) 7	13.5 (13.0–14.3) 6
Tapareba	41.4	36.8	13.4
Cametá	45.8	39.3	14.0
Taiuna	41.7 (39.2–44.8) 13	36.7 (35.0–38.1) 13	13.6 (12.7–14.0) 13
Santarém Highway	40.3	35.6	13.1

Didelphis Marsupialis, Shaw (not Linnaeus), 1800: 476, Pl. 108—*Molucca opossum*.

Didelphis quica, Jentink (not Temminck), 1888:220—part, SURINAME. Schomburgk 1840:344—GUYANA; characters; habits.

Didelphys quica, Waterhouse, 1841:90—part, GUYANA; SURINAME. Waterhouse, 1846:480—part, GUYANA; SURINAME.

D[*idelphys*]. *quica*, Cabanis (not Temminck), 1848, 3: 777—GUYANA.

Metachirops opossum quica, Carvalho (not Temminck), 1958:123—BRASIL: Pará (Graduus, Rio Fresca); local name, *mucura xixica*.

TYPES (Fig. 21)—Name based on Seba's (1734) "*Philander Opossum, sive Carigueja, Brasiliensis*: mas." and "*Philander, Americanus, sive Carigueja, cum catulus, sacrum ventris intranti-*

bus foemina"; the female, in alcohol, designated lectotype by Hershkovitz (1976), is preserved in the Rijksmuseum van Natuurlijke Historie, Leiden.

TYPE LOCALITY—Suriname, determined by J. A. Allen (1900, p. 195), further restricted to Paramaribo by Matschie (1916, p. 262).

DISTRIBUTION (Fig. 5)—Guyana, Suriname, Guyane Française; in Brasil the states of Amapá, Roraima, and equatorial parts of Pará and Amazonas, in the Amazonian basin west of the Rios Tocantins–Araguaia. The hiatus between the west bank of the Rio Negro, north bank of the Rio Solimões and eastern slope of the Andes cannot be attributed to lack of suitable habitat, negative collecting, or preemption of parts of the range by



FIG. 21. Male and female lectotypes of *Didelphis opossum* Linnaeus (1758). Upper, "*Philander opossum* sive Carigueja Brasiliensis mas," the male opossum. Lower, "*Philander americanus*, sive Carigueja, cum catulus, Sacrum ventris intransibus foemina." Figures and quotations from Seba (1734, p. 57, Pl. 36, Fig. 2).

P. andersoni. It may be that during a Pleistocene climatic change, the warm, humidity-loving opossum disappeared from even more extensive areas where savannas replaced forests.

CHARACTERS—General body size larger throughout than *quica* or *melanurus*; molars proportionately smaller; upper parts of trunk grayish to buffy brown, under parts buffy orange to ochraceous orange; tail usually parti-colored.

COMPARISONS—Few individuals of *P. opossum opossum* are as small as average-sized *quica*, and the underparts of none of the specimens at hand show the whitish, pale buff or grayish brown underparts present in many individuals of other races.

MEASUREMENTS—Tables 1 and 9.

TAXONOMY—Sole basis for the Linnaean *Didelphis opossum* is the animals described by the Dutch pharmacist and naturalist collector Albert Seba (1734, in the work entitled *Locupletissimi rerum naturalium thesauri . . .*, 1, p. 56, Pl. 36, Fig. 1 [male], Fig. 2 [female]). Upper parts of the body of the male four-eyed opossum shown in the cited figure reproduced here (Fig. 21) are described as dark chestnut, and the tail base is said to be furred for the length of a human finger, or roughly between 7 and 9 cm. Seba's female, Figure 2 (Fig. 21 here), is fully pouched, but no formal description of the animal appears in the text. Linnaeus (1758, p. 55), in citing Seba, evidently intended that the name *D. opossum* apply to the female. His diagnosis and description, "*D[idelphis]. cauda semipilosa, superciliarum regione pallidore, mammis binis*" and "*abdomen circa mammas contrahitur in marsupium; pollicis postici mutici*," leaves no doubt. Color is not mentioned, but the "*cauda semipilosa*" can be variously translated as hairy for half its length or as partially furred. Whatever the wording, the interpretation must be derived from Seba's woodcut figure of the female (Fig. 21).

VARIATION—The types of *P. opossum opossum* Linnaeus, as described by Seba (1734, pp. 56, 57) are brown-phase individuals. With respect to other Suriname specimens, a male I collected in La Poule and another in Clevia, Paramaribo, are brown phase and resemble the lectotype preserved in alcohol in the Leiden Museum. A young female taken in Lelydorpplan is gray phase. One of two individuals collected by H. A. Beatty in the Wilhelmina Mountains is gray phase, the other brown phase. Other Suriname skins examined are of juvenals.

Gray- and brown-phase individuals and intermediates occur throughout the range of the race. In all, however, underparts are more densely pigmented than in those of neighboring *P. opossum quica*. The large series from the Rio Tocantins (Baiao; Ilha do Taiuna) exhibit the full range of color variation in *P. opossum opossum*.

REMARKS—Under the name *Metacherius* [sic] *opossum*, Sanderson (1949, p. 787) recorded 10 males and 12 females from Suriname. Of the total, 16 are said to have been taken in Paramaribo, and one, a large female, from Zanderij. Other specific localities are not mentioned. I found skins of six males and three females in the British Museum, all labelled Paramaribo, collected by I. T. Sanderson. There is also the female from Zanderij (BM 52.122), but it proves to be *Metachirus nudicaud-*

datus. Its mammae and a sketch of the mammary formula are by Sanderson (1949, Pl. VII, Figs. 3, 4). The remaining 12 of the 22 collected by Sanderson are not among the skins in the British Museum. Husson (1978, p. 28) mentions only the Zanderij *Metachirus* collected by Sanderson but no *Philander*.

SPECIMENS EXAMINED—370. BRASIL. *Amapá*: Ferrovia Amapá, km 192, 1 (LSUMZ); Macapá, Rio Amapari, 3 (MZUSP); Mazagão, Rio Maracá, 1 (MZUSP); Serra do Navio, 59 (USNM, 57; MPEG, 2); Terezinha, Rio Amapari, 1 (LSUMZ); *Amazonas*: Auara Igarapé, 2 (AMNH); Ipixuna, Rio Purús, 1 (USNM); Lago do Baptista, 1 (AMNH); Lago Sampaio, Rosarhino, 2 (AMNH); Rio Madeira, 1 (AMNH); "River Negro," 5 (BMNH); Santo Antônio de Uayara, 1 (AMNH); Santa Clara, Villa Bella Imperatriz, 3 (AMNH); Tefé, 1 (AMNH); *Pará*: Altamira, 54 km S, 150 km W, 3 (USNM); Altamira, Rio Xingú, 3 (USNM); Ananindeua, 2 (MPEG); Arumatheua, 1 (MPEG); Baiao, Rio Tocantins, 14 (AMNH); Belém 2 (AMNH, 1; USNM, 1); Cametá, 17 (MZUSP); Canudos, 1 (FMNH); Capim, 6 (AMNH, 5; MPEG, 1); Cuatipuru, Flor do Prado, 2 (MPEG); Fordlandia, 1 (AMNH); Gradaus, Rio Fresco, 2 (MZUSP); Igarapé Tapereba, 4 (MPEG, 2; MZUSP, 2); Ilha do Taiuna, 85 (AMNH); Ipeau-Apez, Belém, 2 (USNM); Iriteria, 1 (MPEG); Lazaropolis, 4 (MPEG); Macajuba, Rio Tocantins, 3 (AMNH); Marabá, Rio Tocantins, 2 (USNM); Marcos, 1 (MPEG); Mazagão, Rio Tocantins, 1 (MPEG); Murutucú, 5 (BM, 2; FMNH, 3); Peixe-Boi, 1 (MPEG); Rodovia Belém-Brasília, 3 (MPEG); Santa Maria, Bragança, 1 (USNM); Santarém, 10 (MZUSP, 2; USNM, 8); San Miguel do Guamá, 5 (MPEG, 2; MZUSP, 3); Utinga, 22 (MPEG, 6; USNM, 13; AMNH, 1; MZUSP, 2); *Roraima*: Caracará, 2 (MZUSP). GUYANA. *Essequibo Islands-West Demerara*: Buckhall, 2 (BM[NH]); *Upper Takutu-Upper Essequibo*: Kanuku Mts., 5 (BM[NH]); Rupununi River, 1 (BM[NH]); *Demerara-Mahaica*: Better Hope, 1 (BM[NH]); Georgetown, 2 (FMNH); Hyde Park, 4 (BM[NH], 2; FMNH, 2); *Pomeroon-Supenaam*: Supenaam River, 1 (BM[NH]). GUYANE FRANÇAISE. *Guyana*: Cayenne, 5 (BM[NH], 1; FMNH, 4). SURINAME. *Suriname*: Paramaribo, Clevia, 2 (FMNH); Lelydorpplan, 1 (FMNH); Paramaribo, 10 (BM[NH], 9; lectotype, RMNH); no precise locality, 3 (BM[NH]); *Nickerie*: Kaiserberg Airstrip, 1 (FMNH); *Makerie*, West River, 2 (FMNH); *Saramacca*: La Poule, 1 (FMNH); Loksie Hattie, 1 (FMNH). VENEZUELA. *Bolívar*: Ciudad Bolívar, 146 km S, 7 km NE, 2 (USNM); Maripa, 1 (AMNH); Río Yuruán, 10 (AMNH); *Trujillo*: Agua Viva, 18 km N Valera, 1

(USNM); El Dividiri, 30 km NW Valera, 1 (USNM); Motatin, 1 km NNE, 3 (UKMNH); Motatá, 5 km NNE, 1 (UKMNH); Río Motatin, 5 (UKMNH).

Philander opossum quica Temminck

Didelphis quica Temminck, 1824:36. Desmarest, 1827:387—characters. Jentink, 1887:301—BRASIL: Temminck collection. Jentink, 1888:220—part, BRASIL; cotype; *Didelphis larvata* ms. name in synonymy. Hochstetter, 1946:11, Pl. 1, Fig. 2 (brain, sagittal section in skull)—brain, dura mater. Ávila-Pires and Gouvea, 1977:9—BRASIL: *Rio de Janeiro* (Monte Serrat; Benfica; Maceiras); local name, *guaquica*.

Didelphys quica, Waterhouse, 1841:90—part, BRASIL. Waterhouse, 1846:480—part, BRASIL. Burmeister, 1854:136—BRASIL: *Rio de Janeiro* (Novo Friburgo). Pelzeln, 1883:110—BRASIL: *Rio de Janeiro* (Sepetiba); *São Paulo* (Ypanema); *Mato Grosso* (Mato Grosso). Oudemans, 1892:14, Fig. 25 (Cowper's gland)—male accessory reproductive organs.

D[idelphys]. quica, Wagner, 1855:225, Pl. 18 (female)—description, figure, and notes from Natterer manuscript.

Metachirus quica, Burmeister, 1856:70, Pl. 7 (male), p. 11, Fig. 2 (skull)—part, BRASIL: *Rio de Janeiro* (Novo Friburgo); characters. Hensel, 1872:120—BRASIL: *Rio Grande do Sul*; characters. Goeldi, 1894:460—BRASIL: *Rio de Janeiro* (Serra dos Órgãos). J. A. Allen, 1900:195—BRASIL: (type locality, "coast region of Brasil, just south of Rio de Janeiro").

Metachirus opossum quica, J. A. Allen, 1916c:562—BRASIL: *Mato Grosso* (Urucum); *Rio de Janeiro* (Sapitiba [= Sepetiba], restricted type locality). Miller, 1916:589—BRASIL; habits. Carvalho, 1957:3—BRASIL: *Acre* (Serungal Oriente, Rio Juruá).

[*Metachirops*] *quica*, Matschie, 1916:268—BRASIL: *Rio de Janeiro* (type locality, "Sapitibi").

Metachirops quica, Pohle, 1927:243—BRASIL: *Rio de Janeiro* (Barreira; Teresópolis). Schirch, 1932: 85—BRASIL: *Rio de Janeiro* (Teresópolis, 960 m); parasite (*Amblyopinus*).

Metachirops opossum quica, Miranda Ribeiro, 1936: 340—BRASIL: *Rio Grande do Sul* (Porto Feliz, Rio Urugaí); *Rio de Janeiro* (Teresópolis); *Santa Catarina*. Vieira, 1945:421—BRASIL: *Mato Grosso* (Palmeiras). Vieira, 1949:345—BRASIL: *São Paulo*; *Minas Gerais*: *Espírito Santo*; *Mato Grosso*; local names, *quica*, *quaiquica*. Ruschi, 1965:2—BRASIL: *Espírito Santo* (coast); local names, *cui-ca*, *chupata*.

Philander opossum quica, Perondini and Perondini, 1966:28—BRASIL: *São Paulo* (Cantarera Forestal Preserve); sex chromatin in somatic cells. Carvalho, 1965:251—BRASIL: *São Paulo* (Boracéia).

[*Holothylax*] *quica*, Cabrera, 1919:48—classification. *D[idelphys]. quica* [sic], Giebel, 1859:227—"der Guica."

Didelphis myosuroides Temminck, 1824:38—BRASIL: (type locality); cotypes in the Leiden, Vienna,

- Frankfort, and Prince Maximilian zu Wied-Neuwied Museums. Hershkovitz, 1959:343—in synonymy of *Philander opossum frenata* [sic] Olfers; original description based on four-eyed pouched opossum.
- Metachirus nudicaudatus myosurus* [sic], Miranda Ribeiro, 1936:345—BRASIL: *Bahia*; characters; Portuguese translation of original description: "... as femeas tem um sacco completo ...".
- Didelphis larvata* Jentink, 1888:220—Natterer ms. name on label of a syntype of *quica* Temminck.
- Metachirus canus* Osgood, 1913:96—PERÚ: *San Martín* (Moyobamba, type locality); holotype, male, skin and skull, Field Museum of Natural History, no. 19347; collected 4 August 1912 by W. H. Osgood and M. P. Anderson. Osgood, 1914:148—PERÚ: *San Martín* (Moyobamba). Sanborn, 1947:215—type history.
- [*Metachirops*] *canus*, Matschie, 1916:268—classification.
- [*Holothylax griseus*] *canus*, Cabrera, 1919:47—classification.
- Metachirus opossum canus*, Thomas, 1927a:372—PERÚ: *San Martín* (Rioja; Moyobamba; Yurac Yacu). Thomas, 1927b:606—PERÚ: *Huánuco* (Tingo María, 2000 ft). Thomas, 1928a:264—PERÚ: *Ucayali* (Cumeria, 1000 ft; Chicosa, 1000 ft; San Jerónimo, 500 ft).
- M[*etachirus*]. *olpossum*]. *canus*, Thomas, 1928b:294—*crucialis* Thomas a synonym.
- Philander opossum canus*, Sanborn, 1949:277—PERÚ: *Ucayali* (Yarinacocha). Sanborn, 1951:2—PERÚ: *Cuzco* (Hacienda Cadena). Cabrera, 1958:35—*crucialis* Thomas a synonym.
- Metachirus opossum azaricus* Thomas, 1923:604—PARAGUAY: *Paraguari* (Sapucay, type locality); holotype, female, skin and skull, British Museum (Natural History), no. 1903.2.3.36; collected 8 August 1892 by W. Foster.
- Met[*achirops*]. *opossum azaricus*, Krumbiegel, 1941:203, 206—PARAGUAY: (Lapango); BRASIL: *Rio Grande do Sul* (Passo Fundo); BOLIVIA: *Chiquitos* (San Ramón); *crucialis* Thomas a synonym.
- Philander opossum azaricus*, Cabrera, 1958:34—classification. Kantis, 1963:54—ARGENTINA: *Chaco* (Río de Oro, mouth); female with three young. Crespo, 1974:3—ARGENTINA: *Chaco* (Río de Oro, mouth); *Misiones* (Fracrán, San Pedro).
- Metachirus opossum crucialis* Thomas, 1923:604—BOLIVIA: *Santa Cruz* (type locality, Santa Cruz de la Sierra); holotype, female, skin (originally mounted) and skull, British Museum (Natural History), no. 1847.11.22.15; collected by Thomas Bridges.
- Didelphis opossum*, Waterhouse, 1841:90—part, BRASIL. Waterhouse, 1846:485—part, BRASIL. Thomas, 1888:329—ARGENTINA: *Chaco*; BRASIL: *Rio Grande do Sul* (Taquara); BOLIVIA: *Santa Cruz* (Santa Cruz de la Sierra). Winge, 1893:7, 38, Pl. 1, Fig. 7 (ear, foot), Pl. 3, Fig. 1 (skull), Pl. 4, Fig. 7 (humerus)—BRASIL: *Minas Gerais* (Lagoa Santa, Recent and fossil); characters; comparisons.
- D[*idelphis*]. *opossum*, Tschudi, 1844:14, 144, 151—PERÚ.
- Metachirus opossum*, Ihering, 1892:99—BRASIL: *Rio Grande do Sul*; local names, *guaquica*, *guaqui*. Ihering, 1894:10—BRASIL: *São Paulo*. Thomas, 1902a:64—BRASIL: *Paraná* (Roça Nova, Serra do Mar). J. A. Allen, 1916b:201—COLOMBIA: *Meta* (Villavicencio). Bertoni, 1923:51—PARAGUAY: *Central* (Bahía de Asunción); Guaraní name, *guaki*. M[*etachirus*]. *opossum*, Miranda Ribeiro, 1905:189—BRASIL: *Rio de Janeiro* (Monte Serrat, Itatiaya).
- Metachirops opossum*, Bertoni, 1939:6—PARAGUAY. Crespo, 1950:6, Fig. 1 (animal)—ARGENTINA: *Misiones* (Río Uruguay-í, 39 km from Puerto Bemberg); habits; locomotion; local name *guaitica*.
- Philander opossum*, Davis, 1945a:122—BRASIL: *Rio de Janeiro* (Fazenda Boã Fe, Teresópolis). Davis, 1947:1—BRASIL: *Rio de Janeiro* (Fazenda Boã Fe, Teresópolis); life history. Moojen and Ávila-Pires, 1966:397—BRASIL: *cerrado* formation (absent; *Didelphis* and *Monodelphis* only). Gardner and Patton, 1972:5—PERÚ: *Ucayali* (Balta, Yarinacocha); comparisons with *mcilhennyi*. Reig et al., 1977:197, 212, Pl. 1 (karyotype)—part, PERÚ: *Ucayali* (Yarinacocha; Balta). Mello and Moojen, 1979:289—BRASIL: *Distrito Federal* (Brasília gallery forest; Fazenda Agua Limpa, gallery; Guara, gallery); *Mato Grosso* (Baliza, gallery; Barra do Garças gallery; Poconé gallery; Salobra gallery); *Goiás* (Aragarças gallery; Formosa gallery). Correa Gomes, 1984:369—BRASIL: *Mato Grosso* (Salobra); helminth infection. Da Fonseca and Redford, 1984:517—BRASIL: *Distrito Federal* (Parque Nacional, Brasília; humid gallery forest and valley side wet campo; *cerrado* [uncommon]). Mares et al., 1989:19—BRASIL: *Mato Grosso* (Poconé).
- Philander opossum opossum*, da Fonseca and Kierulff (not Linnaeus), 1989: 118, 143—BRASIL: *Minas Gerais* (Fazenda Esmeralda; Fazenda Montes Clarás); reproduction; habits.
- Didelphis nudicaudatus*, Desmarest (part not É. Geoffroy), 1827:390—*myosuros* Temminck a synonym. Waterhouse, 1841:94, Pl. 2 (animal). Jentink, 1888:220—part, syntypes of *myosuros* Temminck and *opossum* of Temminck collection. Thomas, 1888:332—part, *myosuros* in synonymy.
- Philander opossum frenata* [sic], Hershkovitz (part not Olfers), 1959:342—*Didelphis quica* Temminck in synonymy.
- Metachirops opossum quichua* [sic], Krumbiegel, 1941:200, 201, 206—name a reiterated lapsus for *quica* Temminck; BRASIL: *São Paulo* (Juquia, Serra do Mar).

TYPES—An unspecified number of skins, some mounted, skulls and skeletons of both sexes in the Vienna, Leiden, Paris, and Prince Maximilian zu Wied-Neuwied museums; female syntype in the Vienna Natural History Museum, collected 3 March 1818 by Johann Natterer, designated lectotype by Hershkovitz (1959, p. 337).

TYPE LOCALITY—"Bresil," restricted to "Sapitiba" (= Sepetiba), Rio de Janeiro (Rio de Janeiro, 22°58'S, 43°42'W), by J. A. Allen (1900, p. 195; 1916c, p. 562).

TABLE 10. Measurements of *Philander opossum quica*. Means (extremes in parentheses) and number of specimens.

Locality	Head and Body	Tail	Hind Foot	Ear
Brasil ♂♂				
Anápolis	272 (260–285) 5	295 (280–305) 5	42 (38–45) 5	–
Trinidade	–	–	–	–
Urucum	250, 280, 255	280, 280, 275	40, 38, 40	–, –, –
Santa Teresa, ES	215, 290, 297	245, 195, 355	43, 44, 48	34, 34, –
Campinho	270	300	40	30
Vitória	275	335	42	32
Vila Velha	240, 255	300, 285	38, 39	28, 30
Engenheiro Reeve	265	285	32	30
Juiz de Forna	290	330	42	30
Além Paraíba	273	310	29	38
Fazenda Cardoso	263, 244	280, 291	40, 39	–, –
Teresópolis	228, 252, 296	320, 272, 335	40, 42, 43	–, –, –
Barro Branco	246	346	44	22
Macieiras	–	–	–	–
São João Marcos	270	330	45	30
Margaratiba	250	320	39	–
Boraceia	237 (210–260) 7	288 (272–300) 7	35 (30–40) 7	31 (30–33) 4
Piquete	–	–	–	–
Cotia	–	–	–	–
Butantã	–	–	–	–
São Sebastião	267	295	–	–
Iporanga	–	–	–	–
Roça Nova	260	275	35	30
Joinville	300	300	–	–
Hansa	270	310	41	30
Taquara	–	–	–	–
Brasil ♀♀				
Seringal	245	280	35	34
Anápolis	259 (240–265) 7	269 (235–295) 7	39 (36–42) 7	–
Santa Teresa, MG	230	280	36	39
Santa Teresa, ES	262, 260	–, 305	39, 36	31, 30
Campinho	265	275	40	32
Faz. Floresta	250	310	–	–
Benfica	251	266	36	–
Além Paraíba	220, 247, 250	300, 300, –	–, 34, 40	32, 31, 29
Tereópolis	255	305	45	29
Barro Branco	231	278	36	28
Margaratiba	270, 220, 330	240, 280, 300	34, 32, 35	26, 22, 31
Pedra Branca	–	–	–	–
Boraceia	–, –, –	–, –, –	–, –, –	–, –, –
Piquete	–	–	–	–
Monte Alegre	–	–	–	–
Cotia	265, –	280, –	36, –	31, –
São Sebastião	251, 293	265, 277	–, –	25, 25
Avanhandava	–	–	–	–
Roça Nova	230	220	33	32
Paraguay ♂♂				
Sapucay	286	305	36	35
Tacuati	289	292	32	–
Paraguay ♀♀				
Sapucay	258 (239–279) 8	292 (277–304) 8	34 (32–35) 8	34 (32–36) 8
Argentina ♂♂				
Chaco	–	–	–	–
Bolivia ♂♂				
Hamacas	278	297	–	–
Warnes, 3 locations	255 (240–268) 5	272 (266–280) 5	39 (37–41) 5	39 (38–41) 5

TABLE 10. *Extended.*

Condylbasal Length	Zygomatic Breadth	Preorbital Width	Postorbital Width	Braincase Width
65.3 (63.0-67.9) 5	34.8 (33.4-36.0) 5	11.9 (11.0-12.8) 3	8.6 (8.2-9.0) 5	21.0 (19.2-23.0) 5
-	34.0	13.8	8.8	18.8
65.2, 65.2, 66.0	35.4, 35.6, 36.1	-, -, -	8.0, 8.0, 8.5	21.5, 21.6, 21.1
72.2, 72.4, 74.1	39.5, -, 42.8	-, -, 15.7	8.7, -, 8.8	20.4, -, 21.4
70.4	39.0	14.9	8.6	22.8
66.8	-	-	-	-
69.1, 64.0	41.3, 33.7	14.6, 15.0	8.5, 8.8	20.4, 20.0
63.0	32.7	11.4	9.1	19.3
66.5	36.3	13.4	8.5	19.6
68.3	37.0	15.3	8.4	20.7
64.8, 67.1	33.7, 31.5	-, -	8.6, 8.5	20.5, 20.0
66.1, 63.7, 75.5	33.9, 35.7, 42.3	-, -, -	8.8, 7.8, 9.6	-, -, -
65.9	35.5	-	9.0	19.5
70.6	40.3	-	8.5	23.1
76.4	43.7	-	8.4	-
75.4	43.7	-	8.9	-
63.7 (60.0-68.7) 7	33.1 (30.7-37.8) 7	11.4	8.4 (7.9-9.0) 8	19.3 (18.9-20.6) 8
66.9	39.2	-	8.8	20.7
66.0	36.0	-	9.0	21.1
71.8	39.9	-	8.6	-
66.5	34.1	13.0	8.4	18.2
68.0	38.8	-	8.1	21.3
64.9	33.0	11.8	8.6	20.1
72.6	40.3	-	8.6	22.2
66.8	34.1	11.0	8.2	19.2
71.8	36.6	12.9	7.9	20.3
62.3	32.3	14.6	8.7	18.7
64.1 (61.0-65.7) 8	34.0 (32.6-35.7) 8	11.5 (11.0-12.3) 4	8.6 (8.4-8.7) 8	20.9 (19.7-21.7) 8
61.8	31.6	13.3	7.5	19.2
64.7, 68.0	34.0, 34.9	14.2, 14.9	8.5, 8.6	18.3, 18.5
67.0	35.4	14.7	8.2	18.8
62.9	32.7	-	9.7	20.9
59.0	31.1	-	9.9	20.2
58.8, 63.4, 65.5	30.7, 32.0, 34.4	14.7, 14.2, -	9.4, 8.2, 8.8	20.9, 18.1, 18.5
63.3	-	-	-	-
60.5	-	-	-	-
62.5, 64.7, 67.5	-, -, -	-, -, -	-, -, -	-, -, -
60.9	-	-	-	-
58.9, 62.2, 60.8	30.4, 32.2, -	-, -, -	8.2, 9.1, -	19.8, 19.9, -
62.8	31.0	-	-	19.2
61.5	30.0	-	9.0	18.5
63.4, 62.2	34.7, 31.6	-, -	8.9, 8.6	19.1, 19.2
61.6, 58.5	31.1, 29.4	12.2, 11.4	8.4, 8.7	18.4, 18.0
63.3	34.4	-	8.9	20.0
57.1	28.0	9.7	8.2	18.5
67.2	36.8	13.0	8.6	20.7
64.6	34.7	12.6	8.6	19.3
62.4 (58.3-67.8) 9	32.4 (30.3-35.2) 9	11.5 (10.7-12.4) 9	8.7 (8.4-9.1) 9	20.0 (19.0-21.7) 9
69.0	39.2	13.0	9.0	19.8
66.0	33.5	-	8.5	19.2
61.8 (60.5-62.6) 5	33.0 (31.8-34.6) 5	11.3 (10.8-11.8) 5	7.7 (7.4-8.4) 5	19.7 (19.0-20.1) 5

TABLE 10. *Continued.*

Locality	Head and Body	Tail	Hind Foot	Ear
El Beni, 7 locations	257 (235-271) 5	297 (284-319) 5	41 (35-45) 5	39 (38-42) 5
San Joaquín	200	300	37	38
Bolivia ♀♀				
Santa Cruz, 3 locations	262, 227, 254	242, 305, 295	35, 40, 42	41, 43, 41
El Beni, 9 locations	255 (225-275) 10	267 (249-293) 10	39 (35-44) 10	35 (30-38) 10
San Joaquín	-	-	-	-
Perú ♂♂				
Cadena, Hda.	-	-	-	-
Quincemil	244	267	38	34
Urubamba, Río	-	-	-	-
Balta	248 (232-255) 5	278 (253-299) 5	42 (39-44) 5	35 (31-36) 5
Tingo María	278	292	41	37
Pucallpa	270, 264	290, 304	37, 37	36, 33
Yarinacocha	291	286	48	38
Moyobamba	275	293	45	-
Yurac Yacu	257	292	43	33
Perú ♀♀				
Maldonado, Pto.	302	276	36	35
Boca Colorado	-	-	-	-
Santa Rosa	-	-	-	-
Urubamba, Río	-	-	-	-
Chicosa	241	263	36	32
Balta	238	282	43	31
Cumaria	240	280	38	34
Pucallpa	273	297	40	34
Yarinacocha	292	291	46	36
Sarayacu	-, -, -	-, -, -	-, -, -	-, -, -
Apayacu	-	-	-	-
Colombia ♂♂				
Villavicencio	265	270	40	32
Covaríá, Río	267	-	40	33
Colombia ♀♀				
Villavicencio	-	-	-	-
Venezuela ♂♂				
Motatán	256	288	42	35
Río de Oro	280	295	40	35
Venezuela ♀♀				
Motatán	242, 248	288, 299	41, 41	33, 30
Yuruán, Río	244, 236	289, 279	38, 36	-, -

DISTRIBUTION—Map, Figure 5. PERÚ: Departments of Ucayali, San Martín, Huánuco, Cuzco, Ucayali, Madre de Dios; BOLIVIA: La Paz, El Beni, Cochabamba, Santa Cruz; PARAGUAY, ARGENTINA: Chaco, Misiones; BRASIL: Acre, Rondônia, Mato Grosso do Sul, Goiás, Distrito Federal, Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul; altitudinal range sea level to about 1500 m above. See "Specimens Examined," p. 50, for details.

CHARACTERS—Average body size smallest of

the subspecies; underparts generally pale, sharply defined from sides (except some individuals in eumelanic color phase); tail usually parti-colored; molars relatively large, conule *C* of *m*³ rudimentary. Individuals nurtured in captivity may be exceptionally large.

COMPARISONS—*Philander opossum quica* is the small, "gray," large-toothed form generally regarded as typical of the species. The Guianan *P. opossum* is larger, with more saturate pheomelanin, particularly on underparts. *Philander opossum melanurus* is slightly larger but always distin-

TABLE 10. *Extended (continued).*

Condylbasal Length	Zygomatic Breadth	Preorbital Width	Postorbital Width	Braincase Width
66.5 (64.2-70.2) 7 69.3	34.6 (33.4-36.6) 7 38.2	- 11.6	8.1 (7.8-8.6) 7 8.3	20.5 (19.7-21.2) 7 21.3
59.0, 63.1, 60.0 62.2 (59.0-65.9) 9 61.3 (59.8-62.4) 4	31.2, 33.2, 31.4 32.5 (31.0-35.2) 9 32.8 (31.5-34.0) 4	10.5, 11.1, 11.4 10.3 (9.8-11.5) 6 10.4 (10.2-10.8) 4	8.4, 8.2, 8.0 7.9 (7.7-8.5) 9 7.8 (7.7-8.1) 4	19.2, 19.1, 18.8 19.8 (18.9-21.0) 9 19.4 (18.3-20.0) 4
60.5 62.0 62.0	32.6 31.9 -	- - -	8.5 8.2 8.3	20.8 20.5 -
65.0 (62.5-67.5) 5 68.3 65.1, 64.2 71.5 67.5 64.8	33.3 (31.7-34.3) 5 34.5 36.3, 36.2 40.8 - 32.9	12.0 (11.8-12.3) 5 12.4 11.9, 12.3 14.8 - -	8.5 (8.0-8.8) 4 8.3 8.5, 8.9 8.8 8.9 8.3	19.1 (18.4-19.6) 5 19.6 20.9, 21.4 20.4 19.8 19.7
64.3 63.4 61.7 - 59.4 67.5 61.7 - 72.4 66.9, 68.0, 71.9 63.5	31.2 31.9 - - 30.5 33.0 29.5 33.5 38.3 -, 34.0, 35.9 33.9	12.1 - - - 10.5 12.3 10.4 - 13.4 -, -, - -	8.2 8.6 - 8.3 7.5 7.8 7.5 - 9.0 8.6, 8.4, 9.0 9.3	18.5 20.2 - - 18.1 18.6 19.5 19.9 20.0 -, 20.2, 22.0 21.9
64.9 65.1	34.9 33.6	- 12.0	8.3 8.4	19.6 20.8
64.2	33.0	-	8.7	19.3
64.6 61.8	34.6 34.2	11.9 -	8.4 8.0	20.5 20.8
60.8, 63.4 58.5, 61.2	30.5, 33.3 30.6, -	10.6, - -, -	8.4, 8.0 8.2, -	20.0, 19.9 19.2, -

guishable by its chocolate-brown upper parts and saturate orange underparts.

MEASUREMENTS—Tables 1 and 10.

TAXONOMIC HISTORY—*Didelphis quica* was described by Temminck from several mounted skins and skeletons in the Leiden Museum and from other specimens in the Vienna, Paris, and Prince Maximilian zu Wied-Neuwied museums. Four live and several spirit-preserved individuals are also mentioned as having been seen. In his catalog of the Leiden Museum collection, Jentink (1888, p. 220) lists both the mounted

skin of an adult female as "un des types de l'espèce. Bresil. Des collections de M. Natterer. *Didelphis larvata*" and a mounted subadult male as "un des type l'espèce. Bresil. Du Cabinet de M. Temminck. *Didelphis crassicaudata* Desmarest."

Temminck (1824, p. 37) noted particularly that best knowledge of the species is based on "quicas" shipped to the Vienna Museum by Johann Natterer. This information prompted J. A. Allen (1900, p. 195; 1916c, p. 562) to restrict the type locality of Temminck's *quica* to Sepetiba, Rio de

TABLE 10. *Continued.*

Locality	Palatal Length	i-m ⁴	m ¹⁻⁴
Brasil ♂♂			
Anápolis	39.7 (38.5–41.7) 5	34.4 (34.0–35.4) 5	13.1 (12.8–13.3) 5
Trinidade	37.8	33.8	12.9
Urucum	35.8, 38.7, 38.9	33.8, 32.8, 34.2	12.7, 12.6, 12.6
Santa Teresa, ES	41.1, –, 42.0	35.5, –, 35.0	12.4, 12.4, 12.5
Campinho	–	35.8	12.1
Vitória	–	–	12.5
Vila Velha	–, –	35.5, 34.4	12.2, 12.2
Engenheiro Reeve	37.4	33.2	11.6
Juiz de Forna	39.8	34.3	12.3
Além Paraíba	40.5	34.9	12.4
Fazenda Cardoso	38.8, 34.1	33.6, 30.9	12.3, 11.5
Teresópolis	39.0, 39.4, 44.8	33.5, 34.0, 37.4	12.0, 12.1, 12.6
Barro Branco	38.5	33.5	12.1
Macieiras	41.0	33.9	12.0
São João Marcos	43.3	35.9	12.5
Mangaratiba	43.4	36.6	12.7
Boraceia	37.8 (35.6–40.1) 8	33.3 (32.0–34.3) 8	12.2 (11.9–13.0) 8
Piquete	39.3	33.9	12.7
Cotia	39.1	34.6	12.3
Butantã	42.9	36.6	12.2
São Sebastião	39.4	34.5	12.0
Iporanga	39.8	34.0	12.2
Roça Nova	39.3	34.1	12.3
Joinville	41.7	34.9	11.8
Hansa	40.3	34.8	12.2
Taquara	43.1	37.1	12.8
Brasil ♀♀			
Seringal	38.8	33.6	13.2
Anápolis	38.9 (38.5–40.7) 8	34.0 (33.0–34.8) 8	13.0 (12.6–13.5) 8
Santa Teresa, MG	36.4	32.9	12.3
Santa Teresa, ES	38.2, 40.9	33.0, 34.5	12.3, 12.5
Campinho	39.0	34.1	12.0
Faz. Floresta	37.5	33.0	11.9
Benfica	35.3	31.0	11.8
Além Paraíba	35.5, 37.5, 40.0	32.0, 33.6, 34.0	12.0, 12.1, 12.0
Teresópolis	37.1	32.1	11.9
Barro Branco	–	–	12.5
Mangaratiba	–, –, –	–, –, –	11.6, 12.3, 11.9
Pedra Branca	–	–	12.0
Boraceia	35.6, 37.8, –	30.5, 32.0, –	11.4, 11.5, 11.2
Piquete	37.6	33.3	12.0
Monte Alegre	36.7	32.8	11.8
Cotia	37.8, 37.1	33.1, 32.0	11.5, 11.5
São Sebastião	36.6, 35.1	32.6, 32.0	11.8, 11.9
Avanhandava	37.4	32.5	11.8
Roça Nova	35.2	31.8	12.2
Paraguay ♂♂			
Sapucay	40.7	34.9	12.6
Tacuati	38.0	33.4	12.3
Paraguay ♀♀			
Sapucay	37.3 (35.1–39.0) 9	32.8 (31.5–33.8) 9	12.2 (11.9–12.8) 9
Argentina ♂♂			
Chaco	41.8	36.1	13.5
Bolivia ♂♂			
Hamacas	39.4	34.2	13.0
Warnes, 3 locations	37.2 (36.2–38.0) 5	32.9 (31.5–33.5) 5	12.5 (12.0–12.8) 5

TABLE 10. *Continued.*

Locality	Palatal Length	i-m ⁴	m ¹⁻⁴
El Beni, 7 locations	39.9 (39.1-41.7) 7	34.9 (34.2-36.2) 7	13.3 (12.6-13.7) 7
San Joaquín	38.0	33.7	12.8
Bolivia ♀♀			
Santa Cruz, 3 locations	36.0, 39.0, 37.2	32.4, 33.6, 34.0	12.5, 12.4, 13.0
El Beni, 9 locations	37.8 (35.4-39.8) 9	33.3 (32.0-35.3) 9	12.7 (12.0-13.4) 9
San Joaquín	37.2 (36.6-37.7) 4	32.7 (32.2-33.2) 4	12.2 (11.9-12.5) 4
Perú ♂♂			
Cadena, Hda.	36.6	32.9	12.5
Quincemil	38.6	34.9	13.6
Urubamba, Río	38.2	33.7	12.5
Balta	40.0 (38.0-41.8) 5	35.3 (34.0-36.9) 5	13.5 (12.9-14.3) 5
Tingo María	41.8	36.5	13.2
Pucallpa	39.8, 39.9	34.0, 32.5	13.0, 12.5
Yarinacocha	43.1	37.7	14.4
Moyobamba	40.6	35.7	13.4
Yurac Yacu	39.8	34.7	14.2
Perú ♀♀			
Maldonado, Pto.	39.8	33.8	12.6
Boca Colorado	39.1	33.8	13.1
Santa Rosa	37.8	33.8	12.7
Urubamba, Río	36.3	31.8	12.3
Chicosa	36.5	32.2	12.5
Balta	41.3	37.3	14.5
Cumaria	38.5	33.6	13.1
Pucallpa	-	-	13.1
Yarinacocha	45.7	38.5	14.0
Sarayacu	42.3, 42.4, 44.6	38.0, 36.8, 37.6	13.4, 13.6, 13.5
Apayacu	39.8	34.8	12.2
Colombia ♂♂			
Villavicencio	38.6	33.7	13.1
Covarrá, Río	39.3	34.1	13.1
Colombia ♀♀			
Villavicencio	39.0	33.4	12.3
Venezuela ♂♂			
Motatán	40.0	34.1	13.1
Río de Oro	38.0	34.0	13.5
Venezuela ♀♀			
Motatán	32.5, 38.8	33.0, 33.7	12.9, 12.6
Yuruán, Río	35.5, 37.2	32.5, 32.4	12.9, 12.4

Janeiro. Pelzeln (1883, p. 110) mentioned *Sepe-tiba* as one of four localities where Natterer collected a total of 15 specimens, including one live, all sent to Vienna. Pelzeln (loc. cit.) added the descriptions of an old female collected 3 March 1818 and a male collected 29 March 1818, both from *Sepe-tiba*. The female has since been designated the lectotype.

Didelphis myosuroides Temminck is based on one or more pouched adult female four-eyed opossums and an unspecified number of pouched "jeunes femelles [qui] nous parviennent en peaux des-

seches." Males are not mentioned in the description proper, but Temminck (1825, p. 40) stated he examined individuals of both sexes in the Pays-Bas (Leiden) Museum. He might have seen more in the "Musées de Vienna, de Francfort et du prince de Neuwied." In any event, certain aspects of the description may not have been based solely on "*les femelles [qui] ont une poche complete.*" For example, the tail base is described as furred a distance of 10 lines (about 2 cm) in two adults and nine lines in a subadult. This is characteristic of nonpouched *Metachirus nudicaudatus*. On the

other hand, the nearly equal body and tail proportions of the same individuals and unpigmented tail base indicate the pouched species. The descriptions of external characters lack precision, but some details of the original text apply equally well to both pouched and nonpouched species but in no case to the latter alone.

Despite the apparent composite nature of the description, Temminck (1824, p. 39) denied that his *mysurus* might be identical with *D. nudicaudata* É. Geoffroy, because, he notes, “il est dit dans le texte que la queue de cet animal est toute nue, et que la femelle n’a point de poche.” Temminck (1824, p. 40) drew attention, nevertheless, to a poorly preserved skin of a young female in the Paris museum labeled *D. nudicaudata* that, he said, agreed in every respect with *D. mysuros*. He questioned, however, that this individual may have served É. Geoffroy for the original description of *D. nudicaudata*. Notwithstanding, authors beginning with Wied-Neuwied (1826) and Desmarest (1827, p. 390) concluded that Temminck did indeed identify his *D. mysuros* with *D. nudicaudata*. The mistaken identity gave rise to confusion in later years.

Wied-Neuwied (1826, p. 400, Pl. 2, Fig. 5 [skull]) described one of two male four-eyed opossums captured in “Comechatiba” (= Comoxatibá or Cumuraxatibá, 17°06' S, 39°11' W), between the Rios Prado and Corumbão, Bahia, Brasil, and referred them to *D. mysuros* Temminck. The finely detailed characterizations and the figured skull of the animal are unquestionably those of *Metachirus nudicaudatus*. Wied-Neuwied, however, could not be certain of the propriety of the name *mysuros* because he (1826, p. 405) “had not seen a female which, according to Temminck, has a pouch” (my translation of the original German).

In his supplement to Schreber’s *Säugethiere*, Wagner (1843, p. 43) included *Didelphis mysuros* Temminck, emended to “*Didelphis mysurus*,” in his fully pouched opossum group and short-haired subgroup (Wagner, 1843, p. 37—“*mastotheca ventrali ampla*”; p. 42—“*vellere brevi*”). His description of *D. mysurus*, however, is based on the Berlin Museum’s type specimen of *Didelphis frenata* Lichtenstein (Olfers): *Didelphis nudicaudata* É. Geoffroy was listed as a synonym of *Didelphis mysurus* without explanation.

Waterhouse (1846, p. 482) treated *Didelphis mysuros* Temminck, 1824, as a junior synonym of *Didelphis nudicaudata* É. Geoffroy, 1803. His description, based on a specimen in the British

Museum, is unquestionably that of the pouchless species. Evidently females were not seen, and Waterhouse mistakenly included *Didelphis nudicaudata* along with *D. philander* (= *Caluromys philander*) in his *Didelphis* “Section 1. Opossums in which the pouch is well developed.”

In his account of the mammals of Rio de Janeiro and Minas Gerais, Burmeister (1854, p. 135) accepted Wagner’s (1843) use of the emended form of the name *Didelphis mysurus* Temminck and treatment of *D. nudicaudata* as a synonym. Burmeister saw no specimens of *mysuros* in southeastern Brasil, and he drew on Wied-Neuwied (1826) for a description of the species. Shortly thereafter, Burmeister (1856, p. 68, Pl. 10) described a male and female labeled “*Didelphis mysurus* Temminck” in the Berlin Museum. His characterization of the two animals, believed to have originated in Pará, is somewhat equivocal but fits that of *Didelphis nudicaudata* É. Geoffroy, cited as a synonym. The adult male illustrated in color is identifiable as *Metachirus nudicaudatus*.

Thomas (1888) cited “*Didelphis mysurus*, Temm.” and its usage by other authors, including Wied-Neuwied (1826), Wagner (1843), and Burmeister (1854; 1856), in the synonymy of “*Didelphis nudicaudata* É. Geoffroy.”

Jentink (1888, pp. 220, 221) listed the following skins identified as *Didelphis nudicaudata* É. Geoffroy in his catalog of mammals of the Muséum d’Histoire Naturelle des Pays-Bas, where many of Temminck’s specimens are deposited:

- a. Individu adulte monté, un des types du *Didelphis mysuros* Temminck. Brésil.
- b. Male adulte monté, un des types du *Didelphis mysuros* Temminck. Brésil, 1822.
- c. Male adulte monté. Brésil.
- d. Male semi-adulte monté. Brésil. Du Cabinet de M. Temminck. *Didelphis opossum*.

It is unlikely that most, if any, of the above male and unsexed “types” of *D. mysuros* actually served as bases for the original description of the species. The females of the “*plusieurs individus des deux sexes*” mentioned by Temminck (1825, p. 40) are missing. Individual a, listed by Jentink as a “type,” may be a specimen subsequently labeled “*mysuros*” by Temminck. Specimen b, dated 1822, is certainly one of those collected by Natterer the same year in Registo do Sai (April) or Ypanema (January, June) and sent to the Vienna Museum (Pelzeln, 1883, p. 111). These Natterer specimens represent the opossum

sometimes incorrectly known as *M. nudicaudatus personatus* Miranda Ribeiro.

Misapplication of the name *Didelphis myosuroides* Temminck for pouchless four-eyed opossums was pointed out in 1959 (Hershkovitz, 1959, p. 343), and treatment of the name as a junior synonym of *Philander opossum frenata* [sic] Olfers was suggested. On the other hand, my designation of the Comoxatiba opossum recorded by Wied-Neuwied as lectotype of *myosuroides* Temminck is invalid. The specimen, a male *Metachirus nudicaudatus*, was not mentioned by Temminck in his description of *myosuroides* and likely was not seen by him at any time.

It is now proposed to designate as lectotype of *myosuroides* one of the pouched females used by Temminck in the original description of the taxon. In the absence of evidence to the contrary, the type locality, said to be Brasil, is here restricted to southeastern Brasil. Thus, *myosuroides* (= *myosuroides*) Temminck becomes a synonym of *P. opossum quica* Temminck.

Metachirus canus Osgood (1913), from Moyobamba, Perú, based on a single specimen, was distinguished from western Colombian *grisescens* (= *P. opossum melanurus*) by its generally paler coloration and parti-colored tail. Comparisons were not made with *P. opossum quica*, from which it is indistinguishable, presumably for lack of material at hand from Bolivia, Paraguay, and southeastern Brasil.

The Paraguayan *Philander opossum azaricus* Thomas (1923, pp. 604) was characterized as a "uniform grey subspecies without blackened crown." Thomas' (1923, p. 604) description of *Philander opossum crucialis* from Santa Cruz de la Sierra, Bolivia, is virtually a paraphrase of that of *azaricus*. The type, a "remade skin," "somewhat faded," was collected about a half-century earlier by Thomas Bridges. Later, with "good series" of the Peruvian *canus* and Bolivian *crucialis* before him, Thomas (1928b, p. 294) opined that the "two forms should not be considered as distinct from each other." Krumbiegel (1941, p. 204) regarded *azaricus* and *crucialis* indistinguishable.

Except for the color phases, seasonal differences in pelage, and certain exceptionally large individuals, I find a remarkably high degree of uniformity in the morphology of the common *Philander* opossums of eastern Brasil, northern Argentina, Paraguay, lowland Bolivia, eastern Perú, and Ecuador. Material from Colombia and western Venezuela is similar, but the disjunct distribution suggests convergence.

VARIATION—Material from Rio de Janeiro includes individuals of *P. opossum quica* with saturate coats like those of *P. opossum opossum* from Suriname and others with the typical gray coat. A large series (27) from Anápolis, Goiás, appears to be intermediate between *P. opossum opossum* and the gray, eastern Brazilian *P. opossum quica*. Seven adults in old pelage, taken October through February, appear brown because of exposure of the basal portion of the dorsal hairs. Eight adults in fresh winter pelage (April–August) appear grayish.

In the more southern states of eastern Brasil, and in Paraguay, Bolivia, and Perú, the animals are predominantly grayish or grayish brown dorsally, the underparts pale.

Dichromatism in nine specimens of *quica* from Balta, Ucayali, Perú, parallels that of *P. andersoni mcilhennyi* from the same locality. The color difference, however, is not sexual. In six specimens (two ♀♀, four ♂♂), underparts are pheomelanic, the hairs buffy or orange to the roots, as in female *P. andersoni*. In three specimens (♀, ♂♂), underparts are dominantly eumelanic or grayish, the hairs pheomelanic terminally, eumelanic basally, and showing through at the surface, as in male *P. andersoni*. The tail of the single female of the eumelanic series is entirely pigmented. The terminal whitish portion in all other members of the Balta series varies from about one-third to one-eighth of total length without significant difference otherwise between those of the two color phases. Dorsum and sides are likewise nearly the same in both, but crown and muzzle are more deeply and extensively brown in the eumelanic or gray-phase group.

Convergent dichromatism between the Balta *P. opossum* and *P. andersoni* throws more doubt on the validity of the concept of "character displacement" in mammals.

An extremely large male and a female from Yarinacocha, Río Ucayali, Perú, agree with *P. andersoni mcilhennyi* with respect to body size and dark underparts and limbs but lack the diagnostic dark dorsal band. They are readily distinguished by dorsal coloration and pelage pattern from the intermediate series of *quica* taken at nearby Pucallpa as well as by absence of sexual dichromatism. They also differ from Pucallpa *P. opossum quica* by larger size and darker color throughout but agree in dental and cranial characters. The pigmentation of underparts and limbs is interpreted as the dark-phase coloration of occasional occurrence in *P. opossum quica*. The extremely

large size of each of the Yarinacocha samples may be attributed to extreme old age and possibly unusually favorable living conditions comparable to those of the captive *quica* recorded from eastern Brasil (see above, p. 11).

The opossums from the Río Orinoco basin in Colombia and Venezuela are practically indistinguishable from Peruvian *P. opossum quica* or from the Field Museum material from Bolivia and Brasil. They may represent a case of parallelism or may be a disjunct remnant of an erstwhile widely distributed subspecies *P. opossum quica* which may not have differentiated much if anything from the hypothetical ancestral form of the species.

While this monograph was in preparation, Patton et al. (1995 [1996]) had the opportunity to examine tissues for molecular studies of one specimen of *P. opossum frenatus* from "Brasil; Rio de Janeiro; Najé, Carafão, Est. Teresópolis." Fifteen specimens from Teresópolis in the BM[NH], MNRJ, and USNM I examined were identified on the basis of skins and skulls as *P. opossum quica*. Present knowledge of *P. opossum frenatus* does not permit its synonymy with any other known four-eyed opossum.

According to Patton et al. (1995 [1996], pp. 21, 22), *P. opossum frenatus* "is quite divergent from *P. mcilhennyi* and *P. o. canus* [= *P. o. quica*] (two taxa that are sympatric over much of western Amazonia in Brasil and Perú, with an average divergence of 16.45%). Consequently, *frenatus* and (*opossum canus* + *mcilhennyi*) form a basal trichotomy with the three species of *Didelphis* in all analyses."

There appears to be a contradiction between the 15 Teresópolis specimens I identified as *P. opossum quica* on geographic and morphological grounds and the Teresópolis tissue Patton finds unusually different from the others and the 426 specimens I examined over the range of *P. opossum quica* (Fig. 5). Perhaps the Patton et al. specimen is not *quica*, but it has not been shown to be *frenatus*.

SPECIMENS EXAMINED—415. ARGENTINA. *Chaco*: Río Chico, 1 (BM[NH]). BOLIVIA. *El Beni*: Arruda, 1 (FMNH); Barranquita, 1 (FMNH); Camiaco, 1 (AMNH); Camino Vilches, 1 (USNM); Centinela, 1 (FMNH); El Carmen, 1 (FMNH); Exaltación, 2 (AMNH; FMNH); Guayaramarin, 4 (AMNH); Itonama, 1 (USNM); Magdalena, 5 (FMNH); Mercedes, 1 (AMNH); Palácios, Río Mamoré, 4 km SE, 1 (AMNH); Puerto Caballo, 2 (AMNH); Puerto Siles, 2 (AMNH); Río Ibaré, mouth, 4 (AMNH); Río Ma-

moré, 12°26'S, 3 (AMNH; FMNH, 2); San Ignacio de Moxos, 1 (USNM); San Joaquín, 13 (FMNH); San Pablo, 1 (FMNH); San Ramón, 1 (FMNH); Santa Rosa, 1 (FMNH); Santo Dios, 1 (FMNH); Vaca Díez, Riberalto, 1 (USNM); *Cochabamba*: Río Ichilo, 52 km S, mouth, Río Chaparé, 1 (AMNH); *La Paz*: Chulumani, 1 (BM[NH]); *Santa Cruz*: Ascensión de Guarayos, 2 (FMNH); Buena Vista, 12 (AMNH; BM[NH], 8; FMNH, 3); El Palmar, 2 (USNM); Hamacas, 2 (AMNH); Ibañez, Río Piray, 2 (USNM); Río Chaparé, 2 km S, mouth, 1 (AMNH); Santa Cruz, 3 (BM[NH], holotype of *crucialis* Thomas; USNM, 2); Santa Rosita, 4 (USNM); Tocomechi, Warnes, 1 (USNM); Warnes, 3 (USNM). BRASIL. *Acre*: Seringal Oriente, 4 (MPEG, 3; MZUSP); *Espírito Santo*: Cachoeira Bonita, Parque Nacional do Caparaó, 1 (MNRJ); Campinha, 4 (MNRJ); Engenheiro Reeve, 3 (BM[NH]); Pedra Roxa, Parque Nacional do Caparaó, 1 (MNRJ); Santa Teresa, 7 (MNRJ, 5; MZUSP, 2); Sierra, 3 (MNRJ); Vale Verde, Parque Nacional do Caparaó, 8 (MNRJ); Vila Velha, Morro de Angoles, 3 (MNRJ); Vitória, 2 (MNRJ); *Goiás*: Anápolis, 27 (AMNH); Aragarças, 2 (MPEG); Trindade, 1 (MPEG); *Mato Grosso*: Cáceres, 1 (USNM); Monte Alegre, 5 (MZUSP); Santa Teresa, 1 (USNM); Uruçum, 5 (AMNH); *Minas Gerais*: Alem Paraíba, 4 (MNRJ); Benfica, Serra de Itatiaia, 1 (AMNH); Bõa Esperança, Serra de Caparaó, 3 (AMNH); Conceição de Mato Dentro, Boca de Ulaba, 1 (MNRJ); Fazenda Cardosa, Serra de Caparaó, 2 (AMNH); Fazenda de Floresta, Rio Matipó, 2 (MZUSP); Fazenda S. Francisco de Caparaó, 1 (BM[NH]); Juiz de Fora, 2 (MNRJ); Quartel de Sacramento, 1 (MZUSP); "S. Francisco de C.," 1 (BM[NH]); *Paraná*: Rio Paracai, 1 (BM[NH]); Roça Nova, Serra do Mar, 3 (BM[NH]); *Rio Grande do Sul*: no precise locality, 1 (BM[NH]); *Rio de Janeiro*: Barro Branco, 2 (MNRJ); Itatiaia, Maceira, 2 (MNRJ); Itatiaia, Parque Nacional, 1 (MNRJ); Mangaratiba, 5 (MNRJ); Pedra Branca, Paratí, 4 (MNRJ); Rio de Janeiro, 2 (AMNH); Rodico, Serra do Mar, 1 (BM[NH]); São João Marcos, 2 (MNRJ); Teresópolis, 15 (BM[NH]; MNRJ, 13; USNM); *Rondônia*: Porto Velho, 1 (USNM); *Santa Catarina*: Hansa, 4 (BM[NH]); Joinville, 1 (FMNH); *São Paulo*: Alto da Serra, 1 (MZUSP); Boraçeira, 26 (MZUSP, 25; USNM, 1); Butantã, Serra da Cantareira, 3 (MZUSP); Casa Grande, 3 (MZUSP); Cobia, 3 (MZUSP); Costão dos Engenhos, 1 (MZUSP); Iporanga, 5 (MNRJ); Lageado de Iporanga, 1 (MZUSP); Lageado do Aranhadavá, 1 (MZUSP); Monte Alegre, Amparo, 3 (MZUSP); Piquete, 2 (MZUSP); São Sebastião, 4 (BM[NH]); Serra de Itatiaia, 1 (MZUSP); Vila Oliveira, Mogi das Cruzes, 1 (MZUSP). PERÚ. *Cuzco*: Hacienda Cad-

ena, 2 (FMNH); Quincemil, 3 (FMNH); *Huánuco*: Tingo Maria, 2 (BM[NH]); *Ucayali*: Apayacu, 1 (AMNH); Balta, Río Curanja, 9 (LSUMZ); Chicosa, 5 (BM[NH]); Cumaria, 1 (BM[NH]); Iquitos, 1 (AMNH); Itaya, Iquitos, 1 (AMNH); Lagarto Cocha, 2 (AMNH); Pucallpa, 3 (USNM); Río Urubamba, mouth, 5 (AMNH); San Jerónimo, 1 (BM[NH]); Santa Rosa, 1 (AMNH); Sarayacu, 8 (AMNH); Yarinacocha, 4 (FMNH; LSUMZ, 3); *Madre de Dios*: Boca Colorado, 1 (FMNH); Río Tambo, 1 (USNM); *San Martín*: Moyobamba, 3 (BM[NH], 2; FMNH); Rioja, 1 (BM[NH]); Yurac Yacu, 10 (BM[NH]). PARAGUAY. Sapucay, 21 (BM[NH], 8, including holotype of *azaricus*; USNM, 13); Tacuati, 1 (USNM).

Philander opossum frenatus Olfers

D[idelphys]. frenata Illiger, 1815 (1804–1811):107—nomen nudum.

D[idelphys]. frenata Olfers, 1818:204.

[*Metachirops*] *frenata*. Matschie, 1916:268—BRASIL: *Bahia* (type locality).

Met[achirops]. opossum frenatus, Krumbiegel, 1941: 206 (in text)—explicitly omitted from taxonomic review.

Philander opossum frenata [sic], Hershkovitz, 1959: 338, 342—taxonomy; part, synonyms (*superciliaris* Olfers, *myosuros* Temminck).

D[idelphys]. superciliaris Illiger, 1815(1804–1811): 107—nomen nudum. Olfers, 1818:204—no locality.

D[idelphis]. myosurus [sic], Wagner, 1843, footnote 25, p. 44—BRASIL: *Bahia*; type of “*frenata* Lichtenstein” from *Bahia*; collected by Kaehne.

Metachirus quica, Burmeister (part, not Temminck), 1856:70, Pl. 8 (female)—BRASIL: *Bahia*; type of *Didelphys frenata* Illiger [Olfers] in Berlin Museum, figured.

Metachirus nudicaudatus nudicaudatus, Cabrera (part, not É. Geoffroy, 1803), 1958:48—“*frenata* Lichtenstein (Wagner)” in synonymy.

TYPE—Adult female, skin mounted, Berlin Museum; collected before 1815 by Herr Kaehne.

TYPE LOCALITY—Originally given as Brasil; according to Wagner (1843, footnote 25, p. 44) the specimen labeled *D. frenata* in the Berlin Museum was collected by Herr Kaehne in *Bahia*, presumably in the present São Salvador, which may be taken as the restricted type locality (cf. Matschie, 1916, p. 268).

DISTRIBUTION (Fig. 5)—Known only from the ascribed type locality.

CHARACTERS—Olfers' (1818, p. 204) description of *frenata* (and *superciliaris*) reproduced below is little more than the indication required to validate the specimen label names first published as *nomina nuda* by Illiger.

“*D[idelphys]. Opossum* L[innaeus]

“*Sarigoy*, *Sarigue* Var.

“*Carigueia* Marc. 222. Piso 323 (excl. ic.)

“*D. frenata* und *supercilia* Ill. gehören als varietaten hierher. Das Männchen hat Gelbe Flecken, das Weibchen grössere Weisse über den Augen.”

REMARKS—A pouched four-eyed opossum perhaps representative of *P. opossum quica*, may well have ranged into the erstwhile coastal forests of southern Bahia and possibly farther north. Pending examination of the type or specimens from Bahia, if any, the name *frenatus* is retained.

The specimens identified as *P. opossum frenatus* by Patton et al. (1995 [1996], pp. 7, 21, 22) are from Teresópolis in the state of Rio de Janeiro and well within the range of *P. opossum quica*. It has not been shown that the Teresópolis specimen is not *P. opossum quica* nor that it is representative of *P. opossum frenatus*.

Philander opossum melanurus Thomas

[?] *Didelphis opossum*, Thomas, 1888:329—part, EC-UADOR: *Guayas* (Guayaquil).

Metachirus opossum melanurus Thomas, 1899:285—type description. Lönnberg, 1913:36—ECUADOR: *Pichincha* (Gualea).

[*Metachirops*] *melanurus*, Matschie, 1916:268—classification.

[*Holothylax opossum*] *melanurus*, Cabrera, 1919:48—classification.

Metachirops opossum melanurus, Lönnberg, 1921: 68—ECUADOR: *Pichincha* (Gualea).

Philander opossum melanurus, Cabrera, 1958:35—part, not *melantho* (= *fuscogriseus*) in synonymy.

P[hilander]. o[pposum]. melanurus, Baker, 1974: 135—ECUADOR: *Esmeraldas* (Quinindé).

TYPE—Old male, skin and skull, British Museum (Natural History), no. 1897.11.7.61; collected 11 April 1897 by W. F. H. Rosenberg.

TYPE LOCALITY—Paramba, Río Mira, Imbabura, western Ecuador; altitude, 1100 m.

DISTRIBUTION (Fig. 5)—The humid forests of northwestern Ecuador in the provinces of Esmeraldas, eastern Manabí, and bordering parts of western Imbabura and Pichincha. Nothing is known of the opossums in the Colombian departments of Nariño and Cauca, where *fuscogriseus* and *melanurus* may intergrade or prove to be sympatric.

CHARACTERS—Dorsum dominantly brownish agouti, underparts buffy to deep orange often with dark basal portions of hair showing through; tail brown but extreme tip sometimes whitish.

TABLE 11. Measurements of *Philander opossum melanurus*. Means (extremes in parentheses) and number of specimens.

Locality	Head and Body	Tail	Hind Foot	Ear
Ecuador ♂♂				
Mindo, below	—	—	—	—
Paramba	269 (258–283) 5	262 (250–276) 5	41 (40–43) 5	30 (27–35) 5
San Javier	260	270	38	28
Carondelet	296	269	37	28
Ecuador ♀♀				
Río Caoní	284	270	35	28
San Javier	282	229	37	32

COMPARISONS—Dark agouti upper parts, heavily pigmented pheomelanin underparts mixed with gray, and entirely or almost entirely brown tail distinguish *melanurus* from nearly all *fuscogriseus* and *quica*; size averages less than *fuscogriseus*, greater than *quica*.

MEASUREMENTS—Tables I and 11.

REMARKS—Comparatively small size, dark agouti upperparts and dark tail are the most distinctive characters of *P. opossum melanurus*; distinction from *fuscogriseus* is doubtful.

SPECIMENS EXAMINED—15. ECUADOR. *Esmeraldas*: Carondelet, 1 (USNM); *Esmeraldas*, 1 (AMNH); San Javier, 5 (USNM); *Imbabura*: Paramba, 6 (BM[NH], holotype of *melanurus*; FMNH, 2; USNM, 3); *Pichincha*: Mindo, below, 1 (FMNH); Río Caoní, 1 (FMNH).

Philander opossum subspecies nov. 1

Philander opossum subsp. nov. Pérez-Hernández, 1989:373, 377—VENEZUELA: *Monagas* (Cerro Papelón); *Territorio Federal, Delta Amacuro* (Tobesobe, Guayo; Los Gires; Güiniquina).

DISTRIBUTION (Fig. 5)—The original description is that of an opossum with “a markedly different color pattern which could be suggestive of an undescribed subspecies for Venezuela.” Pérez-Hernández (1989, p. 377) added that the “*Orinoco Delta* has a particular climate and vegetation, and can be defined biogeographically by an endemic subspecies of *Philander opossum* with a more melanistic coloration compared to other specimens of that species (Pérez-Hernández in preparation).”

Four specimens were examined by Pérez-Hernández, each from a different locality, one from *Monagas*, the others from *Delta Amacuro*. Five localities are shown on his map (Fig. 18, p. 404).

Philander opossum subspecies nov.?

Metachirus opossum (subsp. nov.?), J. A. Allen, 1916b:201—COLOMBIA: *Meta* (Villavicencio).

Metachirus opossum, Lyne, 1959:84—VENEZUELA: *Mérida*—vibrissae.

Philander opossum, Reig et al., 1977:197—part, VENEZUELA: *Barinas* (Guaquitas)—karyotype ($2n = 22$). Tyndale-Biscoe, 1980:712—part, COLOMBIA: *Meta* (Villavicencio).

Philander opossum griscescens, Pérez-Hernández (not J. A. Allen), 1989:373—VENEZUELA: *Barinas* (Ticopore); *Apure* (Nulita); *Aragua* (Las Bonitas); *Táchira* (La Panchera); *Trujillo* (Motatán; Dividivi); *Zulia* (Encontrados; Alguacil; Churuli; Puerto Catatumbo).

DISTRIBUTION—Map, Figure 5.

SPECIMENS EXAMINED—10. VENEZUELA. *Apure*: La Blanquito, 4 km N Nula, 2 (USNM); Nulita, 3 km N Nula, 1 (USNM); *Zulia*: Encontrados, 2 (USNM). COLOMBIA. *Boyacá*: Rio Covarí, 1 (FMNH); *Meta* (Caney, Restrepo), 2 (AMNH); Finca El Capuchó, 38 km E Villavicencio, 2 (UKMNH).

Philander opossum fuscogriseus

J. A. Allen

Didelphys quica, Alston (not Temminck), 1880:198—MEXICO; GUATEMALA: (Dueñas; Cobán); COSTA RICA: (Tucurriqui).

Didelphys opossum, Thomas, 1888:331—part, GUATEMALA: (Vera Paz; Cobán).

Philander opossum, Tyndale-Biscoe, 1980—COLOMBIA: *Valle del Cauca* (Cali Buenaventura). Tuttle et al., 1981:233—PANAMÁ: *Canal Zone* (Barro Colorado Island); acoustical location of vocalizing frogs.

Metachirus fuscogriseus J. A. Allen, 1900:194; 1901b:213—NICARAGUA: (Greytown; Bluefields); variation.

Metachirus opossum fuscogriseus, J. A. Allen, 1911:247—NICARAGUA: (Greytown).

TABLE 11. *Extended.*

Condylbasal Length	Zygomatic Arch	Preorbital Width	Postorbital Width	Braincase Width
68.9	36.6	—	8.7	22.3
69.1 (64.6–71.0) 5	36.1 (33.8–37.8) 5	13.1 (12.3–13.9) 5	9.3 (8.8–9.7) 5	21.4 (20.4–23.5) 5
70.9	38.1	—	9.0	20.5
71.9	37.3	13.7	9.3	22.0
64.1	33.5	—	9.4	20.9
65.8	34.2	12.5	8.4	19.3

TABLE 11. *Extended (continued).*

Locality	Palatal Length	i-m ⁴	m ¹⁻⁴
Ecuador ♂♂			
Mindo, below	40.8	36.2	13.4
Paramba	41.8 (38.6–43.0) 5	36.3 (34.7–37.4) 5	13.6 (13.3–14.0) 5
San Javier	42.9	37.2	13.8
Carondelet	43.1	37.5	13.8
Ecuador ♀♀			
Río Cauní	38.8	34.6	13.0
San Javier	39.9	34.8	13.0

Metachirops fuscogriseus, Matschie, 1916:268—classification.

[*Holothylax fuscogriseus*] *fuscogriseus*, Cabrera, 1919:47—classification.

Metachirops opossum fuscogriseus, Enders, 1935:410, Pl. 2 (animal)—PANAMÁ: (Barro Colorado); life history.

Philander opossum fuscogriseus, Goodwin, 1942:113—NICARAGUA (type locality, Greytown); HONDURAS; characters. Hall and Kelson, 1959:11—classification; distribution in Middle America. Yates and Froehlich, 1984:512—HONDURAS (Río Plátano Biosphere Reserve, Gracias a Dios).

Metachirus fuscogriseus pallidus J. A. Allen, 1901b:213—MÉXICO: *Vera Cruz* (type locality, Orizaba); holotype, male, skin and skull, U.S. National Museum of Natural History, no. 51858; collected 24 January 1894 (not 24 June 1894 as in original description) by E. W. Nelson and E. A. Goldman; *Tabasco* (Monte Cristo; Frontera; Teapa); *Chiapas* (Huehuetán; Chicharras); *Vera Cruz* (Orizaba; Montzorong; Tuxtepec); *Puebla* (Metlatoyuca).

[*Holothylax fuscogriseus*] *pallidus*, Cabrera, 1919:47—classification.

Metachirops opossum pallidus, Goodwin, 1934:4—GUATEMALA; characters; distribution; habits.

Philander opossum pallidus, Baker, 1951:207—MÉXICO: *Tamaulipas* (70 km S Ciudad Victoria, 2 km W El Carrizo, 2500 ft). Hall and Kelson, 1959:11—classification; distribution. Hall and Dalquest, 1963:195—MÉXICO: *Vera Cruz* (distribution, near sea level to 5600 ft above); characters; habits; common names (“comadreja”; “raton tla-

uache”). Álvarez, 1963:394—MÉXICO: *Tamaulipas* (E slope Sierra Madre Oriental to 2500 ft); variation; habits.

Metachirus grisescens J. A. Allen, 1901b:217—COLOMBIA: *Valle del Cauca* (“Río Cauca,” type locality); holotype, female, skin and skull, American Museum of Natural History, no. 15072; collected June 1888 by J. H. Batty. Goodwin, 1953:227—type history.

[*Metachirops*] *grisescens*, Matschie, 1916:268—classification.

[*Holothylax grisescens*] *grisescens*, Cabrera, 1919:47—classification.

Metachirus opossum grisescens, J. A. Allen, 1916b:201—COLOMBIA: *Valle del Cauca* (Río Frío).

Philander opossum grisescens, Goodwin, 1953:227—classification; type history.

Metachirus opossum melanotho Thomas, 1923:602—COLOMBIA: *Chocó* (type locality, Condoto; altitude, 300 ft); holotype, young adult male, skin and skull, British Museum (Natural History), no. 1914.5.28.30; collected 1 February 1914 by H. G. F. Spurrell.

Metachirus opossum melanurus, J. A. Allen (not Thomas), 1912:73—COLOMBIA: *Cauca* (Cocal). J. A. Allen, 1916a:116; 1916b:201—COLOMBIA: *Cauca* (Cocal); *Chocó* (Bagadó); *Antioquia* (Alto Bonito). Cabrera, 1958:35—part, *Metachirus opossum melanotho* Thomas in synonymy.

HOLOTYPE—Probably female, skin and skull, American Museum of Natural History, no. 9920/

TABLE 12. Measurements of *Philander opossum fuscogriseus*. Means (extremes in parentheses) and number of specimens.

Locality	Head and Body	Tail	Hind Foot	Ear
Ecuador ♂♂				
Ventura	294, 308, 308	261, 268, 293	45, 48, 49	-, -, -
Piñas	-, 214	-, 261	-, 41	-, -
Bucay	292, 307, 307	261, 275, 257	44, 48, 47	-, -, -
Puente de Chimbo	247, 278	250, 240	46, 47	-, -
Seboyal	260	262	42	-
Limón	280, 271, 275	260, 271, 285	42, 43, 45	-, -, -
Ecuador ♀♀				
Salvias, El Oro	237	246	38	-
Bucay	246, 270, 274	264, 270, 260	42, 41, 45	-, -, -
Ríos Chimbo-Coco	259, 271	249, 240	43, 43	-, -
La Papaya	256	268	38	26
Colombia ♂♂				
Bagadó	-	-	-	-
Bellavista	271	294	46	34
Colombia ♀♀				
Río Cauca	-	-	-	-
Alto Bonito	-	-	-	-
Bagadó	-	-	-	-
Panamá ♂♂				
Puerto Armuelles	303	299	49	39
La Zumbadora	265, 255	275, 265	44, 45	35, 33
Cocoli	247, 280	293, 295	43, 45	37, 35
Empire	290	300	41	32
Frijoles	289	275	46	35
Camp Piña	282 (255-305) 5	313 (290-335) 5	49 (46-52) 5	38 (34-40) 5
El Valle	287	296	43	35
Cerro Hoya	275	280	42	36
Isla Cebaco	205, 288, 290	278, 280, 302	45, 46, 50	36, 35, 37
El Volcán	276	272	48	33
Progreso	296	273	44	36
Cayo Agua	286 (261-300) 8	283 (270-290) 8	45 (38-48) 8	36 (34-38) 8
Isla Bastamentos	285, 300, -	300, 300, -	45, 47, -	36, 38, -
Boca del Drago	285 (261-301) 4	291 (269-300) 4	43 (37-48) 4	38 (36-40) 4
Almirante	274 (248-299) 8	300 (282-321) 8	45 (41-46) 8	36 (33-40) 8
Changuinola	279 (271-290) 9	296 (275-332) 9	44 (42-45) 9	36 (34-37) 9
Río Changuena, Camp	275	290	40	35
Panamá ♀♀				
La Zumbadora	251, 263, 282	278, 302, 253	41, 44, 44	31, 35, 35
Camp Piña	280 (250-305) 9	296 (263-320) 9	43 (40-50) 9	35 (34-38) 9
Isla Cebaco	298	275	43	35
Progreso	331	331	47	37
Cayo Agua	271 (255-280) 4	264 (250-270) 4	42 (41-44) 4	34.5 (34-35) 4
Boca del Drago	282 (255-294) 5	300 (273-320) 5	41 (37-42) 5	37 (35-40) 5
Almirante	270 (263-279) 3	300 (286-312) 3	42 (40-45) 3	36 (32-39) 3
Changuinola	272	280	45	33
Costa Rica ♂♂				
Savanillas de Piri	297	291	46	36
Costa Rica ♀♀				
Villa Quesada	285	275	39	30
Nicaragua ♂♂				
Río Escondido	305	320	46	-
Guatemala ♂♂				
Concepción del Mar	279	310	44	-

TABLE 12. *Extended.*

Condylbasal Length	Zygomatic Breadth	Preorbital Width	Postorbital Width	Braincase Width
72.3, 72.3, 75.0 -, 61.9	39.7, 40.4, 41.1 -, -	-, -, - -, -	9.3, 9.2, 9.5 -, -	21.8, 22.2, 22.5 -, -
71.2, 71.4, 73.5 64.7, 68.5	38.9, 36.3, 38.9 32.2, 33.9	-, -, - -, -	8.7, 9.1, 9.2 8.5, 9.3	23.1, 22.3, 21.7 20.3, 19.8
68.1 68.4, 71.9, 73.0	34.1 33.6, 40.4, 49.1	- -, -, -	8.7 8.8, 9.2, -	21.1 21.0, 23.2, 22.7
60.0 63.0, 67.0, 69.3 62.9, 66.4 -	30.7 33.0, 32.4, 33.0 32.5, 33.8 -	- -, -, - -, - -	8.7 8.6, 9.3, 8.9 9.3, 8.4 -	20.4 20.4, 21.1, 21.3 22.0, 20.5 -
72.9 67.8	40.2 33.9	- -	9.4 9.1	21.6 21.3
66.2 64.8 67.2	36.3 34.1 32.9	- - -	9.4 8.8 8.4	22.1 20.6 19.6
79.7 70.9, 76.4 72.0, 77.2 76.6 75.9 77.8 (74.4-81.5) 5 73.5 69.6 70.8, 71.7, 74.6 69.7 73.5 72.4 (67.8-75.0) 8 73.0, 73.3, 75.2 74.0 (72.0-75.3) 4 71.9 (68.7-75.6) 8 73.8 (68.0-76.3) 9 73.2	41.2 35.0, 43.0 37.2, 42.8 39.8 42.3 40.5 (38.3-42.5) 5 38.5 36.6 39.3, 38.6, 40.3 35.9 37.5 38.3 (35.5-41.5) 8 39.2, 40.3, 40.6 39.9 (37.9-42.0) 4 37.5 (34.6-41.2) 8 38.0 (35.5-40.6) 9 38.9	15.4 12.5, 14.7 13.2, 14.5 13.7 13.3 14.0 (12.8-15.7) 6 12.8 13.1 12.8, 13.7, 13.3 12.0 13.4 13.2 (11.8-14.5) 8 13.5, 13.9, 15.0 13.9 (12.5-14.8) 4 13.1 (12.2-15.2) 8 13.6 (12.5-15.5) 9 13.7	8.9 8.4, 8.7 8.8, 8.6 8.6 9.0 9.0 (8.6-9.4) 6 8.9 8.9 9.1, 9.2, 9.0 8.4 9.1 8.8 (8.5-9.0) 8 9.0, 9.0, 8.7 8.7 (8.5-8.9) 4 8.7 (8.5-9.3) 8 8.9 (8.6-9.4) 9 8.9	20.1 19.5, 20.9 20.0, 20.9 20.0 23.5 21.4 (20.5-22.3) 6 21.6 19.8 20.1, 20.1, 21.0 20.6 20.3 20.0 (19.1-21.4) 8 20.9, 22.2, 21.6 22.1 (21.7-22.6) 4 20.5 (19.2-22.7) 8 20.3 (19.8-20.8) 9 22.2
67.6, 71.5, 72.1 72.4 (68.9-74.5) 9 73.5 80.5 67.6 (64.3-70.2) 4 72.4 (65.4-76.5) 5 68.6 (65.7-72.2) 4 67.8	33.7, 34.6, 36.7 37.7 (34.5-38.6) 9 39.7 40.0 35.4 (33.9-35.2) 4 38.0 (34.3-43.1) 5 36.1 (34.4-39.1) 4 35.5	12.0, 12.7, 13.1 12.9 (11.6-13.8) 8 13.8 14.0 12.5 (12.1-12.9) 4 12.7 (11.8-13.3) 4 13.0 (12.5-13.5) 4 13.2	9.1, 8.7, 9.0 8.9 (8.3-9.3) 8 9.2 9.2 8.7 (8.5-8.8) 4 9.0 (8.7-9.4) 5 8.9 (8.8-9.1) 4 8.9	19.8, 19.3, 22.1 20.3 (19.5-21.7) 8 19.9 21.0 19.1 (18.7-19.4) 4 21.8 (20.3-23.6) 5 20.2 (19.5-21.3) 4 19.4
78.7	43.0	15.7	9.0	23.5
66.1	32.7	11.5	8.0	19.6
76.5	-	-	-	-
69.7	35.9	11.8	9.0	22.2

TABLE 12. *Continued.*

Locality	Head and Body	Tail	Hind Foot	Ear
Guatemala ♀♀				
Los Amatos	—	—	—	—
México ♂♂				
Palenque	280	316	—	—
Achotal	269 (252–292) 4	289 (258–310) 4	44 (40–47) 4	36 (34–37) 4
México ♀♀				
Tekom	—	—	—	—
Achotal	300	300	45	36

TABLE 12. *Extended (continued).*

Condylbasal Length	Zygomatic Breadth	Preorbital Width	Postorbital Width	Braincase Width
70.0	—	11.8	9.0	21.8
73.1	—	12.6	8.5	21.2
68.8 (64.1–74.5) 5	36.1 (33.0–39.1) 5	11.9 (10.9–13.0) 5	8.7 (8.3–9.1) 5	21.6 (20.4–22.7) 5
69.8	37.0	12.4	8.5	22.3
71.8	39.0	12.4	8.9	21.9

8252; presented by Albert Smith. The skin is labeled female, skull tag and box are labeled male. The skin is in poor condition but appears to be that of a female; the last molar is not fully erupted.

TYPE LOCALITY—"Found [in New York, 11 January 1895] in a bunch of bananas in unloading a fruit steamer from a Central American port, most likely Colon . . ." (J. A. Allen, 1900, p. 194); subsequently fixed as Greytown (= San Juan del Norte), Nicaragua, by Goodwin (1942, p. 113). According to Allen (1901b, p. 213), "a number of specimens from Greytown and Bluefields, Nicaragua agree with the type of this species, supposed to have come from a point somewhat further south on the coast." This statement does not constitute a fixation of type locality as claimed by Goodwin (1946, p. 284; 1953, p. 227), but Goodwin's designation is.

DISTRIBUTION (Fig. 5)—In México the states of Tamaulipas on the east, Vera Cruz (Oaxaca, 1851/9705) on the west, south through Middle America into western Colombia, Andean valleys, and neighboring parts of Guayas in western Ecuador, to the Peruvian border. Altitudinal range sea level to 1000 m above. The distributional gap between

the range of *fuscogriseus* in southwestern Colombia and that of *P. opossum melanurus* in northwestern Ecuador leaves moot the question of possible intergradation or sympatry between the taxa.

CHARACTERS—Intermediate in coloration between saturate *melanurus* and pale *quica*; conule C of m³ comparatively well developed, as in *P. andersoni*.

COMPARISONS—Individuals of *P. opossum fuscogriseus* with dorsal surface like that of *P. opossum melanurus* and with tail entirely brown are usually much paler on ventral surface. Conule C is most developed in *fuscogriseus*, least in the smaller, generally grayer *quica*.

MEASUREMENTS—Tables 1 and 12.

TAXONOMY—The type of *M. grisescens* J. A. Allen from the Río Cauca valley in southwestern Colombia was distinguished from the Middle American opossums by its paler coloration and uniformly brown tail. Tail color of *grisescens* agrees with that of *P. opossum melanurus* Thomas, but the generally paler coloration identifies *grisescens* with western Colombian representatives of *P. opossum fuscogriseus*. Two specimens from Río Frío, Cauca Valley, which agree closely

TABLE 12. *Continued.*

Locality	Palatal Length	i-m ⁴	m ¹⁻⁴
Ecuador ♂♂			
Ventura	43.7, 43.2, 44.8	37.7, 36.8, 37.5	14.0, 13.2, 13.4
Piñas	-, 37.9	-, 34.3	-, 12.4
Bucay	41.6, 42.6, 43.5	36.5, 35.9, 37.2	14.3, 13.3, 13.5
Puente de Chimbo	39.5, 42.2	35.5, 36.2	13.3, 14.0
Seboyal	39.7	36.0	13.4
Limón	41.7, 43.5, 43.9	37.2, 37.4, 38.2	14.1, 14.3, 14.0
Ecuador ♀♀			
Salvias, El Oro	37.0	34.0	13.3
Bucay	38.1, 41.5, 41.7	33.9, 36.9, 36.9	13.5, 13.9, 14.0
Ríos Chimbo-Coco	39.1, 40.1	34.7, 34.5	14.1, 12.8
La Papaya	40.5	35.2	13.3
Colombia ♂♂			
Bagadó	44.3	37.6	11.7
Bellavista	41.2	37.2	13.8
Colombia ♀♀			
Río Cauca	40.6	34.7	12.9
Alto Bonito	38.8	34.1	12.8
Bagadó	41.7	36.7	13.9
Panamá ♂♂			
Puerto Armuelles	48.7	41.3	14.8
La Zumbadora	43.6, 45.3	37.7, 39.0	15.0, 15.2
Cocoli	43.3, 45.9	37.7, 39.5	14.3, 14.2
Empire	46.7	40.3	15.2
Frijoles	46.4	39.3	14.8
Camp Piña	47.0 (44.7-50.2) 6	40.2 (39.5-41.8) 6	15.0 (14.6-15.6) 6
El Valle	46.1	39.3	15.4
Cerro Hoya	43.1	37.3	14.2
Isla Cebaco	43.5, 44.1, 45.4	37.6, 38.3, 39.0	14.5, 14.7, 15.1
El Volcán	41.7	37.6	14.7
Progreso	45.0	39.6	14.5
Cayo Agua	43.8 (41.9-47.2) 8	37.4 (36.4-39.5) 8	14.0 (13.6-14.4) 8
Isla Bastamentos	43.7, 44.3, 45.1	37.8, 38.8, 38.9	14.6, 14.8, 15.0
Boca del Drago	44.8 (43.6-45.5) 4	38.3 (36.9-39.0) 4	13.9 (13.2-14.4) 4
Almirante	43.5 (42.5-44.6) 5	37.8 (35.9-39.3) 8	14.1 (13.1-14.5) 8
Changuinola	44.6 (41.5-46.6) 9	38.6 (37.0-40.0) 9	14.4 (14.1-14.9) 9
Río Changena, Camp	44.6	37.4	13.9
Panamá ♀♀			
La Zumbadora	41.0, 44.5, 44.4	37.0, 38.7, 38.5	14.8, 15.2, 15.3
Camp Piña	44.6 (42.7-46.0) 9	38.3 (36.0-39.5) 9	14.5 (13.5-15.1) 9
Isla Cebaco	44.8	38.5	14.5
Progreso	48.7	41.2	15.3
Cayo Agua	41.2 (39.3-43.1) 4	35.4 (34.6-36.3) 4	13.6 (13.4-13.9) 4
Boca del Drago	43.6 (39.6-45.8) 5	36.8 (34.5-38.7) 5	13.4 (13.1-14.0) 5
Almirante	42.1 (39.5-44.4) 3	37.0 (35.5-38.3) 4	13.7 (13.5-13.4) 4
Changuinola	42.0	37.7	14.5
Costa Rica ♂♂			
Savanillas de Piri	48.3	41.0	14.7
Costa Rica ♀♀			
Villa Quesada	40.2	35.9	13.4
Nicaragua ♂♂			
Río Escondido	45.8	39.4	14.0
Guatemala ♂♂			
Concepción del Mar	42.0	38.1	14.2

TABLE 12. *Continued.*

Locality	Palatal Length	i-m ⁴	m ¹⁻⁴
Guatemala ♀♀			
Los Amatos	42.3	36.0	13.4
México ♂♂			
Palenque	43.3	37.3	14.1
Achotal	43.6 (38.4-49.5) 5	37.2 (35.7-38.8) 5	13.9 (13.5-14.3) 5
México ♀♀			
Tekom	42.2	37.6	13.4
Achotal	42.5	37.3	13.0

with the type of *griseus*, except for parti-colored tail, are undoubtedly *fuscogriseus*.

The type and only specimen of *griseus* was collected June 1898 (not 1899) by J. H. Batty. Specific locality data were not given. Judged by his itinerary, reconstructed from other dated specimens (cf. Goodwin, 1953, p. 384), Batty must have taken the type in the upper Río Cauca Valley, probably between Cali and Río Frío.

Metachirus fuscogriseus pallidus J. A. Allen, from Orizaba, Vera Cruz, México, was distinguished from the Nicaraguan form of *fuscogriseus* by paler coloration, larger supraorbital patches, and paler and narrower crown. Measurements were given for 21 adults of both sexes from various localities in the Mexican states of Vera Cruz, Oaxaca, Chiapas, Puebla, and Tabasco.

Characters attributed to *pallidus* are demonstrable in other material from Vera Cruz but are not consistent in specimens from elsewhere throughout the range assigned to *pallidus* west of Honduras and Salvador. Variation in specimens from México, Guatemala, Belize, and Honduras and others reported from Salvador (Felten, 1958; Burt & Stirton, 1961) falls well within the limits of variation of Costa Rican, Panamanian, and Colombian *P. opossum fuscogriseus*.

Metachirus opossum melantho Thomas from Condoto, northwestern Colombia, was compared with *andersoni* Osgood of the Peruvian Amazonas, whereas the genetically and geographically relevant *griseus*, *fuscogriseus*, and *melanurus* were ignored in the original description. Typologically, *melantho* could be assigned to any one of the three forms named. Its nearly whitish underparts and sides and parti-colored tail, however, cast *melantho* with *fuscogriseus*. The Field Museum series from nearby Río Docampado, near the type locality of *melantho*, definitely belongs with *fuscogriseus*.

REMARKS—The more or less unpigmented terminal portion of the tail averages about 20% (0-30%) in Colombian and Ecuadorian opossums but becomes increasingly more extensive from Panamá into México. Álvarez (1963, p. 395) noted that the terminal whitish area averaged 53.1% (43.3-62.8%) in 13 specimens from Tamaulipas and 38.7% (30.9-48.2%) in 14 specimens from Vera Cruz.

Bibliographic citations in the synonymies of Middle American representatives of *P. opossum fuscogriseus* are restricted to primary synonyms, selected taxonomies, and distributional references.

SPECIMENS EXAMINED—255. MEXICO. *Chiapas*: Palenque, 1 (FMNH); *Vera Cruz*: Achotal, 9 (AMNH); Orizaba, holotype of *pallidus* J. A. Allen (USNM); *Yucatán*: Tekom, 1 (FMNH). HONDURAS. San Pedro, near Lake Ticamaya, 1 (FMNH). BELIZE. Central Farm, 3 (USNM). NICARAGUA. 4 (AMNH, holotype of *fuscogriseus* J. A. Allen, of unknown origin, but with type locality restricted to Greytown; USNM, 3); Escondido River, 50 mi from Bluefields, 2 (USNM). COSTA RICA. *Alajuela*: San Carlos, 1 (FMNH); Villa Quesada, 1 (FMNH); *San José*: Fuentes, 1 (FMNH); *Savanillas de Pirris*, 1 (FMNH). GUATEMALA. *Escuintla*: Concepción del Mar, 2 (FMNH); *Izabal*: Bobos, 3 (FMNH); Los Amates, 1 (FMNH). PANAMÁ. *Bocas del Toro*: Almirante, 25 (USNM); Boca del Drago, 10 (USNM); Cayo Agua, 20 (USNM); Changuinola, 21 (USNM); Isla Bastamentos, 7 (USNM); Isla Colón, 2 (USNM); Río Changena Camp, 3 (USNM); *Canal Zone*: Cerro Campana, 1 (USNM); Cocolí, 4 (USNM); Empire, 1 (USNM); Fort Sherman, Camp Piña, 31 (USNM); Frijoles, Bahía Peninsula, 51/2 km WNW, 5 (USNM); Puma Island, 1 (USNM); no precise locality, 2 (USNM); *Chiriquí*: Boquerón, 1 (AMNH); Progreso, 4 (USNM); Volcán, 4100 ft, 1 (AMNH); *Cocle*: El Valle, 14 (USNM); *Colón*: Salud, 2 (USNM); *Darién*: Jaqué, 1 (USNM); Puerto Ar-

muelles, 3 (USNM); *Los Santos*: Cerro Hoya, 5 (USNM); *Panamá*: Cerro Azul, 21 (USNM); Cerro Jefe, 4 (USNM); La Zumbadora, Gorgas Laboratory, 3 (USNM); *Veraguas*: Isla Cebaco, 14 (USNM); Isla Gobernado, 2 (USNM). COLOMBIA. *Antioquia*: Alto Bonito, 3 (AMNH); Bellavista, 4 km NE, 1 (FMNH); *Caldas*: Río Hondo, Samaná, 1 (FMNH); *Cauca*: Cocal, upper Río San Juan, 1 (AMNH); La Boca, Río Saija, 3 (FMNH); Upper Río Cauca Valley, holotype of *grisescens* J. A. Allen (AMNH); *Chocó*: Bagadó, 8 (AMNH); Condoto, holotype of *melantho* Thomas (BM[NH]); Novita, 1 (AMNH); Río Docampado, 3 (FMNH); Río Sando, Río Baudó, 6 (FMNH); *Valle del Cauca*: Buenaventura, 1 (FMNH); Río Frío, 2 (AMNH). ECUADOR. *El Oro*: El Chiral, 2 (AMNH); Punta Santa Ana, 1 (AMNH); Salvias, 1 (AMNH); *Guayas*: Bucay, Río Chimbo, 8 (AMNH); Piñas, 4 (AMNH); Puente de Chimbo, 6 (AMNH); Ríos Chimbo-Coco, 6 (AMNH); Ventura, 3 (AMNH); *Loja*: Cebollal, 1 (AMNH); *Manaví*: La Papaya, 1 (AMNH); Río de Oro, 1 (AMNH); Río Pescado, 2 (AMNH); Limón, 1200 ft, 3 (AMNH, not located).

Philander andersoni Osgood

(Synonymies under subspecies headings)

DISTRIBUTION (Fig. 5)—Amazonian basin of Perú, Ecuador, Colombia, Venezuela, and Acre in western Brasil; altitudinal range from near sea level to about 1900 m above.

CRANIAL CHARACTERS—Cranial characters as for the genus.

DENTAL CHARACTERS—Dental characters as for the genus.

COLORATION—Dorsal surface of trunk with broad, blackish (dark brown) longitudinal stripe, or entirely blackish, the dominant guard hairs usually coarse, elongate and uniformly colored or with a pale, narrow subterminal band; neck, chest, and belly often dark brown to blackish with gray basal portions of hairs showing through; lateral line, if present, restricted to a poorly defined hip patch; forefeet usually paler beneath than above, hind feet darker beneath than above; tail usually parti-colored with proximal half to four-fifths brown or blackish, remainder unpigmented, rarely entirely dark; ears usually blackish except sometimes with unpigmented band or patch extending from base to mid-center or margin.

PELAGE—The muskrat-like pelage, particularly of the dorsum, more so in *P. andersoni mcilhennyi*

than in *P. andersoni andersoni*, points to aquatic habits. The notably shorter, more woolly coat of *P. opossum* is less adapted for an aquatic environment.

The long-haired basal portion of the tail, according to Gardner and Patton (1972, p. 3), averages 26.6% of tail length in nine specimens of *P. andersoni mcilhennyi* from Balta and averages 16.9% in 10 specimens of *P. opossum quica* from the same locality. Ratios of a sampling from both species with m^4 fully erupted, measured in the dry skin, are shown in Table 13. The data reveal that the thickly furred basal portion is most extensive in the Balta series of *P. andersoni mcilhennyi* and the Brazilian, French Guianan, and Surinam *P. opossum opossum* and, with few individual exceptions, is less in all others. The survey did not take into account seasonal differences, if any, in hair growth. Collectors' tail measurements recorded on field tags are usually reliable, or comparable, but may account for a few disparities in the ratios.

COMPARISONS—The broad, strongly defined dark middorsal longitudinal band or stripe of long coarse, apparently erectile hairs is the principal external character distinguishing *P. andersoni* from *P. opossum*. Sympatric and parapatric populations of the latter average slightly smaller in bodily and cranial dimensions (Table 14). Dorsum of *P. opossum* is nearly uniformly grayish brown with never more than a faint indication of dark dorsal band, which often may be an artifact of dry, folded-over skin, hind limbs grayish or buffy, not dark brown.

SEXUAL DICHROMATISM—Sexual dichromatism is most strongly marked in the Pucallpa, Río Ucayali, series of *andersoni*. In females, pheomelanin is saturate on underparts and dominant in the banding of the agouti hairs of other bodily parts. In males, the agouti pattern persists on underparts, with the pheomelanin subterminal bands thinly pigmented or pale buff. Irregular pheomelanin patches on belly and chest are paler than in females. Underparts of one of two female *andersoni* only from Santa Elena, Río Samiria, are completely saturate (i.e., monochromatic) pheomelanin.

Sexual dichromatism in remaining material is not as clear, but in general pheomelanin saturation in underparts and sides of body is dominant in females. In males, the trend is toward pigmentary dilution on all parts except for pheomelanin saturation of throat, midline of neck and chest, and pubic region. The intensity of sexual dichromatism varies from population to population. Adap-

TABLE 13. Ratio of hairy basal portion of tail, in dry skin, to total length of tail (collector's measurement) in *Philander andersoni* and *P. opossum*. Figures are of individuals from each locality.

Taxon	Locality	Individual Ratios
<i>P. andersoni mcilhennyi</i>	Balta, Perú	26, 28, 33
<i>P. andersoni andersoni</i>	Pucallpa, Perú	17, 21, 21, 23, 24
	Yurimaguas, Perú	21 (holotype <i>andersoni</i>)
	Chanchamayo, Perú	24
	San Juan, Oxapampa, Perú	27
	Ecuador	18, 19, 19, 23, 23
	Colombia	17, 19, 20, 20
	Venezuela	17, 19, 22, 24
<i>P. opossum opossum</i>	Suriname	25, 27, 33
	Guyane Française	28
	Amapá, Brasil	20
	Pará, Brasil	26
<i>P. opossum quica</i> (selected specimens)	Goiás, Brasil	22
	Mato Grosso, Brasil	25
	Yarinacocha, Perú	24, 24
	Moyobamba, Perú	27
	Pucallpa, Perú	16, 22
	El Beni, Bolivia	23, 23, 24

tive or behavioral correlation with sexual dichromatism is not readily interpretable. The affected parts of the body may or may not be used for display. The bright orange underparts of females and contrastingly brown marsupium are conspicuous to the human eye.

GEOGRAPHIC VARIATION—The melanistic *Philander andersoni* may have differentiated from the nearest ancestor of the already dark *P. opossum*, presumably during a Late or post-Pleistocene dry period in a forest refuge on the eastern base of the equatorial Andes. The postulated area incorporates the Napo refuge described by Haffer (1969). With return of humid, warmer climate, the species advanced north within its sylvan habitat into Colombia south across the Río Marañón into

Perú, east through gallery forests, into the forested highlands of southwestern Venezuela. In all outward spreading, the opossum became darker. One population isolated in the upper Río Purús south of the Marañón evolved into the extremely eumelanistic *P. andersoni mcilhennyi*.

Melanism in *P. andersoni mcilhennyi* is heaviest on head, trunk, tail base, and limbs except digits of forefeet. In the paler *P. andersoni andersoni*, the pigment is more concentrated on crown, nape, middorsal stripe, and over most of trunk. The geographic cline of increasing pigmentation is most notable in the Río Ucayali basin from Pucallpa south, east into headwaters of the Río Purús, and west into the Río Huallaga basin (Yurimaguas).

TABLE 14. Sympatric populations of *Philander andersoni* and *P. opossum* compared in size. Means (extremes in parentheses), specimens examined.

	Balta, Perú		Pucallpa, Perú	
	<i>P. andersoni mcilhennyi</i> (1♂, 3♀)	<i>P. opossum quica</i> (5♂)	<i>P. andersoni andersoni</i> (1♂, 3♀)	<i>P. opossum quica</i> (2♂, 1♀)
Head and body	290 (280–299) 4	248 (232–255) 5	290.5 (279–298) 4	269 (264–273) 3
Condylobasal length	73.9 (73.5–74.4) 3	65.0 (62.5–67.5) 5	71.2 (70.2–73.1) 3	64.7 (64.2–65.1) 2
Zygomatic breadth	37.1 (36.8–37.6) 3	33.3 (31.7–34.3) 5	35.4 (34.2–36.5) 3	35.3 (33.5–36.3) 3
Braincase width	21.1 (21.0–21.2) 3	19.1 (18.4–19.6) 5	20.6 (20.2–20.8) 3	20.7 (19.9–21.4) 3
Molar row	15.2 (14.9–15.3) 3	13.5 (12.9–14.3) 5	14.2 (13.7–14.6) 4	12.9 (12.5–13.1) 3

HABITS—According to notations on specimen labels, individuals of *Philander andersoni andersoni* had been shot out of trees and trapped on the ground.

At Tres Troncos, Río Caquetá, Colombia, two live suckling young, each about 6 cm in combined head and body length, were detached from their trapped, dead mother (FMNH 70985) and left to fend for themselves in camp, where I could observe them. At first, they tottered uncertainly on weak legs, but quickly adapted to life without mother. They ate ripe bananas, plantains, and papayas, lapped blood from animals being skinned, and ate some of the flesh. When not otherwise engaged the two fought with each other, the victor putting the loser to flight. Both animals disappeared after 2 days.

Philander andersoni andersoni Osgood

[?] *D[idelphys] myosuroides*, Tschudi (not Temminck), 1844:14, 145, 151—PERÚ: female with well-developed pouch. Tschudi, 1844:250—PERÚ.

Metachirus andersoni Osgood, 1913:95; 1914:149—PERÚ: Ucayali (type locality, "Yane Yacu," Río Paranapura, 8 mi from Yurimaguas). Sanborn, 1947:215—type history.

M[etachirops] andersoni, Matschie, 1916:268—classification.

[Holothylax] andersoni, Cabrera, 1919:47—classification.

M[etachirus] opossum andersoni, Thomas, 1923:603—classification.

Metachirus opossum andersoni, Thomas, 1928b:294—PERÚ: Ucayali (Iquitos).

Philander opossum andersoni, Cabrera, 1958:34—classification. Pérez-Hernández, 1989:373—VENEZUELA: Territorio Federal Amazonas (Caño Majagua; Cerro Cucurito; San Juan, Río Manapiari; Tamatama; Belén; Capibara; Campamento La Nebolina; Mavaca; Sierra Parima).

[Philander] opossum andersoni, Gardner and Patton, 1972:5—PERÚ: Ayacucho (Huanhuachayo; San José); characters; comparisons.

[Philander] o[possum]. andersoni, Baker, 1974:135—ECUADOR: Napo—Pastaza (Santa Cecilia).

Philander andersoni, Emmons and Feer, 1990:18—part. "upper Amazon Basin of Venezuela, probably Colombia, Ecuador to Ucayali Department."

Metachirus opossum nigratus Thomas, 1923:603—PERÚ: Junín (type locality, Utcuyacu, 1600 m; Chanchamayo); type, male, skin and skull, British Museum (Natural History), no. 1900.7.7.62; collected 21 April 1900 by P. O. Simons. Thomas, 1928a:250, footnote—PERÚ: Junín (Inañez). Gardner and Patton, 1972:5—"more likely a synonym of *andersoni*" than *P. opossum canus*, *apud* Cabrera, 1958.

Metachirus opossum Tate, 1939:161—VENEZUELA: Amazonas (Mt. Duida).

Philander opossum, Gardner and Patton, part (not

Linnaeus), 1972:5—PERÚ: Ayacucho (San José, Río Santa Rosa, 1000 m; Huanhuachayo, 1660 m); comparisons. Reig et al., 1977:197—PERÚ: Ayacucho (San José, Río Santa Rosa; Huanhuachayo). *Philander opossum canus* Cabrera (part, not Osgood) 1958:35—*nigratus* Thomas only, a synonym.

TYPE—Male, skin and skull, Field Museum of Natural History, no. 19655; collected 11 September 1912 by M. P. Anderson.

TYPE LOCALITY—"Yane Yacu" [= Yanayacu], a *chacra*, or farm, on the Paranapura River about 8 mi from Yurimaguas. The latter is on the Río Huallaga at the mouth of the Río Paranapura (cf. Osgood, 1914, p. 147).

DISTRIBUTION (Fig. 5)—Southeastern Colombia, eastern Ecuador, the Río Huallaga Valley in the Peruvian departments of Amazonas, Pasco, Junín, and Ayacucho, the Río Ucayali Valley, Ucayali, and the disjunct population of Territorio Federal Amazonas, Venezuela.

CHARACTERS—Dark middorsal band well defined from sides and continuing over rump to less than basal fifth of tail; hind limbs pale brown, grayish brown or buffy, forelimbs paler with digits usually unpigmented; ventral surface ochraceous orange to buffy or grayish buff.

COMPARISONS—Distinguished from *Philander andersoni mcilhennyi* mainly by paler coloration throughout and narrower, more sharply defined middorsal band; from sympatric representatives of *P. opossum* by larger size, dark middorsal band and darker coloration throughout.

MEASUREMENTS—Tables 1 and 15.

VARIATION—The Andean *andersoni* from Huanhuachayo, Ayacucho, Perú, is dark like *mcilhennyi* but with dorsal pelage shorter, finer, dorsal band not clearly defined from sides, underparts and limbs paler, tail entirely pigmented except for some mottling on terminal portion. A second Andean specimen, from San José, Ayacucho, is slightly paler throughout except for a similarly dark brown tail. Its poorly defined dorsal band and nearly uniformly dark tail suggest intergradation with *P. opossum*. Nearest geographic representatives of *P. opossum*, however, from Cuzco and Madre de Dios are distinct. The third Andean specimen of *andersoni* from Chanchamayo, Junín, and another from San Juan, Oxapampa, also lack the well-defined blackish dorsal band of the subspecies. In all other respects, they agree. The condylobasal length of the last two, 76.3 and 81.2 mm, respectively, are among the largest of the species. The heavily furred basal portion of the tail is notably extensive in the San Juan individ-

TABLE 15. Measurements of *Philander andersoni andersoni*.

Locality	Head and Body	Tail	Hind Foot	Ear	Condylobasal Length	Zygomatic Breadth
Colombia ♀♀						
La Tagua	270, 274, 264	292, 278, 270	37, 40, 37	34, 36, 39	65.9, 69.1, 64.6	31.6, 34.0, 32.3
Venezuela ♂♂						
Capibara	—, 270	—, 305	45, 45	42, 45	67.3, 74.5	32.3, 37.6
Tamatama	266, —, —	295, —, —	44, 42, —	43, 42, —	—, —, 73.7	36.3, —, 38.2
Acanana	—	—	—	—	71.4	36.4
Mount Duida	243	285	45	—	67.9	36.5
Belén	—	—	—	—	75.7	39.9
Venezuela ♀♀						
Capibara	265	285	41	40	67.3	32.3
Esmeralda	258	267	45	41	67.6	33.7
Tamatama	250	290	36	33	—	—
Belén	225	300	41	38	67.7	36.5
Merrey	250	255	41	—	69.1	35.0
Perú ♂♂						
Chanchamayo	280	275	47	30	76.3	38.1
San José	275	300	48	34	71.3	36.6
Yurimaguas	284	288	40	—	76.3	37.8
Pucallpa	279	313	40	35	73.1	36.5
Santa Luisa	267, 304	265, 282	40, 42	33, 35	—, 73.6	—, 39.3
Río Curaray	—	—	—	—	73.0, 68.9	37.0, —
Perú ♀♀						
Huanhuachayo	270	300	45	35	71.7	36.5
Utcuyacu	265	275	40	35	68.2	32.3
Oxapampa	300	332	51	36	81.2	40.0
Yurimaguas	275	278	35	—	68.6	30.8
Pucallpa	298, 295, 290	279, 280, 290	36, 40, 40	37, 35, 38	—, 70.2, 70.3	—, 35.5, 34.2
Santa Elena	278, 277	270, 263	41, 40	35, 33	68.6, 67.1	33.3, 31.7
Río Curaray	—, —, —	—, —, —	—, —, —	—, —, —	68.7, 65.3, 72.3	36.7, 32.9, 35.8
Ecuador ♂♂						
Pindo Yacu	250, 300	255, 315	40, 40	34, 38	68.3, 76.5	34.0, 39.8
Yana Rumi	278	285	40	32	72.4	38.5
Montalvo	250, 264	280, 262	35, 37	35, 35	74.9, 66.7	37.5, 34.9
Ecuador ♀♀						
San José	—	—	—	—	68.5	34.8

ual. A skull from Chanchamayo in the British Museum (Natural History), assigned to *nigratus* (= *andersoni*) by Thomas (1923, p. 603), measures 80.7 mm in condylobasal length.

Two specimens from Santa Elena, Río Samiria, between the Ucayali and Huallaga, are intermediate between typical *andersoni*, the Pucallpa series of *andersoni*, and the Balta topotypes of *mcilhennyi*. The same departure from heavier pigmentation continues westward into the Peruvian Andes (Junín). In Amazonian Venezuela, however, individuals of *P. andersoni andersoni* are blackish but with underparts and limbs pale (Capibara, USNM 406960; Belém, USNM 388412).

TAXONOMIC HISTORY—The dark Peruvian *phi-*

lander identified by Tschudi (1844, p. 145) as *Didelphys myosuroides* Temminck may well be the earliest mention of the form described by Osgood as *P. andersoni*. Tschudi (1844, pp. 14, 144, 151) also noted the occurrence in Perú of the then-called *D. opossum* Linnaeus but mentioned no specimens.

In his review of four-eyed pouched opossums, Thomas (1923, p. 603) treated all recognized forms as subspecies of *Philander* (then *Metachirus*) *opossum*. His description of *Metachirus opossum nigratus* (1923, p. 603) conforms to that of a sexually dichromatic male *P. andersoni andersoni*.

SYMPATRY—H. Hinse, who collected in the Pucallpa region, took both *P. andersoni andersoni*

TABLE 15. *Extended.*

Preorbital Width	Postorbital Width	Braincase Width	Palatal Length	i-m ⁴	m ¹⁻⁴
10.4, 12.5, 10.6	8.3, 8.8, 8.9	19.9, 21.1, 19.7	40.1, 41.1, 39.7	35.5, 35.4, 34.2	13.6, 13.0, 12.6
12.3, 14.3	8.8, 8.5	19.6, 22.0	41.2, 44.6	36.5, 38.1	13.5, 13.8
12.6, -, 13.7	8.6, 8.4, 9.4	19.6, -, 22.4	42.6, 43.8, 42.6	37.8, 38.2, 38.5	14.0, 14.0, 14.1
12.6	8.2	21.0	42.5	37.0	13.4
-	8.9	20.8	40.8	36.8	13.5
14.4	8.6	22.4	44.3	38.2	13.5
12.3	8.8	19.6	41.2	36.5	13.5
12.3	8.7	20.0	41.2	36.7	12.9
12.8	8.8	-	41.3	36.3	13.6
12.6	8.0	19.9	40.5	36.3	13.2
-	8.5	19.8	41.2	36.2	13.4
-	9.2	-	48.9	43.3	16.0
-	9.2	21.6	43.4	39.1	14.5
13.7	9.3	21.5	45.8	39.3	13.7
13.5	8.4	20.8	44.5	38.4	14.6
-, -	-, 9.0	-, 22.5	40.9, 44.2	36.0, 38.9	13.2, 14.4
-, -	8.0, -	22.6, -	44.0, 42.4	38.9, 37.2	14.4, 14.0
14.0	9.8	21.0	44.9	38.8	14.3
12.5	9.4	19.6	42.5	38.7	14.6
15.3	10.1	23.9	49.6	42.9	15.0
13.0	8.0	19.8	41.8	36.8	14.0
-, 13.7, 12.7	-, 8.8, 8.7	-, 20.2, 20.7	-, 42.0, 43.0	-, 36.4, 37.2	14.2, 14.1, 13.7
13.0, 12.9	9.3, 8.2	20.5, 19.3	42.2, 41.0	37.3, 37.0	14.8, 14.2
-, -, -	9.1, 8.5, 8.9	22.3, 20.5, 22.1	41.6, 39.7, 44.6	36.5, 35.2, 36.8	14.0, 13.4, 13.5
11.8, 14.5	8.7, 8.7	21.2, 21.0	41.8, 46.5	35.2, 38.6	12.0, 13.4
13.6	8.6	21.2	43.3	38.0	14.3
13.9, 13.2	8.8, 9.0	19.9, 20.0	45.0, 40.3	37.8, 35.8	13.9, 13.6
-	9.0	21.3	42.0	37.5	14.0

and the smaller *P. opossum quica* 59 km W of Pucallpa, October 1971 and 1972 and November 1971, but only *P. opossum* 59 km NE of Pucallpa (September 1972) and 59 km SW of Pucallpa (October 1972).

SPECIMENS EXAMINED—82. ECUADOR. *Napo*: Río Napo, 3 (BM[NH]); Río Yana Rumi, 1 (FMNH); San José, below, 2 (AMNH); *Pastaza*: Copataza, 3 (AMNH, 2; FMNH); Río Pindo Yacu, 2 (FMNH); Montalvo, Río Bobonaza, 2 (FMNH); Sarayacu, 1 (AMNH). COLOMBIA. *Caquetá*: Tres Troncos, Río Caquetá, 4 (FMNH); *Putumayo*: 17 km N Puerto Asis, 1 (UKMNH). VENEZUELA. *Territorio Federal Amazonas*: Capibara, Casiquiare Canal, 7 (USNM); Belén, Río Cunucunumá, 1 (USNM); Acan-

aña, Río Cunucunumá, 1 (USMN); Tamatama, 9 (USNM); Playa del Río Base, Mt. Duida, 2 (AMNH); Mery, Río Casiquiare, 1 (AMNH); San Juan, Río Manapiare, 2 (USNM); Esmeralda, 2 (USNM). PERÚ. *Amazonas*: 5 mi W Huampani, Río Cenepa, 1 (MVZUC); La Poza, Río Santiago, 1 (MVZUC); *Ayacucho*: Huanhuachayo, 1 (LSUMZ); San José, Río Santa Rosa, 1 (LSUMZ); *Junín*: Chanchamayo, 2 (BM[NH]; fmnh); Inañez, 1 (BM[NH]); Utcuyacu, 1, holotype of *nigratus* Thomas (BM[NH]); *Ucayali*: Iquitos, 3 (BM[NH], 2; AMNH); Santa Elena, Río Samiria, 2 (FMNH); Santa Luisa, 2 (FMNH); Yana Yacu, Yurimaguas, 3, including holotype of *andersoni* Osgood (FMNH); Orosa, 1 (FMNH); Río Curaray, mouth, 7 (AMNH);

TABLE 16. Measurements of *Philander andersoni mcilhennyi*.

Locality	Head and Body	Tail	Hind Foot	Ear	Condylbasal Length	Zygomatic Breadth
Perú ♂♂						
Balta	299	276	43	41	74.4	37.6
Perú ♀♀						
Balta	290, 292	304, 305	44, 43	42, 35	73.9, 73.+	36.8, 36.8

Lago Mirañes, Río Napo, 2 (BM[NH]); Pucallpa, Río Ucayali, 8 (USNM); Pasco: San Juan, Oxapampa, 1 (USNM).

Philander andersoni mcilhennyi
Gardner and Patton

Philander mcilhennyi Gardner and Patton, 1972:2, Fig. 1 (furred tail base), Fig. 2 (skull). Reig et al., 1977: 197, 212, Pl. 2E (karyotype)—PERÚ: Ucayali (Balta, Río Curanja); karyotype ($2n = 22$). Patton et al., 1995 [1996]:7, 20, 21—BRASIL: Amazonas (Alto Rio Uruçu); relationships based on molecular evidence.

Philander andersoni Engstrom and Gardner, 1988:231—*P. mcilhenni* [sic] a synonym. Emmons and Feer, 1990:18—part, PERÚ: Ucayali; BRASIL: Acre.

TYPE—Adult female, skin and skull, Louisiana State University, no. 16395 (originally no. 11541); collected 10 April 1971 by Alfred L. Gardner.

TYPE LOCALITY—Balta, Río Curanja, upper Río Purús, Ucayali, Perú; altitude about 300 m.

DISTRIBUTION (Fig. 5)—Known only from the banks of the upper Río Purús, Ucayali, Perú. Emmons and Feer (1990, p. 18) included Acre, Brasil, in the geographic range based on specimen in the U.S. National Museum of Natural History.

CHARACTERS—Darkest of four-eyed opossums; dorsal band broad and more or less differentiated from sides, its long, coarse dorsal pelage often manelike, extending over basal fourth or fifth of tail; fore- and hind limbs brown except for contrastingly pale or unpigmented digits of forefeet; ventral surface of body dominantly dark brown, variously mixed with gray; throat, chest, and belly often marked with large, irregular, whitish, buffy, or ochraceous patches; two-fifths to three-fifths of terminal portion of tail sharply contrasted pale brown or whitish.

COMPARISONS—Distinguished from *P. andersoni andersoni* by darker coloration throughout, pelage of dorsal band longer, wider, coarser; tail base bushy, 4–6 cm; from sympatric representa-

tives of *P. opossum* by larger size, overall darker coloration, and broad, dark dorsal band.

MEASUREMENTS—Tables 1 and 16.

REMARKS—Morphologically, *P. andersoni mcilhennyi* intergrades completely with *P. andersoni andersoni* through the Pucallpa, Río Ucayali (8 specimens), and Santa Elena, Río Samiria (2 specimens). The two groups are assigned to *P. andersoni andersoni*.

The geographic origin of the tissue studied by Patton et al. (1995 [1996]) and identified as that of *P. mcilhennyi* lies well within the area of projected sympatry between *P. andersoni mcilhennyi* and *P. opossum quica* (map, Fig. 5). Patton et al. did not explain why they prefer the junior synonym *mcilhennyi* as the species name for the dark gray four-eyed opossum, *P. andersoni*.

Hutterer et al. (1995, p. 15) believe that *Philander mcilhennyi* and *P. andersoni* are distinct species, but comparisons were made only between *P. mcilhennyi* and *P. opossum*, which are indeed distinct. They point to differences in the color pattern of the head and the clipped genal vibrissae of *P. opossum*. Normally, all facial vibrissae in *P. opossum* are as in *P. mcilhennyi* (= *P. andersoni mcilhennyi*). They also claim that *andersoni* and *opossum* are “probably separately confined to the western and eastern cordillera [sic] of the Andes.” In fact, both subspecies are confined to the eastern side of the Andes in Perú (infra map, Fig. 5).

SPECIMENS EXAMINED—4. PERÚ. Ucayali: Balta, 4, including holotype of *mcilhennyi* Gardner and Patton (LSUMZ).

Behavior of the Four-Eyed Pouched Opossums (*Philander opossum*)

The activities and traits are arranged alphabetically.

TABLE 16. *Extended.*

Preorbital Width	Postorbital Width	Braincase Width	Palatal Length	i-m ⁴	m ¹⁻⁴
14.0	9.0	21.2	45.1	39.8	15.3
14.7, 13.9	9.2, 9.2	21.0, 21.0	44.5, 44.7	39.7, 39.3	15.3, 14.9

Aggression, reaction, defense
 Associations
 Barbara: The pale-phase four-eyed opossum
 Blood values
 Fat storage
 Foraging
 Grooming
 Habitat
 Home range and territoriality
 Hydrotropism
 Locomotion
 Longevity
 Maternal care
 Mobility
 Nest
 Population density

Breeding
 Cannibalism
 Diet
 Display
 Enemies, predators
 Eye shine
 Population dynamics
 Posture
 Reproduction
 Sleep
 Sociability
 Spontaneous bleeding
 Stress
 Tail transport
 Taming
 Thermoregulation
 Vocalization
 Weight

Miller (in J. A. Allen, 1916c, p. 589; Mato Grosso, BRASIL)

“When trapped it does not feign death but fights viciously, biting at any object within reach and holding on until its strength fails. They do not hesitate to bite iron bars or steel traps even though it may break the teeth.”

Wilson (1970; Barro Colorado Island, PANAMÁ)

“About 8:07 PM on the evening of 3 February, 1969, I observed an aggressive encounter between *Didelphis marsupialis* and *Philander opossum*. The incident occurred in the laboratory clearing near the animal house on Barro Colorado Island, Panama Canal Zone. A loud hissing noise attracted my attention to a small *Didelphis* and a *Philander* that were circling slowly and snapping at each other on the lawn. Neither showed signs of wounds and both moved adeptly. Each attempted to grasp the rostrum of its opponent. Whenever the *Didelphis* secured this grasp, it quickly threw the *Philander* to the ground and held it down with both forefeet and hindfeet, at the same time biting it in the head. Twice in 2 minutes, the *Philander* broke loose and tried to escape but each time was attacked by the *Didelphis*. Soon the *Philander* was effectively pinned on its back and by 8:22 PM had died from the repeated bites on the head, or at least no longer responded to the attacker.”

Hershkovitz (field notes; COLOMBIA)

The usual reaction to apparent or presumed aggression is a bipodal or tripodal stance, mouth-open hissing, often with a lurch forward of the body as if to attack.

Aggression, Reaction, Defense

Enders (1935, pp. 410, 412; Canal Zone, PANAMÁ)

“Next to the Brown Opossum [*Metachirus nudicaudatus*], this is the fiercest fighter of the opossums studied. Allen’s opossum is ready to fight at all times and no amount of handling appears to diminish its resentment.”

One shipped live in the same box with a *Metachirus* of approximately the same size “had been thoroughly cowed by the more aggressive *Metachirus* and showed signs of having been bitten severely about the head and neck, while the aggressor was scatheless.”

Goldman (1920, p. 52; PANAMÁ)

“Unlike *Didelphis* when taken in steel traps these opossums are always ready to fight savagely.”

Associations

Hershkovitz (field notes; COLOMBIA)

Philander opossum was captured in the same

trap lines with species of *Metachirus*, *Chironectes*, *Didelphis*, *Caluromys*, *Monodelphis*, and mouse opossums (Marmosinae). All inhabit the same forests.

Barbara: The Pale-Phase Four-Eyed Opossum

Hershkovitz (field notes, October 1992)

A pale-phase female was live-trapped 17 October 1992 in a wooded area about 1200 m above sea level in the Parque Nacional do Caparaó, eastern Minas Gerais, Brasil. Her nearly completely closed pouch sheltered six attached young, possibly no more than 1 week old. She was kept in her cage for observation of behavior and litter development. Dubbed Barbara, she accepted captive life with equanimity, making no attempt to escape even when the door of her cage was opened for feeding or cleaning. She ate everything served, whether beef, chicken legs, insects, peanut butter, bananas, or mice. Live mice dropped into the cage were instantly attacked, the head and neck seized and crunched in her jaws. The mice were completely devoured with nothing left of flesh, entrails, skin, or bones.

Barbara slept most of the day curled up under the cut grass provided for nesting. Prepared food or raw fruit given during the day was usually consumed at night. Water was imbibed at all hours. Although normally nocturnal, should a live insect or mouse be dropped into the cage during the day, Barbara would awake with a start and make an instant kill and a fast meal. She easily devoured an entire mouse 10 to 15% of her own weight and looked for more.

When wanting food Barbara would fix her eyes on the nearest person, raise her muzzle, and sniff expectantly.

On one occasion Barbara left intact hide and fur of a mouse otherwise completely consumed.

Barbara washed her face frequently after and during meals. One or both paws were used. Grooming forequarters, sides, and underparts usually followed in that order without particular attention to the pouch and none to the young.

On the 26th of October, head-rump length of the six still-attached pouch young ranged from 1 to 2 cm. Mother and offspring were transported the next day to Rio de Janeiro, where facilities were available for their care.

Blood Values

Tyndale-Biscoe (1980, p. 718; COLOMBIA)

Blood values measured at sea level (Buenaventura), 500 m above (Villavicencio), and 1600 m above (Cali) revealed correlations with age and altitude. Hemoglobin concentrations and hematocrit values were lowest at lowest altitudes, and those for pouch young lower than for adults.

Breeding

Natterer (in Pelzeln, 1883, p. 110—Sepetiba, Rio de Janeiro, BRASIL)

Female captured 8 March 1818 with five naked, blind pouch young.

Female captured 29 September 1822 in Ipanema, Rio de Janeiro, with four blind pouch young ("*D. dichrura*").

Miller (in J. A. Allen, 1916c, pp. 563, 589—Urucum, Mato Grosso, BRASIL)

"Number of young is usually small, between three and eight."

Davis (1947, p. 2—Teresópolis, Rio de Janeiro, BRASIL)

Seven of 32 females captured in Teresópolis had pouch young, average number, 4.5. Two females each had seven young and seven nipples in pouch. Breeding begins in August and continues until February.

Fonseca and Kierulff (1989, p. 119—Atlantic forest, Minas Gerais, BRASIL)

Female captured February and another in August had five pouch young each.

Corqueira et al. (1993—Rio de Janeiro, Restinga de Barra de Maricá, BRASIL)

	Total ♀ ♀ cap- tured	Lac- tant
January	12	7
April	16	0
July	15	7
October	9	6

Tyndale-Biscoe (1980, p. 713—Buenaventura, Valle, 10 m; near Villavicencio, Meta, 500 m; near Cali, Valle, 1000 m, COLOMBIA)

Four females captured August and September 1971, one pregnant, three lactating, and each with five pouch young.

Charles-Dominique et al. (1981, p. 425—Ile de Cayenne, GUYANE FRANÇAISE)

Litter size, 4.24 (1–7).

Litters mature in 70 days.

Lactating females three of 16 in June, two of 13 in July, zero of nine in August.

Pouch young survival and food availability: first litter following dry season, 97% ($n = 36$); second litters, 97% ($n = 38$); third litters, food scarce, 28% ($n = 67$).

Interval between litters, 90 days.

Sexual maturity, 150 days.

Seventy-nine percent of October–November population ($n = 42$) born in preceding season.

Ovarian cycle inhibited by lactation but not by gestation.

Charles-Dominique (1983, p. 409, GUYANE FRANÇAISE)

Didelphoid breeding is continuous throughout the year, but successful reproduction is dependent on a rich diet for the female and is seasonal. Up to three successive litters may be produced in 1 year. The third litter “generally occurs at the beginning of the period of food scarcity and in most cases the females lose weight and young die in the pouch at a more or less early stage. Exceptionally, another litter can follow and abort, but generally reproduction is interrupted until the beginning of good recrudescence of fruiting. Among the Didelphidae, *P. opossum* behaves more like an *r*-strategist in favoring rapid population increase in an unstable environment.”

Charles-Dominique (1983, p. 409, GUYANE FRANÇAISE)

Comparison of breeding conditions between *Philander opossum* and *Caluromys philander* of Guyane Française, two similar-sized species occupying different ecological niches:

Philander opossum

Caluromys philander

1. Mainly terrestrial

1. Almost entirely arboreal

2. Omnivorous but largely frugivorous

2. Mostly frugivorous, nectarivorous

3. Food availability variable in undergrowth where foraging is done

3. Food availability less variable in upper strata where foraging is done

4. Birth to weaning 68–75 days

4. Birth to weaning 110–125 days

5. Size weanling, 50–75 g

5. Size weanling, 50–75 g

6. Age at sexual maturity, 6 months

6. Age at sexual maturity, almost 10 months

7. Up to three successive litters in same year (third litter mostly pouch-aborted)

7. Two successive litters in same year

8. Behavior as *r*-strategist¹

8. Behavior more like that of *k*-strategist²

9. Nesting period, 8–15 days

9. Nesting period, 30–45 days

10. Litter size not more than 7

10. Litter size not more than 7

¹ *r* strategist: *r*-selected species, selection favoring a rapid rate of population increase. Typical of species that colonize short-lived environments or of species that undergo large fluctuation in population size.

² *k* strategist: *k*-selected species, selection producing superior competitive ability in stable, predictable environments in which rapid population growth is unimportant as the population is maintained at or near the carrying capacity of the habitat.

Atramentowicz (1986a, p. 125, GUYANE FRANÇAISE)

During a study period from September 1978 through October 1979 in Cayenne, two successive litters were produced between September and June. Some females, however, produced three litters in the same period. The difference is attributed to an abundance of food and a shortened nesting period. In the event of a food shortage, milk production ceases. Death of lactating young starved at the nipple is termed pouch abortion.

Average adult weight, 400 g.

Atramentowicz (1986a, p. 123, GUYANE FRANÇAISE)

During a 26-month (1978–1982) investigation of didelphoid breeding, “animals were live trapped, marked and then released. *Caluromys philander*, *Philander opossum*, and *Didelphis marsupialis* are nocturnal, with a mixed frugivo-

TABLE 17. "Reproductive condition of 22 adult females of *Philander opossum* from Nicaragua" (Phillips & Jones, 1969, p. 345).

Date of Capture	Weight (g)	Pouch Young	Measurements ¹ (mm)
16 February	—	None	—
2 March	—	7	20.0 ²
4 March	—	7	nm ³
5 March	—	7	nm
8 March	—	6	nm
8 March	—	6	nm
10 March	—	7	24.0 ²
13 March	—	3	43.0 ²
17 March	355.0	5 (2♂, 3♀)	44.8
29 March	—	4 young, out of pouch (3♂, 1♀)	107.0
31 March	420.2	5 (1♂, 4♀)	35.2
31 March	402.4	5 (3♂, 2♀)	31.0
2 April	546.3	7 (5♂, 2♀)	63.8
2 April	674.5	6 (4♂, 2♀)	65.5
2 April	361.8	6 (2♂, 4♀)	38.5
15 April	—	7 (4♂, 3♀)	48.0
15 April	521.3	7 (3♂, 4♀)	44.0
15 April	464.9	7 (3♂, 4♀)	47.1
24 April	352.1	6 (4♂, 2♀)	57.0
2 July	256.3	7 (2♂, 5♀)	40.5
6 July	550.0	Lactating, no pouch young	—
15 July	590.0	7 (5♂, 1♀, 1?)	89.0
27 July	282.7	5	nm

¹ Head and body combined.

² "Probably crown-rump length."

³ nm = no measurement.

rous and insectivorous diet. The first species is arboreal, the others mainly terrestrial, but may be seen climbing to the canopy. The percentage of lactating females in the studied population has been compared to food supply in terms of the availability of fruiting food plants."

"The collected data show a direct relation between these two factors. Breeding occurs throughout the year but food scarcity may interrupt reproduction either with no births or 'pouch-abortions' (death of pouch-young) by starvation for lack of milk production."

Atramentowicz (1986b, p. 140, GUYANE FRANÇAISE)

Youngest lactating female, age 8 months.

Pouch young 4.2 (2-7); 179 litters.

Two births between September 1978 and October 1979.

Atramentowicz (1988, p. 55, GUYANE FRANÇAISE)

"Fruits are essential during lactation, the sugars they contain helping the females to cover their increased energy need during this period. On

weaning, the inhibition of the ovarian cycle is removed and a new litter may be produced during the next 15 days. In fact, the ovarian cycle is not inhibited during gestation as in placental mammals, but by the suckling which begins after birth when the embryos attach themselves to the teats."

Phillips and Jones (1969, NICARAGUA)

Size, weight, length, and dates of pouch young of 22 litters are shown in Table 17. Dates range from 16 February to 27 July; pouch litter size, 6.05 (3-7) 21; sex ratios in 13 of the litters with 78 young was 41 (53%) ♂♂, 37 (47%) ♀♀; average head and body length per litter increased from 20.0 to 107.0 mm within above time frame.

Biggers (1966, p. 264, NICARAGUA)

Seventy-three live-trapped males had spermatozoa in testis and epididymis throughout the year; testis weights are lower from September to December inclusive than in remainder of year.

Pouch young found January to October inclusive with peaks in January, May, and August.

Mature animals obtained January to November inclusive. No males trapped in December. No dif-

ference in weight of testes of mature animals throughout the year.

Discrepancies noted in paragraphs one and two above are confusing. Perhaps the mixture of data for *Philander* and *Didelphis* is the cause. Biggers refers readers to the original compilation of data.

Enders (1935, p. 411, PANAMÁ)

Only nonbreeding females captured January to April; starting July, "females with litters outnumber those without; litters of two, four, and five were observed."

Enders (1966, p. 198, PANAMÁ)

"Observations on 18 captured *Philander* indicate that their breeding season . . . begins with onset of the dry season in February."

"The largest litter encountered was five."

Fleming (1973, p. 444, Canal Zone, PANAMÁ)

Females were reproductively active during June, July, and September through December in 1966 and during February through April and June in 1967. Females carrying pouch young or lactating in October and November were anoestrus. Two, possibly more, litters are produced per season.

"Males of *P. opossum* are sexually mature at a body length of 230 millimeters or greater . . . adult males probably are sexually active throughout the year."

Litter size 4.6 (2-7) 34; sex ratio 22 (45%) ♂♂, 27 (55%) ♀♀.

Seba (1734, p. 57, SURINAME)

Eight pouch young were counted.

Seba and Miller (above) are the only authors to record eight pouch young. Maximum number in all other cases is seven, in agreement with number of nipples. *Philander*, unlike *Didelphis* and others, may not produce more young than can be suckled.

Cannibalism

Charles-Dominique (1983, p. 405; Cayenne, GUYANE FRANÇAISE)

Many cases of cannibalism have been observed in captivity of weaned young being eaten by other young and the mother.

Density

Charles-Dominique et al. (1981, p. 383, Cayenne, GUYANE FRANÇAISE)

100-200 individuals per km².

Diet

Temminck (1827, p. 38)

It preys on small birds and insects but also eats fruit. In captivity it feeds on meat.

Pelzeln (1883, p. 111, BRASIL)

Insects found in stomach.

Goldman (1920, p. 52; PANAMÁ)

"The stomach of one taken at Gatun was well filled with fragments of crabs. Stomach contents of several others at the same locality were filled with fragments of birds alone, or of birds including their feathers, and crabs intermixed."

Fleming (1972, p. 623; Canal Zone, PANAMÁ)

"Stomachs of the four-eyed opossum contained unidentified plant material, the pulp of *Corozo oleifera* nuts, insect and fresh water shrimp remains, murid rodent fur, and the tail of a young spiny rat (*Proechimys semispinosus*). One individual was seen feeding on live bats caught in a mist net."

Schomburgk (1840, p. 344; GUYANA)

"They are very destructive to poultry and likewise to fruit. They are often found on those savannahs where the wild pine (*Bromellia* sp. ?) flourishes, to the fruit of which they appear to be partial."

Enders (1935, p. 410; Canal Zone, PANAMÁ)

They "are accused of being poultry- and bird-killers. . . . In captivity they were more carnivorous than any of the other opossums observed. 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. One hungry individual, while fearful of the hand offering a ripe banana, nevertheless sniffed from a safe distance while saliva dripped from its jaws."

Dalquest (1953, p. 19; eastern San Luis Potosí, MÉXICO)

"One animal became entangled when it attempted to climb a net to obtain an entrapped bat, others were taken in traps baited with decayed meat, and two were shot while they were feeding on small wild figs. Remains of insects were usually present in the stomachs of the specimens taken."

Anthony in Goodwin (1934, p. 5; GUATEMALA)

"I was told that these little opossums are often killed in the sugar house [*trapiche*] and that they are quite fond of sweets. . . . At Finca Capres, several times I surprised them at night, feeding on the ripe [bananas]. . . . At Chipore . . . one was attracted by bait composed chiefly of peanut butter and rolled oats."

Hall and Dalquest (1963, p. 198; Veracruz, MÉXICO)

"It has been seen feeding on sweet-lemons, jobo plums, and the fruit of the Chico Zapote (*Sapote achras*) source of chewing gum." One opossum "was seen at the base of a large, hollow fig tree. The upper part of the hollow in the tree served as a retreat for a colony of the large fruit bat, *Artibeus jamaicensis*. Bats were bringing small green figs into the hollow and feeding on them. Parts of the fruit, varying in size from almost whole figs to mere shreds, were dropped by the bats. The four-eyed opossum was feeding on these bits of figs."

The opossum "followed our trap lines, eating mice and other small mammals that had been captured. These opossums were easily trapped by using flesh, preferably much decayed, for bait."

Dubost (in Charles-Dominique, 1971, p. 197, GUYANE FRANÇAISE)

Philander eats tree exudate, and like the primate *Cebuella* (Callitrichidae) or *Microcebus* (Lemuridae) uses its teeth to reopen healed openings in tree trunks to renew the flow of sap.

Charles-Dominique (1983, pp. 397, 398; Cayenne, GUYANE FRANÇAISE)

The diet is opportunistic, consisting of fruits, flowers, nectaries, insects, earthworms, small vertebrates, and carrion. Sympatric *D. marsupialis* subsists on about the same; *Marmosa murina* pre-

fers fruits but takes earthworms and small vertebrates. *Marmosa cinerea* [= *Micoureus demerarae*] and *C. philander* are vegetarian.

"The period of food scarcity determined both by records of fruit and insect abundance and also by body weight changes in the marsupials begins in May, is most critical during June–July–August and ends in September. Data collected in 1976 and from 1976 to 1982 by the Institut Pasteur de Cayenne (variation in weight and reproductive condition of marsupials) suggest that this period of food scarcity is a regular phenomenon, probably correlated with seasonal variations in rainfall."

Charles-Dominique et al. (1981, p. 376; Cayenne, GUYANE FRANÇAISE)

"Eighty percent of stomach contents consisted of a great variety of prey. During the rainy season, earthworms, some of which are as much as 80 cm long, forced above ground, made up a large part of the diet.

"Fallen fruit consumed were mainly *Attalea regia*, *Virola melinonii*, *Virola sebifera*, *Virola surinamensis*, *Ocotea puberula*, *Richardella macrophylla*, *Ficus* spp., *Cordia exaltata*, *Simarouba amara*, *Protium heptaphyllum*. In general the pulp is eaten with only the smallest seeds (*Ficus*, etc.) swallowed, the larger ones spit out. The ground level flowering of the Balanophoracea from January to June is actively sought for the nectar. Losses weight during dry season (September–November in the years 1978, 1979) when fruit is scarce, fatten when fruit is abundant."

Tyndale-Biscoe (1980, p. 716; COLOMBIA)

"They would eat fruit and vegetables provided as well as meat; chicken bones were held in the hands and the ends chewed."

Atramentowicz (1986a, p. 125; Cayenne, GUYANE FRANÇAISE)

Eats ripe pulpy fruit, insects, and small prey such as earthworms, frogs, etc.

Atramentowicz (1988, p. 48; Cayenne, GUYANE FRANÇAISE)

Stomach contents of *Philander opossum* consist of 50% fruit with the remainder invertebrates, small vertebrates, and carrion. A preference is shown for ripe fruit fallen to the ground. The fruit consumed represented 44 species in 21 families.

It was characterized by a fleshy pulp with a high percentage of water. The color may be bright or dull, size large or small, shape variable. The pulp may be rich in sugar or lipids but poor in nitrogen, which the animal finds in animal prey.

Display

Hershkovitz (field notes)

The supraorbital spots are conspicuous at night, at least to the sharp-eyed (see "Sleep," p. 77). Conspicuous supraorbital marking displayed by both nocturnal and diurnal animals may serve for recognition between conspecifics. I find no difference in markings between the sexes, and the signs are usually absent or faint in juvenals.

Enemies, Predators

Most likely predators are the eyra cat (*Herpailurus jagouaroundi*) and smaller spotted cats, large mustelids such as the tayra (*Eira barbara*) and grison (*Galictis vittata*), foxes, large owls, and snakes. Husson (1978, p. 26) found remains of a *Philander opossum* in the stomach of a garden tree boa (*Corallis enhydris*) in Suriname. Schomburgk (1840, p. 344) reported that "they are sometimes eaten by the Creoles and Indians [of Guyana], but as they have a rank and disagreeable smell I doubt if they would prove palatable to us."

Wilson (1970, p. 386) reported an encounter in Panamá between *Didelphis marsupialis* and *Philander opossum* with the former overcoming and devouring skin, flesh, bones, and brain of the latter (see details under "Aggression, Reaction, Defense").

Eye Shine

Anthony in Goodwin (1934, p. 5; GUATEMALA)

"In the beams of the carbide hunting lamps, their eyes were extremely bright, gleaming white, like electric lamps, easily seen at one hundred yards or more."

Enders (1935, p. 412; Canal Zone, PANAMÁ)

The eyes of [*Philander*] show up as a reddish

yellow under the hunting lamps while the eyes of [*Metachirus*] show red."

Hershkovitz (field notes)

The eyes of *Philander*, like those of other didelphoids and *Metachirus*, usually glow bright orange when reflecting the beam of a battery-powered flashlight. There is individual variation in tone of eye shine depending on the amount of environmental light, intensity of directed light, and angle of reflection. These factors and the uncontrolled conditions make it difficult to find significant differences in color of didelphid eye shine. More important for identification is distance between the eyes and animal gait as seen by the reflected light.

Fat Storage

Hall and Dalquest (1963, p. 198; Veracruz, MÉXICO)

"In the lowlands these opossums seldom were fat, but in the highlands, at 5000 feet elevation and higher, in winter, they had a deep layer of yellow [!] fat immediately beneath the skin."

Foraging (Table 18)

Charles-Dominique et al. (1981; Cayenne, GUYANE FRANÇAISE)

Of a total of 294 individuals live-trapped or tracked by radio, 185 were located from 0 to 6 m above ground in the following situations: on ground 70%; fallen logs 7%; small tree trunks 2%; branches 6%; lianas or vines 15%.

Charles-Dominique et al. (1981, p. 343; Cayenne, GUYANE FRANÇAISE)

Nearly always forages on the ground; of 100 individuals live-trapped only three were captured above ground.

Charles-Dominique (1983, p. 397; Cayenne, GUYANE FRANÇAISE)

See Table 18 for body mass and above-ground foraging by five syntopic species of opossums.

TABLE 18. Body mass and above-ground foraging by five syntopic species of opossums.

Taxon	Weight (g)	Substrate
<i>Marmosa murina</i>	40	Low (shrub)
<i>Marmosa cinerea</i> [= <i>Micoureus demerarae</i>]	80	High
<i>Caluromys philander</i>	300	High
<i>Philander opossum</i>	400	Low (essentially ground level)
<i>Didelphis marsupialis</i>	1,000	Low (may climb to feed on fruit)

Grooming

Hershkovitz (field notes, January 30, 1941; northern COLOMBIA)

A captive washed face with hands mouselike; groomed remainder of body with tongue catlike.

Charles-Dominique (1983, p. 407; Cayenne, GUYANE FRANÇAISE)

"We have never observed any allogrooming between [caged] adults, even during mating periods."

Habitat

Hall and Dalquest (1963, p. 196; Veracruz, MÉXICO)

". . . ranges throughout the tropics of Veracruz. At the extreme upper edge of the upper humid division of the Tropical Life-zone, it lives along cold, clear streams at the edge of the oak belt. Lower down but still in the upper humid division, it was found along rivers and streams that flowed through dense jungle, where the tall, broad-leaved trees were thickly hung with orchids, vines, mosses and bromeliads. The four-eyed opossum was found living in the thickets bordering the broad rivers of the coastal plain, in the arid division of the Tropical Life-zone, and along the marshy shores of rivers and streams of the lower humid division of the Tropical Life-zone, in the southern part of the state.

"Most of our specimens were taken on the very shores of rivers or streams . . . however . . . the species is not confined to such habitat . . . seven kilometers west of Potero, workers discovered a family of four young animals in a field of sugar cane, several kilometers from the nearest water at that time of the year. At Jimba, 350 feet elevation, in southern Veracruz, a four-eyed opossum was taken from a tree on a hillside fully three kilo-

meters from the nearest water. These records are unusual, however. Against them are nearly 30 records from in and near water."

Dalquest (1953, p. 19; eastern San Luis Potosí, MÉXICO)

"Found only in the tropics of the eastern part of the state . . . they are taken in dense vegetation growing along the shores of streams and rivers at elevations between 400 and 12,000 feet [more likely 1200 feet]. At El Salto the water is cold and flows swiftly between rocky canyon walls; opossums were found in thickets of ferns, vines, and low, woody plants. Near Huichihuayan, where the water is warmer and sluggish, opossums were taken in thickets of thorny bamboo."

Goodwin (1946, p. 284; COSTA RICA)

"Frequenting forested country from sea level up to about 4000 feet, he is most common at low elevations."

Davis (1947, p. 2; Teresópolis, BRASIL)

"Found more commonly in moist situations although individuals may wander through nearly any kind of vegetation."

Enders (1935, p. 410; Barro Colorado Island, PANAMÁ)

"They are not common on the Island for while they enter traps without hesitation none were taken; but many were captured at Alhajuella in habitats similar to those on the Island . . . why they are not abundant on the Island is a puzzle."

Schomburgk (1848, p. 777; GUYANA)

"It lives mainly in the coastal forests bordering the plantation. During the day it sleeps most of the time in its haunt under tree roots or in hollow trees."

Natterer (in Pelzeln, 1883, p. 111; southeastern BRASIL)

“... Fashions its nest from leaves on low trees.”

Miller (in J. A. Allen, 1916c, p. 589; Mato Grosso, BRASIL)

“... is found in deep forests. I have never known it to venture near houses for the purpose of robbing hen-roosts and nests like its larger relative [*Didelphis marsupialis*], although it may do so.”

Handley (1976, p. 8; VENEZUELA)

Lowlands of western and southern Venezuela, 46 specimens: on the ground, 98%; on a log, 2%; near streams and other moist areas, 100%; evergreen forest, 91%; orchards, croplands, yards, open areas, 9%; elevation 24–324 m.

Hall and Dalquest (1963, p. 198; Vera Cruz, MÉXICO)

“... are usually seen or trapped on the ground, but are sometimes seen in trees.” They prefer the vicinity of streams and seem to be as much at home in rivers as on their banks.

Enders (1935, pp. 410, 411; Barro Colorado Island, Canal Zone, PANAMÁ)

None “were taken in the Island but one was observed high up on a limb on Zetek Trail. . . . While a good climber [it] was usually encountered upon the ground, on or under logs. It is probably more terrestrial in habit than any of the other opossums studied excepting possibly *Didelphis*. This might be surmised from its build, which is well adapted to terrestrial locomotion.”

Davis (1947, p. 2; Teresópolis, BRASIL)

“These opossums seldom climb but are partial to fallen logs and windfalls.”

Farris (1950, p. 259; PANAMÁ)

“About eighteen females were collected in grass fields about 47 miles from Panama City in a location that is low and damp all the year.”

Charles-Dominique (1983, p. 419; Cayenne, GUYANE FRANÇAISE)

The frequency of encounter with *Philander* is

10 to 16 times greater in secondary than in primary forest.

Husson (1978, p. 26; SURINAME)

Some of these opossums were found under the floor of a home at Lelydorp.

Atramentowicz (1986a, p. 123; Cayenne, GUYANE FRANÇAISE)

Philander opossum is mainly terrestrial “but may be seen climbing to the canopy” in the second growth forest.

Da Fonseca and Kierulff (1989, p. 118; Atlantic forest, Minas Gerais, BRASIL)

“Fourteen individuals were caught during the [17-month] course of this study. The occurrence of this large didelphid is apparently tied to the presence of standing or running water. . . . As only a few transects occurred close to streams, this may explain the low trapping success for this species.”

“The species also proved to be primarily terrestrial with only 17% of captures in arboreal traps, and 7% of individuals climbed trees after being released.”

Unpublished (VENEZUELA)

Capture sites recorded by members of the Smithsonian Venezuelan Project (SVP) on field tags of captured specimens are summarized below:

	<u>N</u>
Live-trapped in banana grove	1
Snap-trapped on forest floor	2
Live-trapped on ground	9
Snap-trapped in river	1
Snap-trapped in tree	1
Shot in tree in forest	1
Shot in hollow tree near river	1
Shot in tree alongside river	<u>11</u>
Total	<u>27</u>

All *Philander andersoni* were taken in the Territorio Federal Amazonas. The *P. opossum* were captured in the state of Bolívar, where different ecological conditions prevail (Handley, 1976). It seems that *P. andersoni* is at least as arboreal as it is terrestrial, with perhaps a preference for trees

overhanging rivers. This type of habitat restricts enemy attacks to the forested side of the river and provides the opossum with the opportunity of escaping by diving into the water. The muskrat-like dorsal pelage of *P. andersoni mcilhennyi* and many individuals of *P. andersoni andersoni* seems to be better adapted than that of *P. opossum* for aquatic life. Where the two species occur together, as in Balta and along the Río Ucayali in Perú, *P. andersoni* may be more arboreal-aquatic than terrestrial, whereas *P. opossum* may be more terrestrial-aquatic than arboreal.

Home Range and Territoriality

Miles et al. (1981a, BRASIL)

A small, transparent plastic spool, 6 cm long with 2.2 mm internal and 2.4 mm external diameters, was wound with double-strand terylene thread. The spool was attached to a captive *Philander opossum*, and the free end of the thread was attached to the capture trap or nearby vegetation. As the released animal traveled through the night the thread unwound. The thread tracked during the day led to the diurnal nest or refuge. Distance traveled was calculated from the weight of the spool before release of the animal and after recapture.

Of 21 released animals, 16 were retrieved. The calculated distance for 15 retrievals averaged 438 m (93–1000 m). This compared with a mean of 801 m (51–2450 m) for *Didelphis marsupialis*.

Charles-Dominique (1983, p. 401; Cayenne, GUYANE FRANÇAISE)

Philander explores about 25,000 m² during the night.

"By systematically trapping, marking and releasing we have observed regular loss of individuals, compensated by immigrants from other areas (juveniles and adults of both sexes). Trapping was conducted using Tomahawk and Sherman traps placed on the ground and special 'home-made' traps set at 15 to 20 m in trees; traps were baited with bananas . . . The following data concern new-arrivals [in an over 20-ha study area] from May to October 1979, after 8 months of regular trapping and marking": May, eight immigrants; June, 2; July, 1; August, 3; September, 4; October, 3.

"Migration seems to be more important in *P. opossum* than in *C. philander*—after one year, the entire population of *P. opossum* had been replaced

by new individuals, but only one-third of the original *C. philander* population was replaced."

Atramentowicz (1986b, p. 145; GUYANE FRANÇAISE)

Didelphoids are solitary, not territorial, and many individuals are sedentary. Duration of residence in study area is compared with *Caluromys philander*, *Philander opossum*, and *Didelphis marsupialis* (Table 19).

Charles-Dominique (1983, p. 418)

All American opossums are nocturnal and solitary except during mating and maternal care of young. Territory is not defended. Home ranges overlap between many individuals, male and female, but with close contact avoided. There are no social bonds between adults apart from short copulatory periods; there is no allogrooming.

Hydrotropism (see also Habitat)

Hershkovitz (1962, field notes; SURINAME)

A female with 3 pouch young taken live 20 January 1962 from a snap trap in Lelydorpplan was caged for observation. The animal never recovered from the effects of the blow on the head received from the trap. She slept most of the time and when awake walked slowly with poor coordination. She permitted herself to be petted and seemed to enjoy it, but the docility probably owed to her weakened condition. She ate the insects fed to her and seemed to require large amounts of water. A *Marmosa murina* held captive at the same time derived all its water from fruit.

The *Philander* escaped twice from her cage. On each occasion she sought out the nearest dark, cool, moist refuge. The first time she curled up in an empty but still-wet canvas bucket in the kitchen. The second time, after I had moved to a frame house in La Poule, she snuggled into a dark, wet corner behind a primitive flush toilet.

Fonseca and Kierulff (1989, p. 118; Atlantic forest, Minas Gerais, BRASIL)

"The occurrence is apparently tied to the presence of standing or running water."

Tyndale-Biscoe (1980, p. 716; COLOMBIA)

"All these animals were caught in second

growth forest close to streams, in several caves less than a meter from water. It was thus interesting to observe that a pair in captivity would invariably defecate into the water container rather than elsewhere in the enclosure."

Locomotion

Dalquest (1953, p. 19; eastern San Luis Potosí, MÉXICO)

They "are swift in their actions. For the most part they hunt on the ground, but they climb readily, often to considerable heights, and are skillful swimmers. Animals twice escaped capture by diving into the water of the Rio Naranjos and swimming away beneath the surface."

Crespo (1950, p. 6; Misiones, ARGENTINA)

They "are excellent swimmers, water apparently being their preferred habitat. I have watched them at night swimming swiftly even upstream against the current in rivers such as the Uruguái."

Hall and Dalquest (1963, pp. 197, 198; MÉXICO)

"*Philander* is quick and active. Trapped individuals are able to jump about and twirl in surprising fashion. . . ." The animal "is an agile climber and a skillful swimmer."

"Along the Río Atoyac several four-eyed opossums were taken in a trap set beneath the water level, at the base of a cut-bank. They could have reached the trap only by swimming."

". . . A four-eyed opossum was seen just before midnight, running swiftly over the larger, rounded boulders (six to 18 inches in diameter) along the river bank. When frightened [by us] the animal turned [from the river's bank] and made a smooth, clean dive into the swift water, and as it did not reappear, must have swum away underwater."

Hershkovitz (field notes)

The usual didelphid locomotor pattern on the ground is a measured walking gait, and in climbing an alternating movement of the grasping hands and feet with support of the clinging, prehensile tail. The principal running gait on or above ground is a trot. I have never seen a didelphid leap or bound except in rapid escape. In descending a tree trunk the animal will proceed head first or simply drop to the ground.

Hershkovitz (1941, field notes; northern COLOMBIA)

The prehensile tail was used for swinging the body from limb to limb, the hands for grasping the next higher support. The animal would also use the tip of its tail for clasping an overhead limb, then climb its tail until it could grasp the limb above with its hands. Carrying an opossum by its tail can be hazardous. Marmosids habitually use the tail for climbing.

When attacking live prey, the opossum springs for throat or head with lightning speed.

Longevity

Farris (1950, p. 258)

Life span in captivity, 3 years, 6 months.

Atramentowicz (1986b, p. 140; GUYANE FRANÇAISE)

Based on tooth wear, longevity of wild *Philander opossum* and *Didelphis marsupialis* was calculated as 2.5 years; of *Caluromys philander*, as 3.5 years. Captive *Caluromys philander* (Brunoy, France) lived to 6 years. Maximum life expectancy of *Didelphis marsupialis* was said to be less than 36 months.

Maternal Care

Seba (1734, p. 57)

"The mother does not remove the young from her pouch before they are old enough to enjoy the light of day. When the time is right she retreats to a lookout to assure the safety of her young. She then opens the pouch and permits the offspring to emerge into the sunlight and play with her. At the slightest suspicion of danger she calls her young with a warning cry that sounds *tik, tik, tik*. The young respond immediately by returning to the pouch whereupon the mother runs to a hiding place."

COMMENT—Seba actually beheld the mother and her brood at one time or another. The fanciful description of their relationship (translation), however, must have been confected long after the supposed facts.

Didelphids are nocturnal, but in captivity, especially as household pets, as Seba's opossums

must have been, they generally adjust to the hours they are fed.

Nest

Goldman (1920, p. 52; PANAMÁ)

"A nest of one of these opossums was found three feet from the ground on a fallen log. The log lay in the dense thicket of an old clearing and was heavily overhung with vines and bushes. The nest, globular in form and about a foot in diameter, was placed in a well hidden spot among the vines. It was made entirely of the banana-like leaves of a native plant rather neatly laid together. The opening at one end faced outward along the log. . . . The nest cavity was clean and about the size of the animal's body."

Carriker (in J. A. Allen, 1911, p. 247; Yuruán, VENEZUELA)

"The female with a litter of young was taken out of the hollow stump in a grass field in the [forest] clearing."

Hall and Dalquest (1963, p. 197; Veracruz, MÉXICO)

"Several four-eyed opossums were taken in a trail leading from a dense thicket . . . to a stream ten feet away. . . . A hole, about five inches in diameter that led downward beneath the roots of a tree was discovered near the center of the thicket. This seemed to be the home of at least one of the opossums."

Two "were found in a nest that they had constructed in the palm thatch of the roofs of abandoned houses. These nests consisted of a handful of dry leaves, pushed in between the layers of palm fronds. From outside, a distinct spherical or oval lump in the thatch marked the site of the nest. Inside the house we could see no trace of the nests."

A nest "was found in a cavity in the side of a piece of tree trunk, 15 inches in diameter and three feet long, that was suspended in the air by vines. . . . The nest was of dry leaves, about 11 inches deep and seven inches in diameter."

One animal "was shot from the large hollow in the side of a giant 'ligaron' [higaron?] tree. This tree was fully 12 feet in diameter at waist height, and contained a hollow about 60 feet high and five feet in diameter."

Dalquest (1953, p. 19; eastern San Luis Potosí, MÉXICO)

"A burrow near Huichihuayan was in muddy soil beneath a clump of thorny bamboo, and another was beneath a decayed log, nearly concealed by vines and succulent plants. This burrow was so shallow that when the log was rolled aside the entire burrow was exposed. A nest at the end of the branched burrow consisted of a formless mass of dry leaves a foot in diameter. Two feet away there was an opening to the dense vegetation beside the log. Three feet farther on, the burrow emerged from under the log; and a trough like trail led through the vegetation to the river, twenty feet away."

Murie (1935, p. 16; GUATEMALA)

"In the edges of the pine ridge, especially near the streams, were numerous well worn trails about five inches wide, which were apparently made by these opossums. Many of the trails led from one ground burrow to another. At the end of one of the burrows about fifteen inches from the entrance, I found a nest ten inches in diameter, composed of dry sedges."

Enders (1966, p. 201; PANAMÁ)

After the young are born the female moves about more. Unlike habits during the rest of the year (Enders, 1935, p. 397), they frequent the same nest. Later, when the young are able to detach themselves and so leave the mother, young may continue to use the nest.

Husson (1978, p. 26; SURINAME)

Nest with female and seven young found under a tree. Nothing more is said.

Miles et al. (1981a, p. 341; BRASIL)

"Nests of the opossum were often found 8–10 m above the forest floor in hollow trees or as open nests in tree forks; some nests were, however, terrestrial, in cavities besides buttressed tree roots."

Farris (1950, p. 259; PANAMÁ)

"The animals usually were found in their nests in palm trees, at the branching and in the leaves about 5 feet off the ground where conditions were relatively dry."

Population Density

Charles-Dominique et al. (1981, p. 383; Cayenne, GUYANE FRANÇAISE)

Philander opossum was one of the most abundant mammals on the island. Its biomass, based on 199 observations within a square kilometer, was calculated as between 100 and 200 individuals, with a biomass between 40 and 60 kilograms in the same area. The biomass of each of the five other marsupials of the same area was 25 to 50 kg for *D. marsupialis*, 30 to 60 kg for *C. philander*, 2 to 8 kg for *Marmosa cinerea* [*Micoureus demerarae*], and 0.7 to 3.5 for *M. murina*.

Of the six marsupial species inhabiting the island, *Philander*, *Didelphis*, *Caluromys*, and *M. murina* were most abundant. *Marmosa cinerea* [= *Micoureus demerarae*] were moderately abundant; *Monodelphis brevicaudata*, uncommon.

Cerqueira et al. (1993, p. 513; Restinga de Barra de Maricá, Rio de Janeiro, 22°57'S, 42°51'W, an impoverished small animal community, Atlantic forest, BRASIL)

Average density 1.91/ha; population maintained mostly by recruitment.

Atramentowicz (1986b, p. 144; GUYANE FRANÇAISE)

Density per square kilometer based on observations from September 1978 to October 1979 was 137 *P. opossum*, 143 *C. philander*, and 45 *D. marsupialis*.

Population Dynamics

Atramentowicz (1986b, GUYANE FRANÇAISE)

"Five species of Didelphid marsupials were trapped live, marked, and released in a secondary forest in French Guiana during a 26-mo field study. Data on body weight, body length, dental stage, and reproductive state of females were collected. A total of 851 individuals, including 372 pouch-young, were monitored in 2273 captures. This abundance of data we made led us to a comparative analysis of the population dynamics of three species: *Didelphis marsupialis*, *Philander opossum*, and *Caluromys philander*, which represented 94 percent of the whole captures (Table 19). Some data on the two other species, *Marmosa murina* and *M[icoureus]. cinerea*, were add-

ed for comparison. These sympatric Didelphids are nocturnal, with a basically frugivorous and insectivorous diet. The three main species have high densities, high reproductive rates, short life-spans, and rapid population turnover. There are some differences in these parameters, mainly between the arboreal species, *C. philander*, and both terrestrial species, *D. marsupialis* and *P. opossum*. Although all have few social interactions and show a lack of territoriality, *C. philander* appear to have a longer life-span, a lower reproductive rate and a more sedentary population. *M. cinerea* [*Micoureus demerarae*] were very rare in this area, whereas *M[armosa]. murina* show large density variation."

The well-known tendency of American marsupials to enter baited traps, usually the same ones, time and again ensures a high degree of accuracy in estimating their duration of residence in an area. In general, both sexes of *P.* and *C. philander* are highly sedentary. *Didelphis marsupialis*, on the other hand, tends to wander, particularly the males (Table 19).

Posture

Enders (1935, p. 412; Canal Zone, PANAMÁ)

Philander "used the tripod [sitting] posture more frequently than *Metachirus* although the tail of the latter is a very effective appendage."

Hershkovitz (1941, field notes; northern COLOMBIA)

Sitting was tripod, the body supported by hind limbs and tail.

Sleep

Temminck (1827, p. 38)

It sleeps during the day rolled up into a ball. Its breathing is like that of a ferret, and it leaves its hiding place only at night.

Schomburgk (1840, 348; GUYANA)

They sleep during the day under tree roots or in hollow trees and hunt at night.

Hershkovitz (1941, field notes; northern COLOMBIA)

The animal sleeps rolled up on its side or ex-

TABLE 19. Duration of residence in study area.

	Duration of Residence					
	<i>Caluromys phillander</i>		<i>Phillander opossum</i>		<i>Didelphis marsupialis</i>	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
N total	53 (100%)	38 (100%)	60 (100%)	36 (100%)	27 (100%)	24 (100%)
Individuals captured once	14 (26.4%)	11 (28.9%)	16 (26.6%)	9 (25%)	13 (48.1%)	9 (37.5%)
Individuals residing <31 days	4 (7.5%)	5 (13.1%)	12 (20%)	4 (11%)	6 (22.2%)	5 (20.2%)
Individuals residing 31-100 days	14 (26.4%)	8 (21%)	13 (21.6%)	8 (22.2%)	5 (18.5%)	6 (25%)
Individuals residing 101-200 days	21 (39.6%)	14 (36.8%)	19 (31.6%)	15 (41.6%)	3 (11.1%)	5 (20.8%)
Individuals residing >200 days	12 (22.6%)	7 (18.4%)	5 (8.3%)	6 (16.6%)	1 (3.7%)	1 (4.1%)
Maximum residence	398 days	408 days	325 days	355 days	201 days	333 days
Average residence	150 days	136 days	99 days	134 days	58 days	83 days

tended backside up. The closed eyes are not visible, but the whitish supraorbital spots give the animal an appearance of being awake with eyes widely opened.

Sociability

Hall and Dalquest (1963, p. 179; Veracruz, MÉXICO)

“On a few occasions, two four-eyed opossums were seen as close together as 50 feet, but otherwise they were solitary.”

Charles-Dominique (1983, pp. 405-407; GUYANE FRANÇAISE)

“Didelphids are always solitary day and night. During development immediately after the young have released the nipples, they remain for a short period in a nest (8 to 15 days for *P. opossum* and 30 to 45 days for *C[aluromys]. phillander*). During the first days (the first weeks for *C. phillander*), the young maintain a certain cohesion between themselves (they often grasp each other) and explore the surroundings of the nest. This gregarious behavior indicates the persistence of a need for body contact, directed indiscriminately towards the litter mates as well as towards the mother. Sometimes one or several young of the litter cling to the mother’s fur during nocturnal activity. . . . Individual recognition may not exist between lactating females and young. In the middle of the night, and again at dawn, the mother returns to the nest for 2 to 3 h. This cohesive behavior disappears after weaning, mother and young becoming indifferent or aggressive when they meet.

“We observed no durable social bonds between adult individuals. When two animals met (for example, in a fruiting tree), they often threatened each other with an aggressive vocalization and then continued their individual activities.”

Charles-Dominique (1983, pp. 406, 407; Cayenne, GUYANE FRANÇAISE)

A dominance hierarchy or peck order does not exist among didelphoids. “Nineteen adult four-eyed opossums (10 females; 9 males) habitually fed on a 1 m high platform baited daily with bananas. Animals were identified by collars (radio-transmitters and color bands) and only had access to the platform via a single branch. Observations under weak lighting were made from a distance

of 3 m. Conflicts were observed principally during the first 2 hr of the night when the four-eyed opossums came to take the first meal (12 evenings of observation). Usually an animal which had not eaten chased one which was already eating on the platform. I observed direct fighting (bites) on only three occasions, but usually only threats were exchanged (hissing, open mouth, and start of chase). No rank order was observed and an individual (male or female) chased by another (male or female) one night could chase it in turn the following night depending on the situation (degree of hunger)."

Spontaneous Bleeding

Herskovitz (1941, field notes; northern COLOMBIA)

An adult female *P. opossum* was clubbed by a woodsman and seized as she jumped from its nest in the felled tree. The animal was brought live to my camp, where it recovered without signs of injury. When irritated, however, it bled spontaneously from the tips of the fingers, the tail, and the nose. I had never witnessed or known of this phenomenon before.

Stress

Hunsaker and Shupe (1977, p. 302)

"Tight coiling of the tail . . . occurs in *Philander opossum*, *Didelphis marsupialis* and *Caluromys* as a function of stress. It occurs when an animal is frightened and can be considered a submission posture."

The coiled tail reduces exposure from seizure by a predator.

Tail Transport

Hunsaker and Shupe (1977, p. 301)

"Tail coiling has been observed to facilitate carrying nesting material in *Didelphis virginiana*, *Monodelphis domestica*, *Caluromys derbianus* and *Marmosa robinsoni*. The fact that more species have not been observed to do so is probably a function of inadequate observations." *Philander* does coil its tail in the manner described and may indeed do so for transport of building material.

According to Layne (1951, p. 464), use of the tail for transport by *Didelphis* was first described and illustrated by Pray (1921, p. 109). Layne further elaborated on the subject.

Taming

Herskovitz (1941, field notes; northern COLOMBIA)

The opossum captured alive after being struck with a machete by a woodsman was leashed and brought to me. It objected to being handled, was suspicious of anyone's approach, and reacted like all other didelphoids I've known by hissing with the mouth open. Within a few days, however, the animal became tame and permitted itself to be handled and stroked and seemed to enjoy climbing onto my shoulder and head.

Thermoregulation

Enders and Davis (1936, p. 165; Canal Zone, PANAMÁ)

Body 35.4, environment 26.1 (afternoon).

Miller (in J. A. Allen, 1916c, p. 589; Mato Grosso, BRASIL)

"As a general rule opossums cannot stand great heat and will soon die if left exposed to the direct rays of the tropical sun."

Vocalization

Charles-Dominique (1983, pp. 407, 411, 412; Cayenne, GUYANE FRANÇAISE)

"Two types of calls by adults are the weak sexual call (rarely by the male) and an aggressive call by both sexes.

"The young begin emitting very short high-pitched "clicks" about one month before releasing the nipples, especially when the mother licks the young attached to the nipples in her pouch, or when the young are experimentally pulled off the nipples.

"These clicks progressively disappear when the young release the nipple and the first 'hiss'—associated with the typical posture (opened mouth)—is emitted very early in conditions of fear or when pulled off the nipple."

In the case of *C. philander* the clicking sound was particularly loud, audible at 200 m. The same sound, but muted, was emitted by *Marmosa murina*, *Monodelphis brevicaudata*, and *D. marsupialis*.

The clicking sound has also been recorded by Reynolds (1952, p. 235) for *D. virginiana* as being most pronounced during breeding. Kirsh (1979, p. 392) heard the sound from *Caenolestes fuliginosus*; Thrasher et al. (1971), from *Marmosa robinsoni*. Bruce Patterson (personal communication) heard *Metachirus nudicaudatus* clicking as a signal of aggression.

Apparently all New World marsupials are capable of three types of calls: the standard hiss, usually uttered when standing erect or tripodally in an aggressive posture, is usually fear stimulated; a mouselike squeak, which may be a sexual call; and the click, which is emitted under various conditions.

Weight

Tyndale-Biscoe (1980; *P. opossum*—COLOMBIA)

Weights of adults (g): 8♂♂, 416.9 ± 132.1 (230–675); 4♀♀, 323.8 ± 65.2 (275–420).

Alphabetical List of South American Collecting Localities of *Philander* with Key Numbers to Distribution Map (Fig. 22) and Gazetteer (p. 85)

See Hall and Kelson (1959) for Middle American portion of range.

Acanaña; Territorio Federal Amazonas, Venezuela (107)
Agua Limpia; Brasília, Distrito Federal, Brasil (175c)
Agua Viva; Trujillo, Venezuela (98a)
Albina; Marowijne, Suriname (128)
Além Paraíba; Minas Gerais, Brasil (182)
Alguacil; Zulia, Venezuela (97a)
Altamira; Pará, Brasil (151)
Alto Bonito; Antioquia, Colombia (1)
Alto da Serra; São Paulo, Brasil (202)
Ananindéua; Pará, Brasil (159)
Anapolis; Goiás, Brasil (174b)

Apayacu; Ucayali, Perú (43)
Aragarças; Goiás, Brasil (173)
Arruda; El Beni, Bolivia (73)
Arumateua; Pará, Brasil (157)
Ascención de Guarayos; Santa Cruz, Bolivia (84)
Asunción; Central, Paraguay (91)
Auará; Igarapé; Amazonas, Brasil (144)
Avanavero Falls; Nickerie, Suriname (119)
Avanhandava (Lajeado); São Paulo, Brasil (195)
Ayacucho (Ibáñez); Santa Cruz, Bolivia (88)
Bacaceta; São Paulo, Brasil (199)
Bagadó; Chocó, Colombia (4)
Bahia; Bahia, Brasil (172)
Baião; Pará, Brasil (156)
Balisa; Mato Grosso, Brasil (168d)
Balta; Ucayali, Perú (55)
Barra do Garças; Mato Grosso, Brasil (168c)
Barranquita; El Beni, Bolivia (73)
Barreira; Rio de Janeiro, Brasil (189)
Barro Branco; Rio de Janeiro, Brasil (193)
Baptista (Lago); Amazonas, Brasil (141)
Belém; Pará, Brasil (159)
Belém—Brasília (Rodovia); Pará, Brasil (159)
Belén; Territorio Federal Amazonas, Venezuela (106)
Bellavista; Antioquia, Colombia (2)
Bemberg (Puerto); Misiones, Argentina (95)
Benfica; Minas Gerais, Brasil (181)
Better Hope; East Demerara, Guyana (not located but likely near Georgetown [114] and perhaps same as Hope [6°42'N, 57°57'W])
Boa Esperança; Minas Gerais, Brasil (179)
Boa Fé (Fazenda); Rio de Janeiro, Brasil (189)
Boa Vista (Fazenda); Rio de Janeiro, Brasil (189)
Boa Vista; Roraima, Brasil (134)
Boca Colorado; Madre de Dios, Perú (65)
Bom Jardim; Brasil; not located; many so-named throughout most states
Boracéia (Ponta); São Paulo, Brasil (203)
Boracéia, Rio Tietê; São Paulo, Brasil (196)
Branco (Rio); Amapá, Brasil (133)
Brasília; Distrito Federal, Brasil (175c)
Bucay; Guayas, Ecuador (28)
Buck Hall; Essequibo Islands—West Demerara, Guyana (116)
Buenaventura; Valle del Cauca, Colombia (10)
Buenavista; Santa Cruz, Bolivia (86)
Butantã; São Paulo, Brasil (200)
Cáceres; Mato Grosso, Brasil (168a)
Cachaví (= Cachabí); Esmeraldas, Ecuador (18)
Cadena (Hacienda); Cuzco, Perú (63)
Caixa D'agua; Espírito Santo, Brasil (186)
Cali; Valle del Cauca, Colombia (11)
Cametá; Pará, Brasil (153)



FIG. 22. South American collecting localities of *Philander* species. See Gazetteer (p. 85) for numbered locality names.

Camiaco; El Beni, Bolivia (81)
 Camino Vilches; El Beni, Bolivia (73)
 Campinho; Espírito Santo, Brasil (185)
 Caney; Meta, Colombia (16)
 Cantareira (Serra da); São Paulo, Brasil (200)
 Canudos; Pará, Brasil (149)
 Caoní (Río); Pichincha, Ecuador (22)
 Capibara; Territorio Federal Amazonas, Venezuela (111)
 Capim; Pará, Brasil (164)
 Caracará; Roraima, Brasil (135)

Cardoso (Fazenda); Minas Gerais, Brasil (180)
 Carondelet; Esmeraldas, Ecuador (18)
 Casa Grande; São Paulo, Brasil (203)
 Catatumbo (Puerto); Zulia, Venezuela (97b)
 Cauca (Río); Valle del Cauca, Colombia (11)
 Cayenne; Cayenne, Guyane Française (129)
 Cebollal; Loja, Ecuador (30)
 Cerro Cucurito; Territorio Federal Amazonas, Venezuela (109b)
 Centinela; El Beni, Bolivia (73)
 Chaco; Argentina (94)

- Chalimana; Bolívar, Venezuela (104c)
 Chanchamayo; Junín, Perú (61)
 Chaparé (Río); Santa Cruz, Bolivia (83)
 Chicosa; Ucayali, Perú (53)
 Chimbo (Puente); Guayas, Ecuador (28)
 Chimbo-Coco (Ríos); Guayas, Ecuador (28)
 Chocolatal, Monte, El Beni, Bolivia (75)
 Chulumani; La Paz, Bolivia (67)
 Churulí; Zulia, Venezuela (97a)
 Clevia; Suriname, Suriname (125)
 Cocal; Cauca, Colombia (14)
 Coco (Río); Guayas, Ecuador (28)
 Colônia do Prata; Pará, Brasil (163)
 Colônia Hansa; Santa Catarina, Brasil (209)
 Colorado (Boca); Madre de Dios, Perú (65)
 Colorado (Río); Madre de Dios, Perú (65)
 Commewijne (River); Commewijne, Suriname (127)
 Comochatibá (= Comoxatibá) 17°06'S, 39°11'W.
 Maximilian Wied-Neuwied, July 1816.
 Conceição do Mato Dentro; Minas Gerais, Brasil (176)
 Condoto; Chocó, Colombia (5)
 Copataza (Río); Pastaza, Ecuador (37)
 Corumbá; Mato Grosso do Sul, Brasil (170)
 Costão dos Engenhos; São Paulo, Brasil (201)
 Cotia; São Paulo, Brasil (200)
 Covaría (Río); Boyacá, Colombia (15)
 Cucurito (Cerro); Territorio Federal Amazonas, Venezuela (109b)
 Culturutuín; Suriname, Suriname (125)
 Culumani; La Paz, Bolivia (67)
 Cumaría; Ucayali, Perú (52)
 Cumería; Ucayali, Perú (52)
 Cumuruxotibá (= Comoxatibá = Comochatibá – q.v.)
 Curaray (Río); Napo, Ecuador (39)
 Curaray (Boca); Ucayali, Perú (39)
 De Oro (Río); Chaco, Argentina (94)
 De Oro (Río); Zulia, Venezuela (97)
 Dividive; Trujillo, Venezuela (98a)
 Docampadó (Río); Chocó, Colombia (7)
 Duida (Cerro); Territorio Federal Amazonas, Venezuela (108)
 El Capricho (Finca); 38 km E Villavicencio, Meta, Colombia (16)
 El Carmen; El Beni, Bolivia (78)
 El Chiral; El Oro, Ecuador (29)
 El Dividive; Trujillo, Venezuela (98a)
 El Palmar; Bolívar, Venezuela (102a)
 El Palmar; Santa Cruz, Bolivia (88)
 Encontrados, Río de Oro; Zulia, Venezuela (97b)
 Engenheiro Reeve; Espírito Santo, Brasil (188)
 Engenheiro Rive (see Engenheiro Reeve)
 Esmeralda (Fazenda); Minas Gerais, Brasil (178)
 Esmeralda; Territorio Federal Amazonas, Venezuela (109a)
 Esmeraldas; Esmeraldas, Ecuador (19)
 Estrada de Santarém–Cuiabá; Pará, Brasil (148)
 Exaltación; El Beni, Bolivia (74)
 Fazenda Bõa Fé; Rio de Janeiro, Brasil (189)
 Fazenda Cardosa; Minas Gerais, Brasil (180)
 Fazenda da Floresta; Minas Gerais, Brasil (178)
 Flor do Prado; Pará, Brasil (161)
 Floresta (Fazenda); Minas Gerais, Brasil (178)
 Fordlandia; Pará, Brasil (147)
 Formosa; Goiás, Brasil (174a)
 Fracrán; Misiones, Argentina (96)
 Georgetown; Demerara–Mahaica, Guyana (114)
 Gradaús; Pará, Brasil (152)
 Guala; Pichincha, Ecuador (23)
 Guamá; Pará, Brasil (165)
 Guaquitas; Barinas, Venezuela (100b)
 Guayaquil; Guayas, Ecuador (27)
 Guayaramarín; El Beni, Bolivia (68)
 Güiniquina, Territorio Federal Delta Amacuro, Venezuela (98d)
 Hacienda Cadena; Cuzco, Perú (63)
 Hamacas; Santa Cruz, Bolivia (88)
 Hansa; Santa Catarina, Brasil (209)
 Hato San José; Bolívar, Venezuela (103)
 Hondo (Río); Caldas, Colombia (3)
 Huampami; Amazonas, Perú (56b)
 Huanhuachayo; Ayacucho, Perú (62)
 Hyde Park; Demerara–Mahaica, Guyana (115)
 Ibáñez; Santa Cruz, Bolivia (88)
 Ibaré (Boca); El Beni, Bolivia (79)
 Ichilo (Río); Cochabamba, Bolivia (82)
 Igarapé Açu; Pará, Brasil (163)
 Igarapé Tapereba; Pará, Brasil (150)
 Ilha do Taiuna; Pará, Brasil (153)
 Imperatriz; Amazonas, Brasil (140)
 Inañez; Pasco, Perú (not located)
 “High ground between Chanchamayo and upper Río Pachitea” (Hendee in Thomas, 1928a, *Annals and Magazine of Natural History*, Series 10, 2:250).
 R. W. Hendee, June 1927, at 5000 ft
 Ipanema; São Paulo, Brasil (199)
 Ipeau-Apez; Pará, Brasil (159)
 Ipitanga; Pará, Brasil (160)
 Ipixuna; Amazonas, Brasil (138)
 Iporanga; São Paulo, Brasil (197)
 Iquitos; Ucayali, Perú (42)
 Iriteria; Pará, Brasil (165)
 Itaituba; Pará, Brasil (148)
 Itatiaia (Parque Nacional de); Rio de Janeiro, Brasil (193)

- Itatiaia (Serra de); São Paulo, Brasil (204)
 Itaya; Ucayali, Perú (42)
 Itonama; El Beni, Bolivia (71)
 Joinville; Santa Catarina, Brasil (209)
 Juiz de Fora; Minas Gerais, Brasil (183)
 Juquia; São Paulo, Brasil (201)
 Kaiserberg Airstrip; Nickerie, Suriname (122)
 Kanuku Mountains; Upper Takutu–Upper Essequibo, Guyana (118)
 Km 19; Pará, Brasil (148)
 Km 90; Pará, Brasil (159)
 Km 216; Pará, Brasil (148)
 La Blanquita; Apure, Venezuela (101a)
 La Boca, Río Saijá; Cauca, Colombia (13)
 La Lengueta; Barinas, Venezuela (100c)
 La Neblina; Territorio Federal Amazonas, Venezuela (112b)
 La Papaya; Manabí, Ecuador (not located)
 T. Mena, May 1942, at 50 m
 La Ponchera; Táchira, Venezuela (101b)
 La Poule; Saramacca, Suriname (124)
 La Poza; Amazonas, Perú (56a)
 Lagarto Cocha; Ucayali, Perú (54)
 Lago do Baptista; Amazonas, Brasil (141)
 Lago Mirañes; Ucayali, Perú (40)
 Lagoa Santa; Minas Gerais, Brasil (177)
 Lapango; Central, Paraguay (92)
 Las Bonitas; Barinas, Venezuela (100b)
 Lazarópolis do Prata; Pará, Brasil (not located)
 Lelydorp; Suriname, Suriname (126)
 Lelydorpplan; Suriname, Suriname (126)
 Limón; Ecuador (not located)
 G. H. H. Tate, December 1923, at 1200 ft
 Loksie Hattie; Brokopondo, Suriname (123)
 Los Guires, Territorio Federal Delta Amacuro, Venezuela (98c)
 Macapá; Amapá, Brasil (132)
 Macieiras; Rio de Janeiro, Brasil (193)
 Madeira (Rio); Amazonas, Brasil (142)
 Magdalena; El Beni, Bolivia (76)
 Majagua (Caño); Territorio Federal Amazonas, Venezuela (105)
 Makerie; Nickerie, Suriname (121)
 Maldonado (Puerto); Madre de Dios, Perú (66)
 Mamoré (Rio); El Beni, Bolivia (70)
 Mamoré (Rio); Santa Cruz, Bolivia (83)
 Mangaratiba; Rio de Janeiro, Brasil (192)
 Marabá; Pará, Brasil (158)
 Marco; Pará, Brasil (159)
 Maripa; Bolívar, Venezuela (102b)
 Matipó (Rio); Minas Gerais, Brasil (178)
 Mato Grosso; Mato Grosso, Brasil (167)
 Mavaca; Territorio Federal Amazonas, Venezuela (110c)
 Mazagão; Amapá, Brasil (133)
 Mazagão; Pará, Brasil (154)
 Mazán (Río); Ucayali, Perú (40)
 Mercedes; Santa Cruz, Bolivia (85)
 Merey; Territorio Federal Amazonas, Venezuela (112a)
 Mérida; Mérida, Venezuela (99)
 Merredor; El Beni, Bolivia (69)
 Mindo; Pichincha, Ecuador (24)
 Miranda; Mato Grosso do Sul, Brasil (171a)
 Mirañes (Lago); Ucayali, Perú (40)
 Mocajuba; Pará, Brasil (155)
 Montalvo; Pastaza, Ecuador (36)
 Monte Alegre; São Paulo, Brasil (198)
 Monte Alegre; Mato Grosso, Brasil (169)
 Monte Chocolatal (see San Ramón); El Beni, Bolivia (75)
 Monte Serrat; Rio de Janeiro, Brasil (193)
 Montes Claras; Minas Gerais, Brasil (178)
 Motatán, 1 km E and 5 km NNE; Trujillo, Venezuela (98a)
 Motatán, Rio; Trujillo, Venezuela (98a)
 Moyobamba; San Martín, Perú (57)
 Murutucu; Pará, Brasil (159)
 Napo (Puerto); Napo, Ecuador (33)
 Napo (Río); Napo, Ecuador (33)
 Nauta; Ucayali, Perú (45)
 Navio (Serra do); Amapá, Brasil (131)
 Nickerie (River); Nickerie, Suriname (120)
 Nóvita (Río), Chocó, Colombia (8)
 Novo Friburgo; Rio de Janeiro, Brasil (189)
 Nulita; Apure, Venezuela (101a)
 Órgãos (Serra dos); Rio de Janeiro, Brasil (189)
 Oro (Río de); Chaco, Argentina (94)
 Orosa; Ucayali, Perú (44)
 Ouanary (River); Ouanary, Guyane Française (130)
 Oxapampa; Pasco, Perú (60)
 Pacific Virology Field Camp; Valle del Cauca, Colombia (12)
 Palacios; El Beni, Bolivia (74)
 Palmeiras; Mato Grosso, Brasil (169)
 Papelón (Cerro); Monagas, Venezuela (98b)
 Pará; Pará, Brasil (159)
 Pará (River); Suriname, Suriname (125)
 Paracá (Rio); Paraná, Brasil (207)
 Paramaribo; Suriname, Suriname (125)
 Paramba; Imbabura, Ecuador (21)
 Parima (Sierra); Territorio Federal Amazonas, Venezuela (110b)
 Parintins; Amazonas, Brasil (139)
 Parintins (Serra de); Amazonas, Brasil (139)
 Parque Nacional de Brasília; Distrito Federal, Brasil (175b)

- Parque Nacional de Itatiaia; Rio de Janeiro, Brasil (193)
- Passo Fundo; Rio Grande do Sul, Brasil (210)
- Pedra Branco; Rio de Janeiro, Brasil (194)
- Peixe-Boi; Pará, Brasil (163)
- Pescado (Río); Manabí, Ecuador (25)
- Piñas; El Oro, Ecuador (29)
- Pindo Yacu (Río); Pastaza, Ecuador (38)
- Piquete; São Paulo, Brasil (205)
- Playa del Río Base; Territorio Federal Amazonas, Venezuela (108)
- Pocão, Boa Vista; Roraima, Brasil (134)
- Pocão, Caracará; Roraima, Brasil (135)
- Poconé; Mato Grosso, Brasil (168b)
- Ponta de Boracéia; São Paulo, Brasil (203)
- Porto Velho; Rondônia, Brasil (166)
- Pucallpa; Ucayali, Perú (51)
- Puente de Chimbo; Guayas, Ecuador (28)
- Puerto Asis; Putumayo, Colombia (17a)
- Puerto Bemberg; Misiones, Argentina (95)
- Puerto Caballo; El Beni, Bolivia (74)
- Puerto Catatumbo; Zulia, Venezuela (97b)
- Puerto Maldonado; Madre de Dios, Perú (66)
- Puerto Napo; Napo, Ecuador (33)
- Puerto Siles; El Beni, Bolivia (72)
- Punta Santa Ana; Loja, Ecuador (29)
- Quartel de Sacramento; Minas Gerais, Brasil (178)
- Quincemil; Cuzco, Perú (64)
- Quinindé (Río); Esmeraldas, Ecuador (20)
- Raposo (Río); Valle del Cauca, Colombia (12)
- Restrepo; Meta, Colombia (16)
- Rijweg; Suriname, Suriname (125)
- Río de Janeiro; Rio de Janeiro, Brasil (190)
- Río de Oro; Chaco, Argentina (94)
- Río de Oro; Manabí, Ecuador (26)
- Río de Oro; Zulia, Venezuela (97b)
- Río Frío; Valle del Cauca, Colombia (9)
- Río Hondo; Caldas, Colombia (3)
- Rioja; San Martín, Perú (58)
- Roça Nova; Paraná, Brasil (208)
- Rodeio; Rio de Janeiro, Brasil (191)
- Rodovia Belém-Brasília; Pará, Brasil (159)
- Rosarinho; Amazonas, Brasil (143)
- Rupununi (River); Rupununi, Guyana (117)
- Saijá (Río); Cauca, Colombia (13)
- Salesopolis; São Paulo, Brasil (203)
- Salobra; Mato Grosso do Sul, Brasil (171b)
- Salvador; Bahia, Brasil (172)
- Salvias; El Oro, Ecuador (29)
- San Ignacio de Móxos; El Beni, Bolivia (80)
- San Javier; Esmeraldas, Ecuador (18)
- San Jerónimo; Cuzco, Perú (63)
- San Jerónimo; Ucayali, Perú (49)
- San Joaquín; El Beni, Bolivia (73)
- San José; Ayacucho, Perú (62)
- San José; (Hato); Bolívar, Venezuela (103)
- San José, Abajo; Napo, Ecuador (32)
- San Juan; Territorio Federal Amazonas, Venezuela (105)
- San Martín de Turumbán; Bolívar, Venezuela (104a)
- San Pablo; El Beni, Bolivia (77)
- San Ramón; El Beni, Bolivia (75)
- San Ramón; Santa Cruz, Bolivia (89)
- Sandó (Río); Chocó, Colombia (6)
- Santa Ana, Punta; Loja, Ecuador (29)
- Santa Cecilia; Napo, Ecuador (31)
- Santa Clara; Amazonas, Brasil (140)
- Santa Cruz de la Sierra; Santa Cruz, Bolivia (88)
- Santa Elena; Ucayali, Perú (46)
- Santa Luisa; Ucayali, Perú (41)
- Santa María; Pará, Brasil (162)
- Santa Rosa; El Beni, Bolivia (72)
- Santa Rosa; Ucayali, Perú (54)
- Santa Rosita; Santa Cruz, Bolivia (87)
- Santa Teresa; Espírito Santo, Brasil (184)
- Santa Teresa; Mato Grosso do Sul, Brasil (170)
- Santo Antônio de Uayara; Amazonas, Brasil (145a)
- Santo Dios; El Beni, Bolivia (73)
- Santo Isidoro; Amazonas, Brasil (137)
- Santarém; Pará, Brasil (148)
- Santarém-Cuiabá (Estrada); Pará, Brasil (148)
- São João de Petrópolis; Espírito Santo, Brasil (184)
- São João Marcos; Rio de Janeiro, Brasil (191)
- São Luis de Cáceres; Mato Grosso, Brasil (168a)
- São Miguel do Guamá; Pará, Brasil (165)
- São Paulo; São Paulo, Brasil (200)
- São Sebastião; São Paulo, Brasil (206)
- Sapitiba (see Sepetiba); Rio de Janeiro, Brasil (191)
- Sapucaí; Paraquari, Paraguay (93)
- Sapucajuba; Pará, Brasil (159)
- Sapucay; Paraguarí, Paraguay (93)
- Sarayacu; Pastaza, Ecuador (35)
- Sarayacu; Ucayali, Perú (48)
- Seboyal; Loja, Ecuador (30)
- Sepetiba; Rio de Janeiro, Brasil (191)
- Seringal Oriente; Acre, Brasil (146)
- Serra; Espírito Santo, Brasil (185)
- Serra de Itatiaia; São Paulo, Brasil (204)
- Serra de Parintins; Amazonas, Brasil (139)
- Serra do Navio; Amapá, Brasil (131)
- Serra dos Órgãos; Rio de Janeiro, Brasil (189)
- Serrat Monte; Rio de Janeiro, Brasil (193)

"S. Francisco de C." Minas Gerais, Brasil (not located)
 A. Robert, March 1900, at 1580 m.
 Shahuía; Ucayali, Perú (52)
 Siles (Puerto); El Beni, Bolivia (72)
 Sitio Minas Gerais; Minas Gerais, Brasil (not located)
 Supenam (River) (see Supinaam River); Demerara-Mahaica, Guyana (113)
 Supinaam (River); Demerara-Mahaica, Guyana (113)
 Tacuati; San Pedro, Paraguay (90)
 Taiuana (Ilha); Pará, Brasil (153)
 Tamatama; Territorio Federal Amazonas, Venezuela (110a)
 Tapereba (Igarapé); Pará, Brasil (150)
 Taquara; Rio Grande do Sul, Brasil (211)
 Tefé; Amazonas, Brasil (137)
 Teresinha; Amapá, Brasil (131)
 Teresópolis; Rio de Janeiro, Brasil (189)
 Terezinha (see Teresinha); Amapá, Brasil (131)
 Theresopolis (see Teresópolis); Rio de Janeiro, Brasil (189)
 Ticoporo, Reserva Forestal; Barinas, Venezuela (100a)
 Tingo María; Huánuco, Perú (59)
 Tobesobe, Guayo; Territorio Federal Delta Amacuro, Venezuela (98c)
 Tocomechi; Santa Cruz, Bolivia (88)
 Tres Troncos; Caquetá, Colombia (17b)
 Trinidad; Goiás, Brasil (175a)
 Turumbán (= San Martín de Turumbán); Bolívar, Venezuela (104a)
 Uragua-i (Río); Misiones, Argentina (95)
 Urubamba (Río); Ucayali, Perú (54)
 Urucu, Río; Amazonas, Brasil (145b)
 Urucum; Mato Grosso do Sul, Brasil (170)
 Utcuyacu; Junín, Perú (61)
 Utinga; Pará, Brasil (159)
 Vaca Diez; El Beni, Bolivia (79)
 Valão de São Lourenço; Espírito Santo, Brasil (187)
 Ventura; Guayas, Ecuador (28)
 Vila Oliveira; São Paulo, Brasil (202)
 Vila Velha; Espírito Santo, Brasil (185)
 Villa Bella Imperatriz; Amazonas, Brasil (140)
 Villavicencio; Meta, Colombia (16)
 Vitoria; Espírito Santo, Brasil (185)
 Warnes; Santa Cruz, Bolivia (87)
 Xiriviny (Río); Amazonas, Brasil (136)
 Yana Rumi (Río); Napo, Ecuador (34)
 Yana Yacu; Ucayali, Perú (47)
 Yarinacocha; Ucayali, Perú (50)
 Ypanema (= Ipanema); São Paulo, Brasil (199)
 Yurac Yacu; San Martín, Perú (56c)
 Yurimaguas; Ucayali, Perú (47)

Yuruán (Río); Bolívar, Venezuela (104b).

Gazetteer of South American Collecting Localities of *Philander*

Colombia—*Philander opossum fuscogriseus*, *P. opossum quica*, *P. andersoni andersoni*

Antioquia—*Philander opossum fuscogriseus*

1. Alto Bonito, 7°01'N, 76°17'W, about 400 m, upper Río Sucio, W slope Cordillera Occidental.
L. E. Miller and H. S. Boyle, February 1915.
2. Bellavista, 6°33'N, 75°18'W, upper Río Porce, Cordillera Centra.
P. Hershkovitz, February 1950, at 1200 m.

Caldas—*Philander opossum fuscogriseus*

3. Río Hondo, Samaná, 5°42'N, 75°01'W, Cordillera Central.
P. Hershkovitz, March 1951.

Chocó—*Philander opossum fuscogriseus*

4. Bagadó, 5°25'N, 76°24'W, Río Andagueda.
E. L. Kerr, November 1912, at 650 m.
5. Condoto, 5°06'N, 76°37'W, Río Condoto, tributary of Río San Juan.
H. G. F. Spurrell, February 1914, at 92 m.
6. Río Sandó, Río Baudó, 5°03'N, 76°57'W.
K. von Sneidern, October 1958, at 160 m.
7. Río Docampadó, 4°45'N, 77°18'W.
K. von Sneidern, September 1958, at 75–160 m.
8. Nóvita, 4°57'N, 76°34'W, Río Tamaná.
L. E. Miller, December 1911, at 120 m.

Valle del Cauca—*Philander opossum fuscogriseus*

9. Río Frío, 4°09'N, 76°15'W, enters Río Cauca from east.
A. A. Allen and L. E. Miller, November–December 1911, at 100 m.
10. Buenaventura, 3°53'N, 77°04'W.
K. von Sneidern, February 1958, at near

sea level.

C. H. Tyndale-Biscoe, September 1971.

10. Buenaventura, 28 km NE.

J. A. W. Kirsch, September 1969, at 150 m.

11. Cali, 3°27'N, 76°31'W, upper Río Cauca valley.

C. H. Tyndale-Biscoe, September 1971.

11. "Río Cauca" (see Cali).

J. H. Batty, June 1898.

12. Raposo (Río), 3°43'N, 77°08'W, Pacific Virology Field Camp.

J. Duran, June 1962, at near sea level.

Cauca—*Philander opossum fuscogriseus*

13. Río Saijá, La Boca (= Mouth), 2°52'N, 77°41'W.

K. von Sneidern, June 1958, at near sea level.

14. Cocal, 2°31'N, 77°00'W, upper Río San Juan.

L. E. Miller, July 1911, at 125 and 187 m.

Boyacá—*Philander opossum quica*

15. Río Covaría, 7°03'N, 72°04'W, near mouth, above town of Covaría.

K. von Sneidern, March 1959, at 350 m.

Meta—*Philander opossum quica*

16. Caney, Río Guatiquía (see Restrepo).

16. Restrepo, 4°15'N, 73°33'W.

16. Villavicencio, 4°09'N, 73°37'W, upper Río Guatiquía.

R. Gilmore, February, May, June 1939, at 465 m.

C. H. Tyndale-Biscoe, 1971.

16. El Capricho (Finca), 38 km E Villavicencio, 4°09'N, 73°16'W.

J. A. W. Kirsch, October 1969.

Putumayo—*Philander andersoni andersoni*

17a. Puerto Asis, 17 km N; 0°31'N, 76°31'W.

J. A. W. Kirsch, November 1969, at 330 m.

Caquetá—*Philander andersoni andersoni*

17b. Tres Troncos, 0°08'N, 74°41'W, above La Tagua, Río Caquetá.

P. Hershkovitz, January 1952, at 182 m.

Ecuador—*Philander opossum melanurus*, *P. opossum fuscogriseus*, *P. andersoni andersoni*

Esmeraldas—*Philander opossum melanurus*

18. Cachaví (Cachabí), Río Cachaví, 1°03'N, 78°50'W.

18. Carondelet, 1°03'N, 78°50'W.

G. Fleming, October 1900.

18. San Javier, 1°04'N, 78°47'W.

G. Fleming, August 1900, at 20 m.

19. Esmeraldas, 0°59'N, 79°42'W.

W. Richardson, November 1912, at near sea level.

20. Río Quindindé, 0°20'N, 79°28'W.

Imbabura—*Philander opossum melanurus*

21. Paramba, 0°49'N, 78°21'W, 1100 m.

W. F. H. Rosenberg, April 1897; L. Gomez, June 1941.

Pichincha—*Philander opossum melanurus*

22. Río Caoní, 0°12'N, 79°23'W.

M. Olalla, January 1935.

23. Gualea, 0°08'N, 78°48'W, ca. 1250 m.

L. Söderström, May 1920.

24. Mindo, below 8°02'S, 78°48'W.

L. Söderström, December 1924, at 1000 m.

Manabí—*Philander opossum fuscogriseus*

25. Río Pescado, 1°25'S, 80°15'W.

G. H. H. Tate, May 1922, at 500 m.

26. Río de Oro, 2°10'S, 79°22'W.

W. Richardson, January 1917.

Guayas—*Philander opossum fuscogriseus*

27. Guayaquil, 2°10'S, 79°50'W, near sea level.

E. Belcher, 1838.

28. Puente de Chimbo, 2°10'S, 79°07'W.

G. H. H. Tate, August 1922, at 375 m.

28. Ríos Chimbo-Coco, 2°10'S, 79°50'W.

G. H. H. Tate, July 1922, at 750 m.

28. Bucay, Río Chimbo, 2°10'S, 79°06'W.

G. H. H. Tate, November 1921, at 312 m.

28. Ventura, Río Chanchán, 2°17'S, 79°24'W.

G. H. H. Tate, April 1922, at 750 m.

El Oro—*Philander opossum fuscogriseus*

29. El Chiral, 2°39'S, 79°43'W.
H. E. Anthony, August 1920, at 167 m.
29. Piñas, 3°42'S, 79°42'W.
G. H. H. Tate, September 1921, at 1125 m.
29. Salvias, 3°47'S, 79°21'W.
H. E. Anthony, August 1920, at 1000 m.

Loja—*Philander opossum fuscogriseus*

29. Santa Ana, Punta (?) 3°50'S, 79°25'W, on road from Zaruma to Loja.
H. E. Anthony, December 1920, at 114 m.
30. Seboyal (see Cebollal).
30. Cebollal, 4°02'S, 80°02'W.
G. H. H. Tate, October 1921, at 968 m.

Napo—*Philander andersoni andersoni*

31. Santa Cecilia, 0°03'N, 76°58'W.
32. San José, abajo (= below), 0°31'S, 77°20'W.
Olalla Brothers, April 1924.
33. Puerto Naop, Río Napo, 1°03'S, 77°47'W.
33. Río Napo (near) (see Puerto Napo).
L. Söderström, March 1921.
34. Río Yana Rumi, 1°38'S, 76°59'W.
R. Olalla, October 1934.

Pastaza—*Philander andersoni andersoni*

35. Sarayacu, Río Bobonaza, 1°44'S, 77°29'W.
G. H. H. Tate, March 1924, between 450 and 500 m.
36. Montalvo, Río Bobonaza, 2°04'S, 76°58'W.
R. Olalla, February 1932.
37. Río Copataza, 2°07'S, 77°27'W.
R. Olalla, March 1939; G. H. H. Tate, March 1924.
38. Río Pindo Yacu, 2°08'S, 76°03'W.
R. Olalla, October 1934, at 250 m.

Perú—*Philander opossum quica*, *P. andersoni andersoni*, *P. andersoni mcilhennyi*

Ucayali—*Philander opossum quica* (42, 43, 48–51, 54, 55), *P. andersoni andersoni* (39–41, 44–47), *P. andersoni mcilhennyi* (51, 55).

39. Río Curaray, Boca (= mouth), 2°22'S, 74°05'W.
Olalla Brothers, 1925.
40. Lago Mirañes, Río Napo (see Río Mazán).
40. Río Mazán (mouth, 3°28'S, 73°02'W).
L. Söderström, September 1930.
41. Santa Luisa, Río Nanay, 3°35'S, 74°30'W.
C. Kalinowski, October 1956.
42. Itaya (see Iquitos).
H. Bassler, 1927.
42. Iquitos, Río Marañon, 3°46'S, 73°15'W, 106 m.
H. Bassler, March 1928; C. Kalinowski, October 1956; R. W. Hendee, January 1928; C. Arevalo (H. Bassler collection), March 1930.
43. Apayacu, 3°19'S, 72°07'W.
Olalla Brothers, January 1927.
44. Orosa, 3°26'S, 72°08'W.
Ollalla Brothers, October 1926.
45. Nauta, 4°30'S, 73°25'W, ca. 130 m.
46. Santa Elena, Río Samiria, 4°42'S, 74°12'W, ca. 130 m.
C. Kalinowski, November 1956.
47. Yurimaguas, Río Huallaza, 5°54'S, 76°05'W, 180 m.
47. Yana Yacu, below Yurimaguas, 5°52'S, 76°15'W.
M. P. Anderson, September 1912, at 180 m.
48. Sarayacu, Río Ucayali, 6°44'S, 75°06'W.
A. M. Olalla, March, April 1927.
49. San Jerónimo, 7°45'S, 74°50'W, 300 m.
R. W. Hendee, December 1927.
50. Yarinacocha, 8°15'S, 74°43'W, 160 m.
C. C. Sanborn, March 1946; A. L. Gardner, August 1968, March 1971.
51. Pucallpa, 59 km W, 59 km NE, 59 km SW (see Pucallpa, Río Ucayali).
H. Hinse, October, November 1971, October 1972; H. Hinse, 59 km NE, September 1972; 59 km SW, October 1972.
51. Pucallpa, Río Ucayali, 8°23'S, 74°32'W, 180 m.
52. Cumeria (= Cumaría, across from Shahuía, q.v.).
52. Shahuía, Río Ucayali opposite Cumaría, 9°52'S, 74°01'W.
R. W. Hendee, July 1927, at 312 m.
53. Chicosa, 10°21'S, 74°00'W, ca. 150 m.
R. W. Hendee, September 1927.
54. Lagarto Cocha, Río Ucayali, 10°41'S, 73°48'W.
Olalla Brothers, January 1928.
54. Río Urubamba, mouth, 10°42'S, 73°42'W.

- Olalla Brothers, October, November 1927.
54. Santa Rosa, 10°43'S, 73°53'W.
Olalla Brothers, December 1927.
55. Balta, Río Curanja, 10°08'S, 71°15'W, 300 m.
A. L. Gardner, June 1968, March 1971;
R. Thomas, 1971; A. L. Gardner, July,
August 1966, February 1977, July 1968;
J. P. O'Neil, February 1971.
- Amazonas—*Philander andersoni andersoni*
- 56a. La Poza, Río Santiago, 4°01'S, 77°47'W.
J. L. Patton, August 1979, at 180 m.
- 56b. Huampami, Río Cenepa.
J. L. Patton, July, August 1977, July 1978.
- San Martín—*Philander opossum quica*
- 56c. Yurac Yacu, 5°52'S, 77°14'W.
R. W. Hendee, July 1926, at 780 m.
57. Moyobamba, Río Mayo, 6°03'S, 76°58'W.
W. H. Osgood and M. P. Anderson,
August 1912;
L. Rutter, February 1924, June 1926, at
845 m.
58. Rioja, 6°10'S, 77°10'W, ca. 800 m.
R. W. Hendee, September 1926.
- Huánuco—*Philander opossum quica*
59. Tingo María, 9°08'S, 75°57'W.
R. W. Hendee, January 1927, at 625 m.
- Pasco—*Philander andersoni andersoni*
60. Oxapampa, 10°34'S, 75°24'W.
C. R. Pérez, August 1964, at 280 m.
- Junín—*Philander andersoni andersoni*
61. Chanchamayo, 11°03'S, 75°19'W.
P. O. Simons, August 1900; J. M.
Schunke, August 1948; M. Kalinowski
before 1916.
61. Utcuyacu, 11°12'S, 75°28'W.
P. O. Simons, August 1900, at 1600 m.
- Ayacucho—*Philander andersoni andersoni*
62. San José, Río Santa Rosa, 12°44'S, 73°46'W.
A. L. Gardner, April 1971, at 1000 m.
62. Huanhuachayo, 12°44'S, 73°47'W.
A. L. Gardner, May 1971, at 1660 m.
- Cuzco—*Philander opossum quica*
63. Hacienda Cadena, Marcapata, 13°24'S,
70°43'W, 890 m.
C. Kalinowski, October 1949, August
1950.
63. San Jerónimo, 13°34'S, 71°54'W.
64. Quincemil, 13°16'S, 70°38'W.
C. Kalinowski, June 1953, at 680 m.
- Madre de Dios—*Philander opossum quica*
65. Colorado, Río (mouth) (see Boca Colorado).
65. Boca Colorado, 12°30'S, 70°10'W.
C. Kalinowski, October 1954, at 279 m.
66. Puerto Maldonado, Río Tambo, 12°36'S,
69°11'W, 256 m.
M. L. Kuns, April 1965.
- Bolivia—*Philander opossum quica*
- La Paz
67. Culumani (see Chulumani).
67. Chulumani, 16°24'S, 67°31'W, 2000 m.
P. O. Simons, February 1901, at 2200 m.
- El Beni
68. Guayaramarín, Río Mamoré, 10°51'S,
65°23'W.
A. Ximénez, June 1964; K. F. Koopman,
1964.
69. Merredor, Río Mamoré, 11°41'S, 65°05'W.
D. Edwards, July 1965; A. Ximénez, May
1965.
70. Río Mamoré, 12°26'S, ca. 65°W.
D. E. Añez, October 1965.
71. Itonama, 12°28'S, 64°24'W.
M. L. Kuns, April 1970.
72. Puerto Siles, Río Mamoré, 12°49'S,
65°00'W.
S. Anderson, October 1965.

72. Santa Rosa, 13°01'S, 65°11'W.
M. L. Kuns, June 1964.
73. Barranquita (see San Joaquín).
M. L. Kuns, August 1963.
73. Arruda, 4 km NE San Joaquín (q.v.).
M. L. Kuns, December 1963.
73. Centinela, 1.5 km E San Joaquín (q.v.).
M. L. Kuns, June 1964.
73. Camino Vilches, 1 mi E San Joaquín (q.v.).
M. L. Kuns, February 1966.
73. Santo Dios, 2 km NE San Joaquín (q.v.).
M. L. Kuns, June 1963.
73. San Joaquín, Río Machupo, 13°04'S,
64°49'W.
M. L. Kuns, April, June, July 1963;
February, May 1964.
74. Exaltación, Río Mamoré, 13°16'S, 65°15'W.
M. L. Kuns, May 1964; S. Anderson,
October 1965, at 8 km N.
74. Palacios, 13°34'S, 65°19'W.
D. E. Añez, May 1965.
74. Puerto Caballo, 13°34'S, 65°21'W.
S. Anderson, September 1965.
75. San Ramón, Río Machupo, 13°18'S,
64°37'W.
M. L. Kuns, January 1964.
75. Monte Chocotalal (see San Ramón).
M. L. Kuns, January 1964.
76. Magdalena, 13°20'S, 64°08'W.
M. L. Kuns, July 1963, July 1964.
77. San Pablo, 13°52'S, 65°36'W.
M. L. Kuns, September 1963.
78. El Carmen, Río Blanco, 13°57'S, 63°43'W.
M. L. Kuns, June 1964.
79. Río Ibaré (mouth), 14°37'S, 64°57'W.
D. E. Añez, August 1965.
K. F. Koopman, August 1965.
79. Vaca Diez, 14°47'S, 64°51'W.
M. L. Kuns, May 1969.
80. San Ignacio de Móxos, 14°53'S, 65°36'W.
M. L. Kuns, June 1965.
81. Camiaco, 15°24'S, 64°46'W.
A. Ximénez, August 1965.
84. Ascensión de Guarayos, 14°57'S, 61°24'W.
M. L. Kuns, June 1964.
85. Mercedes, Río Guaporé, 15°36'S, 60°22'W,
6 km S and opposite Buena Hora, Brasil.
A. Ximénez, May 1965.
86. Buenavista, 17°27'S, 63°40'W.
T. Bridges, probably 1846; F. Steinbach,
January 1915; J. Steinbach, June 1921, May
1925, July 1926, June, July 1927, July 1928.
87. Warnes, 17°31'S, 63°10'W.
M. L. Kuns, August 1965.
87. Santa Rosita, Warnes, 17°30'S, 63°10'W.
M. L. Kuns, July 1965.
88. Tocomechi, 17°35'S, 62°55'W.
M. L. Kuns, August 1965.
88. Hamacas, 17°44'S, 63°11'W.
O. Silva (Rockefeller Institution), July
1938.
88. El Palmar, 17°48'S, 63°10'W.
W. Kerr, August 1966, at 500 m; D. R.
Hadden, August 1966.
88. Ayacucho, Ibáñez, 17°51'S, 63°20'W.
J. Riddell, August 1966.
88. 18 km SW Santa Cruz (q.v.).
F. Becerra, August 1966.
88. Santa Cruz (see Santa Cruz de la Sierra).
88. Santa Cruz de la Sierra, 17°48'S, 63°10'W.
F. Becerra, September 1966.
89. San Ramón, 17°33'S, 61°03'S.

Paraguay—*Philander opossum quica*

San Pedro

90. Tacuati, 23°27'S, 56°35'W.
C. Wharton, May 1950.

Central

91. Asunción, 25°16'S, 57°40'W.
92. Lapango, 25°21'S, 57°42'W.
H. Krieg, August 1925.

Paraguarí

93. Sapucay (= Sapucaí), 25°40'S, 56°55'W.
W. Foster, September 1902.

Argentina—*Philander opossum*

Chaco

94. No precise locality.
C. Friend, before 1880.

Cochabamba

82. Río Ichilo, 16°50'S, 64°45'W.
D. E. Añez, July 1965.

Santa Cruz

83. 2 km S mouth, Río Chaparé, Río Mamoré,
15°58'S, 64°42'W.
D. E. Añez, July 1965.

94. Río de Oro (mouth), 27°04'S, 58°34'W.
I. Apostal, October 1962.

Misiones

95. Río Uruguar-í, 30 km from Puerto Bemberg (Libertad). 26°30'S, 54°W.
J. A. Crespo, September, October, November 1949.
96. Fracrán, San Pedro, 26°46'S, 54°16'W.
J. A. Crespo, February 1952.

Venezuela—*Philander opossum* subspecies, *P. andersoni andersoni*

Zulia—*Philander opossum* subspecies

- 97a. Alguacil, Caja Seca, 09°8'N, 71°04'W.
97a. Churulí, Caja Seca, 09°09'N, 71°04'W.
97b. Puerto Catatumbo, 09°07'N, 72°35'W, 50 m.
97b. Boca del Río de Oro, 9°06'N, 72°45'W.
97b. Encontrados, 9°03'S, 72°14'W.
N. E. Peterson, March 1968.
97b. Encontrados, 60 km WNW, 90°03'N, 72°14'W, 73 m.

Trujillo—*Philander opossum* subspecies

- 98a. Motatán, 9°24'N, 70°36'W, 1 km E at 330 m, 5 km NNE at 290 m.
J. A. W. Kirsch, June 1969.
- 98a. Motatán (Río), 9°28'N, 70°34'W at 290 m, 9.8 km NNE at 290 m.
J. A. W. Kirsch, June 1969.
- 98a. Agua Viva, 9°34'N, 70°36'W.
N. E. Peterson, September 1965, at 164 m.
- 98a. El Dividive, 9°29'N, 70°44'W.
N. E. Peterson, October 1965, at 90 m.

Monagas—*Philander* [?] *opossum* subspecies

- 98b. Papelón (Cerro), 10°01'N, 63°54'W.

Delta Amacuro (Territorio Federal)—*Philander opossum* subspecies

- 98c. Los Guires, 09°15'N, 61°54'W.
98c. Tobesobe, Guayo, 09°00'N, 61°25'W.
98d. Güiniquina, 90°10'N, 61°03'W, 0 m.

Mérida—*Philander opossum* subspecies

99. "Merida," 8°36'N, 71°08'W.

Barinas—*Philander opossum* subspecies

- 100a. Ticoporo, Reserva Forestal, 07°48'N, 69°55'W.
100b. Guaquitas, 07°28'N, 71°39'W.
100b. Las Bonitas, Caño Amaru, 07°23'N, 70°44'W.
100c. La Lengüeta, 08°30'N, 70°23'W.

Apure—*Philander opossum* subspecies

- 101a. Nulita, 07°19'N, 71°55'W.
A. Tuttle, January 1968, at 24 m.
- 101a. La Blanquita, 7°12'N, 71°45'W.
A. Tuttle, January 1968, at 24 m.

Táchira—*Philander opossum* subspecies

- 101b. La Ponchera, 07°26'N, 71°52'S.

Bolívar—*Philander opossum opossum*

- 102a. El Palmar, Río Grande, 08°01'N, 61°55'W.
102b. Maripa, Río Caura, 7°26'N, 65°09'W.
S. M. Klages, 1901.
103. Hato San José, 146 km S, 7 km NE Ciudad Bolívar, 6°44'N, 63°27'W.
N. Peterson, D. Peacock, R. Peacock, D. Furman, March 1967, at 302 m.
- 104a. San Martín de Turumbán, Río Cuyuni, 06°59'N, 61°02'W.
104b. Río Yuruán, 06°48'N, 61°50'W.
M. A. Carriker, Jr., March 1910.
- 104c. Chalimana (Raudal), Río Paramichí, Río Paragua, 04°10'N, 62°59'W.

Amazonas (Territorio Federal)—*Philander andersoni andersoni*

105. Majagua (Caño), Río Ventuari, 05°20'N, 65°40'W.
105. San Juan, Río Manapiare, 05°19'N, 66°03'W.
M. D. Tuttle, F. L. Harder, July 1967, at 155 m.
106. Belén, Río Cunucunumá, 03°43'N, 65°42'W.

- M. D. Tuttle, F. L. Harder, January 1967, at 150 m.
107. Acanaña, Río Cunucunumá, 03°39'N, 65°66'W.
M. D. Tuttle, F. L. Harder, June 1967, at 145 m.
108. Playa del Río Base, Mt. Duida, 03°25'N, 65°40'W.
Olalla Brothers, November 1928.
- 109a. Esmeralda, 03°11'N, 65°33'W.
M. D. Tuttle, F. L. Harder, March 1967, at 135 m.
- 109b. Cucurito, Cerro, 03°38'N, 66°25'W.
- 110a. Tamatama, Río Orinoco, 3°08'N, 65°52'W.
M. D. Tuttle, F. L. Harder, April, May, June 1967, at 135 m; D. S. Bremlington, June 1967, at 135 m.
- 110b. Parima (Sierra), 02°40'N, 64°30'W.
- 110c. Mavaca, 02°31'N, 65°10'W.
111. Capibara, Brazo Casiquiare, 2°34'N, 66°18'W.
M. D. Tuttle, F. L. Harder, June 1967, at 130 m.
- 112a. Meray, opposite, Brazo Casiquiare, 2°17'N, 67°11'W.
Olalla Brothers, October 1929.
- 112b. La Neblina (Campamento), Cerro La Neblina, 00°52'N, 66°14'W.

Guyana—*Philander opossum opossum*

Demerara—Mahaica

113. Supinaam River (= Supenam River), 6°58'N, 58°31'W.
Crozier.
114. Georgetown, Demerara River, 6°48'N, 58°10'W.
J. Rodway, June 1929.
115. Hyde Park, Demerara River, 6°30'N, 58°16'W.
S. B. Warren, September 1906.

Essequibo Islands—West Demerara

116. Buck Hall, Essequibo River, 6°56'N, 58°33'W.
S. B. Warren, March 1906.

Upper Takutu—Upper Essequibo

117. Rupununi River, 4°03'N, 58°34'W.
J. J. Quelch, September 1900, at 200 ft.

118. Kanuku Mountains, 3°N, 59°45'W.
E. V. McConnell, J. J. Quelch, November 1900, at 240 ft.

Suriname—*Philander opossum opossum*

Nickerie

119. Avanavero Falls, Kabulebo River, 4°49'N, 57°24'W.
120. Nickerie River, upper, ca. 5°59'N, 56°30'W.
121. Makerie, West River, Wilhelmina Mountains, 3°26'N, 56°45'W.
H. A. Beatty, December 1961, January 1962.
122. Kaiserberg Airstrip, 3°10'N, 56°15'W.
H. A. Beatty, February 1961, at 275 m.

Brokopondo

123. Loksie Hattie, 5°09'N, 55°28'W.
P. Hershkovitz, December 1961.

Saramacca

124. La Poule, 5°47'N, 55°25'W.
P. Hershkovitz, January, February 1962.

Suriname

125. Paramaribo, 5°50'N, 55°11'W.
I. T. Sanderson, February 1938.
125. Clevia, Paramaribo (q.v.).
P. Hershkovitz, February 1962.
125. "Culturutuín," Agricultural Experimental Station in Paramaribo (q.v.).
125. Para River, ca. 10 km SE Paramaribo (q.v.).
125. Rijweg, ca. 9 km W Paramaribo (q.v.).
126. Lelydorp, 5°42'N, 55°16'W.
126. Lelydorpplan (see Lelydorp).
P. Hershkovitz, January, February 1962.

Commewijne

127. Commewijne River, 5°54'N, 55°05'W.

Marowijne

128. Albina, 5°30'N, 54°03'W.

Guyane Française—*Philander opossum opossum*

Cayenne

129. Cayenne, 4°56'N, 52°19'W.
G. K. Cherrie, B. T. Gault, November 1902; S. Klages, January, February 1917; M. Atramentowicz, September 1978–October 1982; P. Charles-Dominique, 1978–1982.

Ouanary

130. Ouanary River, 4°14'N, 51°39'W.

Brasil—*Philander opossum opossum*, *P. opossum frenata*, *P. opossum quica*

Amapá—*Philander opossum opossum*

131. Serra do Navio, 0°59'N, 52°03'W.
T. P. Woodall, June 1966; Instituto Evandro Chagas, 1967, 1968, 1969.
131. Teresinha (= Terezinha), Río Amapari, 0°58'N, 52°02'W.
132. Macapá, Río Amapari, 0°02'N, 51°03'W.
M. Moreira, October, November 1952.
133. Mazagão, Río Maracá, 0°06'S, 51°18'W.
M. Moreira, December 1958.
133. Río Branco, tributary Río Maracá, 0°07'S, 51°17'W.

Roraima—*Philander opossum opossum*

134. Bõa Vista, Río Branco, 2°49'N, 60°40'W.
C. T. Carvalho, M. Sobeiro do Amaral, M. Melo, March 1959.
134. Pocão, Bõa Vista (see Bõa Vista).
135. Caracarái, Río Mucajai, 1°50'N, 61°08'W.
C. T. Carvalho, M. Sobeiro do Amaral, M. Melo, March 1959.
135. Pocão, Caracarái (see Caracarái).

Amazonas—*Philander opossum opossum*

136. Río Xiriviny, 0°59'S, 61°53'W.
K. B. Parker, October 1928, at 80 m.
137. Santo Isidoro, Tefé, 3°27'S, 64°47'W.
Olalla Brothers, August 1928.
138. Ipixuna (Lago do), 3°52'S, 63°52'W.

139. Serra de Parintins, 2°35'S, 56°25'W.
Olalla Brothers, November 1930.
139. Parintins, 2°36'S, 56°44'W.
Olalla Brothers, November 1930.
140. Santa Clara, Villa Bella Imperatriz, 2°50'S, 56°55'W.
Olalla Brothers, August 1930.
141. Lago do Baptista, 3°18'S, 58°15'W.
A. M. Olalla, June 1936.
142. Río Madeira, mouth, 3°22'S, 58°45'W.
Olalla Brothers, February 1930.
143. Rosarthino, 3°43'S, 59°08'W.
Olalla Brothers, June, July 1930.
144. Auará Igarapé, 4°22'S, 59°43'W.
Olalla Brothers, March 1930.
145a. Santo Antônio de Uayara, Río Eirú, 6°43'S, 69°52'W.
Olalla Brothers, April 1930.
145b. Río Urucu, 4°51'S, 65°16'W.
M. N. F. da Silva.

Acre—*Philander opossum quica*

146. Seringal Oriente, 8°48'S, 72°46'W.
M. Moreira, August 1934; M. Moreira, F. Novaes, August 1956.

Pará—*Philander opossum opossum*

147. Fordlandia, Río Tapajóz, 3°40'S, 55°30'W.
R. M. Gilmore, February 1938.
148. Km 19, Itaituba–Jacareacanga, 4°17'S, 56°05'W.
F. Ramos, Instituto Oswaldo Cruz, August 1972.
148. Km 216, Estrada de Santarem–Cuiabá (BR165) (see Itaituba).
Instituto Evandro Chagas, May, June 1973.
149. Canudos, 7°16'S, 58°07'W.
F. Lima, November 1920.
150. Taperebá, Igarapé, Chaves, 0°10'S, 49°55'W.
C. Carvalho, June, July 1958.
151. Altamira, Río Xingú, 3°12'S, 52°12'W.
Instituto Oswaldo Cruz, August 1971.
152. Gradaús, 7°43'S, 51°11'W.
C. T. Carvalho, N. Hidasí, M. Amaral, June, July, August 1957.
153. Cametá, Río Tocantins, 2°15'S, 49°29'W.
A. M. Olalla, February 1934, March, April, May, November 1935, November 1936.

153. Ilha do Taiuna, R o Tocantins, 2 15'S, 49 29'W, opposite Camet . A. M. Olalla, October, November 1931.
154. Mazag o, R o Tocantins, 2 25'S, 49 10'W. F. Lima, November 1912.
155. Mocajuba, R o Tocantins, 2 35'S, 49 30'W. A. M. Olalla, November 1931.
156. Bai o, R o Tocantins, 2 41'S, 49 41'W. A. M. Olalla, December 1931.
157. Arumateua, R o Tocantins, 3 54'S, 49 41'W. F. Lima, October 1912.
158. Marab , R o Tocantins, 5 20'S, 49 10'W. N. Peterson, September 1975.
159. Par  (see Bel m).
159. Km 90, Par , Rodovia E. Sneathlage, April 1909.
159. Bel m do Par  (see Bel m).
159. Bel m, 1 27'S, 48 29'W. M. A. Miles, 1975–1980.
159. Ipeau–Apez, Bel m (see Bel m). E. Sneathlage.
159. Marco, suburb of Bel m (q.v.).
159. Murutucu (= Instituto Agronomico do Norte), Bel m (q.v.). F. Luna, August 1922, March 1925.
159. Utinga, suburb of Bel m (q.v.). Instituto Oswaldo Cruz, June 1963; R. H. Pine, June 1968.
159. Ananind ua, E. F. Bragan a, 1 22'S, 48 23'W. F. Lima, May 1920.
159. Sapucajuba, suburb of Bel m (q.v.).
160. Ipitanga, Rio Acar , 1 57'S, 48 11'W.
161. Flor do Prado, near Quatipuru, 0 52'S, 46 59'W. E. Sneathlage, October 1916.
162. Santa Mar a, Bragan a, 1 03'S, 46 46'W. April 1968.
163. Peixe-Boi, R. R. Bragan a, 1 12'S, 47 18'W.
163. Igarap  A u, 1 32'S, 47 03'W.
163. Col nia do Prata, Igarap  A u (q.v.).
164. Capim, 1 30'S, 48 20'W. Instituto Oswaldo Cruz, 1960.
165. S o Miguel do Guam  (see Guam ).
165. Guam , 1 37'S, 47 27'W. Departamento do Zoologia, S o Paulo, October 1959.
165. Iriteria, S o Miguel do Guam  (see Guam ). M. Amaral, December 1959, January 1960.
- Rond nia—*Philander opossum quica*
166. Porto Velho, 8 46'S, 63 54'W. T. Hibbs, April 1965.
- Mato Grosso—*Philander opossum quica*
167. Mato Grosso, 15 00'S, 59 57'W. J. Natterer, September–November 1824.
- 168a. C ceres, 16 04'S, 57 41'W. M. L. Kuns, September 1965.
- 168b. Pocon , 16 15'S, 56 37'W.
- 168c. Barra do Gar es, 15 53'S, 52 15'W.
- 168d. Balisa, 16 15'S, 52 26'W.
169. Monte Alegre, Palmeiras, 16 03'S, 55 30'W. A. M. Olalla, June 1944; A. Aggio, June 1944.
- Mato Grosso do Sul—*Philander opossum quica*
170. Corumb , R o Paraguay, 19 01'S, 57 39'W. M. L. Kuns, September 1965.
170. Urucum, 19 13'S, 57 33'W. L. E. Miller, December 1913, at 125 m.
170. Santa Teresa (see Urucum). M. L. Kuns, September 1965.
- 171a. Miranda, 20 14'S, 56 22'W. A. M. Olalla, 1957; J. Lima, September 1937.
- 171b. Salobra, 21 14'S, 57 08'W. L. Travassos, May 1942.
- Bahia—*Philander opossum frenata*
172. Bahia (= Salvador), 12 59'S, 38 31'W. Herr Kaehne, before 1815.
- Goi s—*Philander opossum quica*
173. Aragar as, 15 55'S, 52 15'W. M. Amaral, May 1958.
- 174a. Formosa, 15 32'S, 47 20'W.
- 174b. Anapolis, 16 20'S, 48 58'W. R. M. Gilmore, 1936–1937.
- 175a. Trindade, 16 40'S, 49 30'W. S. Hidasi, June 1962.
- Distrito Federal—*Philander opossum quica*
- 175b. Parque Nacional, 15 35'S, 48 54'W.
- 175c. Bras lia, 15 47'S, 47 55'W.
- 175c. Agua Limpa (Fazenda), 15 57'S, 47 54'W.

Minas Gerais—*Philander opossum quica*

176. Conceição do Mato Dentro, 19°01'S, 43°25'W.
177. Lagoa Santa, 19°38'S, 43°53'W.
P. W. Lund, between 1833 and 1880.
178. Quartel de Sacramento, 19°44'S, 42°31'W.
J. Pinto Fonseca, July 1919.
178. Fazenda de Floresta, Rio Matipó, 19°53'S, 42°33'W.
J. Pinto Fonseca, July 1919.
178. Esmeralda (Fazenda), ca. 19°20'S, 42°50'W.
178. Montes Claras, 19°25'S, 42°35'W.
179. Boa Esperança, Serra de Caparaó, 20°10'S, 41°46'W.
E. Kaempfer, August 1929.
180. Fazenda Cardoso, Serra de Caparaó, 20°22'S, 41°48'W.
E. G. Holt, June 1922.
181. Benfca, Serra de Itatiaia, 21°41'S, 43°26'W.
E. H. Holt, June 1922, at 2000 ft.
182. Além Paraíba, 21°52'S, 42°41'W.
183. Juiz de Fora, 21°45'S, 43°20'W.
Serviço do Estudos e Pesquisas sobre a Febra Amarela (SEPSFA).

Espírito Santo—*Philander opossum quica*

184. Santa Teresa, 19°55'S, 40°36'W.
A. M. Olalla, October 1942.
184. São João de Petrópolis, 19°49'S, 40°40'W.
C. Lako, June 1940.
185. Serra, 20°07'S, 40°18'W.
C. Lako, September 1949, at 50 m.
185. Campinho, 20°07'S, 40°17'W.
C. Lako, April 1940, at 500 m.
185. Vitória, 20°19'S, 40°21'W.
C. Lako, April 1940.
185. Vila Velha, Morro de Angoles, 20°20'S, 40°17'W.
C. Lako, March, April 1940, June 1941.
186. Caixa D'água, 20°38'S, 40°55'W.
C. Lako, June 1940.
187. Valão de São Lourenço, Santa Teresa, 20°37'S, 41°41'W.
C. Lako, June 1940.
188. Engenheiro Reeve (now Rive), 20°46'S, 41°28'W.
A. Robert, March, April 1903.

Rio de Janeiro—*Philander opossum quica*

189. Teresópolis (see Teresópolis).
189. Teresópolis, 22°27'S, 42°57'W.

G. R. Hancock, September 1923, at 3000 ft; R. Kellogg, March 1943; G. Perreira, September 1942; D. E. Davis, May, September, October 1943; C. Guinle, Perreira, January 1943; C. Guinle, P. M. Britto, November 1942, March 1943, May 1943; C. Guinle, November 1942; C. Guinle, H. W. Laemmert, April 1943; P. M. Britto, January, May 1943.

189. Boa Vista, Fazenda, Teresópolis (see Teresópolis).
189. Boa Fé, Fazenda, Teresópolis, 22°22'S, 41°53'W.
D. E. Davis, October, September 1943; P. M. Britto, January 1943; G. Perreira, September 1942; C. Guinle, November 1942; C. Guinle, P. M. Britto, March, May 1943; C. Guinle, H. W. Laemmert, April 1943.
189. Novo Friburgo, 22°16'S, 42°32'W.
Herr Beschke.
189. Barreira, Serra dos Órgãos, 22°56'S, 42°56'W.
Schind in Pohle, 1927.
189. Serra dos Órgãos, 22°56'S, 42°56'W.
190. Rio de Janeiro, 22°54'S, 43°14'W.
R. M. Gilmore, January, February 1938.
191. Rodeio, Serra do Mar, 22°33'S, 43°41'W.
G. B. Flowers.
191. Sepetiba, 22°58'S, 43°42'W.
J. Natterer, March 1818.
191. Sapatiba (see Sepetiba).
191. São João Marcos, 22°54'S, 43°58'W.
C. Lako, October 1938, January 1939.
192. Mangaratiba, 22°57'S, 44°02'W.
C. Lako, July, September 1938, February 1939.
193. Itatiaia Parque Nacional, 22°30'S, 44°34'W.
F. Gouvêa, July 1957.
193. Monte Serrat, Parque Nacional de Itatiaia.
C. Moreira, 1901; F. Gouvêa, March 1951, at 800 m, August 1957, at 850 m.
193. Macieiras Itatiaia, 22°30'S, 44°34'W.
F. Lima, December 1949; F. Gouvêa, December 1949.
193. Barro Branco, 22°23'S, 44°30'W.
A. Passarell, April 1941.
194. Pedra Branco, Paratí, 23°13'S, 44°43'W.
C. Lako, July 1943.

São Paulo—*Philander opossum quica*

195. Avanhandava, Lajeado, 20°57'S, 48°46'W.
E. Garbe, April 1910.

196. Boracéia, upper Rio Tietê, 22°10'S, 48°45'W.
J. Pinto, May 1958; L. Travassos, March, April 1958; see also Boracéia (203).
197. Iporanga, Lajeado, 24°36'S, 48°34'W.
E. Dente, December 1944.
198. Monte Alegre, Amparo, 22°40'S, 46°41'W.
J. Lima, June 1944.
199. Ypanema (Ipanema = Bacaetava), 23°26'S, 47°36'W.
200. São Paulo, 23°30'S, 46°30'W.
200. Cotia, 12 km W São Paulo (q.v.).
"I.A.L.," January, July 1961, January 1962, November 1963.
200. Cantareira, Serra da, 23°25'S, 46°39'W.
200. Butantã, Serra da Cantareira (q.v.).
J. Navas, April 1910.
201. Juquia, 24°19'S, 47°36'W.
201. Costão dos Engenhos, 24°41'S, 47°25'W.
A. M. Olalla, July 1964.
202. Alto da Serra, 23°47'S, 46°19'W.
202. Vila Oliveira, Magi das Cruzes, 23°31'S, 46°11'W.
J. Lima, September 1943.
203. Salesópolis, Boracéia, 23°32'S, 45°51'W.
J. Oliveira, June, July 1961.
203. Casa Grande, 20 km S Salesópolis (q.v.).
O. de Sousa Lopez, April 1962, May 1966, May 1968.
203. Boracéia, Ponta de, 23°48'S, 45°49'W.
Near Salesópolis Biological Station; not to be confused with Boracéia (196).
204. Serra de Itatiaia, 22°55'S, 45°28'W.
205. Piquete, 22°37'S, 45°10'W.
Zech, January 1897.
206. São Sebastião, 23°48'S, 45°25'W.
A. Hempel, July, August 1900.

Paraná—*Philander opossum quica*

207. Rio Paracá, 23°41'S, 53°57'W.
E. Dente, S. Siraglia, January 1954.
208. Roça Nova, Serra do Mar, 25°30'S, 48°50'W.
A. Robert, August, September 1901.

Santa Catarina—*Philander opossum quica*

209. Joinville, 26°18'S, 48°50'W.
E. Steiger, August 1930.
209. Hansa, 26°27'S, 48°50'W.
W. Ehrhardt, August 1928.

209. Colônia Hansa (see Hansa).

Rio Grande do Sul—*Philander opossum quica*

210. Passo Fundo, 28°15'S, 52°20'W.
211. Taquara, 29°31'S, 50°47'W.
R. Hensel, before 1867; H. von Ihering, before 1888.

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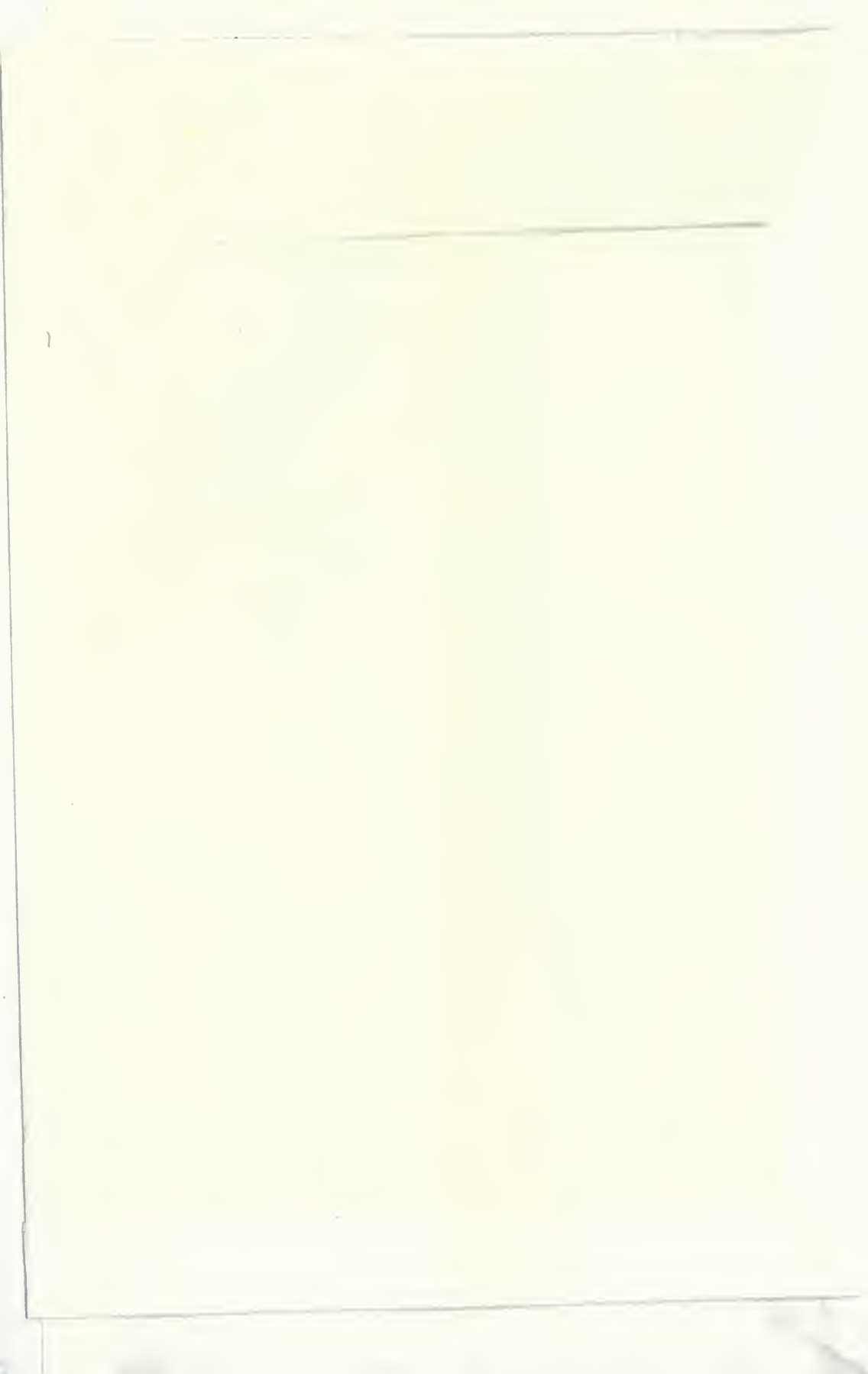
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