

DEFINITION OF SPECIES OF POUCHED FOUR-EYED OPOSSUMS (DIDELPHIDAE, *PHILANDER*)

JAMES L. PATTON AND MARIA NAZARETH F. DA SILVA

*Museum of Vertebrate Zoology, University of California,
Berkeley, CA 94720 (JLP, MNFS)*

*Coordenação de Entomologia, Instituto Nacional de Pesquisas da Amazônia,
Correio Postal 478, 69083 Manaus, Amazonas, Brazil (MNFS)*

We hypothesize phyletic relationships among taxa of the didelphid marsupial genus *Philander*, based on sequences of the mitochondrial cytochrome *b* gene. Data are available for six taxa recognized at either the specific or subspecific levels; *P. opossum opossum* Linnaeus (eastern and northeastern Amazonia), *P. opossum canus* Osgood (western Amazonia), *P. opossum fuscogriseus* J. A. Allen (southeastern Central America), *P. opossum frenata* Olfers (southeastern Brazil), *P. andersoni andersoni* Osgood (northwestern Amazonia), and *P. andersoni mcilhennyi* Gardner and Patton (west-central Amazonia). Haplotype divergence is minimal to non-existent (<1% on average) between individuals within and among localities for each taxon. The taxon inhabiting the Atlantic forest of coastal Brazil (*P. o. frenata*) is highly divergent from all others, averaging nearly 14% in sequence divergence. Maximal divergence among haplotypes representative of the other taxa examined is <8%. The combination of phylogenetic relationships and local sympatry suggests a greater degree of species diversity for the genus than the two species *P. opossum* and *P. andersoni*. We recognize the Brazilian coastal *P. frenata*, as well as both *P. andersoni* and *P. mcilhennyi*, as valid species in addition to *P. opossum*. It is possible *P. opossum* is a composite, and that further studies will accord species status to the Middle American, western Amazonian, and eastern Amazonian-Guianan gray four-eyed opossums.

Key words: *Philander*, marsupials, Didelphidae, mtDNA sequence, Neotropical forests, species limits, phylogenetics

Pouched four-eyed opossums of the genus *Philander* are among the more common large, terrestrial didelphid marsupials in the moist Neotropical forests. The genus ranges from Tamaulipas, Mexico, to northern Argentina. In South America, it occurs from the lowland rain forests of Amazonia, the Guiana coast, the Chocó of Colombia and northwestern Ecuador, and the Mata Atlântica (Atlantic rain forest) of Brazil to upper tropical forests above 1,200 m on both eastern and western Andean slopes (Emmons and Feer, 1990; Hall, 1981). The nomenclatural status of the generic name *Philander* has been debated (Gardner, 1981; Hershkovitz, 1949, 1976, 1981; Husson, 1978; Pine, 1973; summarized in Gardner, 1993), and the number, as well as geographic range

of the species recognized, has been uncertain.

These opossums are quite variable geographically in external color, color pattern, and body size. Nonetheless, most accounts considered the genus to be monotypic, comprised of the single species *Philander opossum* Linnaeus 1758, until *P. mcilhennyi* was described by Gardner and Patton (1972). The latter is a nearly totally black animal, known at the time of description from a single locality in the lowland Amazonian forest of eastern Peru where it was found to be sympatric with the widely distributed and gray *P. opossum*. This represented the first reported case of sympatry between forms that were readily separable by cranial, dental, pelage, and coloration characters.

Philander opossum (exclusive of *P. mcilhennyi*) comprised 12 subspecies according to Cabrera (1958) and Hall (1981). Some of these (e.g., *andersoni* Osgood, *nigratus* Thomas, *melanurus* Thomas, and *melantho* Thomas) exhibit aspects of the blackish coloration otherwise diagnostic of *P. mcilhennyi*. Gardner and Patton (1972) recognized a possible relationship between *mcilhennyi* and *andersoni*, but preferred to treat the latter as a geographic race of *opossum* and the former as a separate species. Subsequently, Emmons and Feer (1990) and Gardner (1993) re-evaluated this arrangement, and listed *mcilhennyi* as a synonym of *andersoni*, thus linking within this species those Amazonian forms that typically are larger and have blackish fur at least along the mid-dorsum. Emmons and Feer (1990) mapped the distribution of *P. andersoni* from northern Peru and adjacent Ecuador southeast to the type locality of *mcilhennyi* in eastern Peru, east into adjacent states of Acre and Amazonas in Brazil, and north to southern Venezuela. Gardner (1993) included both *mcilhennyi* and *nigratus* in his concept of *andersoni*. Neither Emmons and Feer (1990) nor Gardner (1993) provided documentation for their conclusions, and the geographic extent of color variants of four-eyed opossums has not been evaluated.

Here we evaluate the systematic position of *mcilhennyi* in relation to geographic representatives of other taxa of *Philander*, including *andersoni* from northern Peru and Ecuador, as well as taxa usually treated as geographic representatives of *P. opossum* (e.g., Cabrera, 1958; Gardner, 1993). Our perspective is based on sequence variation in the mitochondrial cytochrome *b* gene, supplemented by comments on morphological characters.

MATERIALS AND METHODS

Liver tissues, obtained from animals captured in the field, were frozen in liquid nitrogen or preserved in 95% ethyl alcohol. DNA was extracted using the sodium dodecyl sulfate-proteinase K/phenol/RNase method (Maniatis et al.,

1982), sodium-chloride method (Miller et al., 1988), or Promega®-Wizard minipreps (Beckman et al., 1994). Mitochondrial sequences containing the cytochrome *b* gene (*cyt-b*) were isolated via the polymerase chain reaction (PCR) using primer combinations MVZ05-MVZ14 or MVZ05-MVZ16 for both double-strand and asymmetrical single-strand amplifications. Sequences for the first 660 base pairs (bp) of the light strand of the *cyt-b* gene were obtained using MVZ05 and MVZ19 or MVZ65 as sequencing primers (oligonucleotide sequences given by da Silva and Patton, 1993; Smith and Patton, 1991, 1993; Patton et al., 1996). Complete *cyt-b* sequences are available for three taxa of *Philander* (*canus*, *frenata*, and *mcilhennyi*) in Patton et al. (1996) and as GenBank accession numbers U34678–U34680.

Specimens examined are listed in the Appendix I, and sampled localities are mapped in Fig. 1. All phylogenetic analyses were based on unique haplotypes. Maximum parsimony trees were constructed using PAUP (Swofford, 1993), with a heuristic search of 100 random orders of haplotypes with tree bisection-reconnection (TBR) branch swapping. Hypotheses of relationship depicted at specific internal nodes were evaluated using bootstrap analyses (Felsenstein, 1985), with 500 replicates and 10 random orders of input taxa for each replication. The Molecular Evolutionary Genetics Analysis (MEGA—Kumar et al., 1993) and the Minimum Evolutionary Tree (METREE—Rzhetsky and Nei, 1992) programs were used to generate neighbor-joining trees of all haplotypes from a matrix of Kimura 2-parameter distances (Kimura, 1980). Confidence limits at nodes were based on the standard error test of Rzhetsky and Nei (1992, 1993), with 2,000 replicate analyses. Additionally, the dataset was pared to 18 terminal taxa (divergent haplotypes) and analyzed by the same distance methods and by the branch-and-bound procedure in PAUP, which guarantees that the shortest tree will be found. When more than one minimal-length tree was found, a strict consensus topology was produced, and was used to summarize the hierarchical patterns observed.

RESULTS AND DISCUSSION

Levels and patterns of sequence divergence.—Thirty-one distinct haplotypes of cytochrome *b* sequence were identified for the 43 *Philander* examined, with a total of

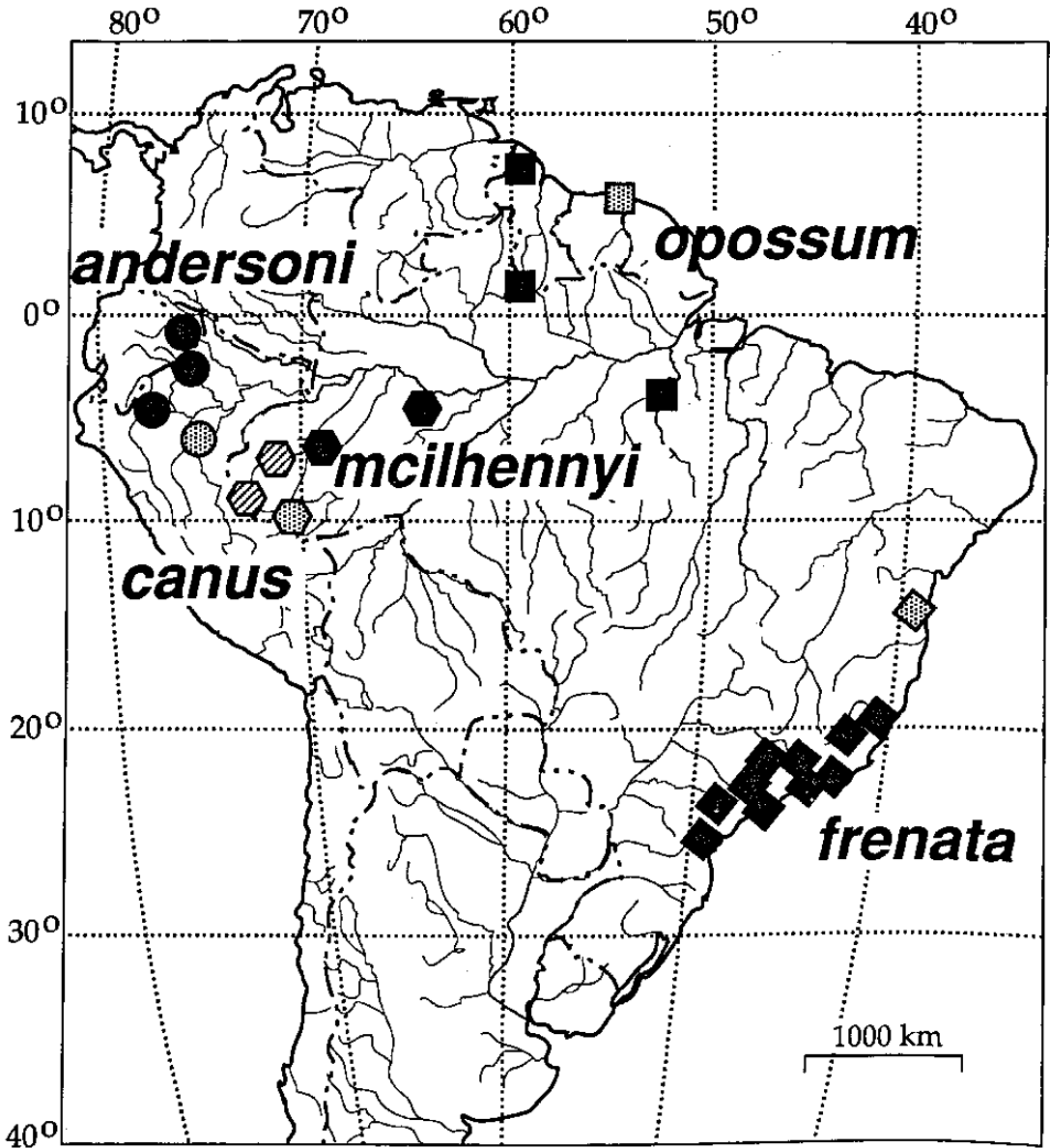


FIG. 1.—Map of sample localities of mitochondrial cytochrome *b* sequences for five taxa of South American *Philander*. Stippled symbols are the type localities for *andersoni* (circle), *opossum* (square), *mcilhennyi* (hexagon), and *frenata* (diamond). The two diagonally hatched hexagons identify sympatric localities of *canus* and *mcilhennyi* in the upper R \ddot{u} Juru \acute{a} , states of Acre and Amazonas, Brazil.

190 variable sites among the 660 bases examined for all individuals. Divergence levels are minimal among the haplotypes within local populations and among geographic samples of single taxa of *Philander*, averaging <1.5% in all comparisons (Table 1).

In no case does variation between or among haplotypes from the same locality exceed the level observed among localities of the same taxon. Only two haplotypes that differed by a single site mutation were found among the four individuals of *canus* ex-

TABLE 1.—Levels of divergence in comparisons of 660 base pairs of the light strand of the mitochondrial cytochrome *b* gene for taxa of *Philander*, estimated by the Kimura 2-parameter method (Kimura, 1980). Data are given as means and ranges for comparisons among haplotypes within and between taxa. The number of unique haplotypes relative to the number of individuals examined is given.

Taxon	Taxon					
	<i>frenata</i>	<i>andersoni</i>	<i>fuscogriseus</i>	<i>opossum</i>	<i>mcilhennyi</i>	<i>canus</i>
<i>frenata</i> (12/16)	0.71 (0.2–1.5)	14.16 (13.7–14.7)	13.14 (12.6–13.5)	14.85 (13.7–15.8)	13.57 (12.4–14.9)	12.43 (11.8–12.8)
<i>andersoni</i> (5/5)		1.12 (0.5–1.4)	7.55 (7.4–7.8)	6.74 (6.6–6.9)	7.53 (7.3–8.1)	6.69 (6.6–6.7)
<i>fuscogriseus</i> (1/2)				6.07 (5.9–6.2)	7.24 (7.1–7.5)	6.77
<i>opossum</i> (4/6)				1.34 (0.2–2.0)	4.16 (3.6–4.6)	3.88 (3.6–4.1)
<i>mcilhennyi</i> (7/10)					1.49 (0.1–2.4)	3.97 (3.6–4.3)
<i>canus</i> (2/4)						0.15

amined from three localities along the Rio Juruá in western Brazil. Variation among the four haplotypes of *opossum* from Guyana and eastern Brazil is likewise negligible, averaging only 1.34%, while that between the 12 haplotypes of *frenata* average 0.71% with a maximum of 1.5% between individuals from the states of São Paulo and Minas Gerais. The greatest degree of haplotype divergence observed within recognizable taxa is that for *mcilhennyi*, for which maximal divergence values of 2.4% were observed between individuals from localities >1,000 km apart in western Amazonia, although average values were only ca. 1.5%. These levels of within and among locality variation are rather typical for other species of small mammals for which data on the same gene are available (e.g., da Silva and Patton, 1993; Myers et al., 1995; Patton and Smith, 1992; Smith and Patton, 1991, 1993).

Divergence values between taxa, however, are several fold higher (Table 1). Comparisons between the coastal Brazilian *frenata* and all other taxa examined, average nearly twice the level of divergence (13.63%) as that observed between any other pair of taxa. The divergence value be-

tween *andersoni* and *fuscogriseus* (7.6%) is nearly equivalent to the levels of divergence between these taxa and to all other taxa, ranging between 6.1 (*fuscogriseus* to *opossum*) and 7.5% (*andersoni* to *mcilhennyi*). Divergence between the remaining three taxa (*opossum*, *canus*, and *mcilhennyi*) also are nearly equal, but average 4.0% (an average of 3.88% between *opossum* and *canus*, 3.97% between sympatric *canus* and *mcilhennyi*, and 4.16% between *opossum* and *mcilhennyi*). Clearly, *andersoni* and *mcilhennyi* are not as similar in their cytochrome *b* sequences as would be expected if these two forms were members of the same species (sensu Emmons and Feer, 1990; Gardner, 1993). As mentioned above, it is the extremely high levels of sequence divergence between populations currently allocated to the species *opossum* from the Amazon Basin in comparison to those from the Mata Atlantica of coastal Brazil that is most striking.

Phylogenetics of Philander.—Estimates of phylogenetic relationships among haplotypes belonging to each of the taxa of *Philander* examined were made using both distance and parsimony approaches. Sequences from species of other didelphid

genera were used as out-groups, including *Metachirus*, *Caluromys*, *Marmosa*, *Marmosops*, *Micoureus*, and *Monodelphis* (Patton et al., 1996; GenBank accession numbers U34663–U34682). The choice of out-group made no difference in the topological relationships among the haplotypes of *Philander* examined herein.

Distance and parsimony methods differ in their respective assumptions regarding the mode of sequence divergence, and each approach has its proponents and detractors. For the *Philander* dataset, the same topology was produced, with the same general level of support for specific nodes, regardless of the method of analysis. Initially, trees were generated for the entire group of 31 separate haplotypes. Placement of haplotypes varied only at terminal nodes within local geographic-taxonomic units when multiple trees were obtained. Consequently, the taxonomic structure represented by all trees produced by either method was consistent. Given the high degree of sequence similarity within taxonomic units and the extent of divergence among them (Table 1), this is perhaps not surprising. For example, the 12 haplotypes of the 16 specimens of *frenata* invariably clustered as a single phylogenetic unit that was the sister to all other *Philander* sequences, although the specific relationships of these haplotypes differed among the individual trees. In both distance and parsimony analyses, each of the six terminal taxa is comprised of monophyletic sets of haplotypes, with both confidence limits and bootstrap values 99% or higher.

For final analyses, data were reduced to 18 haplotypes that represented the range of variation found among each of the six taxa examined. The strict consensus parsimony tree for these haplotypes is shown in Fig. 2. The topology depicted is identical to that obtained by the neighbor-joining algorithm on the Kimura 2-parameter distance matrix, with one exception. The distance tree includes both *andersoni* and *fuscogriseus* in an unresolved polytomy with the triad of

opossum, *canus*, and *mcilhennyi*, while the parsimony tree resolves this polytomy. The level of support for nearly all internal nodes obtained by both tree-building methods, whether measured as the statistical confidence limit or by a bootstrap value, is essentially equivalent and uniformly strong. The distinctness of *frenata* is evident, as this taxon forms the sister group to all other *Philander*, with a confidence limit of 99% and bootstrap of 100%. The taxon *andersoni* is positioned sequentially outside *fuscogriseus* and a polytomous clade consisting of *canus*, *opossum*, and *mcilhennyi*. The node linking *andersoni* with these four taxa also is strongly supported, with a confidence limit of 99% and bootstrap value of 100%, but that linking *fuscogriseus* with the remainder is less well supported (confidence limit of 0% and bootstrap of 77%). Finally, in both analyses, *opossum*, *canus*, and *mcilhennyi* form an unresolved polytomous relationship, although their grouping is well supported with a confidence limit of 99% and a bootstrap value of 83%. The lack of clear resolution between these three taxa is not surprising, given their approximately equal levels of pairwise divergence (Table 1).

Species boundaries in Philander.—Figure 2 is a gene tree of relationships among the sampled mitochondrial-sequence haplotypes. Consequently, this tree, no matter how well individual nodes are supported, may not reflect the true phylogeny of the taxa under consideration because of the potentially confounding problems of differential lineage sorting and the retention of ancestral polymorphisms. For the data available on *Philander*, the retention of ancestral polymorphisms does not seem a problem of concern, because haplotypes of each recognizable taxon form strongly supported monophyletic units. However, it remains possible that the phylogenetic relationships among these lineages of haplotypes do not reflect the true phylogenetic history of the taxa. Only the addition of other, genetically independent data (such as nuclear sequenc-

regardless of the species concept that one might apply (Cracraft, 1983; de Queiroz and Donoghue, 1990; McKittrick and Zink, 1987).

Under a phylogenetic species concept (Cracraft, 1983; McKittrick and Zink, 1987), the coastal-Brazilian *frenata* would be clearly recognized by virtue of its unique phylogenetic position and highly divergent *cyt-b* sequence relative to other taxa examined. The same argument can be made for the superficially similar black forms *andersoni* and *mcilhennyi*, by virtue of their lack of phylogenetic sister relationship. It is even possible to extend this same argument to *fuscogriseus*, *canus*, and *opossum*, because together they form a paraphyletic relationship with *mcilhennyi*. However, their phylogenetic separation may reflect the vast geographic distance between the respective sample localities (Panama, western Amazonia near the Peru-Brazil border, and eastern Amazonia). Additional material from central and northern Brazil, from Colombia and Venezuela, and from Central America and Mexico would be needed to determine the degree of phyletic separation of these gray four-eyed opossums.

Based on the analyses presented, including the degree of sequence divergence within taxa across their sampled geographic ranges, as well as that among them, and the robust set of phylogenetic relationships, we suggest that there are at least four species of pouched four-eyed opossums that deserve recognition. In making this suggestion, however, we recognize that: 1) There are considerable lacunae in the available geographic (and taxonomic) samples. Consequently, additional data will possibly modify the recommendations we make below. And, 2) mitochondrial-DNA sequences, while optimal for defining lineages because of their rapid rate of evolution, are none-the-less potentially problematic in depicting true relationships (e.g., Melnick et al., 1993; Patton and Smith, 1994). Species defined by cohesive or reproductive criteria (Templeton, 1989) will not necessarily be

those recognized by cladistic ones (Cracraft, 1983). Thus, our current views as to the species status among the various pouched four-eyed opossums rests on two elements: demonstrable sympatry between readily definable forms (as, for example, between *canus* and *mcilhennyi* in western Amazonia) and the assumption that the cytochrome-*b* tree is an accurate reflection of organismal history, and thus can be used to define taxa in a phylogenetic context. Given these principles, and the data available, species of *Philander* that are definable include the following:

Philander andersoni (Osgood, 1913:95)

Type locality.—"Yurimaguas, [Loreto,] Peru."

Synonyms.—*nigratus* Thomas, 1923:603; type locality "Utcuyaco, Dept. Junin, 1600 m," Peru. Synonymy follows Gardner (1993).

Characteristics.—This is a dark-colored subspecies, typically with a well-marked black, median-dorsal stripe ca. 3–4 cm wide, gray sides, and self-colored (unicolored) creamy to gray-based creamy venter. The dorsal fur is short and dense, equal in length to that along the sides (ca. 10 mm long), without conspicuously elongated and coarse guardhairs. The base of the tail, which is covered with short hairs, is furred for ca. 18% of its length. The cheek and eye-spots are cream, and a distinctly pale cream spot at the medial base of the pinna usually is present.

Distribution.—Specimens that we have seen of this taxon occur from the Cerro Duida region of southern Venezuela (AMNH, MZUSP) west to the Sierra de Macarena of Colombia (AMNH), and south through eastern Ecuador and northern Peru (AMNH, FMNH, MVZ). North of the Río Marañón-Río Amazonas axis, specimens are known from localities in the Andean foothills and Amazon Basin proper. For example, in northern Peru, we have collected specimens on the lower Andean slopes in the basins of the Cenepa and Santiago riv-

ers, and have examined specimens from the lowland forests on the Río Tigre (KU), Río Curaray, and Río Amazonas near Iquitos, Orosa, and Sarayaca (AMNH). South of the Río Marañón, specimens of *andersoni* are only known from the type locality (Yurimaguas, near the mouth of the Río Huallaga in Loreto Department, Peru). Specimens from foothill valleys of the Andes in Junín and Ayacucho departments have been allocated to this species (Gardner and Patton, 1972), but this allocation needs confirmation (see comments below, under *mcilhennyi*).

Philander frenata (Olfers, 1818:204)

Type locality.—"Südamerica;" restricted to Bahia, Brazil, by Wagner (1843:44, footnote 25).

Synonyms.—*frenata* Illiger, 1815:107 (*nomen nudum*); *superciliaris* Illiger, 1815:107 (*nomen nudum*); *superciliaris* Olfers, 1818:204; type locality "Südamerica"; *quica* Temminck, 1824:36; type locality "Brésil;" restricted to Sapitiba (= Sepetiba, Rio de Janeiro) by von Pelzeln (1883:110; also see J. A. Allen, 1916:563, and Hershkovitz, 1959:342).

Characteristics and distribution.—This is a large, dark-gray form distributed along the coastal region of eastern and southeastern Brazil, at least from the state of Paraná north to Bahia and inland to the states of Minas Gerais and Goiás. Some specimens have a darker mid-dorsum, but without the distinctness of a stripe; the sides are invariably dark gray, and the venter cream-gray. The relationship of *frenata* to *azarica* in the Paraná Basin remains to be established. We align *azarica* here with *opossum*, but without any justification beyond its current placement (*sensu* Cabrera, 1958).

Philander mcilhennyi Gardner and Patton, 1972:2

Type locality.—"Balta (10°08'S, 17°13'W), Río Curanja, ca. 300 meters, Departamento de Loreto [now Departamento de Ucayali], Perú."

Characteristics.—This is a large, almost entirely black animal. The dorsum is blackest along the midline, usually without the distinct mid-dorsal black stripe characteristic of *andersoni*. The sides become grayer, with hairs tipped in silver, but the dark-gray coloration continues onto the venter where the fur is completely gray-based throughout with short silver tips. Specimens from the type locality are somewhat blacker in overall appearance than those from farther to the east in Brazil; those from the Río Urucu in central Brazil can have the chin and a thoracic patch covered with pale self-colored hairs instead of being completely gray ventrally. Some specimens, particularly young ones, from the Río Juruá and Río Urucu in western Brazil also exhibit an indistinct blackish stripe in the shoulder region, but this becomes diffuse posteriorly. All specimens of *mcilhennyi* that we have seen lack the pale cream spots at the medial base of the ears that are characteristic of *andersoni*. The dorsal fur is distinctly longer than in *andersoni*, with dense and coarse guardhairs (ca. 18 mm in length) extending beyond the underfur. Guardhairs, which are especially dense along the back, give the animal a shaggy appearance; they are also prominent, if more sparsely distributed, on the sides. The fur at the base of the tail is black to the tip, long, and the furred base averages >23% of the length of tail. Cranial characteristics listed by Gardner and Patton (1972) include anteriorly expanded lacrimal bones, distinctly notched posterior aspect to the expanded portion of the nasal bones, and deep indentation of the labial margin of M3. The expanded lacrimal bones characterize all specimens we have examined from western Brazil, but there is variation in the degree to which the posterior nasals are notched. Hutterer et al. (1995) noted differences in number and length of vibrissae in comparisons between sympatric *mcilhennyi* and *opossum*.

Distribution.—Known from eastern Peru in the Río Ucayali Basin (Panguana, Río Pachitea, Hutterer et al., 1995; 59 km SW

Pucallpa, USNM) southeast to the type locality at Balta in the headwaters of the Río Purus (MVZ, LSU) and east into states of Acre and Amazonas of Brazil along the upper Río Purus (USNM), central and upper Río Juruá, and Río Urucu (INPA, MVZ). We have seen color photographs of specimens from the biological station at Jenero Herrera and the Río Yarapa, on the east side of the Río Ucayali near its mouth in Loreto department, northeastern Peru (D. W. Fleck, pers. comm.); we believe these specimens to be *mcilhennyi*, although they were recorded as *andersoni* by Fleck and Harder (1995). *P. mcilhennyi* is broadly sympatric with *P. opossum* (subspecies *canus*) throughout most of its range; the two co-occur at all known localities for *mcilhennyi*, except at the site on the Río Urucu in central Brazil (Fleck and Harder, 1995; Gardner and Patton, 1972; Hutterer et al., 1995). From our experiences along the Río Juruá, *mcilhennyi* typically is found in upland, non-seasonally flooded (terra firme) forest, while *opossum* is more prevalent in the seasonally flooded forest (várzea).

Remarks.—As mentioned above, the relationship of blackish animals from the Andean foothills in eastern Peru to *andersoni* or *mcilhennyi* remains to be ascertained. Based on general morphology, Gardner and Patton (1972) allocated specimens from the Río Apurimac drainage in Departamento Ayacucho to *andersoni* rather than to *mcilhennyi*, while Hutterer et al. (1995) allocated individuals from the more northern sites at Panguana in the Río Pachitea drainage to *mcilhennyi*. The name *nigratus* Thomas 1923 (with type locality of Utcuyaco, in the Chanchamayo Valley of eastern Junín department) usually is treated as a junior synonym of *andersoni* (Gardner, 1993; Gardner and Patton, 1972), because of Thomas' (1923:603) reference to a black dorsal stripe observed in the type specimen. However, Thomas also noted that the venter was "dull muddy greyish brown, with a small patch only on the chest buffy to the bases of the hairs." These descriptions of *nigra-*

tus mix the dorsal coloration of *andersoni* with the ventral coloration of *mcilhennyi*. If future analyses indicate that *nigratus* is conspecific with *mcilhennyi*, then *nigratus* would have priority for this species.

Philander opossum (Linnaeus, 1758:55).

Type locality.—"America", restricted to Surinam by J. A. Allen (1900:195); further restricted to Paramaribo, Surinam, by Matschie (1916:268).

Characteristics.—As currently understood, this species has an extremely wide distribution encompassing the entirety of the Amazon Basin, the dry forests of eastern Bolivia and Paraguay, the coastal region of Guiana, the Pacific coast of Colombia and Ecuador, the lowlands of Central America, and eastern Mexico as far north as the state of Tamaulipas. *P. opossum* exhibit geographic variation in color and color pattern. However, there is no tendency in specimens of this species to have a dark dorsal-median stripe, although some individuals are slightly darker along the mid-back. We recognize the following subspecies, although future studies may suggest that one or more be raised to species status:

Philander o. opossum (Linnaeus). This uniformly pale-gray subspecies is known from coastal Venezuela and the Guianas through the eastern Amazon Basin of Brazil. Pérez-Hernández (1989), based on color pattern, suggested that specimens from Portuguesa and Territorio Federal Delta Amacuro in Venezuela represent an undescribed subspecies.

Philander o. azarica (Thomas, 1923:604). Type locality "Sapucay," Paraguarí, Paraguay. A pale-gray subspecies, *P. o. azarica*, distributed from the Paraná Basin of northern Argentina and Paraguay west probably into eastern Bolivia and north into southwestern Brazil. It is likely that *crucialis* Thomas (1923:604), with type locality "Santa Cruz de la Sierra," Santa Cruz, Bolivia, is a synonym. However, if *azarica*, as noted above, is a synonym of *frenata* from the Brazilian Mata Atlantica, rather than as

listed here, then the Bolivian *crucialis* is probably a recognizable subspecies of *opossum*.

Philander o. canus (Osgood, 1913:96). Type locality "Moyobamba, [San Matín,] Peru." *P. o. canus* is a small, gray subspecies that occurs throughout the western Amazon Basin of central Peru south of the Marañón-Amazonas axis into northern Bolivia and western Brazil. It is usually darker in color than *opossum* to the east. It is sympatric with *mcilhennyi* at many localities in eastern Peru and western Brazil. Although the type localities of *canus* and *andersoni* are relatively close, there are no known points of sympatry. Characters distinguishing *canus* from *mcilhennyi*, other than color and quality of pelage, were given by Gardner and Patton (1972) and Hutterer et al. (1995).

Philander o. fuscogriseus (J. A. Allen, 1900:194). Type locality "Central America," restricted to Graytown, Nicaragua, by J. A. Allen (1911:247). This dark-gray subspecies is known from northern Colombia and southern Central America as far north as Honduras. It probably includes *grises-cens* (J. A. Allen, 1901:217), known only from its type locality of "Rio Cauca, Colombia." Allen (1901) considered *grises-cens* to be distinct by virtue of its uniformly dark tail.

Philander o. melanurus (Thomas, 1899:285). Type locality "Paramba, Rio Mira, N. Ecuador; alt. 1100 m." This is a dark-gray to blackish subspecies, typically with a dark-brown to black tail. It is distributed in the Pacific lowlands of Colombia and Ecuador. Specimens become somewhat paler and have an increasing amount of white on the tip of the tail from north to south. We consider *melanthero* (Thomas, 1923:602), with its type locality at "Condoto, 300'," Chocó, Colombia, to be a synonym.

Philander o. pallidus (J. A. Allen, 1901:215). Type locality "Orizaba, Veracruz", Mexico. This is a pale-gray subspecies distributed from central Honduras north to Tamaulipas, Mexico (Hall, 1981).

ACKNOWLEDGMENTS

We thank the following curators for allowing us to examine specimens under their care: A. L. Gardner and M. D. Carleton, United States National Museum of Natural History; G. G. Musser, American Museum of Natural History; B. D. Patterson, Field Museum of Natural History; M. S. Hafner, Louisiana State University; R. M. Timm, University of Kansas; P. Vanzolini, Museu de Zoologia, Universidade de São Paulo. R. M. Timm (University of Kansas), J. F. Jacobs (United States National Museum of Natural History), M. D. Engstrom (Royal Ontario Museum), M. C. Lara and M. A. Mustrangi (Museum of Vertebrate Zoology), E. Hingst (Universidade Federal do Rio de Janeiro), and G. da Fonseca, Y. Leite, and L. Costa (Fundação Biodiversitas, Belo Horizonte) graciously provided samples of tissues. R. H. Pine and two anonymous reviewers offered thoughtful comments on the manuscript, although they should not be held accountable for the final contents. M. N. F. da Silva was supported by a fellowship from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). Permits for field work in Brazil were provided by CNPq and the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA); in Peru, permits were issued by the Ministerio de Agricultura. Grants to J. L. Patton, M. N. F. da Silva, and J. R. Malcolm from the National Geographic Society (4453-91) and Wildlife Conservation Society provided financial support for fieldwork; a grant to J. L. Patton from the National Science Foundation (DEB 9317685) supported the laboratory work.

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Submitted 20 September 1995. Accepted 15 May 1996.

Associate Editor was Janet K. Braun.

APPENDIX I

Specimens examined.—Voucher specimens for the individuals sequenced in this report are from the following collections: Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); United States National Museum of Natural History, Washington, D.C. (USNM); University of Kansas Natural History Museum, Lawrence, Kansas (KU); Museu Na-

cional, Rio de Janeiro, Brazil (MNRJ); Museu de Zoologia, Universidade de São Paulo, Brazil (MZUSP); Royal Ontario Museum, Toronto, Canada (ROM); Fundação Biodiversitas, Belo Horizonte, Minas Gerais, Brazil (FBMG). Specimens prefixed by initials JLP and MNFS are field catalog numbers of materials collected during the authors' 1991–1992 expedition to the Rio Juruá in western Brazil; vouchers from these specimens are available and will be cataloged eventually into the collections of the Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA), the Museu Paraense Emílio Goeldi, Belém (MPEG), or the MVZ. Most taxa and localities examined are shown in Fig. 1. Individuals included in the phylogenetic analysis depicted in Fig. 2 are indicated by an asterisk.

Philander andersoni.—ECUADOR (2): Napo; Parque Nacional Yasuni, Onkone Sur, 38 km S Pompeya Sur (ROM 104496*, ROM 104030). PERU (3): Amazonas; Huampami, Río Cenepa, 180 m (MVZ 153265*, MVZ 153267). Loreto; San Jacinto, Río Tigre, 2°18'S 75°51'W (KU-NW 844*).

Philander frenata.—BRAZIL (16): Espírito Santo; Estação Biológica Santa Lúcia, Santa Tereza, 500 m (MZUSP-MAM 189*); Mato do Lava d'Água, 1.7 km (by road) from Santa Tereza (MNRJ 31462). Minas Gerais; Parque Estadual do Ibitipoca, 30 km N Lima Duarte, 1,000 m (MZUSP-MAM 208*, MAM 210); Fervedouro (FBMG-GM 001). São Paulo; Fazenda Intervalles, Capão Bonito, 700 m (MVZ 182066*); Fazenda da Toca, Ilha de São Sebastião, Ilhabela, 150 m (MZUSP-MAM 63, MVZ 182067); Praia do Félix, Ubatuba, 150 m, 44°58'W 23°23'S (MZUSP-MAM 74, MVZ 182068); Estação Biológica Boracéia (MZUSP-MAM 97, MAM 98); Serra do Japí, 7 km W Jundiá, 46°57'W 23°14'S (MZUSP-MAM 211). Rio de Janeiro; Parque Nacional de Itatiaia, Penedo, Município de Itatiaia, 500 m (MZUSP-MAM 183*); Maricá (MNRJ-ML 137); Garrafão, Estacion Río Terezópolis, Majé (MNRJ-ORG1).

Philander mcilhennyi.—BRAZIL (10): Acre; Igarapé Porongaba, right bank Río Juruá (MNFS 1103*, MNFS 1196); Seringal Sobral, left bank Río Juruá (MNFS 1435, MNFS 1437). Amazonas; Seringal Penedo, right bank Río Juruá (MNFS 383*); Seringal Condor, left bank Río Juruá (JLP 15702*); Seringal Altamira, right bank Río Juruá (JLP 16067, 16069*); alto Río Urucu (INPA-MNFS 146*, MNFS 147).

Philander opossum opossum.—GUYANA (4): Rupununi; Surama, 30 km SE of Surama (ROM 98045*, ROM 98046). North West; Santa Cruz (ROM 98839); Waikerebi (ROM 98910*). BRAZIL (2): Pará; east bank Río Xingu, 52 km SSW Altamira, 52°22'W 3°39'S (USNM 549297*, USNM 549299).

Philander opossum canus.—BRAZIL (4): Acre; Fazenda Santa Fé (=Flora), left bank Río

Juruá (MNFS 1031); Seringal Ocidente, right bank Río Juruá (MNFS 1039*, 1040). Amazonas; Nova Empresa, left bank Río Juruá (JLP 15395*).

Philander opossum fuscogriseus.—PANAMÁ (2): Bocas del Toro; Old Point, Isla Bastimentos (USNM 464248*); Isla Popa, 1 km SE Deer Island Channel (USNM 464254).