

CHAPTER TWO

Taxonomy and Distributions of Mesoamerican Primates

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INTRODUCTION

Geoffroy's tamarin, a squirrel monkey, a night monkey, the white-throated capuchin, two or three species of howling monkey, and one or two spider monkeys comprise the primate fauna of Middle America, historically throughout the subtropical and tropical forests from about 24°N in Tamaulipas, Mexico, extending south along the coast of the Gulf of Mexico, through Central America to the border of Colombia and Panama. This is the simple description, and hides a remarkable, and still poorly understood, diversity of 7–9 species and up to 22 taxa,

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New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior, and Conservation, edited by Alejandro Estrada, Paul A. Garber, Mary S. M. Pavelka, and LeAndra Luecke. Springer, New York, 2005.

all with ranges restricted to Middle America and west of the Andes, through Colombia and Ecuador to the Tumbes region of extreme northern Peru.

In this review, we will follow, as far as the evidence permits, the Phylogenetic Species Concept (PSC), as outlined by Groves (2001). This means that homogeneous taxa, diagnosable by unique, apparently consistent (fixed) heritable features, are ranked as species. Subspecies are geographic segments within a species, characterized by high frequency but not fixed differences from other such segments.

While Geoffroy's tamarin, *Saguinus geoffroyi*, and the night monkey, *Aotus*, are considered distinct and monotypic, some have considered them to be subspecies, others species. In recent years, the night monkey has been assigned four different names as a result of differing opinions concerning its affinities with, and the taxonomy of, the diverse forms in Colombia. There are two broadly accepted subspecies of squirrel monkey, *Saimiri oerstedii*, restricted to a small area of the Pacific lowlands of Panama and Costa Rica. They are separated from all other squirrel monkeys, their nearest relatives being east of the Río Magdalena in Colombia, and in the past were considered to have arisen from human introduction in pre-Columbian times. A genetic study by Cropp and Boinski (2000) indicated that this is unlikely, however, and their isolated presence in Central America in this case can only be explained by prehistoric geographic and climatic changes and the extinction of the intervening populations through vegetation changes. The white-throated capuchin, *Cebus capucinus*, extending from Panama to northern Honduras, may comprise three subspecies—Hershkovitz (1949) listed them, but neither Hernández-Camacho and Cooper (1976) nor Groves (2001) accepted their validity.

Lawrence (1933), Smith (1970), Horwich (1983), and Cortés-Ortiz *et al.* (2003) have consolidated evidence for the existence of two howling monkeys in Central America, the black howler, *Alouatta pigra*, from the Yucatán Peninsula, and the mantled howling monkey, *A. palliata*, from southeastern Mexico into Colombia and Ecuador. Froehlich and Froehlich (1986, 1987) argued that the diminutive Coiba Island howler was also a distinct species, *A. coibensis*. Groves (2001) accepted their arguments, but Cortés-Ortiz *et al.* (2003) were unable to confirm this in their study of the molecular genetics of the genus. Groves (2001) otherwise found the evidence insufficient to distinguish a further three mantled howlers listed here: *aequatorialis*, *mexicana*, and *trabeata*.

Perhaps, the most confusion surrounds the spider monkeys. For many years, the taxonomy was based on Kellogg and Goldman's (1944) careful revision

of cranial morphology and pelage. They recognized two species for Middle America, *A. geoffroyi* and *A. fusciceps* (Froehlich *et al.* [1991] and Collins and Dubach [2000] have suggested that *A. fusciceps* is a synonym of *A. geoffroyi*), and all but two of the forms they described are still recognized today. The strong indications are that they gave the wrong name to the Colombian black spider monkey (Heltne and Kunkel, 1975); Napier (1976) argued that *A. geoffroyi panamensis* is a synonym of *A. g. ornatus*; and Silva-López *et al.* (1995, 1996) argued that *A. g. pan* is a synonym of *A. g. vellerosus*. It is only recently that there has been a tendency to further lump the subspecies of *A. geoffroyi*. Collins (1999) and Collins and Dubach (2000) divided them into two: northern *geoffroyi* and southern Central American *geoffroyi*. Groves (2001) provisionally recognized only five of Kellogg and Goldman's (1944) nine subspecies of *A. geoffroyi*.

Biogeographical considerations are of course fundamental for our understanding of the diversity of these primates. For this reason, we also present here a review of the current information regarding the historical ranges of the various species and subspecies. Historical is the key word. Our understanding of where these animals occurred naturally is increasingly dependent on the relatively scarce collections in museums. They are hunted and their forests are now severely reduced, degraded, and fragmented throughout Middle America (Estrada and Coates-Estrada, 1984; Horwich and Johnson, 1984, 1986; Luecke, 2004; Silva-López *et al.*, 1995; Estrada *et al.*, this volume). This diminution of the geographic extent of their occurrence makes it extremely difficult to achieve an understanding of the full diversity of the species in terms of pelage variation, morphology and genetics, and as such to make confident decisions concerning their taxonomy. This is particularly critical for the Central American spider monkeys, a group that is evidently still very poorly known in many regions (Konstant *et al.*, 1985; Hines, 2004).

The destruction of the Middle American forests has severely reduced population diversity over the majority of the ranges of all the Middle American primates. The distribution maps provided here are hypotheses of the historical ranges—they overestimate by far the actual area of occupation. The reality today is that each of the taxa is restricted to few and isolated forest fragments. Now, the real distributions are scattered and isolated localities—remnant forest patches—and there is an urgent need for regionwide and detailed surveys to identify and map them, to determine the status of the populations remaining. The GIS is a powerful tool for mapping these forests and populations, with an

accuracy and scale never achieved before (for example, Luecke, 2004; Estrada *et al.*, 2004; Pavelka *et al.*, this volume). The conservation of these remnant forests is vital: in the future, the ranges of these primates (Table 1) will undoubtedly be described as lists of protected areas.

SPECIES AND SUBSPECIES OF MESOAMERICAN PRIMATES

Saguinus geoffroyi (Pucheran, 1845)

Geoffroy's tamarin, red-crested bare-face tamarin (Hershkovitz, 1977; Reid, 1997), rufous-naped tamarin (Moynihan, 1970), tití or bichichi in Colombia and Panama (Hernández-Camacho and Cooper, 1976; Reid, 1997). Panama, Colombia (Figure 1).

Type: The type specimen is a mounted skin and a (separate) skull of a female in the Muséum National d'Histoire Naturelle, Paris. Skin No. 112, Skull No. 621. Originally donated to the Jardin des Plantes, and died there on 25 August, 1845 (Hill, 1957; Hershkovitz, 1977).

Type locality: Panama. Restricted by Hershkovitz (1949) to the Canal Zone.

There are a considerable number of synonyms, listed and discussed by Hill (1957), Hershkovitz (1949, 1977), and Groves (2001). *Oedipomidas spixi* (Reichenbach, 1862) was the name used by Hill (1957), following the recommendation of Cabrera (1940), who argued that the specific name *geoffroyi* was preoccupied by *Simia geoffroyi* (Humboldt, 1812), the white-face marmoset of the Brazilian Atlantic forest. Hershkovitz (1949) disagreed with Cabrera (1940) (as pointed out by Hill [1957, p. 260] himself) and listed the tamarin as *Marikina geoffroyi*. Hershkovitz (1949) argued at length that the two species had never been placed in the same genus and as such "a real state of homonymy never existed" (1977; p. 759). Cabrera (1958) evidently later accepted Hershkovitz's argument, listing the Panamanian tamarin as *Leontocebus geoffroyi* Pucheran. Eisenberg (1989) confused the authorship, attributing *geoffroyi* to Reichenbach (1862), author in fact of the junior synonym *spixi*.

Oedipomidas salaquiensis was the name given by Elliot (1912b) to a specimen from the Chocó, Río Salaquí (a tributary of the Río Atrato), a skin and skull in the American Museum of Natural History, New York. Elliot distinguished *salaquiensis* by its larger and differently proportioned skull, chestnut rather than burnt umber crown and nape, and buffy yellow (instead of pure white)

Table 1. The primates of Mesoamerica.

Callitrichidae		
<i>Saguinus geoffroyi</i> (Pucheran, 1845)	Geoffroy's tamarin, rufous-naped tamarin	Colombia, Panama
Cebidae		
<i>Saimiri oerstedii oerstedii</i> (Reinhardt, 1872)	Black-crowned Central American squirrel monkey	Costa Rica, Panama
<i>Saimiri oerstedii citrinellus</i> ^a (Thomas, 1904)	Grey-crowned Central American squirrel monkey	Costa Rica
<i>Cebus capucinus capucinus</i> (Linnaeus, 1758)	White-throated capuchin	Colombia, Panama
<i>Cebus capucinus imitator</i> ^b Thomas, 1903	Panamanian white-throated capuchin	Costa Rica, Nicaragua, Panama
<i>Cebus capucinus limitaneus</i> ^b Hollister, 1914	Honduran white-throated capuchin	Honduras, Nicaragua
Aotidae		
<i>Aotus zonalis</i> Goldman, 1914	Panamanian night monkey	Colombia, Costa Rica (?), Panama
Atelidae		
<i>Alouatta palliata palliata</i> (Gray, 1849)	Golden-mantled howling monkey	Costa Rica, Honduras, Nicaragua, Panama
<i>Alouatta palliata mexicana</i> ^b Merriam, 1902	Mexican howling monkey	Mexico, Guatemala
<i>Alouatta palliata</i> <i>aequatorialis</i> ^b Festa, 1903	Ecuadorian mantled howling monkey	Colombia, Ecuador, Panama
<i>Alouatta coibensis coibensis</i> ^a Thomas, 1902	Coiba Island mantled howling monkey	Panama
<i>Alouatta coibensis trabeata</i> ^b Lawrence, 1933	Azuero mantled howling monkey	Panama
<i>A. pigra</i> (Lawrence, 1933)	Black howling monkey	Belize, Guatemala, Mexico
<i>Ateles geoffroyi geoffroyi</i> Kuhl, 1820	Geoffroy's or Nicaraguan spider monkey	Costa Rica, Nicaragua
<i>Ateles geoffroyi azuerensis</i> Bole, 1937	Azuero spider monkey	Panama
<i>Ateles geoffroyi frontatus</i> (Gray, 1842)	Black-browed spider monkey	Costa Rica, Nicaragua
<i>Ateles geoffroyi grisescens</i> Gray, 1866	Hooded spider monkey	Panama, Colombia (?)
<i>Ateles geoffroyi ornatus</i> Gray, 1870	Ornate spider monkey	Costa Rica, Nicaragua
<i>Ateles geoffroyi vellerosus</i> Gray, 1866	Mexican spider monkey	El Salvador, Honduras, Guatemala, Mexico
<i>Ateles geoffroyi yucatanensis</i> ^b Kellogg and Goldman, 1944	Yucatán spider monkey	Belize, Guatemala, Mexico
<i>Ateles fusciceps rufiventris</i> ^a Sclater, 1871	Colombian black spider monkey	Colombia, Panama

^a Subspecific versus specific status needs further examination.^b Validity dubious.



Figure 1. The distribution of *Saguinus geoffroyi*. Based on Eisenberg (1989), Emmons and Feer (1997), Hernández-Camacho and Cooper (1976), Hershkovitz (1977), Matamoros and Seal (2001), Mast *et al.* (1993), Reid (1997), Rodríguez-Luna *et al.* (1996), Rylands *et al.* (1993), and Skinner (1985). Map drawn by Mark Denil and Kimberly Meek (Center for Applied Biodiversity Science, Conservation International, Washington, DC).

underparts. It was, however, not listed in Elliot's (1913) "*A Review of the Primates*", and Elliot (1914) reported that the investigation of further material from Colombia had indicated that the yellowish underparts were due to staining (Hershkovitz [1977] argued that it is in fact natural) and that the skull size, although large, was within the natural variation of that found for *O. geoffroyi*. Hernández-Camacho and Cooper (1976, p. 41) recorded that "of the few museum specimens of *S. geoffroyi* known for Colombia as well as those seen in captivity (largely from the region of Acandí), a large percentage have distinct sulfurous yellowish underparts, including lightly pigmented areas of the limbs." Hershkovitz (1977) found that *S. geoffroyi* does in fact get paler from south to north. The most saturate series he examined was from Sandó (locality 28) in the Chocó. Anthony (1916) remarked on the yellowish underparts of animals he

observed in Panama (along the Canal Zone, the Maxon Ranch [Río Trinidad], and localities on the Río Tuyra, Darién—Boca de Cupe, Chepigana, Cituro, Tacarcuna, and Tapalisa), concluding that it was variable and had no diagnostic value.

Hershkovitz (1977) classified the Panamanian tamarin as a subspecies of *S. oedipus* (the cotton-top tamarin from northern Colombia) based on pelage patterns and color, cranial and mandible morphology, and pinna size. Mittermeier and Coimbra-Filho (1981; see also Mittermeier *et al.*, 1988; Rylands, 1993) regarded the forms *oedipus* and *geoffroyi* to be distinct species, arguing that there is no evidence of intergradation between them and that “*S. oedipus* and *S. geoffroyi* are at least as differentiated from one another as are the members of the *Callithrix jacchus* group” (which they also argued to be valid species). Also influential was the suggestion of Thorington (1976) that the cotton-top tamarin was more closely related to *S. leucopus* (the silvery-brown bare-face tamarin of northern Colombia) than to *S. geoffroyi*. Hanihara and Natori (1987) carried out a multivariate comparative analysis of the dental morphology of a number of species of *Saguinus*, and confirmed Thorington’s (1976) view. Skinner (1991) examined body weight and a number of morphological characters and found that *S. geoffroyi* was significantly larger than *S. oedipus*, and morphologically more similar to *S. leucopus* than to *S. oedipus* in 16 of the 17 morphological characters studied. Skinner also discussed the pelage color and patterns of the three forms (emphasizing differences rather than the similarities demonstrated by Hershkovitz, 1977), along with aspects concerning hybridization and intergradation in *Saguinus* in general. Moore and Cheverud (1992, p. 73) concluded that “... A variety of multivariate statistical analyses including discriminant function and cluster analysis suggest that *S. oedipus* and *S. geoffroyi* differ morphologically at a level consistent with species-level distinctions. The extent of differences between these taxa is large ...” and later “... a comparison of collecting localities revealed that the variation we observed among *S. oedipus* and *S. geoffroyi* was not clinal but presented a large morphological discontinuity at the boundary between taxa ...”. Like Skinner (1991), they found that *S. leucopus* was more similar to *S. oedipus*.

Elliot (1913), Hershkovitz (1977), Eisenberg (1989), Rylands *et al.* (1995), and Emmons and Feer (1997) all indicated that *S. geoffroyi* occurs from northwest Colombia, through Panama to the border with Costa Rica, entering its southeasternmost tip on the Pacific coast. Reid (1997) pointed out that this is based on a sight record by Carpenter (1935), who noted that the tamarins were

very scarce in the Cotó region. Hershkovitz (1977, p. 924) listed two localities in his gazetteer, which would evidently be mistakes in this case: “Puntarenas, Cotó Region, 8°35'N, 83°05'W, C. R. Carpenter, June 1932, February–March, 1933”, and an unspecified locality in Chiriquí, Panama, “arbitrarily indicated on the map, fig. XIII.3”. Baldwin and Baldwin (1976) reported on a survey of 71 forest areas in Chiriquí between August 1968 and December 1970, and made no mention at all of *S. geoffroyi*. Reid (1997) cited a Panamanian zoogeographer (F. Delgado, in litt. to D. Engleman) as saying that the record is questionable and certainly does not reflect the species' current distribution, which is limited to central and eastern Panama (and Colombia). The exact western limit is not clearly defined, but marked by Reid (1997) at just a little west of the Canal Zone. Their range is restricted to the east of the Azuero peninsula.

In discussing habitat preference in Panama, Moynihan (1970) stated that “Rufous-naped tamarins are abundant in some parts of the Pacific coastal region, and also occur in some central areas approximately equidistant from both coasts. To our knowledge however, they are completely absent from the whole of the Atlantic coast of the isthmus, except for one small, highly modified or “unnatural” area.” (p. 2). The exception he mentioned is around the Canal Zone, the city of Colón, and Lake Gatún where the original forest has been almost entirely destroyed, and Moynihan (1970, 1976) argued that their occurrence there is the result of a recent range extension. The map of localities provided by Hershkovitz (1977, p. 915) confirms Moynihan's observation, with only two records on the Atlantic side of the isthmus except in the vicinity of the Canal Zone. The two outlying Atlantic coast records listed in the gazetteer (p. 925) are: Locality 6c, San Blas, Mandinga, 9°27'N, 79°04'W, C. O. Handley, Jr., May 1957, a series of six specimens in New York; and locality 6d, San Blas, Armila, Quebrada Venado, 8°40'N, 77°28'W, C. O. Handley, Jr., February–March 1963, a series of 12 specimens, also in the US National Museum. Moynihan (1970, 1976) suggested that their absence from the Atlantic coast was related to a preference for drier forests (“of moderate humidity”) typical of the Pacific coast. Skinner (1985) confirmed their occurrence in San Blas and reported the presence of *S. geoffroyi* in 21 sites all in moist tropical forest from the western Río Chagres basin to the Darién, from the Atlantic to the Pacific coasts.

In Colombia, it occurs along the Pacific coast, south as far as the Río San Juan. The Río Atrato was believed to be the eastern limit to its range (Hernández-Camacho and Cooper, 1976; Hershkovitz, 1977), but Vargas (1994, cited in

Defler, 2003) found the species occurring around the National Natural Park of Las Orquídeas in the vicinity of the village of Mandé, Antioquia, at elevations as high as 1000 m, extending its range to the west of the upper Río Cauca. Barbosa *et al.* (1988, in Mast *et al.*, 1993) also recorded the species at Quibdo, a town just east of the upper Río Atrato.

Saimiri oerstedii (Reinhardt, 1872)

Central American squirrel monkey, mono ardilla, mono tití.
Costa Rica, Panama (Figure 2).

The two subspecies listed here are recognized by Hill (1960) and Hershkovitz (1984). Cabrera (1958) and Thorington (1985), on the other hand, regarded the Central American squirrel monkey to be a subspecies of



Figure 2. The distribution of *Saimiri oerstedii*. Based on Boinski (1985, 1987), Boinski *et al.* (1998), Reid (1997), Sierra *et al.* (2003), Matamoros and Seal (2001), Rodríguez-Luna *et al.* (1996), and Wong (1990). Map drawn by Mark Denil and Kimberly Meek (Center for Applied Biodiversity Science, Conservation International, Washington, DC).

S. sciureus (Linnaeus, 1758); both sharing the Gothic-arch superciliary pattern. Thorington (1985) wrote, however, that his classification resulted from him also placing the form *boliviensis* (d'Orbigny, 1834) as a subspecies of *sciureus*—“In coat color and pattern and in craniometric analyses, *oerstedii* seems no more different from *S. sciureus sciureus* in Colombia than does *boliviensis*. Because I am treating *boliviensis* as a subspecies of *S. sciureus*, I should treat *oerstedii* as a subspecies of *sciureus* as well. A demonstration that *boliviensis* is a valid species would change the way I treat *oerstedii*.” (p. 22). Hershkovitz (1984) and Groves (2001) recognized *sciureus*, *boliviensis*, and *oerstedii* as distinct species, and *citrinellus* as a subspecies of *oerstedii*. Costello *et al.* (1993) and Silva *et al.* (1993) recognized the distinctiveness of *S. oerstedii* compared to all other squirrel monkeys, which they lump as *S. sciureus*. Studies by Boinski and Cropp (1999) using mtDNA, behavioral and morphological data, and Cropp and Boinski (2000) using two nuclear genes (IRBP and ZFX) and one mitochondrial (D-Loop) also confirmed that *sciureus*, *boliviensis*, and *oerstedii* should be considered distinct species. Their DNA study included specimens of both putative subspecies of *S. oerstedii*, and these formed homogeneous clades, raising the question of whether they might better be ranked as two distinct species (*S. oerstedii* and *S. citrinellus*); there is a need for further study to determine whether the described phenotypic differences are also consistent.

Hershkovitz (1969, 1984) presented a number of circumstantial arguments that these squirrel monkeys were introduced into Central America by humans, probably by sea from the Pacific coast of Ecuador or Peru. They included: their tameness; the “beach-head sized range”; their discrete distributions (well separated from *S. sciureus* to the east of the Río Magdalena), which cannot be explained by natural dispersal; and the extremely derived pelage color patterns of the two forms. Furthermore, Hershkovitz (1984) argued that *oerstedii* is the more derived of the two subspecies, and yet *citrinellus* is geographically the most peripheral. A study of nuclear and mtDNA by Cropp and Boinski (2000), however, provided divergence dates (3–4.4 mya—mtDNA; 420,000–260,000 years ago—nuclear DNA) that clearly negate Hershkovitz’s (1969) introduction hypothesis.

Hill (1960), Hershkovitz (1984), and Groves (2001) provide descriptions of pelage color patterns. Both *S. o. oerstedii* and *S. o. citrinellus* are predominantly orange to reddish-orange with a characteristic dark cap. In *S. o. oerstedii*, both males and females have a black cap. Compared to *S. o. citrinellus*, the limbs are more yellowish, and there is a stronger yellowish tinge in the underparts

(abdomen, groin, and medial aspects of thigh) (Hill, 1960). The outer side of the leg is orange like the arms (Groves, 2001). Thomas (1904) distinguished *citrinellus* by its less black head and less yellow limbs. Elliot (1913) regarded these features as variable (the head color with age) and considered *citrinellus* a synonym of *oerstedii*.

Saimiri oerstedii oerstedii (Reinhardt, 1872)

Black-crowned Central American squirrel monkey, red-backed squirrel monkey, or Panamanian red-backed squirrel monkey (Hill, 1960), tití, mono ardilla, mono tití.

Costa Rica, Panama (Figure 2).

Type: Skin and skull in the Zoological Museum, Copenhagen. Collected by A. S. Örsted.

Type locality: Vicinity of David, Chiriquí, Panama.

S. o. oerstedii occurs along the Pacific coast of Costa Rica, from the left bank of the Río Grande de Térraba to the Osa Pensinsula, along the coast of the Golfo Dulce and the Burica Peninsula to the western part of the Chiriquí Province, mouth of the Río Fonseca, including the Archipelago of the Golfo de Chiriquí, in Panama (Hershkovitz, 1984; Boinski *et al.*, 1998). Surveys by Baldwin and Baldwin (1972, 1976) recorded its presence on the Burica Peninsula, but indicated that it is now restricted to a narrow strip of scattered lowland coastal forest fragments, not extending to the type locality David, although it possibly occurred as far east as Remedios (well to the east of David) prior to the 1950s. Altitudinal range is 0–500 m asl (Hershkovitz, 1984). Rodríguez-Vargas (2003) mapped the remaining populations in Panama.

Saimiri oerstedii citrinellus Thomas, 1904

Grey-crowned Central American squirrel monkey or Costa Rican red-backed squirrel monkey (Hill, 1960), tití, mono ardilla, mono tití.

Costa Rica (Figure 2).

Type: Male, skin and skull in British Museum (Natural History), No. 1904.2.72, collected 31 May, 1902, by C. F. Underwood (Napier, 1976; Hershkovitz, 1984).

Type locality: Pozo Azul, Río Pirris or Parrita, San José, Costa Rica. According to Carriker (1910, p. 349, see Hershkovitz, 1984, p. 197), Pozo Azul is a

locality on the Río Grande de Pirris about 10 miles from the Pacific Ocean, reached by cart-road from San José.

The historic range of *S. o. citrinellus* is along the Pacific coast of Costa Rica, to altitudes of up to 500 m asl. The northeastern limit is marked by the Río Tulín in the north Herradura Mountains (9° 40'N, 84° 35'W) and Dota Mountains (9° 37'N, 84° 35'W), and the southern limit is the north bank of the Río Grande de Térraba (8° 25'N, 84° 25'W) (Arauz, 1993; Sierra *et al.*, 2003). Its occurrence is sporadic, and the surviving populations are entirely fragmented (Alfaro, 1987; Wong, 1990; Sierra *et al.*, 2003). As mentioned above, we recommend further study of the differences between this subspecies and nominotypical *S. o. oerstedii* to determine if they are correctly ranked taxonomically.

Cebus capucinus (Linnaeus, 1758)

White-throated capuchin, mono carablanca, cariblanco, mono capuchino.
Colombia, Costa Rica, Ecuador, Honduras, Nicaragua, Panama (Figure 3).

Cebus capucinus is the only capuchin monkey in Central America, ranging from Honduras in the north, through Nicaragua, Costa Rica, and Panama and through the Chocó-Darién into Colombia (Hernández-Camacho and Cooper 1976, Rodríguez-Luna *et al.*, 1996, Reid, 1997, Marinero and Gallegos, 1998). It is easily distinguished from other members of the genus in the black pelage on the crown, nape, back, flanks, limbs, and tail. The face, forehead, sides of head, throat, sides and front of neck, shoulders, and chest are white (off-white or slightly yellowish). The Colombian *C. c. nigripictus* was distinguished by Elliot (1913) for its black chest (but see below). Hershkovitz (1949) listed five subspecies of *Cebus capucinus*: *C. c. nigripictus* (from the upper Río Cauca in Colombia), *C. c. capucinus* (Colombia and eastern Panama), *C. c. imitator* (western Panama, Coiba Island [Panama], and Costa Rica), *C. c. limitaneus* (Honduras and Nicaragua), and *C. c. curtus* (Gorgona Island, Colombia, possibly introduced in the 16th or 17th century); yet he went on to say that “None of the distinguishing characters attributed to the described races of *C. capucinus* appears to be valid” (pp. 346–347), while considering it desirable to retain the named subdivisions pending a thorough study. Hernández-Camacho and Cooper (1976) argued that variability in populations on the upper Río Cauca did not support the validity of *C. c. nigripictus*, and considered that the Central American populations were subject to the same limitation. Hernández-Camacho and Defler (1991) and Defler (1994) listed just two subspecies of



Figure 3. The distribution of *Cebus capucinus*. Based on Defler (2003), Eisenberg (1989), Hill (1960), Hall (1981), Hernández-Camacho and Cooper (1976), Marineros and Gallegos (1998), Matamoros and Seal (2001), Reid (1997), and Rodríguez-Luna *et al.* (1996). The numbers indicate two localities where capuchin monkeys have been reported but their presence has yet to be confirmed; 1: Mayan Mountains of western Belize (the Chiquebul forest and in the region of the Trio and Bladen branches of the Monkey River); 2: Sierra del Espíritu Santo near the Guatemala–Honduras border (see text). Map drawn by Mark Denil and Kimberly Meek (Center for Applied Biodiversity Science, Conservation International, Washington, DC).

C. capucinus for Colombia: *C. c. capucinus* and *C. c. curtus*. Groves (1993, 2001), having reviewed specimens in the US National Museum, the American Museum of Natural History, and the Museum of Comparative Zoology at Harvard University, also regarded all the subspecies listed by Hershkovitz (1949) and Hill (1960) to be junior synonyms of a monotypic *C. capucinus*. Here, we list the three Mesoamerican forms separately to draw attention to each one, but this should not be taken to imply that we endorse their status as separate subspecies. There are no records of this species in El Salvador or Mexico. There are unconfirmed reports of its occurrence in southern Belize and eastern Guatemala.

Cebus capucinus capucinus (Linnaeus, 1758)

White-throated capuchin, mono carablanca.

Type: None exists.

Type locality: Not known, but Hershkovitz (1949) indicated “Northern Colombia”.

Colombia, Ecuador, Panama (Figure 3).

According to Hill (1960, p. 425), *C. c. capucinus* differs from other subspecies in the “general whiteness of the pallid areas of head, neck, shoulders, arms, and underparts, including the chest”. It is larger than *C. c. limitaneus*, and the females do not have the frontal tufts of *C. c. imitator*. In Colombia, the white-throated capuchin occurs south from the Panamanian border along the Pacific Coast, west of the Andes into northwestern Ecuador. It is apparently restricted to the west bank of the Río Cauca and extends north across the Río Sinu into Córdoba, Sucre, and Atlántico to the town of Barranquilla on the northern coast of Colombia (Hernández-Camacho and Cooper, 1976; Defler, 2003). In Central America, *C. c. capucinus* extends west as far the Panama Canal (Hall, 1981).

Cebus capucinus imitator Thomas, 1903

Panamanian white-throated capuchin, mono carablanca.

Costa Rica, Nicaragua, Panama (Figure 3).

Type: Adult female (skin and skull) in British Museum (Natural History), No. 1903.3.3.13. Collected 15 October, 1902, by H. J. Watson (Napier, 1976).

Type locality: Chiriquí, Boquete, western Panama, altitude 4000 ft.

Much resembling typical *C. c. capucinus*, but females have elongated frontal tufts, entirely altering the facial appearance. Hall (1981) places this subspecies in western Panama, west from the Canal, and in adjacent areas of Costa Rica. Populations also occur on the islands of Coiba and nearby Jicarón. Baldwin and Baldwin (1976, 1977) documented the occurrence of *C. capucinus* in a number of localities in the Province of Chiriquí, southwestern Panama. Crockett *et al.* (1997) listed localities in Nicaragua, and Allen (1908, 1910) recorded specimens of *C. capucinus* (referred to as *C. hypoleucus* in Allen, 1908), from Ocotol (northern highlands, 4500 ft), and localities on the east slope of the highlands, Savala (800 ft), Chontales (lowlands east of Lake Nicaragua, altitudes 500–1500 ft), and the Río Tuma (500 ft) and Muy Muy (Matagalpa Province, 1500–2000 ft).

Cebus capucinus limitaneus Hollister, 1914

Honduran white-throated capuchin monkey, white-faced capuchin monkey.
Honduras, Nicaragua (Figure 3).

Type: Adult male, skin and skull in United States National Museum, collected by C. H. Townsend in 1887 (Hill, 1960).

Type locality: Segovia River, eastern Honduras. Restricted by Hershkovitz (1949) to Cabo Gracias a Dios at the mouth of the river, eastern border between Honduras and Nicaragua.

Described by Hollister (1914) as similar to *C. c. imitator* Thomas of western Panama and Costa Rica, but slightly smaller with a “decidedly smaller skull”. This is the most northerly population of the species and genus. Besides the type locality, Hollister (1914) recorded specimens from Patuca, Honduras, and the Río Escondido, Nicaragua. In Honduras, Marineros and Gallegos (1998) recorded it from throughout the north (Departments of Gracias a Dios, Colón, Atlantida, and Cortés) besides Santa Bárbara in the northwest, and Olancho and El Paraíso in the east.

Hollister (1914) also listed a skin from British Honduras (Belize). There have been unauthenticated reports of capuchins in the Mayan Mountains of western Belize (the Chiquebul forest and in the region of the Trio and Bladen branches of the Monkey River) and in Sarstoon National Park on the southern border. Its occurrence in Belize has never been confirmed (McCarthy, 1982; Dahl, 1984, 1987; Hubrecht, 1986). Silva-López *et al.* (1995; Silva-López, 1998) also reported on the possible occurrence of *C. c. limitaneus* in Guatemala, in the Sierra del Espíritu Santo near the Guatemala–Honduras border. This also remains to be substantiated.

Aotus zonalis Goldman, 1914

Panamanian night monkey, owl monkey, mono de noche, marteja, jujuná (Reid, 1997).

Colombia, Costa Rica (?), Panama (Figure 4).

Type: In the National Museum of Natural History, Washington, DC, Accession No. USNM 171231, collected 29 April, 1922, by E. A. Goldman.

Type locality: Lake Gatún, Canal Zone (Panama), altitude 100 ft.

Hershkovitz (1949) recognized two night monkeys in northern Colombia and Central America, both as subspecies of *A. trivirgatus* (Humboldt, 1812):



Figure 4. The distribution of *Aotus zonalis*. Based on Defler (2003), Hall (1981), Hernández-Camacho and Cooper (1976), Hershkovitz (1983), Matamoros and Seal (2001), Reid (1997), Rodríguez-Luna *et al.* (1996), and Timm (1988). The numbers indicate two unconfirmed localities in Costa Rica: 1: La Selva Biological Reserve, a field station of the OTS, 1 km south of Puerto Viejo de Sarapiquí, Heredia (10°26'N, 83°59'W, altitude 35–150 m) (three sightings; Timm, 1988); 2: Near Bribri, Limón Province, about 70 km north northwest of Isla Bastimentos, Panama, the northernmost documented population of night monkeys (reported; Vaughan, 1983). Map drawn by Mark Denil and Kimberly Meek (Center for Applied Biodiversity Science, Conservation International, Washington, DC).

A. t. lemurinus (I. Geoffroy, 1843) and *A. t. griseimembra* Elliot, 1912a. He proposed that *griseimembra* in the northern lowlands and far northwestern Colombia (*Type locality*: Hacienda Cincinnati, northeast of Santa Marta, northwestern slope of the Sierra Nevada de Santa Marta, Magdalena, Colombia, altitude 1480 m) was the form extending into Panama, and included *zonalis* Goldman, 1914 as a synonym. Hill (1960) provided a very similar appraisal, one perhaps significant difference being that he placed the form *bipunctatus* Bole, 1937 from the Azuero Peninsula as a synonym of *griseimembra*, whereas Hershkovitz (1949, p. 404) had stated that “The night monkey of the Azuero

Peninsula, Panama, described as *A. bipunctatus*, is certainly a member of the common species but requires further comparison with additional material to determine its exact relationship to *griseimembra*. Most characters of *bipunctatus* described as distinctive, appear to be, rather, individual variables". It is not clear on what basis Hill (1960) synonymized *bipunctatus* with *griseimembra*, however, when Hershkovitz (1949) was reluctant to do so.

Hill (1960) listed the form *rufipes* Sclater, 1872 as a subspecies of *Aotes* [*sic*] *trivirgatus*. This was a live animal received by the Zoological Society of London from San Juan del Norte, Nicaragua. Night monkeys have never otherwise been recorded from Nicaragua, and Hershkovitz (1949) argued that the original description and color plate identify the animal as having come from Brazil. Allen (1910) simply said that the locality was unquestionably erroneous, a sentiment repeated by Elliot (1913).

Hernández-Camacho and Cooper (1976) restricted both *lemurinus* (Colombian Andes, elevations from 1000 to 1500 m up to 3000 to 3200 m) and *griseimembra* (northern lowlands, Santa Marta mountains, west to Río Sinú, Río San Jorge, lower Río Cauca, and lowlands of middle and upper Río Magdalena) to Colombia, while recognizing the form *zonalis* as the night monkey of northwestern Colombia (Chocó) and Panama. Hershkovitz (1983) continued to recognize *lemurinus* and *griseimembra* as distinct, but considered them to be subspecies of a single species; he made no mention of the name *zonalis*, but as he ascribed Central American night monkeys to *A. lemurinus lemurinus*, by implication he was regarding it as a synonym of this latter form. Unfortunately, a full explanation of his research and views regarding *Aotus* taxonomy was never published, but this switch from his 1949 arrangement was probably due to interpretation of the variable diploid numbers in the genus (*A. l. lemurinus* $2n = 55/56$; *A. l. griseimembra* $2n = 52/53/54$).

Reviewing the entire taxonomy and distributions of the night monkeys, Ford (1994) carried out multivariate analyses of craniodental measures and pelage patterns and color, and also took into consideration chromosomal data and blood protein variations. She concluded that there was "good support" for just two species north of the Río Amazonas: *A. trivirgatus* (Humboldt, 1812) to the east and north of the Río Negro, and the polymorphic *A. vociferans* to the west of the Río Negro. *A. vociferans*, as such, would include all the forms north of the Río Amazonas/Solimões in Brazil (west of the Río Negro), Peru, Colombia, and Ecuador, and in the Chocó, northern Colombia and Colombian Andes, and Panama: *brumbacki*, *lemurinus*, *griseimembra*, and *zonalis*. Torres

et al. (1998) identified six karyomorphs in Colombia, but concluded that a larger sample is required (both in numbers and geographic spread) in order to elucidate whether they represent different species.

Groves (2001) followed Hernández-Camacho and Cooper (1976) in recognizing *zonalis* as the form in Panama, and listed it as a subspecies of *lemurinus* along with *griseimembra* and *brumbacki* Hershkovitz, 1983. Defler *et al.* (2001) concluded that the karyotype of *A. herskovitzi* Ramirez-Cerquera, 1983; (from the upper Río Cusiana, Boyacá, Colombia; $2n = 58$) was in fact that of true *lemurinus*, and that the karyotypes that Hershkovitz (1983) had considered to be those of *lemurinus* were in fact of *zonalis*. Defler *et al.* (2001; Defler, 2003; Defler and Bueno, 2003) concluded that *A. lemurinus* of Hershkovitz (1983) is in fact three karyotypically well-defined species, and that the night monkeys of the lowlands of Panama and the Chocó region of Colombia belong to the species *A. zonalis*, and those of the Magdalena valley to *A. griseimembra*, while those above altitudes of 1500 m should correctly be referred to as *A. lemurinus*. *A. zonalis* is distinguished from *griseimembra* by the darker upper surfaces of the hands and feet; blackish in Panama, but brownish in Colombia (Hershkovitz, 1949; Hernández-Camacho and Cooper, 1976). In the Canal Zone, they are brownish in overall body color, but grade into paler, grayer forms along the upper Río Tuira (Hershkovitz, 1949). In Colombia, they again have a brownish tinge to the pelage.

Spix's night monkey, *A. vociferans* (Spix, 1823), is recognized by Hershkovitz (1983), Groves (2001), and Defler (2003) as the form occupying a large part of the Colombian Amazon, north of the Río Amazonas, north to the Río Tomo (Hershkovitz, 1984) or Río Guaviare (Defler, 2003). It extends into Venezuela, Brazil, Peru, and Ecuador.

The distribution in Panama was mapped by Hall (1981; see also Hershkovitz, 1949; Reid, 1997). It would appear that it occurs west as far as the Río San Pedro in Veraguas along the Pacific coast, and from there is restricted to the Atlantic side of Panama through the province of Bocas del Toro, west as far as the Río Changuinola. It is absent from Chiriquí (Baldwin and Baldwin, 1976). Anthony (1916) recorded specimens from the Río Tuyra (Tuira), and Darién (Boca de Cupe and Tapalisa).

There have been a number of unconfirmed reports of night monkeys in Costa Rica (Reid, 1997). Timm (1988) examined the curious history and confusion of a specimen collected by Dr. van Patten in the highlands of Costa Rica that was recorded by Sclater (1872) and found by him to be the same as night

monkeys from Bogotá. There was, however, confusion about the locality, and the specimen has been lost. Timm (1988; Timm *et al.*, 1989) argued that night monkeys should still be widely distributed in the eastern Caribbean lowlands of Costa Rica. This is based on three sightings in La Selva Biological Reserve, a field station of the Organization for Tropical Studies (OTS), 1 km south of Puerto Viejo de Sarapiquí, Heredia (10°26'N, 83°59'W, altitude 35–150 m). Lowland evergreen forest is predominant there. Timm (1988) also cited Vaughan (1983) who obtained information indicating the presence of night monkeys in Limón Province, around Bribri, near the Panamanian border, and only about 70 km north northwest of Isla Bastimentos, Panama, the northernmost documented population of night monkeys. In Colombia, *A. zonalis* occurs in the Pacific lowlands, south at least to the Río Raposo, south of Buenaventura, the region of Urabá and east to the Sinú valley, possibly through the San Jorge valley to the region of Puerto Valdivia in northern Antioquia (Hernández-Camacho and Cooper, 1976; Defler *et al.*, 2001).

Alouatta palliata (Gray, 1849)

Mantled howling monkey.

Colombia, Costa Rica, Ecuador, Honduras, Guatemala, Mexico, Nicaragua, Panama (Figure 5).

The current taxonomy of the mantled howling monkey is based on a thorough and detailed study of the pelage, crania, and taxonomic history of the Mesoamerican howlers by Lawrence (1933). It was inspired by the arrival at Harvard University's Museum of Comparative Zoology of several specimens from Herrera Province on the Azuero Peninsula, Panama, which Lawrence was unable to identify. Her findings resulted in her describing the form *trabeata* for the newly arrived specimens, besides *pigra* from Guatemala (replacing the name *villosa* in use previously) and *luctuosa* from Belize. She recognized seven subspecies in all.

Hill (1962) followed the taxonomy of Lawrence (1933) but continued to list the monotypic Guatemalan howling monkey, *A. villosa* (Gray, 1845), as a separate species, following Elliot (1913), but noting that *pigra* might turn out to be a synonym of *A. villosa*. In this, he was followed by Hall and Kelson (1959) and Napier (1976). The type of *A. villosa* is a skull (skin untraceable) of an adult female in the British Museum (Natural History), Accession No. 1843.9.14.3, unsexed (Napier, 1976). Smith (1970), however, regarded the name *villosa* as



Figure 5. The distributions of *Alouatta palliata* and *Alouatta coibensis*. Based on Aquino and Encarnación (1994), Curdts (1993), Defler (2003), Eisenberg (1989), Estrada and Coates-Estrada (1984), Froehlich and Froehlich (1987), García-Orduña and Canales-Espinosa (1995), García-Orduña *et al.* (1999), Hall (1981), Hernández-Camacho and Cooper (1976), Horwich and Johnson (1986), Reid (1997), Rodríguez-Luna *et al.* (1996, 2001), Silva-López *et al.* (1995), Smith (1970), Tirira (2001), Watts *et al.* (1986), and Watts and Rico-Gray (1987). Map drawn by Mark Denil and Kimberly Meek (Center for Applied Biodiversity Science, Conservation International, Washington, DC).

indeterminable, as had Lawrence (1933), and used *A. pigra* for the Guatemalan black howler. The type locality was given as “Brazils” by Gray (1845), but Sclater (1872) was convinced that it was attributable to a skin of a black howler from Vera Paz, Guatemala: a specimen collected by a Mr. Salvin, who also provided an account of howler monkeys in Guatemala. The account was published by Sclater (1872), and parts were reproduced *verbatim* in Elliot (1913) and Lawrence (1933), listing a number of localities in the Petén region of Guatemala. Apart from being all black, Sclater (1872) indicated that the direction of the hairs on the head was diagnostic, but this was ruled out by both Elliot (1913) and

Lawrence (1933) as too variable to be of use. The tenuous connection between Gray's *villosa* and Salvin's black howler from Guatemala, and the lack of a skin for the holotype (the skull is not diagnostic), resulted in Lawrence (1933, p. 336) concluding that it was "advisable to reidentify the howler monkeys of this region [Guatemala] and to regard *M[ycetes]. villosus* as indeterminable due to the absence of a type locality and the imperfect condition of the type." Hence, she described the form *A. palliata pigra* for the Guatemalan howler; the name used today, and recognized as a species distinct from *A. palliata* following the analyses of Smith (1970), Horwich (1983), and Horwich and Johnson (1984).

Lawrence's (1933) taxonomy included another all-black howler she described as *A. p. luctuosa* from a single specimen, adult male (skin and skull) from Mountain Cow, Cayo District, British Honduras (Belize), collected by O. L. Austin Jr., 12 April, 1928, and kept in the Museum of Comparative Zoology at Harvard University (Accession No. 20459). Smith (1970, p. 375) examined it, however, and found that it fell well within the range of individual variation observed in *pigra*, and considered it a junior synonym as a result. The resulting taxonomy of a monotypic *A. pigra* and five subspecies comprising *A. palliata* (*A. p. palliata*, *A. p. aequatorialis*, *A. p. mexicana*, *A. p. trabeata*, and *A. p. coibensis*) was accepted by Hall (1981), and modified only slightly by Froehlich and Froehlich (1986, 1987; in litt. to RAM 17 March 1987) whose study of dermatoglyphs convinced them that the forms *coibensis* and *trabeata* were quite distinct from the rest, and placed them as subspecies of *A. coibensis* Thomas, 1902.

Rylands *et al.* (2000) listed three species of howling monkeys in Mesoamerica: *A. palliata* (with three subspecies), *A. coibensis* (two subspecies), and *A. pigra*. Groves (2001) likewise recognized these three howling monkey species, but none of their subspecies. The forms *mexicana* Merriam, 1902 and *aequatorialis* Festa, 1903 were considered by him to be synonyms of *A. palliata*, and he listed *trabeata* Lawrence, 1933 as a synonym of *coibensis*. Smith (1970; see also Hall, 1981) found that the cranial characteristics (size and shape), dental cusp pattern and styler development of the upper molars, and the color of the pelage (all features which he demonstrated clearly distinguished *A. p. mexicana* from sympatric *A. pigra*) were very similar in the forms *palliata*, *mexicana*, *trabeata*, and *coibensis*, indicating not just that they are closely allied but only weakly definable as subspecies. He, like others who followed, however, was reticent about actually subsuming all as junior synonyms because of the lack of an extensive analysis of geographic variation (Hall, 1981; Rylands

et al., 2000; Groves, 2001; Cortes-Ortiz *et al.*, 2003). To date, nobody has superseded the detailed, considerate, and thorough study of Lawrence (1933), but we recommend a reexamination of the status of *coibensis* and *trabeata*.

Alouatta palliata palliata (Gray, 1849)

Golden-mantled howling monkey or Nicaraguan mantled howling monkey (Hill, 1962), mono congo, mono aullador.

Costa Rica, Guatemala, Honduras, Nicaragua, Panama (¿) (Figure 5).

Type: Syntypes, an adult female (skin and skull) and adult male (skin) in the British Museum (Natural History), collected by A. Sallé. Accession Nos. 1848.10.26.1 and 1848.10.26.2, respectively (Napier, 1976).

Type locality: Shores of Lake Nicaragua (*vide* Sclater, 1872; given in original description by Gray [1849] as Caracas, Venezuela).

Lawrence (1933) remarked that, excepting the small *coibensis* and the black howlers from Guatemala, she found it very difficult to distinguish the subspecies of *A. palliata* due to individual differences almost coinciding with variation over the total range of the species. She described *A. p. palliata* as a large race of generally black pelage relieved by light yellowish flank hairs, but showing much individual variation. Especially difficult she found was the separation of *palliata* from *aequatorialis* in the region of Panama where they intergrade. *A. p. palliata* differs from *aequatorialis* in being generally blacker and with more rufous than yellowish golden hairs forming the mantle. It differs from *A. p. mexicana* mainly in some aspects of skull morphology (Lawrence, 1933).

The range limits separating *A. p. aequatorialis* from *A. p. palliata* are not clear. Lawrence (1933) cited a specimen of *A. p. palliata* from Cotó, extreme western Panama, and Hill (1962, p. 106) mentioned that specimens from Sevilla Island, western Panama, collected by J. H. Batty were “manifestly” *A. p. palliata*. Hall (1981), on the other hand, lists Sevilla Island, and Puerto Cortez, Costa Rica, as marginal records for *A. p. aequatorialis*. Many individuals from Panama are intermediate (Lawrence, 1933). From eastern Costa Rica, at least, *A. p. palliata* extends through Nicaragua to northern Honduras and, according to Curdts (1993), it just extends into Guatemala to the Río Motagua and possibly along the coast a short distance to the Cabo de Tres Puntas, where it meets *A. pigra*. It is not known to occur in El Salvador to the south (Burt and Stirton, 1961).

Alouatta palliata mexicana Merriam, 1902

Mexican howling monkey, mono aullador, mono aullador pardo, saraguato, mono zambo.

Mexico, Guatemala (Figure 5).

Type: Adult male, skin and skull, US National Museum, Accession No. 79398, collected by E. W. Nelson and E. A. Goldman, 23 April, 1906. Biological Survey Collection.

Type locality: Minatitlán, Vera Cruz, Mexico (Hill, 1962; Groves, 2001).

According to Merriam (1902), *A. p. mexicana* is similar to but much smaller than *palliata* (Gray, 1849), and he also provided a number of distinguishing (qualitative) cranial features. Lawrence (1933) was unable to establish any consistent difference in size from *A. p. palliata*, but recognized the subspecies due to some differences in pelage and certain cranial traits. The main feature is a more diffuse distribution of light-banded hairs over the back, and the paler more silvery bases of the hairs on the flank and on parts of the dorsum. The head, shoulders, limbs, tail, and (occasionally) spinal region are black.

The range of *A. p. palliata* extends eastward from southeastern Mexico, provinces of Vera Cruz, Tabasco, and northern Chiapas and Oaxaca. As discussed by Smith (1970), in Tabasco *A. p. mexicana* meets, and is sympatric with, *A. pigra* in a region 5 miles southeast of Macuspana. García-Orduña *et al.* (1999) found mixed populations of the two species in small habitat fragments in Tabasco (see also Rodríguez-Luna *et al.*, 2001). From there it extends east in a swathe through central Guatemala, skirting the southern limits of the range of *A. pigra*, but not extending south into El Salvador. Historically, at least, it would meet *A. p. palliata* only on the border with Honduras. Whether the two subspecies, *mexicana* and *palliata*, are still in contact is not known.

Alouatta palliata aequatorialis Festa, 1903

South Pacific blackish howling monkey, Ecuadorian mantled howling monkey. Peru: Mono coto de Tumbes, coto mono or coto mono de Tumbes (Aquino and Encarnación, 1994; Encarnación and Cook, 1998). Colombia: Aullador negro (Defler, 2003). Ecuador: Aullador de la costa, coto negro, mono mongón (Tirira, 2001). Panama: mono negro.

Colombia, Costa Rica (?), Ecuador, Panama, Peru (Figure 5).

Type: Four cotypes, two adult males, one female, and one young (skin numbers 101, 102, 103, and 104, and skull numbers 4688, 4886, 4692, and 4693), Museum of Zoology and Comparative Anatomy, University of Turin. Collected in September, year uncertain but between 1895 and 1898 by Enrico Festa.

Type locality: Vinces, Guayas Province, west coast of Ecuador.

Described by Elliot (1913)—who listed it as a species—as “similar to *A. palliata* but general color chocolate-brown instead of black”. Lawrence (1933) found the mantle hairs to be golden-ochraceous, slightly shorter than in *palliata*, and most numerous posteriorly, hardly extending as far forward as the axillary region (note difference in this aspect to *trabeata*). She noted the original account of Festa who said that the general color was chocolate-brown with the bases of the hairs yellowish fulvous, the tips yellow, and the flanks golden yellow. The females, according to Festa, are browner with less golden than the males. Lawrence (1933) pointed out that the overall color is actually quite variable and can range from the bright-colored individuals to “quite black”. The general color of the paler forms, however, is very different from that of *palliata*—paler and more golden brown than the orange-rufous of *palliata*, and the bright coloring extends farther down the hind limbs than in *palliata*. Even where the bright mantle is almost totally absent, the back is still broadly and more evenly sprinkled with paler hairs than is found in *palliata*. Lawrence (1933) failed to find any cranial characters to distinguish *aequatorialis* from *palliata*. Smith (1970) found that *aequatorialis* resembles typical *palliata* in most respects, and the few specimens he examined from Panama seem to indicate the presence of a well-defined zone of intergradation. In some ways, *aequatorialis* resembles *A. pigra*—both are large (Smith [1970] reported that the dental arcade does not exhibit such a marked trend in size reduction as seen in typical *palliata*), and the typical mantle coloration of *palliata* is frequently reduced or lost completely in *aequatorialis*. Cortés-Ortiz *et al.* (2003), who analyzed mtDNA of 19 *A. palliata* (from Panama to southern México), found a maximum level of sequence divergence of 0.5% but “a minor phylogeographic break separating northern and southern *A. palliata* [...] near Panama’s Sona Pensinsula” (p. 75).

A. p. aequatorialis occurs in Panama, from the southern limit to the range of *A. p. palliata* (either in western Panama or extreme eastern Costa Rica), through the Serranía del Darién (Anthony, 1916; Lawrence, 1933) into western Colombia, north through the basins of the Ríos Sinú and Atrato to the Caribbean coast, and south through the Serranía del Baudó (Defler, 2003)

and the foothills, lowlands, and lower montane areas west of the Andes to the Pacific coast, through Colombia and Ecuador, just into the Tumbes region of northern Peru (Aquino and Encarnación, 1994; Encarnación and Cook, 1998; Tirira, 2001).

Alouatta coibensis Thomas, 1902

Coiba Island howling monkey.

Panama (Figure 5).

Froehlich and Froehlich (1987) concluded that the howlers on Coiba Island and the Azuero Peninsula (*trabeata*) are close to, but quite distinct from, *A. palliata* in Panama, Costa Rica, and Nicaragua. Their argument was based on an analysis of fingerprint data, which they used as a surrogate to indicate genetic distance. Citing Bartlett and Barghoorn (1973), Froehlich and Froehlich (1987) indicated that the islands of Coiba and Jicarón were last connected to the mainland about 24,000 to 15,000 years ago, and they argued that *coibensis* should be considered a distinct species, with two subspecies—*coibensis* and *trabeata*. *A. coibensis coibensis* is smaller and has a less distinctive (duller) color than *trabeata*.

Cortés-Ortiz *et al.* (2003) found, however, that both *trabeata* and *coibensis* shared mtDNA haplotypes with *A. palliata* and were unable to substantiate the classification of *coibensis* (or *trabeata*) as a distinct species. The mitochondrial DNA divergence between *A. palliata* and *A. coibensis* was very low, showing only 0.1% sequence divergence—more than an order of magnitude fewer nucleotide substitutions than were observed between any other pair of *Alouatta* species. Divergence between *A. palliata* and *A. coibensis* was found to be similar to mitochondrial DNA distances observed between geographically separated populations within each of these two species. This, of course, does not by itself mean that the species *A. coibensis* should be sunk, but it does suggest that the morphological characters should be reassessed for their consistency. A morphometric study by Guadalupe Méndez is indicating that the howler monkeys from Azuero and Coiba are well differentiated from other Central American forms, and that they are certainly distinct subspecies (A. Cuarón, in litt. 21 May, 2003). Rylands *et al.* (2000) and Groves (2001) followed Froehlich and Froehlich (1987) in recognizing *coibensis* as a full species. We continue to recognize both *trabeata* and *coibensis* as distinct, but fully accept the possibility that they should be considered subspecies of *A. palliata*.

Alouatta coibensis coibensis Thomas, 1902

Coiba Island howling monkey.

Panama (Figure 5).

Type: An old male (skin and skull, Accession No. 1902.3.5.9) in the British Museum (Natural History), collected 18 May, 1901, by J. H. Batty (Napier, 1976).

Type locality: Coiba Island, Pacific coast of Panama.

This howling monkey is known only from Coiba Island and neighboring Jicarón, off the Pacific coast of Panama. It is smaller than other Central American howling monkeys, and has a duller pelage than the closely related form from the Azuero Peninsula, *A. c. trabeata*. Compared to *A. c. trabeata*, the mantle is more confined to the flanks. Hill (1962) described the head and fore part of the back as “seal brown, appearing almost black in most lights”. The lower back is paler and the rump and proximal parts of the hind limbs are walnut. The flank hairs are elongated—orange-rufous to cinnamon-rufous according to Hill (1962), and golden as described by Groves (2001). The type specimen has a large pedunculated and unpigmented scrotum (Hill, 1962). The females are similar in color to the males, but smaller.

Alouatta coibensis trabeata Lawrence, 1933

Azuero howling monkey, golden howling monkey (Froehlich and Froehlich, 1987).

Panama (Figure 5).

Type: Adult male (skin and skull, Accession No. 29545) in the Museum of Comparative Zoology, Harvard, collected by Thomas Barbour, in March 1933.

Type locality: Capina, Herrera Province, Panama.

According to Hill (1962), this howling monkey is distinguished principally by its golden flanks and loins (golden-ochraceous tips to hairs), together with a browner appearance of the rest of the body. Lawrence (1933) described it as having a walnut-colored back and very long silky golden flank hairs extending from the axilla to the groin. Besides this, she noted a greater degree of sexual dimorphism in skull measurements than in other populations of Central American howlers. Froehlich and Froehlich (1987) found it to be more closely related to *coibensis* Thomas, 1902 than to other Central American forms and, recognizing *coibensis* as a full species, placed it as a subspecies. Although listing it as a synonym of *coibensis*, Groves (2001, p. 180) recognized that “the mainland

and insular populations of this species [*coibensis*] differ considerably and are presumably (at least?) subspecifically distinct.” Froehlich and Froehlich (1987) provide an interesting discussion regarding the zoogeography of the region and how and why the Azuero peninsula may have been relatively isolated in the past, resulting in the differentiation of its howlers (and spider monkeys) and a relatively depauperate mammal fauna. Rylands *et al.* (2000) and Groves (2001) followed Froehlich and Froehlich (1987) in recognizing *trabeata* as a subspecies of *coibensis*. It is endemic to the Azuero Peninsula, Panama (Froehlich and Froehlich, 1987; Rowe, 2000).

Alouatta pigra Lawrence, 1933

Black howling monkey, Lawrence’s howler monkey (Hall, 1981), Yucatán black howler (Reid, 1997), saraguato negro (Mexico).

Belize, Guatemala, Mexico (Figure 6).



Figure 6. The distribution of *Alouatta pigra*. Based on Curdts (1993), Eisenberg (1989), Hall (1981), Horwich and Johnson (1986), Jones *et al.* (1974), Reid (1997), Rodríguez-Luna *et al.* (1996), Silva-López *et al.* (1995), Smith (1970), and Watts and Rico-Gray (1987). Map drawn by Mark Denil and Kimberly Meek (Center for Applied Biodiversity Science, Conservation International, Washington, DC).

Type: Adult male, skin and skull, in the Museum of Zoology, University of Michigan, collected 4 May, 1931 by A. Murie. One of a series of 12 specimens (five adult males, five adult females, and a young female; Lawrence, 1933).

Type locality: Uaxactún, Petén, Guatemala.

Although placed as a subspecies of *A. palliata* by Lawrence (1933) and Hill (1962), Smith (1970) (see also Jones *et al.*, 1974; Horwich, 1983; Horwich and Johnson, 1984) demonstrated that the black howling monkey from the Yucatán peninsula (Mexico), Belize, and northern Guatemala is a valid species. *A. pigra* is larger than typical *palliata* and distinguished from other Central American howlers by absence in both sexes of light areas along flanks. Smith (1970) found a zone where the two species are sympatric in Tabasco, Mexico (5 miles SE of Macuspana; see also García-Orduña *et al.*, 1999; Rodríguez-Luna *et al.*, 2001; Serio-Silva and Rico-Gray, 2004), and compared the pelage, dental and cranial morphology, and the articulation of the mandible in the two species. Hall (1981) described the cranial differences between *A. pigra* and *A. palliata*. Silva-López (1998) recorded that it occurs in sympatry with *A. palliata* in the Biotopos Chocón Machacas and the Mario Dary Rivera Biosphere Reserve, and there is a need to study the mechanics of their coexistence in these areas.

The westernmost locality given by Hall (1981) is at Frontera, in the Mexican state of Tabasco; *A. palliata* has been recorded just west of there along the coast, 6 miles south of Cárdenas. Further localities that define the western and southern limits of its range include 5 miles southeast of Macuspana, Tabasco, and San Mateo Ixtatán (*ca.* 11,000 ft) in Guatemala. Hall (1981) identified the southern limits of its range in the east with three localities along the Río Motagua basin in Guatemala, including Quirigua and Zacapa (right bank of the river). Curdts (1993), on the other hand, found that the southern and southwestern limits of the range of *A. pigra* in Guatemala were defined by the Lago de Izabel, El Golfete, and the Río Dulce. He noted large numbers of *A. pigra* in the Río Polochic delta, entering the west end of the Lago de Izabel. These are just to the north of the Río Motagua, where Curdts (1993) identified *A. palliata*.

Ateles geoffroyi Kuhl, 1820

Geoffroy's spider monkey, mono araña.

Belize, Colombia, Costa Rica, El Salvador, Honduras, Guatemala, Mexico, Nicaragua, Panama (Figure 7).



Figure 7. The distributions of *Ateles geoffroyi* and *Ateles fusciceps*. Based on Defler (2003), Eisenberg (1989), Estrada and Coates-Estrada (1984), Hall (1981), Heltne and Kunkel (1975), Hernández-Camacho and Cooper (1976), Hershkovitz (1949), Horwich and Johnson (1986), Kellogg and Goldman (1944), Konstant *et al.* (1985), Marineros and Gallegos (1998), Reid (1997), Rodríguez-Luna *et al.* (1996), Silva-López *et al.* (1995), Tirira (2001), Watts *et al.* (1986), and Watts and Rico-Gray (1987). 1: Pico Bonito National Park, Honduras. Map drawn by Mark Denil and Kimberly Meek (Center for Applied Biodiversity Science, Conservation International, Washington, DC).

The Mesoamerican spider monkeys are variable in their pelage color and are difficult to resolve taxonomically. The classic study of Kellogg and Goldman (1944) resulted in the recognition of 16 taxa of spider monkeys, 10 of them in Mesoamerica: 9 taxa of *A. geoffroyi* and, extending into Panama from north-western Colombia, *A. fusciceps robustus*. Over the last 60 years, little has been done that has shaken the foundation laid down by Kellogg and Goldman (1944): Hill (1962), Hall (1981), and Konstant *et al.* (1985) maintained their taxonomy of the Central American spider monkeys and, till recently, all but one have stood the test of time. Schultz (1960) who studied geographic variation

in the crania of 203 adult *A. geoffroyi* concurred with the taxonomic arrangement of Kellogg and Goldman (1944). Silva-López *et al.* (1996) concluded that *A. geoffroyi pan* Schlegel, 1876, a very dark form from Guatemala, was a variant of the Mexican spider monkey, *A. g. vellerosus*, while Napier (1976) showed that *A. g. panamensis* is a synonym of *A. g. ornatus*.

Having disqualified *A. g. pan* and *panamensis*, however, the remaining eight Mesoamerican spider monkeys identified by Kellogg and Goldman (1944) are still poorly defined. Their taxonomy was based on cranial morphology, body size, and pelage color patterns although the cranial differences were minimal. Silva-López *et al.* (1996) suspected that, like *pan*, the form *A. geoffroyi yucatanensis* is merely a color variant of *A. g. vellerosus*. The validity of the remaining forms requires a good understanding of the geographic patterns of natural variation; something which is increasingly difficult to attain due to the widespread loss and fragmentation of their forests and populations.

Collins (1999) and Collins and Dubach (2000) divided the subspecies into two groups: northern (*velerosus* and *yucatanensis*) and southern (*frontatus*, *ornatus*, *geoffroyi*, *panamensis*, and *griscens*). Groves (2001) recognized only five subspecies: *A. g. yucatanensis*, *A. g. vellerosus* (synonym *A. g. pan*), *A. g. geoffroyi* (synonym *A. g. frontatus*), *A. g. ornatus* (synonyms *azuerensis* and *panamensis*), and *A. g. griscens*. The taxonomy we follow here is essentially that of Kellogg and Goldman (1944).

Ateles geoffroyi geoffroyi Kuhl, 1820.

Nicaraguan spider monkey (Kellogg and Goldman, 1944).

Costa Rica, Nicaragua (Figure 7).

Type: Adult female, Muséum National d'Histoire Naturelle, Paris (menagerie specimen acquired in 1819; registered in I. Geoffroy, Catalog méthodique del la collection des mammifères, pt 1 (Catalog des Primates), p. 49, 1851) (Kellogg and Goldman, 1944).

Type locality: Unknown, but restricted to San Juan del Norte (Greytown), Nicaragua by Kellogg and Goldman (1944) who refer to a specimen of Sclater (1862) from the Río Rana, Gorgon Bay, near San Juan del Norte, which was listed by Gray (1870) as "*Ateles hybridus*" from St. Juan, Nicaragua.

The nominotypical subspecies of Geoffroy's spider monkey is silvery to brownish gray on the back, upper arms, and thighs (Konstant *et al.*, 1985). The black on the elbows, knees, and upper and lower arms and legs is variable, but the hands and feet are always black. Chest is similar to the back but the

lower abdomen can be quite golden. The face is black with flesh-colored eye rings. According to Kellogg and Goldman (1944), it most closely resembles *frontatus* from northwestern Costa Rica, and the light buff (silvery to brownish gray) color of the back contrasts with that of *ornatus* of eastern Costa Rica, which they described as rich rufescent. The skull is very similar to *ornatus* but apparently smaller (Kellogg and Goldman, 1944). Groves (2001) considered the form *frontatus*, also from Costa Rica and Nicaragua, to be a junior synonym of *A. g. geoffroyi*, but this needs further study (see below).

Its distribution is given by Kellogg and Goldman (1944) as the coastal region around San Juan del Norte or Martina Bay, southeastern Nicaragua; probably ranging across the lowlands to the vicinity of Lake Managua and Lake Nicaragua on the Pacific coast. It possibly extends into northern Costa Rica. Specimens examined by Kellogg and Goldman (1944) were from Monagua, Nicaragua.

Ateles geoffroyi azuerensis Bole, 1937

Azuero spider monkey.

Panama (Figure 7).

Type: Adult female, Cleveland Museum of Natural History, Accession No. 1235.

Type locality: Altos Negritos, 10 miles east of Montijo Bay (part of the spur forming south drainage divide of Río Negro), Mariato Suay Lands, Azuero Peninsula, Veraguas Province, Panama; altitude 1500 ft.

Distinguished from neighboring forms by a general color of light tawny or ochraceous-tawny. Konstant *et al.* (1985) summarized the description of *azuerensis* (two skins from the type locality) by Kellogg and Goldman (1944), as follows: the back is grayish brown, and a little darker than the underside; outer surfaces of limbs black, but top of head, black or blackish brown. Believed by Groves (2001) to be a probable junior synonym of *A. g. ornatus* of Nicaragua and Costa Rica.

Definitely known only from the western (Veraguas) side of the forested mountains of the Azuero peninsula in the vicinity of Ponuga, where it appears to be isolated. Kellogg and Goldman (1944) indicated that it may occur to the west along the Pacific coast to the Burica Peninsula, near the Panama–Costa Rica border. Kellogg and Goldman (1944) tentatively attributed a series of 25 skulls from the collection of Adolph H. Schultz (no skins, but reported to have been light-colored) from Río La Vaca, near Puerto Armmuelles, Burica Peninsula to *A. g. azuerensis*. Baldwin and Baldwin (1976) found no evidence that spider monkeys ever occurred in the Province of Chiriquí. Konstant *et al.*

(1985) reported that the Azuero Pensinsula was widely deforested and it is likely to be surviving only in western parts. It occurs in the Cerro Hoya National Park (Matamoros and Seal, 2001).

Ateles geoffroyi frontatus (Gray, 1842)

Black-browed spider monkey, black-foreheaded miriki (Kellogg and Goldman, 1944).

Costa Rica, Nicaragua (Figure 7).

Type: Adult female with young (paratype) shot by Capt. Sir Edward Belcher (skin and skull), British Museum (Natural History). Accession No. 1842.10.30.4 (Napier, 1976).

Type locality: South America (= harbor of Culebra, León = Culebra, Bay of Culebra, Guanacaste, northwestern Costa Rica) according to Gray (1843 in Kellogg and Goldman, 1944).

According to Kellogg and Goldman (1944), *frontatus* is similar in color pattern (restriction of black areas to top of head and, irregularly, to outer surfaces of limbs) to *geoffroyi* of southeastern Nicaragua, but the body is darker, with the upperparts brown and underparts honey yellow to tawny, rather than light buff. It differs from *panamensis* in having a brownish instead of deep ferruginous general body color, and from *vellerosus* of Veracruz in the restriction of black areas to the anterior part of the back and more yellowish tone of the lumbar region. Apart from the type in the British Museum from northwestern Costa Rica, little is definitely known of its characters or distribution. The genetic analyses of Collins and Dubach (2000) included a sample from a Nicaraguan spider monkey, which, by its pelage, they tentatively identified as *A. g. frontatus*. It was quite distinct from *panamensis* and *vellerosus/yucatanensis*, and their findings suggested that it was a sister clade to northern, or even all, *A. geoffroyi*. Groves (2001) did not recognize this form as a valid subspecies, considering it a synonym of *A. g. geoffroyi*.

A. g. frontatus is believed to range through northwestern Costa Rica and extreme western and northern Nicaragua (Kellogg and Goldman, 1944). Specimens from Nicaragua examined by Kellogg and Goldman (1944) were from the following localities: Lavalá; Peña Blanca; Río Siquia; Río Yoya, a tributary of the Río Principolca; Tuma; and Uluce. Allen (1908, 1910) recorded *A. geoffroyi* from the east slope of the Nicaraguan highlands, Savala (800 ft), Tuma (1000 ft), Peña Blanca (high point in low Atlantic coast forests, 1500 ft), and

Uluce (about 1000 ft), and in the highlands of northern Nicaragua at Matagalpa (2000 ft).

Ateles geoffroyi grisescens Gray, 1866

Hooded spider monkey.

Panama, Colombia (?) (Figure 7).

Type: Skin of an adult, sex unknown, in the British Museum (Natural History), Accession No. 1865.4.20.2 (Napier, 1976).

Type locality: Unknown, but restricted by Kellogg and Goldman (1944) to the Río Tuyra, southeastern Panama.

According to Kellogg and Goldman (1944), the adults have long, lax pelage and a peculiar dusky coloration, with a general admixture of yellowish gray or golden hairs, the hairs on the upperparts are golden at the base. The skull, they concluded, indicates a close relationship to *panamensis*, despite the latter's contrasting deep reddish color. Specimens examined by Kellogg and Goldman (1944) were from Chepigana, Darién. Konstant *et al.* (1985) examined specimens (no locality given) that were much paler than the descriptions of Kellogg and Goldman (1944) and Hernández-Camacho and Cooper (1976) would indicate.

Kellogg and Goldman (1944) presumed that it occurred in the valley of the Río Tuyra and probably southeastward through the Serranía del Sapo of extreme southeastern Panama and the Cordillera de Baudó of northwestern Colombia. Matamoros and Seal (2001) indicate its occurrence in the basin of the lower Río Tuira in Panama and the frontier zone with Colombia. Heltne and Kunkel (1975) indicated Cerro Pirre or Río Tucutí as marking the limits of its range with *A. f. rufiventris* to the north. Hernández-Camacho and Cooper (1976) indicated that *grisescens* occurs in Colombia: "...[it] is known only from the vicinity of Juradó very near the Panamanian border on the Pacific coast. It is undoubtedly restricted by the Baudó Mountains to a narrow coastal strip that may extend as far south as Cabo Corrientes." (p. 66). Defler *et al.* (2003) recorded that there is no recent information regarding its presence or otherwise along the Panamanian border, but that colonists near the northern parts of the Serranía de Baudó region talk of two "types" of *Ateles*, one in the lowlands (definitely *A. fusciceps*) and another form above 500–600 m altitude (J. V. Rodríguez-M., unpubl. data): the only real suggestion is that this taxon might actually be present in Colombia. *A. fusciceps* in the central part of the

Sierra de Baudó would indicate that the occurrence of *grisescens* there would be limited to the portion immediately abutting Panama, and not the entire mountain range (Defler *et al.*, 2003).

Ateles geoffroyi ornatus Gray, 1870

Ornate spider monkey (Kellogg and Goldman, 1944), Mono Colorado. Costa Rica, Nicaragua (Figure 7).

Type: Juvenile (skin and skull) of unknown sex, British Museum (Natural History), Accession No. 1850.1.26.2 (Napier, 1976).

Type locality: Unknown, but restricted by Kellogg and Goldman (1944) to Cuabre, Talamanca region, southeastern Costa Rica.

Type of panamensis: Adult female, skin and skull, U.S. National Museum, Accession No. 171489 (Biological Surveys collection); collected by E. A. Goldman, 8 June, 1911. Original No. 21165.

Type locality: Cerro Brujo, about 15 miles southeast of Portobello, Province of Colón, Panama; altitude 2000 feet (Kellogg and Goldman, 1944).

This most intensely red of the Central American spider monkeys was described by Kellogg and Goldman (1944), under the name *panamensis*, as a rather large, deeply rufescent race, similar to *ornatus* of the Caribbean slope of Costa Rica, but with a more intense reddish tone (back of shoulders to base of tail, backs of thighs, and sides of body), the back less obscured by overlying dusky hairs; inner side of upper arms pinkish cinnamon to ferruginous. It differs from *azuerensis* in its deep reddish instead of cinnamon or tawny general coloration. A black (sometimes freckled with a pale skin) face.

Kellogg and Goldman (1944) described *ornatus* as being “a dark golden yellowish subspecies, the upper parts in strong light having a glossy, golden yellow sheen, owing to the yellowish subterminal bands of hairs”. Napier (1976: 88) found that the type specimen falls well within the range of variation of Panamanian specimens, and implied that Kellogg and Goldman (1944) would not have described *panamensis* had they not been prevented by wartime constraints from traveling to London to examine the type of *ornatus*, which they knew only from the somewhat misleading type description.

The ornate spider monkey is found in forested regions of Panama, east of the Canal Zone (Cordillera San Blas), and west through Chiriquí to central western Costa Rica. Heltne and Kunkel (1975) give the following localities

as marking the eastern limit of its range: San Juan, Cerro Brujo, Cerro Azul, and Río Pequeñi—all on or within the boundary line of the Madden Lake watershed, and nowhere more than 30 miles east of the Panama Canal. The Río Bayano basin just to the east is occupied by *A. fusciceps rufiventris* (see Handley, 1966; Heltne and Kunkel, 1975). This is the spider monkey of the Osa Peninsula, Corcovado National Park, and Carara Biological Reserve in Costa Rica (Matamoros and Seal, 2001). The population on the Island of Barro Colorado is introduced (Carpenter, 1935; J. F. Eisenberg, pers. comm. in Konstant *et al.*, 1985). Crockett *et al.* (1997; see also Cody, 1994; Querol *et al.*, 1996) observed spider monkeys in the Refugio Bartola/ Reserva Indio-Maíz (300,000 ha), along the Río Bartola, north of the Río San Juan along the frontier with Costa Rica. They were unable to identify the subspecies but said that, unlike *A. g. geoffroyi*, they were “distinctly reddish on the back and on the top of the tail; the ends of the limbs were dark” (p. 73).

Ateles geoffroyi vellerosus Gray, 1866

Mexican spider monkey (Kellogg and Goldman, 1944). Mono araña.
El Salvador, Honduras, Guatemala, Mexico (Figure 7).

Type: Skin (Accession No. 1845.11.2.2) and skull (Accession No. 1845.12.8.16) in the British Museum (Natural History). Napier (1976) inferred that it was a female. Figured in Sclater (1872).

Type locality: Originally assigned by Gray to Brazil, but restricted by Kellogg and Goldman (1944) to Mirador, about 15 miles northeast of Huatasco, Veracruz, Mexico; altitude 2000 feet (the type locality of the junior synonym *A. neglectus*, Reinhardt, 1873).

A. g. vellerosus occurs in the forests of Veracruz and eastern San Luis Potosí and southeastward through Tabasco, across the Isthmus of Tehuantepec in eastern Oaxaca, including the highlands of Guatemala (thought by Kellogg and Goldman to have been occupied by *A. g. pan*, here considered a synonym) through El Salvador and Honduras, including the north coast to the lowlands of the Mosquitia in the Department of Gracias a Dios.

Kellogg and Goldman (1944, p. 33) described *A. g. vellerosus* as “a subspecies distinguished by a combination of black or brownish-black top of head, neck, and shoulders, in contrast with buffy lumbar region, and pinkish-buff to cinnamon-buff underparts. Differs from *yucatanensis* of Quintana Roo in

deeper buff underparts (underparts in *yucatanensis* are silvery-white or light buff)". According to Konstant *et al.* (1985), dorsal surfaces range from black to dark brown, except for a light band across the lumbar region, and contrast strongly with its lighter abdomen and inner limbs. Exposed flesh-colored skin is often present about the eyes. Silva-López *et al.* (1996) reported that this description is compatible with *A. g. vellerosus* at Sierra de Santa Marta, Veracruz, Mexico, although there is also considerable variation, for example, in lighter dorsal surfaces, a less distinct band across the lumbar region, and lack of contrast between the color and tones of the dorsal surfaces and the inner limbs. Konstant *et al.* (1985) also indicated the absence, or marked reduction, of the white triangular forehead patch and sideburns (present in *A. belzebuth* and the darker *A. hybridus*). Some spider monkeys at the Sierra Santa Marta have distinct white forehead triangles, and Silva-López *et al.* (1996) found that *vellerosus* there is quite variable, with the pelage ranging from very dark to very pale. In Tikal, Guatemala, they observed whitish *vellerosus*, with a darker distal third of the tail. In El Salvador, Burt and Stirton (1961, p. 21) described *vellerosus* as follows "Top of head, arms, legs and tip of tail nearly black; from shoulders to rump golden slightly washed with dark brown; cheeks, throat, belly, and undersides of limbs whitish (washed with pale yellow on breast)". According to Marineros and Gallegos (1998) in Honduras, it has a black pelage, paler on the back (grizzled coffee color) and underparts, with pale circles of naked skin around their eyes.

The very dark *A. g. pan* from Cobán, Alta Vera Paz, Guatemala (co-types: an adult male and two adult females in Leiden) was listed by Kellogg and Goldman (1944) as the species of the central highlands of Guatemala. Konstant *et al.* (1985) noted its similarity to the darker *vellerosus*, differing only in the relative lack of contrast between dorsal and ventral color and lack of a lighter-colored saddle on its lumbar region, and doubted its validity. Its supposed range is broadly covered by pine forest, dominated by *Pinus*, *Quercus*, and *Liquidambar* with some remnants of tropical forest in the lowlands of Alta Verapaz and Quiché (including the locality of Barillas), to the north; near Chilascó and in the Biotopo Mario Dary Rivera, in the east; and in Escuintla and Retalhuleu, in the south (Silva-López *et al.*, 1996). Only howling monkeys have been found in the Sierra de Chamá (Alta Verapaz, Quiché), 300–1500 m asl; the Sierra de Chuacús (Baja Verapaz, Quiché), 600–2100 m asl; and the Sierra de los Cuchumatanes (Huehuetenango, Quiché), 1500–2700 m asl (Silva-López *et al.*, 1996). Kellogg and Goldman (1944) believed that *A. g. pan* intergraded

with *vellerosus*, Konstant *et al.* (1985) were doubtful of its validity, and Silva-López *et al.* (1996) concluded that it was not a valid taxon.

The spider monkeys of Honduras have been very poorly documented. They are based on samples from the Tegucigalpa area (Cantoral and Guaymaca), Olancho (Catacamas), and Octopeque (El Chorro), all from central and southern Honduras, south of the Cordillera Nombre de Dios. Recent studies in the Pico Bonito National Park in northern Honduras (Hines, 2004) have indicated that the spider monkeys there are neither *A. g. vellerosus* nor *A. g. yucatanensis*. Unlike *vellerosus*, the North Honduran *Ateles* have a bright-reddish-orange back, similar to *panamensis*. *A. g. yucatanensis* is a much darker auburn-brown. The underparts in the northern Honduran *Ateles* are closer to the silver-white of *A. g. yucatanensis*, although the lower stomach tends towards a darker buff color. The white on the inside of the arms and legs of the northern Honduran specimens extend to the ankles and wrists, as in *A. g. yucatanensis*, whereas in *A. g. vellerosus*, the light color generally extends only as far as the elbows and knees. The Honduran specimens examined by Kellogg and Goldman (1944) were from the central and southern parts of the country where the climate is much drier than along the northern coast. The climate is markedly drier on the southern side of Pico Bonito, particularly in the Ahuan Valley, which has desert-like conditions and a flora that contrast with the more humid coastal side of the park. It is quite common to encounter agave and cacti in the Ahuan Valley and throughout the areas along the southern side of the park. Specimens from southern Honduras are less intense in the red-orange color on their back, but retain the similar bright silver-white upper chest, and a darker buff coloration on the lower chest and stomach.

Ateles geoffroyi yucatanensis Kellogg and Goldman, 1944

Yucatán spider monkey (Kellogg and Goldman, 1944).

Belize, Guatemala, Mexico (Figure 7).

Type: Adult male, skin and skull, U. S. National Museum, Accession No. 108531 (Biological surveys collection), collected 2 April, 1901, by E. W. Nelson and E. A. Goldman; original number 14652.

Type locality: Puerto Morelos, northeast coast of Quintana Roo, Mexico; altitude 100 ft.

Kellogg and Goldman (1944, p. 35) wrote that *A. g. yucatanensis* is a “rather small, slender, light-colored race with underparts silvery whitish or very pale

buff, pelage short and thin. Size about as in *vellerosus* of Veracruz but decidedly paler, especially on the underparts where in typical specimens a whitish silvery tone extends to neck and inner sides of limbs; underside of tail cream-buff to near callosity; frontal outline of skull more prominent". Konstant *et al.* (1985) described it as having a brownish-black head, neck, and shoulders, lighter brown on the lower back and contrasting with silvery-white underside, inner limbs, and sideburns. In the south of its range (Campeche and Guatemala), Kellogg and Goldman (1944) noted that specimens from Apazote, Campeche, and Uuxactúm, Guatemala, are referable to *yucatanensis* but with slightly darker and more buffy underparts, indicating gradation towards neighboring *vellerosus*.

Jones *et al.* (1974) studied the crania of spider monkeys from the Yucatán peninsula, from Veracruz and Oaxaca (*vellerosus*) and from Nicaragua (*frontatus*) and found that they differ mainly in breadth dimensions. They also examined pelage color, and concluded that whereas *frontalis* from Nicaragua was quite distinct (almost entirely yellowish except for a blackish area on the head and neck), specimens from the Yucatán did not differ from adjacent *vellerosus*, and therefore considered *yucatanensis* a synonym, while Konstant *et al.* (1985) noted that *yucatanensis* can be confused with lighter individuals of *vellerosus*. Silva-López and Rumiz (1995) reported that spider monkeys in the Río Bravo Conservation and Management Area in Belize resembled the descriptions of *vellerosus* more than *yucatanensis*, and noted that inter-individual variation in the color made it difficult to assign individuals to a particular subspecies. The genetic studies of Collins and Dubach (2000) indicated that *vellerosus* and *yucatanensis* were inseparable in mtDNA (based on three individuals: one from Belize, second from Yucatán, and the third from the Guatemala). Further morphological and genetic studies and most importantly field observations and a modern review of pelage variation are needed to clarify the validity or otherwise of this taxon (Silva-López *et al.*, 1995), but the evidence that *yucatanensis* is separable appears poor.

A. g. yucatanensis occurs in the forests of the Yucatán peninsula, north-eastern Guatemala, and adjoining parts of Belize, intergrading to the south in Mexico (Campeche) and Guatemala with *vellerosus*. Parra Lara and Jorgenson (1998) reported on a survey of 36 localities in the state of Quintana Roo. They confirmed the presence of spider monkeys in 11 of them, and received reports of their occurrence in a further 19, extending from the Ejido Tres Garantías in the south to locations way in the north, near Cancún, at Cenote Notnozot. Ramos-Fernández and Ayala-Orozco (2003) have studied the population size and habitat use of *A. g. yucatanensis* around the Punta Laguna, Quintana Roo.

Ateles fusciceps rufiventris Sclater, 1871

Colombian black spider monkey (Kellogg and Goldman, 1944). Panama: mono araña, mono negro.

Panama, Colombia (Figure 7).

Type: Juvenile skin (date and collector unknown), BM 1876.1.31.24 (Napier, 1976: 95).

Type locality: Río Atrato, Darién, Colombia.

The Colombian black spider monkey was described by Kellogg and Goldman (1944) as nearly all black, except for a brownish tinge on the forehead of one individual they examined, and a few inconspicuous whitish hairs on the chin and around the mouth. Heltne and Kunkel (1975) examined pelage color and patterns in detail, and added that the specimens they examined from eastern Panama had white or golden hairs on the cheeks and reddish or golden-banded hairs on the ventral surface of the trunk and limbs to a varying extent. Only 6 of the 24 specimens they examined were completely black on the frontal region. A series from the region of Tacarcuna showed all possible combinations of the distribution of white hairs on the facial and frontal areas and all black or brick-red tinged hairs in the ventral (genital) region, extending to the inner thigh.

There is still some confusion as to the taxonomy of the Colombian black spider monkey, despite the fact that a careful reading of Heltne and Kunkel (1975) leaves no doubt regarding the validity of the name *rufiventris* Sclater, 1871 as opposed to *robustus* Allen, 1914. Mittermeier and Coimbra-Filho (1981), Groves (2001), and Defler (2003) listed *A. fusciceps rufiventris* (= *robustus*), whereas Konstant *et al.* (1985) and Mittermeier *et al.* (1988) listed *Ateles f. robustus* (= *rufiventris*). Hernández-Camacho and Cooper (1976) also used the name *robustus*. Rylands *et al.* (2000) misidentified the author—listing *rufiventris* but ascribing it to Allen (1914) rather than Sclater (1871). Basing themselves only on the description of Sclater, an illustration, and a more detailed description of the type by Elliot (1913), Kellogg and Goldman (1944) argued that Sclater's *rufiventris* was probably a young female *A. p. aequatorialis*. Hershkovitz (1949) concluded, without saying why, that *rufiventris* was a color variant of *A. g. griseescens*; in this, he was followed by Napier (1976). Hill (1962) studied the type of *rufiventris* and decided it was a valid species. While not comparing it with *robustus*, his notes on pelage variation showed it to be similar, and especially similar to *Ateles dariensis* Goldman, 1915, from “near head of Río Limón, Mount Pirre, eastern Panama; altitude 5200 feet”, which

was considered later by Goldman himself to be a synonym of Allen's *robustus* (Kellogg and Goldman, 1944). It is of interest that, contra Hershkovitz (1949), Hill (1960: 502) found that "of all the races of *A. geoffroyi*, *A. g. griseascens* shows the least resemblance to *A. rufiventris*".

Another question, yet to be resolved, is whether *rufiventris* is a subspecies of the brown-headed spider monkey, *A. fusciceps* Gray, 1866, of Ecuador, or should be aligned with *geoffroyi*, or should be regarded as a distinct species. Having decided that the pelage of the type of *A. rufiventris* "merely represents a pattern variant certainly within the spectrum of variation implied by the USNM [US National Museum] series of *A. f. robustus*" (p. 98), Heltne and Kunkel (1975) pointed out that none of the USNM specimens they examined, and only one reported by Kellogg and Goldman (1944), showed the slightly brownish tinge on the forehead—the character (along with some cranial details) that Kellogg and Goldman (1944) used to align it with *fusciceps*. Kellogg and Goldman (1944, pp. 3–4) indicated that "perhaps the most clearly defined line of demarcation between the species, as we understand them, is in eastern Panama, where the range of the deep reddish *panamensis*, a member of the *geoffroyi* group, meets or closely approaches the range of the nearly all black *robustus* [*rufiventris*]". Color it would seem is the basis for them separating *fusciceps* from *geoffroyi*, but Kellogg and Goldman (1944) commented later (p. 30) that "Despite the marked contrast in color between this black form [*robustus*, here a synonym of *rufiventris*] and the red monkey of eastern Panama [*panamensis*], the agreement in nearly all cranial details suggests close relationship". Hernández-Camacho and Cooper (1976) recorded that the southernmost specimens in Colombia (Barabacoas, Department of Nariño) show nothing of the brownish color typical of Ecuadorian *A. f. fusciceps*. Cranial and dental morphometric analysis led Froehlich *et al.* (1991) to lump all northwestern South American spider monkeys (*fusciceps* and *hybridus*) as subspecies of *geoffroyi*. Rossan and Baerg (1977) bred a hybrid between *rufiventris* and *panamensis*, and recorded two specimens from the wild that resembled this animal, although they were careful to add that the two taxa are evidently quite homogeneous, and the (anecdotally reported) putative hybrid zone must be very narrow. Medeiros *et al.* (1997) concluded that *A. f. rufiventris* may be genetically isolated from both *hybridus* and *geoffroyi* subspecies (differs in two chromosome pairs, 5 and 6, according to Kunkel *et al.*, 1980), and argued that the mere occurrence of hybrids is inconclusive unless the degree of fertility is established. In their mtDNA analysis, Collins and Dubach (2000), like Froehlich *et al.* (1991), found that *A. f. robustus* (as they called it) formed

a clade with the subspecies of *A. geoffroyi*. As a result, they too recommended that it be regarded as another subspecies of *A. geoffroyi*. Within this clade, however, all the “*robustus*” specimens (from three different localities) formed one subclade, and all *A. geoffroyi* subspecies formed another; so the two taxa are consistently different in this character. Collins and Dubach (2000) were unable to sample *A. f. fusciceps*, so we do not know whether “*robustus*” (i.e., *rufiventris*) is distinct from this taxon or not.

Ateles f. rufiventris ranges from the western cordillera of the Andes from southwestern Colombia, northward on the west side of the Río Cauca to eastern Panama (Cerro Pirre and the basin of the Río Bayano of the Pacific coast). The Cerro Pirre or the Río Tucutí mark the border with *A. g. griseescens*. In Colombia, *A. f. rufiventris* occurs throughout the Pacific lowlands except for Juradó, northwestern part of the Department of Chocó, supposedly the domain of *A. g. griseescens* (Hernández-Camacho and Cooper, 1976; Defler, 2003). It occurs in the Urabá region in northwestern Antioquia, Córdoba, Sucre, and northern Bolívar east to the lower Río Cauca along the western bank to south-central Antioquia. The most southerly record in Colombia is Barabacoas, Department of Nariño, and the most northerly is southern bank of the Canal del Dique, Cartagena. Hernández-Camacho and Cooper (1976) believed that it formerly occurred as far north as Pendales.

SUMMARY

In this chapter, we review the taxonomy and distributions of the 21 primate taxa occurring in Central America and southern Mexico, from about 24°N in Tamaulipas, Mexico, extending south along the coast of the Gulf of Mexico, through Central America to the border of Colombia and Panama. In our appraisal, we follow the PSC, as outlined by Groves (2001). Panama (with eight species) has the richest primate community; Costa Rica has four species (five if night monkeys, *Aotus* are included). Capuchin monkeys, *C. capucinus*, extend north as far as Nicaragua and Honduras, and only spider monkeys (*A. geoffroyi*) and howling monkeys (*A. palliata* and *A. pigra*) occur in Belize, Guatemala, and Mexico. Only spider monkeys have been recorded from El Salvador.

Geoffroy’s tamarin, *S. geoffroyi*, and the night monkey, *Aotus*, both regionally restricted to Panama, are considered distinct and monotypic. There are two broadly accepted subspecies of squirrel monkey, *S. oerstedii*, occurring in a small area of the Pacific lowlands of Panama and Costa Rica. The white-throated capuchin, *C. capucinus*, extending from Panama to northern Honduras, may

comprise three subspecies, although their validity is doubtful. There are two distinct howling monkey species, the mantled howler (*A. palliata*) and the black howler (*A. pigra*). The howling monkeys of Coiba Island and the Azuero Peninsula have some distinct morphological features that argue for their classification as a third species, *A. coibensis*, but a recent molecular genetics' study failed to distinguish them from *A. palliata*. We list three subspecies of *A. palliata* but they are of doubtful validity. The spider monkeys, *A. geoffroyi*, are highly variable. Seven subspecies are listed, and there is the possibility of an eighth undescribed subspecies in northern Honduras. The variability is still poorly understood, however, and the possibility remains that a number of taxa are not valid. The Colombian black spider monkey, *A. fusciceps rufiventris*, extends a short way into Panama.

A notable finding while researching this review was the lack of modern published revisions of the taxonomy and distributions of the region's primates; the major references are still those of Kellogg and Goldman (1944), Hershkovitz (1949), and Hall (1981, based on Hall and Kelson, 1959). The spider monkeys, howler monkeys, and capuchin monkeys are in urgent need of major taxonomic revision, while it is probable that the establishment of the precise historic distributions of all of the Mesoamerican primates is now an impossible task due to introductions, hunting, and forest loss and fragmentation. The widespread loss of population diversity makes taxonomic and biogeographic research on the Mesoamerican primates an increasingly difficult task. All are now restricted to few, diminishing, and isolated forest fragments, and there is an urgent need for regionwide and detailed surveys to identify and map them, to determine the status of the populations remaining.

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(Eds.)

2006, XVI, 600 p., Hardcover

ISBN: 978-0-387-25854-6