Chapter 3
The Taxonomy of Howler Monkeys: Integrating Old and New Knowledge from Morphological and Genetic Studies

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Abstract The taxonomic history of the howler monkeys, genus *Alouatta*, has been long, complex, and filled with omissions and mistakes. This has created confusion over the validity of different taxa. Here we review the taxonomic history of the genus and evaluate the validity of the different taxa based on current knowledge generated through morphological and genetic studies. We recognize nine species of howlers (*A. palliata*, *A. pigra*, *A. seniculus*, *A. arctoidea*, *A. sara*, *A. macconnelli*, *A. guariba*, *A. belzebul*, *A. caraya*) and three more taxa that we tentatively consider full species (*A. nigerrima*, *A. ululata*, *A. discolor*), but for which genetic and/or morphological studies are required to confirm this status. We recognize five subspecies in *A. palliata* (*A. p. mexicana*, *A. p. palliata*, *A. p. coibensis*, *A. p. trabeata*, and *A. p. aequatorialis*), three in *A. seniculus*, (*A. s. seniculus*, *A. s. juara*, and *A. s. puruensis*), two in *A. guariba* (*A. g. guariba* and *A. g. clamitans*), and acknowledge the possibility that *A. pigra* may have two subspecies (*A. p. pigra* and *A. p. luctuosa*). Most species and subspecies require field studies to determine their actual distribution ranges. Furthermore, a combination of morphological and genetic analyses is needed to confirm the validity of several taxa. Given the broad presence of howler monkeys in the Neotropics, these studies would require the collaboration of a multidisciplinary network of researchers across the range of distribution of the genus.

Resumen La historia taxonómica de los monos aulladores, género *Alouatta*, ha sido larga, compleja y llena de omisiones y errores. Esto ha creado confusión respecto la validez de los distintos taxa. En este capítulo revisamos la historia taxonómica del género y evaluamos la validez de los distintos taxa con base en el conocimiento actual generado a través de estudios morfológicos y genéticos.

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Reconocemos nueve especies de monos aulladores (*A. palliata*, *A. pigra*, *A. seniculus*, *A. arctoidea*, *A. sara*, *A. macconnelli*, *A. guariba*, *A. belzebul*, *A. caraya*) y tres taxa que tentativamente consideramos como especies verdaderas (*A. nigerrima*, *A. ululata*, *A. discolor*), pero que requieren de estudios morfológicos y/o genéticos para confirmar su estatus específico. Reconocemos cinco subespecies en *A. palliata* (*A. p. mexicana*, *A. p. palliata*, *A. p. coibensis*, *A. p. trabeata* y *A. p. aequatorialis*), tres en *A. seniculus*, (*A. s. seniculus*, *A. s. juara* y *A. s. puruensis*), dos en *A. guariba* (*A. g. guariba* y *A. g. clamitans*) y consideramos la posibilidad de que *A. pigra* pueda tener dos subspecies (*A. p. pigra* y *A. p. luctuosa*). La mayoría de las especies y subespecies requieren de trabajos de campo que permitan delimitar sus rangos de distribución. Además, se precisa de análisis de datos genéticos y morfológicos para confirmar la validez de varios de estos taxa. Dada la amplia presencia de los monos aulladores en el Neotrópico, estos estudios requerirán de la colaboración de una red multidisciplinaria de científicos a través del rango de distribución del género.

Keywords *Alouatta* • Morphology • Genetics • Systematics

3.1 Introduction

Howler monkeys (*Alouatta* Lacépède, 1799) are the most widespread primate genus in the Neotropics. They range from southern Veracruz State in Mexico to northern Argentina (Fig. 3.1), and can be found in numerous forest types across the region (Neville et al. 1988; Glander and Pinto 2013). They are among the largest of the platyrrhines (Hill 1962; Peres 1994) along with the muriquis (*Brachyteles*), the spider monkeys (*Ateles*), and woolly monkeys (*Lagothrix*).

Until the 1980s, *Alouatta* was classified in the Cebidae (with all of the non-clawed platyrrhines) in the subfamily Alouattinae Elliot, 1904 (Hill 1962; Napier and Napier 1967; Napier 1976; Hershkovitz 1977). The revision of Rosenberger (1980, 1981, 2011; see also Schneider and Rosenberger 1996) placed *Alouatta* in the family Atelidae—the large, prehensile-tailed platyrrhines that also include *Ateles*, *Lagothrix*, and *Brachyteles*. Initially (1981), Rosenberger's revolutionary rearrangement had what he termed the "large suspensory frugivore-folivores" in a subfamily, Atelinae, as part of the family Pitheciidae, and, as a consequence, moved the howlers one step down to a tribe, Alouattini in the Atelinae; the spider monkeys, woolly monkeys, and muriquis being placed in the tribe Atelini. Subsequent compelling molecular phylogenetic evidence has placed the large prehensile-tailed frugivore-folivores as a distinct family, the Atelidae, with two subfamilies Alouattinae and Atelinae (for a review, see Schneider and Sampaio 2013), an arrangement accepted by Rosenberger (2011; see also Perelman et al. 2011; Halenar and Rosenberger 2013). The tribe Alouattini is composed of *Alouatta* and four extinct fossil genera *Stirtonia*, *Paralouatta*, *Solimoea*, and *Cartelles* Halenar and Rosenberger, 2013 (Rosenberger et al. 2015). The Atelini contains *Ateles*, *Brachyteles*, and *Lagothrix*, and two extinct forms, *Caipora* and *Protopithecus*.

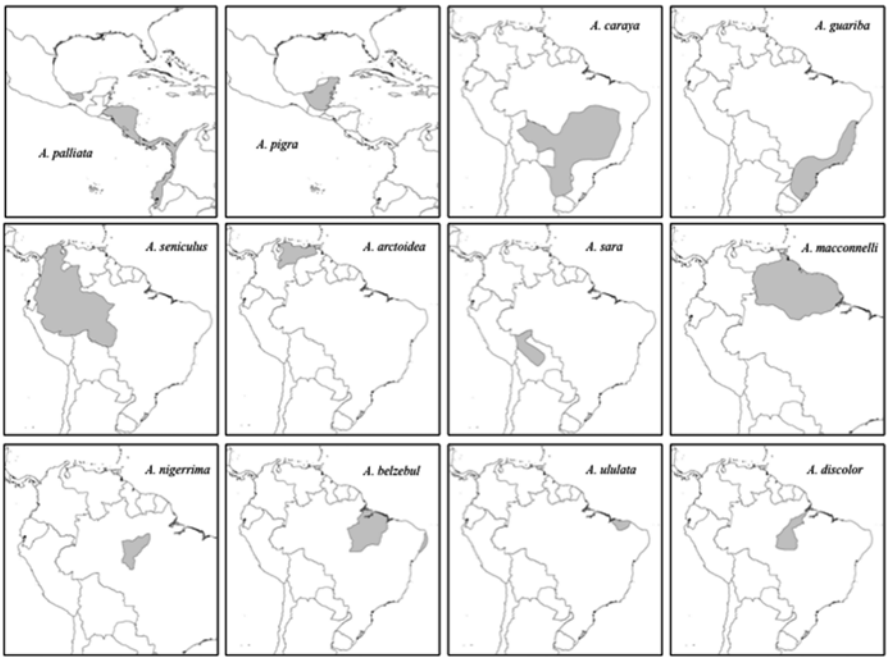

Fig. 3.1 Geographic distribution of currently recognized species of howler monkeys, genus *Alouatta* (distributions modified from IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. http://www.iucnredlist.org. Downloaded on September 24th, 2013)

Elliot (1913) provided the first comprehensive twentieth-century review of the howler monkey species. He listed twelve, *A. beelzebul* [sic] (Linnaeus, 1766), *A. seniculus* (Linnaeus, 1766), *A. caraya* (Humboldt, 1812), *A. ursina* (Humboldt, 1805), *A. villosus* (Gray, 1845), *A. palliata* (Gray, 1849) (with subspecies *mexicana* Merriam 1902, and *coibensis* Thomas 1902), and *A. aequatorialis* Festa, 1903, and five that he himself had described and named, *A. macconnelli* Elliot, 1910, *A. insulanus* Elliot, 1910, *A. juara* Elliot, 1910, *A. sara* Elliot, 1910, and *A. ululata* Elliot, 1912 (see Tables 3.1 and 3.2).

Ihering (1914) reviewed the Brazilian species of howlers and clarified the confusion created by Humboldt (1805) when he described the Venezuelan howler (*A. ursina*) but provided an illustration of the brown howler of the Brazilian Atlantic forest. Elliot (1913) did not catch this mistake, and Ihering (1914) named the brown howler *A. fusca* (Geoffroy Saint-Hilaire, 1812). Despite Humboldt's confusion, Cabrera (1957), Hill (1962), and Groves (2001, 2005) attributed the name *guariba* Humboldt, 1812 to the brown howler (see Rylands and Brandon-Jones 1998), although Gregorin (2006) affirmed that *A. fusca* is the correct name, as was also argued by Hershkovitz (1963).

Table 3.1 Names given to different forms of howler monkeys over time and the correspondence to the taxa recognized in this publication (derived or misspelled names are not included)

Name	Publication	Taxon as considered in this publication	Reference	Type locality
seniculus	Linnaeus (1766)	*A. seniculus*	*Syst. Nat.*, 12th Ed. I:37	Cartagena, Colombia
belzebul	Linnaeus (1766)	*A. belzebul*	*Syst. Nat.*, 12th Ed. I:37	Brazil, Pará, Rio Capim
ursina	Humboldt and Bonpland (1805)	*A. arctoidea*	*Rec. Obs. Zool. Anat. Comp.* 1:8	Caracas, Venezuela
caraya	Humboldt (1812)	*A. caraya*	In: Humboldt & Bonpland 1811 (1812). *Rec. Obs. Zool. Anat. Comp.* 1:355	Paraguay
guariba	Humboldt (1812)	*A. guariba*	In: Humboldt & Bonpland 1811 (1812). *Rec. Obs. Zool. Anat. Comp.* 1: pl. 30	Brazil, restricted by Cabrera (1957) to the Rio Paraguassú, Bahia
niger	Geoffroy Saint-Hilaire (1812)	*A. caraya*	*Ann. Mus. d'Hist. Nat. Paris* 19:108	"Bresil"
stramineus	Geoffroy Saint-Hilaire (1812)	*A. caraya*	*Ann. Mus. d'Hist. Nat., Paris* 19:108	"Gran Pará"
fusca	Geoffroy Saint-Hilaire (1812)	*A. guariba*	*Ann. Mus. d'Hist. Nat. Paris* 19:108	Brazil, restricted by Cabrera (1957) to the Rio Paraguassú, Bahia
rufimanus	Kühl (1820)	*A. belzebul*	*Beitr. Zool. Vergl. Anat.* 1:31	Unknown
barbatus	von Spix (1823)	*A. caraya*	*Sim. Vespert. Brasil.* p.48, pl. XXXII and XXXIII	Between the rios Negro and Solimões
discolor	von Spix (1823)	*A. discolor*	*Sim. Vespert. Brasil.* p.48, pl. XXXIV	Forte Gurupá, state of Pará
chrysurus	I. Geoffroy Saint-Hilaire (1829)	*A. macconnelli or A. seniculus*?	1828 (1829). *Mem. Mus. d'Hist. Nat. Paris*, 17:166, 171	Spanish Guiana (Venezuela) or Colombia

laniger	Gray (1845)	*A. seniculus*	*Ann. Mag. Nat. Hist.* 16:219	Colombia
bicolor	Gray (1845)	*A. guariba*	*Ann. Mag. Nat. Hist.* 16:219.	Brazils
villosus	Gray (1845)	*A. pigra*	*Ann. Mag. Nat. Hist.* 16:220	Vera Paz, Guatemala
auratus	Gray (1845)	*A. macconnelli*	*Ann. Mag. Nat. Hist.*, 16:220	Brazils (Orinoco on label)
palliata	Gray (1849)	*A. palliata*	*Proc. Zool. Soc. Lond.*, 1849:138, pl. VI	Shores of Lake Nicaragua
nigra	Slack (1863)	*A. caraya*	*Proc. Acad. Nat. Sci. Philadelphia* 1863 (1862):518	Brazil, Paraguay and Bolivia
mexicana	Merriam (1902)	*A. palliata mexicana*	*Proc. Biol. Soc. Washington* 15:67	Minatitlan, state of Veracruz, Mexico
coibensis	Thomas (1902)	*A. palliata coibensis*	*Novit. Zool.* 9:135	Coiba Island, off the Pacific coast of Panama
aequatorialis	Festa (1903)	*A. palliata aequatorialis*	*Boll. Mus. Zool. ed Anat. Comp. Univ. Torino* 18:3	Vinces, Guayas Province, Ecuador
caucensis	J. A. Allen (1904)	*A. seniculus*	*Bull. Am. Mus. Nat. Hist.* 20:462, figs. 2, 4, Nov. 28, 1904	Charingo, upper Río Cauca, Colombia
rubicunda	J. A. Allen (1904)	*A. seniculus*	*Bull. Am. Mus. Nat. Hist.* 20:458, figs. 1, 3	Bonda, Santa Marta, Colombia
metagalpa	J. A. Allen (1908)	*A. palliata palliata*	*Bull. Am. Mus. Nat. Hist.* 24:670	Lavala, Nicaragua
mexianae	Hagmann (1908)	*A. belzebul*	*Arch. Rass. Ges. Biol.* p.6	Isle of Mexiana, Amazon Delta
insulanus	Elliot (1910)		*Ann. Mag. Nat. Hist.* 8th Series, 5:79	Island of Trinidad
macconnelli	Elliot (1910)	*A. macconnelli*	*Ann. Mag. Nat. Hist.* 8th Series, 5:80	Coast of Demerara

(continued)

Table 3.1 (continued)

Name	Publication	Taxon as considered in this publication	Reference	Type locality
juara	Elliot (1910)	*A. juara*	*Ann. Mag. Nat. Hist.* 8th Series, 5:80	Río Juara, Peruvian Amazon
sara	Elliot (1910)	*A. sara*	*Ann. Mag. Nat. Hist.* 8th Series, 5:81	Province of Sara, Bolivia
ululata	Elliot (1912)	*A. ululata*	*Bull. Am. Mus. Nat. Hist.* 31:32	Miritiba, Maranhão, northeastern Brazil
inclamax	Thomas (1913)	*A. palliata aequatorialis*	*Ann. Mag. Nat. Hist.*, 8th Series. 12:567	Intac, about 50 miles north of Quito, Ecuador
quichua	Thomas (1913)	*A. palliata aequatorialis*	*Ann. Mag. Nat. Hist.*, 8th Series, 12:567	Río Blanco 20 miles west of Mindo, about 75°10′W on Equator, Alt. 2500 ft., northwest Ecuador
inconsonans	Goldman (1913)	*A. palliata aequatorialis*	*Smithson. Misc. Coll.*, 60 (22):17	Cerro Azul, Panama
bogotensis	J. A. Allen (1914)	*A. seniculus*	*Bull. Am. Mus. Nat. Hist.* 33:648	Subia, Cundinamarca near Bogotá, Colombia
caquetensis	J. A. Allen (1914)	*A. seniculus*	*Bull. Am. Mus. Nat. Hist.* 33:650	La Murelia = Muralla, Caquetá, Colombia
trabeata	Lawrence (1933)	*A. palliata trabeata*	*Bull. Mus. Comp. Zool.* 75:328	Capina, Herrera Province, Panama
pigra	Lawrence (1933)	*A. pigra*	*Bull. Mus. Comp. Zool.* 75:333	Uaxactun, Petén, Guatemala
luctuosa	Lawrence (1933)	*A. pigra*	*Bull. Mus. Comp. Zool.* 75:337	Mountain Cow, Cayo District, British Honduras (Belize)

arctoidea	Cabrera (1940)	*A. arctoidea*	*Ciencia*, *Méx.* 1:404	Caracas, Venezuela (same as that of *ursina* Humboldt 1812)
clamitans	Cabrera (1940)	*A. guariba clamitans*	*Ciencia Méx.* 1:404	State of São Paulo
amazonica	Lönnberg (1941)	*A. seniculus*	*Ark. Zool.* 33A (10):16	Codajáz, north of Rio Solimões, Amazonas, Brazil
puruensis	Lönnberg (1941)	*A. puruensis*	*Ark. Zool.* 33A (10):16	Rio Purus, Amazonas, Brazil
juruana	Lönnberg (1941)	*A. juara*	*Ark. Zool.* 33A (10):18	Upper Rio Juruá
iheringi	Lönnberg (1941)	*A. guariba clamitans*	*Ark. Zool.*, 33A (10):23	Serra de Cantareira, São Paulo, Brazil
beniensis	Lönnberg (1941)	*A. sara*?	*Ark. Zool.* 33A (10):24	Puerto Salinas, Río Beni, Bolivia
tapajozensis	Lönnberg (1941)	*A. discolor*	*Ark. Zool.* 33A (10):27	Brazil, restricted by Bonvicino et al. (1989) to Aveiros, Amazonas
nigerrima	Lönnberg (1941)	*A. nigerrima*	*Ark. Zool.* 33A (10):33	West of Rio Tapajóz and south of the Amazon, Brazil (Patinga, Amazonas, Brazil)

Table 3.2 The taxonomy of the howlers (*Alouatta*) according to Elliot (1911), Cruz Lima (1945), Cabrera (1957), Hill (1962), Rylands et al. (2000), Groves (2001), Gregorin (2006), and Glander and Pinto (2013)

Elliot (1912)	Cruz Lima (1945) Brazilian Amazonian species	Cabrera (1957) South American species	Hill (1962)
A. belzebul [sic] (Linnaeus, 1766)	*A. b. belzebul*	*A. b. belzebul*	*A. b. belzebul*
A. ululata Elliot, 1912	*A. b. ululata*	*A. b. ululata*	*A. b. ululata*
discolor (von Spix, 1823) is a synonym of *A. belzebul*	*A. b. discolor* (Spix, 1823)	*A. b. discolor*	*A. b. discolor*
A. b. mexianae (Hagmann, 1908) was not considered	Not considered	*A. b. mexianae*	*A. b. mexianae*
–	*A. nigerrima* Lönnberg, 1941	*A. b. nigerrima*	*A. b. nigerrima*
A. seniculus (Linnaeus, 1766)	*A. s. seniculus*	*A. s. seniculus*	*A. s. seniculus*
A. s. stramineus[a] is a synonym of *A. seniculus*	*A. s. straminea*[a]	*A. s. straminea*[a]	*A. s. stramineus*
A. macconnelli Elliot, 1910	Synonym of *A. s. straminea*	Synonym of *A. s. straminea*	*A. s. macconnelli*
A. insulanus Elliot, 1910	–	Not considered	*A. s. insulanus*
A. juara Elliot, 1910	*A. s. juara*	Synonym of *A. s. seniculus*	*A. s. juara*
–	*A. s. puruensis* Lönnberg, 1941	Synonym of *A. s. seniculus*	*A. s. puruensis* Lönnberg, 1941
–	*A. s. amazonica* Lönnberg, 1941 is a synonym of *A. s. straminea*	Synonym of *A. s. straminea*	*A. s. amazonica*

–	–	*A. s. arctoidea* Cabrera, 1940	*A. s. arctoidea*
A. sara Elliot, 1910	–	*A. s. sara*	*A. s. sara*
A. caraya (Humboldt, 1812)	–	*A. caraya*	*A. caraya*
A. ursina (Humboldt, 1812)	Synonym of *A. s. seniculus*	Synonym of *A. s. arctoidea*	Synonym of *A. s. arctoidea*
A. palliata palliata (Gray, 1849)	–	*A. p. palliata*	*A. p. palliata*
A. p. mexicana Merriam, 1902	–	–	*A. p. mexicana*
A. aequatorialis Festa, 1903	–	*A. p. aequatorialis*	*A. p. aequatorialis*
A. palliata coibensis Thomas, 1902	–	–	*A. p. coibensis*
–	–	–	*A. p. trabeata* Lawrence, 1933
A. villosus (Gray, 1845)	–	–	*A. villosa*
			A. p. pigra Lawrence, 1933
			A. p. luctuosa Lawrence, 1933
A. guariba considered to be a synonym of *A. ursinus*	–	*A. guariba guariba* (Humboldt, 1812)	*A. g. guariba*
–	–	*A. guariba clamitans* Cabrera, 1940	*A. g. clamitans*
–	–	*A. guariba beniensis* Lönnberg, 1941	*A. g. beniensis*

(continued)

Table 3.2 (continued)

Rylands et al. (2000)	Groves (2001, 2005)	Gregorin (2006) Brazilian species	Glander and Pinto (2013)
A. belzebul belzebul	*A. belzebul*	*A. belzebul*	*A. belzebul*
A. b. ululata	Synonym of *A. belzebul*	*A. ululata*	*A. ululata*
A. b. discolor	Synonym of *A. belzebul*	*A. discolor*	*A. discolor*
A. b. mexianae not considered	Synonym of *A. belzebul*	Synonym of *A. discolor*	Synonym of *A. discolor*
A. nigerrima	*A. nigerrima*	*A. nigerrima*	*A. nigerrima*
A. s. seniculus	*A. s. seniculus*	–	*A. s. seniculus*
Type of *A. s. straminea* is a female *A. caraya*	Type of *A. s. straminea* is a female *A. caraya*	Synonym of *A. macconnelli*	Type of *A. s. straminea* is a female *A. caraya*
A. seniculus ssp.	*A. macconnelli*	*A. macconnelli*	*A. macconnelli*
A. s. insulanus	Synonym of *A. macconnelli*	–	Synonym of *A. macconnelli*
A. s. juara	*A. s. juara*	*A. juara*	*A. s. juara*
A. s. puruensis	Synonym of *A. s. juara*	*A. puruensis*	*A. s. puruensis*
A. s. amazonica	Synonym of *A. s. juara*	Synonym of *A. s. juara*	Synonym of *A. s. juara*
A. s. arctoidea	*A. s. arctoidea*	–	*A .arctoidea*
A. sara	*A. sara*	–	*A. sara*
A. caraya	*A. caraya*	*A. caraya*	*A. caraya*
A. ursinus not considered	Synonym of *A. s. arctoidea*	–	Not considered
A. palliata palliata	*A. palliata*	–	*A. palliata palliata*
A. p. mexicana	Synonym of *A. palliata*	–	*A. p. mexicana*
A. p. aequatorialis	Synonym of *A. palliata*	–	*A. p. aequatorialis*

A. c. coibensis	*A. coibensis*	–	*A. p. coibensis*
A. c. trabeata	Synonym of *A. coibensis*	–	*A. p. trabeata*
A. pigra	*A. pigra*	–	*A. pigra*
A. villosa and *A. p. luctuosa* are synonyms of *A. pigra*[b]	*A. villosa* and *A. p. luctuosa* are synonyms of *A. pigra*		
A. g. guariba	*A. g. guariba*	*A. fusca*	*A. g. guariba*
A. g. clamitans	*A. g. clamitans*	*A. clamitans*	*A. g. clamitans*
A. g. beniensis not considered	Synonym of *A. guariba*	–	Not considered

[a]Elliot (1912), Cruz Lima (1945), Cabrera (1957) and Hill (1962) attribute authorship to Humboldt (1812), we attribute the name to É. Geoffroy Saint-Hilaire (1812) (see text)

[b]Following the revision by Smith (1970)

A number of reviews of the howler monkey taxa from particular geographic regions (e.g., Lawrence 1933; Tate 1939; da Cruz Lima 1945; Hershkovitz 1949; Cabrera 1957) continued to modify the taxonomy of the genus for the next 30 years (Table 3.2). Osman Hill published another complete review of the genus in 1962. The taxonomic arrangement that he proposed was accepted with minor modifications (e.g., Smith 1970) until the late 1980s, when cytogenetic and molecular genetic analyses began to contribute new evidence that challenged the taxonomy based primarily on morphological characters.

In this chapter, we integrate the knowledge provided by studies on morphological and genetic characters and propose a taxonomic arrangement for the genus that is congruent with both. We briefly summarize the main issues regarding the taxonomy of each recognized taxa and provide our reasoning on why they are considered in their respective taxonomic levels. We also attempt to guide the reader on the important gaps of information that permeate the taxonomy of the genus in an attempt to stimulate new integrated genetic and morphological studies, based on individuals of known geographic origin.

3.2 Mesoamerican Howler Monkeys

The current taxonomy of Mesoamerican howler monkeys is based on morphological and genetic studies (Lawrence 1933; Smith 1970; Horwich 1983; Cortés-Ortiz et al. 2003; Steinberg et al. 2008). Lawrence (1933) conducted a comprehensive study of Mesoamerican howlers, reviewing the taxonomy of all taxa described for the region through an analysis of both cranial features and pelage coloration of a large number of specimens, including type specimens. She considered all Mesoamerican howlers to be subspecies of *A. palliata*, seven in all: *A. p. mexicana*, *A. p. palliata*, *A. p. aequatorialis*, *A. p. pigra*, *A. p. luctuosa*, *A. p. coibensis*, and *A. p. trabeata. Alouatta villosa* (Gray, 1845) she argued was indeterminable given the lack of a skin of the holotype (only a damaged skull remained) and confusion regarding the actual locality of the type. She thus assigned the name *A. palliata pigra* for the Guatemalan howler and *A. p. luctuosa* (Lawrence 1933) as the form in Belize. Hall and Kelson (1959), Hill (1962) and Napier (1976) continued to use the name *A. villosa*. Brandon-Jones (2006) provided a detailed analysis of the evidence that the *A. villosa*-type specimen is recognizably distinct from *A. palliata* (and other black howlers such as *A. nigerrima* and *A. caraya*) and that the type locality was recorded as Mexico. He argued, as such, that *A. villosa* is correctly a senior synonym of *A. pigra*. However, as the type specimen is reduced to a cranium (the skin was lost, Napier 1976) and without a proper study of this specimen, we conservatively continue listing this species using the name *A. pigra*, as did Smith (1970), Hall (1981), Groves (2001), and Rylands et al. (2006).

3.2.1 Alouatta palliata *(Gray, 1849)*

Type: Syntypes, adult female, skin and skull, No. 1848.10.26.1, and adult male, skin, 1848,10.26.2, British Museum (Natural History) (Napier 1976).
Type locality: Nicaragua (shores of Lake Nicaragua).
Common name: Mantled howler.

This species ranges from southern Veracruz State in Mexico, south through Central America and the Pacific slopes of the Andes in Colombia and Ecuador reaching the Tumbes region in northern Peru (Fig. 3.1).

Only five of the seven subspecies recognized by Lawrence (1933) for *A. palliata* are currently accepted: *A. p. mexicana*, *A. p. palliata*, *A. p. aequatorialis*, *A. p. coibensis*, and *A. p. trabeata*. Lawrence (1933) commented on the difficulty in distinguishing the subspecies of *A. palliata*, with the exception of the Guatemalan (*A. p. pigra*) and the Coiba Island (*A. p. coibensis*) forms. Smith (1970), likewise, analyzed cranial and dental patterns, and pelage coloration of *A. palliata*, and concluded that the forms *palliata*, *mexicana*, *coibensis*, and *trabeata* were only weakly definable as subspecies. Froehlich and Froehlich (1986, 1987), however, analyzed patterns of dermal ridges of howler monkeys from Nicaragua, Costa Rica, and Panama, and found that individuals from Coiba Island and the Azuero Peninsula were distinct from those of Nicaragua, Costa Rica, and the rest of Panama. They considered that differences in the dermal ridge patterns of the hands and feet were congruent with genetic distances, and that the difference found between *coibensis/trabeata* and *palliata/aequatorialis* groups was comparable to that of either of them and the South American howler monkey species. They, therefore, suggested that the forms *coibensis* and *trabeata* be treated as subspecies of a distinct species, *A. coibensis*. Glander and Pinto (2013) adhered to this view, Groves (2001, 2005) considered *trabeata* to be junior synonym of *A. coibensis*, and Rylands et al. (1995, 2000) maintained them as subspecies of *A. palliata* (as per Lawrence 1933). The molecular genetic studies (mtDNA) of Cortés-Ortiz et al. (2003) produced no evidence to back this distinction. *Alouatta palliata coibensis* individuals were found to share mitochondrial haplotypes with *A. palliata* from Costa Rica and Mexico, and *A. p. trabeata* individuals shared haplotypes with *A. p. aequatorialis* from central Panama. These two clades represented northern and southern mitochondrial lineages separated around the Sona Peninsula in western Panama (Cortés-Ortiz et al. 2003). Interestingly, recent phylogeographic analyses based on nuclear markers (microsatellites) support the phylogeographic brake between *A. p. palliata* and *A. p. aequatorialis*, but show closer proximity of *A. p. coibensis* and *A. p. trabeata* to *A. p. aequatorialis* (Cortés-Ortiz et al. unpublished). This discrepancy between mitochondrial and nuclear markers in the Coiba population may be the result of a secondary intergradation between formerly distinct lineages when Coiba Island was connected to the mainland (see Ford 2006). Studies including a larger number of individuals from Coiba Island, the Azuero Peninsula, and other regions in western and central Panama are necessary to corroborate the subspecific status of *A. p. coibensis* and *A. p. trabeata*, as well as to identify the limits of the ranges of *A. p. palliata* and *A. p. aequatorialis*.

3.2.2 Alouatta pigra *Lawrence, 1933*

Type: Adult male, collected by A. Murie, 4 May 1931, Museum of Zoology, University of Michigan.
Type locality: Uaxactun, Petén, Guatemala.
Common name: Central American black howler.

Alouatta pigra is distributed across the Peninsula of Yucatán in Mexico, Belize, and north and eastern Guatemala (Fig. 3.1). Most authors followed Lawrence's taxonomic arrangement of the Mesoamerican howlers, until 1970, when James D. Smith analyzed two sympatric populations of howler monkeys from the state of Tabasco, Mexico. He examined the skulls, teeth, and/or pelage of 238 specimens from across the range of *A. palliata* (*sensu* Lawrence 1933) and maintained that the two (partially sympatric) forms from his sample constituted two well-differentiated species, *A. palliata* and *A. pigra. Alouatta palliata luctuosa* Lawrence, 1933, he considered a junior synonym of *A. pigra*, given that the only extant specimen (from Mountain Cow, Cayo District, Belize) fell within the range of variation of *A. pigra*. Horwich (1983) supported Smith's recognition of two distinct species and commented on differences in group size between *A. palliata* and *A. pigra* (the latter having consistently smaller group sizes than the former), as well as differences in male genitalia; *A. pigra* males have fully descended testes from infancy, the testes of *A. palliata* males do not descend until they are subadults. Cortés-Ortiz et al. (2003) using mitochondrial DNA sequence data corroborated that *A. palliata* and *A. pigra* fall into two reciprocally monophyletic groups that separated approximately 3 MA, supporting their status as distinct species. Steinberg et al. (2008) also supported this distinction based on chromosome number (*A. palliata* 2n = 54 and *A. pigra* 2n = 58) and on the male sex determination system (X_1X_2Y in *A. palliata* and $X_1X_2Y_1Y_2$ in *A. pigra*). All samples of *A. pigra* analyzed by Cortés-Ortiz et al. (2003) and Steinberg et al. (2008) came from Mexico, and the validity of *A. pigra luctuosa* from the Cayo District in Belize has yet to be evaluated with genetic data.

Regarding the proper name for the Central American black howler monkey, as already mentioned, Brandon-Jones (2006) provided evidence that the *A. villosa* type (skull of a young adult female in the British Museum [Natural History]) is recognizably distinct from *A. palliata* and that the type locality can be identified as "Mexico." However, further studies exploring the similarities of the *A. villosa*-type specimen to a large sample of crania from *A. pigra* from Mexico, Guatemala, and Belize, as well as the differences with other black howlers (i.e., *A. nigerrima* and *A. caraya*) of known geographical provenance would provide compelling evidence for the suggested status of *A. villosa* as senior synonym of *A. pigra*. Given the widespread use of *A. pigra* and the benefits of taxonomic stability, we continue to call this taxon *A. pigra* until further studies are completed.

3.3 South American Howler Monkeys

The taxonomy of South American howler monkeys has been subject to multiple revisions. Linnaeus (1766) was the first to describe species of South American howler monkeys under his genus *Simia*. He recognized two: *S. belzebul* and *S. seniculus*. To date there have been over 48 names used to refer to the different forms of South American howlers (Table 3.1), which has caused considerable confusion in the taxonomy of the genus. Many of these names have become synonyms, and some forms are still recognized as distinct despite the need for taxonomic revision. Below we summarize the currently recognized species and subspecies following Groves (2001), Gregorin (2006), Rylands et al. (2000, 2012), Rylands and Mittermeier (2009), and Glander and Pinto (2013). It is reasonable to assume, however, that some of these species still require specific studies to determine their validity, and so this taxonomic arrangement should be considered a working hypothesis.

3.3.1 Alouatta caraya *(Humboldt, 1812)*

Type: No type preserved.
Type locality: Paraguay.
Common name: Black and gold howler, Paraguayan howler.

This species has a broad distribution including Brazil (Pantanal, and parts of the Cerrado and Caatinga), northern Argentina, Paraguay, and Bolivia (Fig. 3.1). Most authors have recognized this taxon as a full species given the presence of a distinct sexual dichromatism: males are mostly black and females have a yellowish or brindled tawny color (Groves 2001). Morphological analyses of the hyoid bone in males distinguish this species from other howlers, particularly by the lack of a tentorium (see Hershkovitz 1949; Gregorin 2006). *Alouatta caraya* has a diploid number of 2n = 52, which does not vary in specimens from distinct localities (de Oliveira et al. 2002). This species presents a sex chromosome system of $X_1X_1X_2X_2/X_1X_2Y_1Y_2$ (Mudry et al. 2001; de Oliveira et al. 2002), also observed in taxa of the *A. seniculus* group (*A. macconnelli*, *A. sara*, *A. arctoidea*) (Seuánez et al. 2005) and in *A. pigra* (Steinberg et al. 2008). This quadrivalent sex chromosome system differs from those of *A. guariba*, *A. belzebul*, and *A. palliata* (see chapter by Mudry et al. 2015). Chromosome painting with human chromosome probes suggests that the rearrangements that gave rise to this system in *A. caraya* and the *A. seniculus* group may have a single origin (Mudry et al. 2001), whereas the origin of the *A. pigra* quadrivalent sex chromosome system seems to be separate (see chapter by Mudry et al. 2015). The possible single origin of the sex chromosome system between *A. caraya* and the *A. seniculus* group suggests that *A. caraya* may have a close phylogenetic affinity

with the Amazonian red howler taxa. Indeed, *A. caraya* shares one chromosome painting association pattern with the red howlers (*A. seniculus*, *A. sara*, *A. macconnelli*) and *A. guariba*, but not with *A. belzebul* (see Stanyon et al. 2011). A phylogenetic reconstruction by de Oliveira et al. (2002) based on parsimony analysis of chromosomal changes in different species of *Alouatta* places *A. caraya* as a sister group of *A. belzebul*, but phylogenetic studies based on mitochondrial and/or nuclear sequence data include *A. caraya* in a clade with species from the *A. seniculus* group (Cortés-Ortiz et al. 2003; Nascimento et al. 2005; Perelman et al. 2011), or show this species as basal to all howlers (e.g., Bonvicino et al. 2001). The actual phylogenetic position of *A. caraya* in the genus may require additional multilocus analyses that contain representatives of all the main lineages of howler monkeys, and include multiple samples from distinct geographic localities for each taxon.

Nascimento et al. (2005, 2007) and Ascunce et al. (2007) analyzed interspecific variation in *A. caraya* using mitochondrial DNA markers (the control region and the cytochrome *b* gene). In both cases they found evidence of divergent mitochondrial haplotypes consistent with individuals from different geographical regions (Mato Grosso, Brazil vs. Santa Cruz, Bolivia vs. Goiás, Brazil in Nascimento et al. 2005, and Mato Grosso, Brazil vs. northern Argentina/Paraguay vs. Goiás, Brazil in Ascunce et al. 2007). However, some of these divergent haplotypes can be found in both Argentina and Brazil and therefore they may be the result of ancestral polymorphism or the expansion and secondary contact of formerly allopatric populations (Ascunce et al. 2007). The structuring of mitochondrial haplotypes in these localities suggests that these populations could represent different subspecies. Whether these populations constitute different taxa, however, remains to be explored with further studies that include samples of individuals from a wider range of locations.

3.3.2 Alouatta guariba *(Humboldt, 1812)*

Type: No original type available. Hill (1962) notes for *Mycetes bicolor* (Gray, 1845) (in the British Museum, adult male, skin and skull, 1844. 5.14.16) that the label indicates it was collected by Parzudaki on the Orinoco. Napier (1976, p. 76) noted that "it appears to be more closely related to *A. belzebul*," and she catalogued it under *Alouatta* sp. (p. 88).
Type locality: Brazil. Restricted by Cabrera (1957) to Rio Paraguassú, Bahia (Hill 1962; Napier 1976).
Common name: Brown howler.

This species inhabits the Atlantic Forest of Brazil, south of the Rio São Francisco (Rylands et al. 1996) (Fig. 3.1). The taxonomy of this taxon is quite complex and there is some confusion about its correct name. Rylands and Brandon-Jones (1998) argued that É. Geoffroy Saint-Hilaire (1806) mentioned the name "guariba" in reference to *A. belzebul* not as a binomial but as a common name. "Guariba" is the name for howlers in the Brazilian Amazon and É. Geoffroy Saint-Hilaire used it to distinguish *A. belzebul* from the spider monkey *Ateles belzebuth*. The name *guariba*, used for the brown howler by Humboldt (1812), is not as such a junior homonym as

argued by Hershkovitz (1963) and is available for this taxon. (Humboldt [1812] predated the *Stentor fuscus* of É. Geoffroy Saint-Hilaire [1812] by 2 months [Thomas 1913]). Gregorin (2006) disagrees with this, however, and supports the view of Hershkovitz (1963) that *guariba* is an objective junior homonym and that the correct name to use for this taxon is *A. fusca* (Geoffroy Saint-Hilaire, 1812). Here we follow the interpretation of Rylands and Brandon-Jones (1998) in using the name *A. guariba* for this species.

Two different forms have been identified based on pelage coloration: a northern brown howler *A. g. guariba* and a southern form in which males are darker than females, the southern brown howler *A. g. clamitans* Cabrera, 1940. This distinction is supported by cytogenetic (de Oliveira 1995; 1996; de Oliveira et al. 2002) and molecular (Harris et al. 2005; de Mello Martins et al. 2011) data. Based on morphological analyses of cranial and hyoid bone features, Gregorin (2006) considers that these two forms should be considered full species. Analyses of mitochondrial DNA variation among the populations of *A. guariba* in three localities (in the states of Rio de Janeiro, São Paulo, and Santa Catarina) show the existence of two mitochondrial lineages (de Mello Martins et al. 2011). These monophyletic lineages are apparently consistent with the northern and southern forms, which are in contact in the state of São Paulo. Unfortunately, de Mello Martins et al. (2011) do not provide information on the genetic distance between these lineages, but according to their Fig. 2, it is similar to that observed among different haplotypes of *A. belzebul*. Although this study supports some distinction between *A. g. guariba* and *A. g. clamitans*, the taxonomic recognition as full species will require further genetic analyses that include a larger number of samples across the range of this species, representatives of other recognized howler species, as well as the use of multiple loci.

3.3.3 Alouatta belzebul *Group*

3.3.3.1 *Alouatta belzebul* (Linnaeus, 1766)

Type: Inexistent or unknown.
Type locality: Brazil. Thomas (1911) restricted the type locality to the state of Pernambuco, based on the materials collected by Marcgrave (1648), on which Linnaeus based his description (Gregorin 2006).
Common name: Red-and-black howler, red-handed howler.

Alouatta belzebul has been recognized as a full species ever since Linnaeus (1766) first described it in his genus *Simia*. Hill (1962) recognized five subspecies: *A. b. belzebul*, *A. b. discolor*, *A. b. mexianae*, *A. b. ululata*, and *A. b. nigerrima*. Morphological, cytogenetic, and molecular studies have provided evidence that *A. nigerrima* is more closely related to *A. seniculus* than to *A. belzebul*, and here we consider it tentatively as a full species (see below). Groves (2001, 2005) considered *mexianae*, *discolor*, and *ululata* as synonyms of *A. belzebul*; however, here we cautiously follow Gregorin (2006) who placed *mexianae* as a junior synonym of *A. discolor* and recognized *belzebul*, *discolor*, and *ululata* as full species based on

morphological analyses of the cranium and hyoid apparatus, and pelage color pattern. Below we comment on the need to validate some of these species with genetic data.

Alouatta belzebul has a disjunct distribution with populations in the lower Amazon region in Brazil, to the south of the Rio Amazonas, as well as in isolated populations in the coastal forests of northeastern Brazil (Langguth et al. 1987; Coimbra-Filho et al. 1995) (Fig. 3.1). Genetic analyses have shown little divergence in haplotypes of populations of *A. belzebul* in north-east Brazil and the Amazon basin (Bonvicino et al. 2001; Cortés-Ortiz et al. 2003), and a phylogeographic study based on the mitochondrial cytochrome *b* gene fails to distinguish populations from Paraíba from those of the left margin of the Rio Tocantins in the state of Pará (Nascimento et al. 2008).

3.3.3.2 *Alouatta discolor* (von Spix, 1823)

Type: Juvenile male, Munich Museum.
Type locality: Forte Curupá (=Gurupá), south margin of Rio Amazonas, between Rio Tapajós and Rio Xingu, state of Pará, Brazil. [Not the Island of Gurupá].
Common name: Spix's red-handed howler monkey.

This species is distributed from the right bank of the rios Tapajós and Juruena to the rios Xingú and Irirí (Gregorin 2006; Glander and Pinto 2013) (Fig. 3.1). Elliot (1913) regarded this taxon as a synonym of *A. belzebul* given that he considered that the type (a juvenile with a darker pelage) presented pelage coloration within the range of this species. Lönnberg (1941) described a new subspecies of *A. belzebul* to the east of the Rio Tapajós, naming it *A. b. tapajozensis*, but Cruz Lima (1945) argued that Lönnberg's *tapajozensis* was a synonym of Spix's *discolor*. He included this form as a subspecies of *A. belzebul* (*A. b. discolor*). Later authors (e.g., Cabrera 1957; Hill 1962) followed Cruz Lima in recognizing the form *discolor* as a subspecies of *A. belzebul*. Groves (2001, 2005) considered *discolor* as a synonym of a monotypic *A. belzebul*, but Gregorin (2006), after a detailed analysis of morphometric data and pelage coloration patterns of over 70 individuals from Pará, concluded that the diagnostic characters of the hyoid bone and pelage coloration clearly distinguish *A. discolor* from the other two phylogenetically close taxa (*A. belzebul* and *A. ululata*) and are sufficiently trustworthy to validate its specific status. To date, there are no genetic data from individuals of this region, so we only tentatively consider *A. discolor* as a full species following Gregorin (2006).

3.3.3.3 *Alouatta ululata* Elliot, 1912

Type: Adult male, skin and skull, No. 1911.10.16.10, British Museum (Natural History) (Napier 1976).
Type locality: Miritiba, northern Maranhão State, Brazil.
Common name: Maranhão red-and-black howler.

Alouatta ululata is distributed in the north-east of Brazil, in the north of the states of Maranhão, Piauí, and Ceará (Gregorin 2006) (Fig. 3.1). The typical pelage coloration pattern of this form was first described by Dollman (1910) from individuals

collected in Miritiba (Maranhão), but he believed that the specimens that he was analyzing belonged to *A. discolor*, given that their pelage coloration pattern was similar to the description given by Spix (1823). Later, Elliot (1912) recognized the specimens as part of a distinct species, given that he considered that the type specimen and figure from Spix (1823) portrayed a young *A. belzebul* individual with the typical darker coloration, and did not accurately match Spix's description of *discolor*. Furthermore, Elliot considered that Spix's description could not be applied to any species of howler known at that time (Elliot 1913). However, Elliot found consistent differences between the specimens from Miritiba and the specimens from the west of Pará, which he considered to be *A. belzebul* (here *A. discolor*) and he therefore described it as a distinct species, *A. ululata*. Ihering (1914), in his review of the genus *Alouatta*, analyzed a number of specimens of howler monkeys from Brazil and Venezuela with the aim of resolving the problematic positioning of the forms *discolor*, *ululata*, and *belzebul*. Based on his analyses of cranial measurements and pelage coloration, he concluded that the three forms belonged to a single species, *A. belzebul*. Since then, most authors either considered *ululata* as a synonym (e.g., Lönnberg 1941; Groves 2001) or as subspecies of *A. belzebul* (e.g., da Cruz Lima 1945; Hill 1962). Gregorin (2006) considered that the specimens he analyzed from Ceará and Maranhão presented a conspicuous coloration (sexually dichromatic) not described for any individual of *A. belzebul* or *A. discolor*, and therefore agreed with the recognition of *A. ululata* as a distinct species. As mentioned earlier, there are no genetic studies that include specimens of this taxon, and therefore the question of their genetic distinctiveness from *A. belzebul* and *A. discolor* remains an open question.

3.3.4 Alouatta seniculus *Group*

3.3.4.1 *Alouatta seniculus* (Linnaeus, 1766)

Type: Inexistent or unknown.
Type locality: Cartagena, department of Bolivar, Colombia.
Common name: Colombian red howler.

This is one of the two species of howler monkeys originally described by Linnaeus (1766) in his genus *Simia*. It was originally believed that it was broadly distributed in South America to the north of the Rio Amazonas, but morphological and genetic analyses have yielded enough evidence to conclude that the howlers in this area belong to a species complex (see below) rather than to a single species. Hill (1962) recognized nine subspecies of *Alouatta seniculus* (*seniculus*, *arctoidea*, *stramineus*, *insulanus*, *amazonica*, *macconnelli*, *juara*, *puruensis*, and *sara*), most of which are considered valid taxa today; a couple are considered synonyms, and others have even been reclassified as full species (see below). The only taxon not recognized as valid is *stramineus*, the holotype of which is a female *A. caraya* (see Rylands and Brandon-Jones 1998). Here we recognize three possible subspecies of *A. seniculus*: *A. s. seniculus*, *A. s. juara*, and *A. s. puruensis*. Three more taxa

formerly included as part of the *seniculus* group (*A. arctoidea*, *A. macconnelli*, and *A. sara*) are considered to be distinct species, based primarily on genetic information (see below). Unfortunately, genetic information is not available for the entire species group. Gregorin (2006) elevated *A. s. juara* and *A. s. puruensis* to the species level; however, we consider that more studies (particularly on their geographic distribution and genetics) are needed before categorizing these taxa as distinct species. Nonetheless, we present each subspecies separately to allow a better understanding of the variation already observed by Gregorin.

3.3.4.2 *Alouatta seniculus seniculus* (Linnaeus, 1766)

The distribution of *A. s. seniculus* is restricted to Colombia (east of the Andes), northwestern Venezuela (around Maracaibo Lake), Brazilian Amazon to the north of the Rio Solimões and south of the Rio Negro, eastern Ecuador, and eastern Peru (east of the Río Huallaga, to the upper Marañon, and rios Napo and Putumayo).

This subspecies represents the typical *seniculus* described by Linnaeus (1766). A number of genetic studies have included individuals sampled from within the distribution range of this subspecies (e.g., Yunis et al. 1976; Cortés-Ortiz et al. 2003) showing clear genetic differences with other species. However, phylogeographic studies that include representatives of the different subspecies here considered are still lacking, preventing a better understanding of the distribution of genetic variation within the species and limiting our abilities to correctly classify these forms.

3.3.4.3 *Alouatta seniculus juara* Elliot, 1910

The Juruá red howler monkey is distributed through the western portion of the Brazilian Amazon, in the states of Acre and Amazonas, south of the Rio Solimões and west of the Rio Purus (Fig. 3.1). Its range extends to Peru, but the range limits are not known. The taxonomic position of *juara* has been debated, sometimes considering it a junior synonym of *A. seniculus* (e.g., Cabrera 1957), other times including it as one of its subspecies (e.g., Groves 2001) or as a distinct species (e.g., Elliot 1910; Gregorin 2006). These discrepancies are mainly due to the lack of comprehensive studies. Gregorin (2006) examined 31 specimens from Brazil that occur within the supposed range of this taxon. He found statistical differences on morphometric variables between *juara* and *A. macconnelli* and *A. nigerrima*, but he did not present data for these types of analyses comparing *juara* to *A. seniculus*. Nonetheless, he found differences in pelage coloration between *juara* and *A. seniculus* from northern Colombia. Regarding hyoid morphology, Gregorin (2006) found a high similarity between *juara* and *A. seniculus* and concluded that they must be phylogenetically proximate.

Lima and Seuánez (1991) reported on the karyotype of one individual sampled in Tefé, in the range of *juara*, and mentioned that the karyotype of this individual was "basically the same as that of the Colombian specimens" analyzed by Yunis et al. (1976)

and that "this finding indicates that the geographic range of this subspecies might extend further south to the Solimões River." Gregorin (2006) used this information as evidence supporting the distinction of *juara* from *A. macconnelli* and *A. nigerrima*, but it remains unclear whether this taxon is distinct from *A. seniculus*.

3.3.4.4 *Alouatta seniculus puruensis* Lönnberg, 1941

This subspecies is distributed along both margins of the Rio Purus, to the lower Rio Madeira and the middle Rio Aripuanã, extending eastward to the Rio Teles Pires. To the south, it is restricted to the northern margin of the Rio Abunã on the border of Bolivia (Glander and Pinto 2013) (Fig. 3.1). Gregorin (2006) reported the southernmost locality for this species to be Placido de Castro in Acre, Brazil.

The main diagnostic character for this subspecies is the sexual dichromatism, with males being dark rufous (back mahogany red and flanks and limbs maroon [Hill 1962]) and females golden orange with the distal portions of the limbs, tails, and beard dark rufous (pale yellowish, with the flank fringe partially orange and the limbs and tail also showing some orange [Hill 1962]). Gregorin (2006) found morphological differences in the shape of the hyoid bone, and proposed that it be considered a full species. We continue to place this taxon as a subspecies of *A. seniculus* until genetic studies reveal the degree of divergence (if any) with the other members of this species.

3.3.4.5 *Alouatta arctoidea* Cabrera, 1940

Type: Adult male, Paris Museum.
Type locality: Caracas, Venezuela, fixed by J. A. Allen (1916) on the basis of Humboldt's vernacular name (Hill 1962), further restricted by Cabrera (1957) to the valley of Aragua (Groves 2001).
Common name: Venezuelan red howler, Ursine red howler.

Alouatta arctoidea occurs on the island of Trinidad and in northern Venezuela, from the coastal region of Falcón to the state of Miranda (north of the Orinoco) (Fig. 3.1). Bodini and Pérez-Hernández (1987) reported a possibly distinct form in the Venezuelan llanos; however, no further studies have reported the existence of this howler and here we consider it as part of *A. arctoidea*. This species was initially described by Humboldt and Bonpland (1805) as *Simia ursina* but he created confusion due to the disagreement between the description and the figure given by the author (which depicted *A. guariba*). The name *ursina* (Humboldt) is now considered a synonym of *guariba*. J. A. Allen (1916) designated this form as a subspecies of *A. seniculus* (*A. s. ursina*), and Cabrera (1940) proposed to call it *A. s. arctoidea*, as the name *ursina* was inadmissible for this form given that it is a homonym to *Simia hamadryas ursinus* Kerr, 1792 and *Simia ursina* (Bechstein 1800) used to refer to the "ursine baboon" (Cabrera 1940).

Based on cytogenetic differences recognized by Stanyon et al. (1995), this taxon is currently accepted as a full species. The 14 chromosomal rearrangements found by these authors between *A. arctoidea* (four individuals from Hato Masaguaral, Venezuela) and *A. sara* (one individual captured in Bolivia, held at the San Diego Zoo) are more typical of differences between species, and are on the same order of magnitude as those found between *A. sara* and *A. seniculus* by Minezawa et al. (1985). However, until now no *A. arctoidea* specimens have been analyzed using molecular techniques and no monkeys from northern Venezuela have been cytogenetically characterized. Therefore, further validation of this species is necessary and the extent of its distribution range remains to be studied.

3.3.4.6 *Alouatta macconnelli* Elliot, 1910

Type: Adult male, skin and skull, No. 1908.3.7.3, British Museum (Natural History) (Napier 1976).
Type locality: Coast of Demerara, Guiana.
Common name: Guianan red howler, Golden howler.

Alouatta macconnelli is distributed throughout the Guiana Shield, including French Guiana, Suriname and Guyana, southern Venezuela (south of the Río Orinoco), and northern Brazil (from the coast of the state of Amapá to the eastern margins of the rios Negro and Branco, including Gurupá island in the Amazon delta) (Fig. 3.1).

There has been confusion about the name that should be used for the howler monkeys that inhabit the Guiana Shield, as well as whether one or two taxa should be recognized. The confusion started with É. Geoffroy Saint-Hilaire's (1812) description of *Stentor stramineus*,[1] which was based on a specimen of a female *A. caraya* from Central Brazil (Elliot 1913; Rylands and Brandon-Jones 1998; Gregorin 2006). Later, Elliot (1910) described *A. macconnelli* from one specimen from French Guiana, and synonymized *stramineus* with *A. seniculus* (Elliot 1913), which he deemed as clearly different from *A. macconnelli*. Tate (1939) considered both *macconnelli* and *stramineus* as subspecies of *A. seniculus*, and da Cruz Lima (1945) considered *A. macconnelli* (Elliot 1910) a synonym of *A. seniculus straminea* (Geoffroy Saint-Hilaire 1812). Hill (1962) still included both *straminea* and *macconnelli* as subspecies of *A. seniculus*, but wrote "There is every indication that both *macconnelli* and *amazonica* fall within the range of variation of *stramineus* and they should accordingly be treated as synonyms thereof, an action already taken by Cabrera (1957)."

Bonvicino et al. (1995), based on morphological analyses of individuals in the range of the two putative subspecies (*A. s. stramineus* and *A. s. macconnelli*), concluded that the howlers from the northern bank of the Amazon can be divided into two species separated by the Rio Trombetas, and argued that this is supported

[1] Although some authors, for example, Hill (1962), attribute the name *stramineus* to Humboldt (1812) (*Simia straminea*) published two months before É. Geoffroy Saint Hilaire's *Stentor stramineus*, Humboldt (1812) gave specific credit to Geoffroy Saint-Hilaire for the name; he merely placed it in Linnaeus' genus *Simia* and changed the gender accordingly. (See Article 50.1.1 of the *International Code of Zoological Nomenclature* <http://iczn.org/code>.)

by the biochemical and karyological analyses of Sampaio et al. (1991) and Lima et al. (1990) and Lima and Seuánez (1991), respectively. However, as discussed by Rylands and Brandon-Jones (1998, p. 887), the main "confusion regarding the identity of the Guianan howler is compounded by the inadequate, or imprecise information and uncorroborated conjectures about its geographic distribution." Rylands and Brandon-Jones (1998) found that the same specimens analyzed by different authors as part of one taxon were regarded as the alternative taxon by others. This is true throughout the taxonomic history of these two taxa, but was particularly true in the case of the analyses done by Bonvicino et al. (1995).

Molecular analyses by Sampaio et al. (1996) using biochemical data concluded that the genetic distance between populations from opposite sides of the Rio Trombetas, and those to the east of the Rio Jari are too small to justify their separation even at the subspecific level. Figueiredo et al. (1998) analyzed mitochondrial DNA sequence data of individuals from the same locations as those of Sampaio et al. (1996) and found that genetic distances among them were small and similar to those found among populations, and that individuals from different localities were sometimes less divergent than individuals from the same population. They concluded that both biochemical and mitochondrial DNA data strongly suggested gene flow among the three studied populations and the existence of a single species within the studied area.

Gregorin (2006) studied pelage coloration and morphometric data from specimens sampled in Brazil, and compared them to specimens from the rest of the Guiana Shield (French Guiana, Suriname, and southern Venezuela). He found that the Brazilian and "Guianan" specimens presented great variation in pelage coloration, which was not distinguished geographically. The same was true when analyzing the morphology of the hyoid bone. Principal Component Analyses of morphometric data also did not support the recognition of two taxa for the Guiana Shield (Gregorin 2006). In all, Gregorin's study supported Figueiredo et al.'s (1998) conclusion that there is a single taxon of howler in the Guiana Shield, which is easily distinguishable from the other recognized species of howlers. The description of Elliot's *A. macconnelli* type falls within the spectrum of variation found in the specimens from the Guiana Shield by Gregorin (2006), and he concluded that this taxon should be conservatively named *A. macconnelli*, but acknowledged the observation by Rylands and Brandon-Jones (1998) that given that the type locality of *Mycetes auratus* Gray is in the west of the range of *A. macconnelli*, the correct name for this species may well be *Alouatta auratus* (Gray, 1845).

3.3.4.7 *Alouatta sara* Elliot, 1910

Type: Adult female, skin and skill, No. 1907.8.2.1 British Museum (Natural History) (Napier 1976).
Type locality: Province of Sara, Bolivia.
Common name: Bolivian red howler.

Distributed in Bolivia, this species occurs from the department of Pando south along the Andean Cordillera, and east into Bolivia, including the Río Beni basin and east as far as the Mamoré-Guaporé interfluvium (Anderson 1997; Büntge and Pyritz 2007) (Fig. 3.1).

Alouatta sara was initially considered a distinct species by Elliot (1910) and later regarded as a subspecies of *A. seniculus* by Cabrera (1957) and Hill (1962). Minezawa et al. (1985) conducted cytogenetic analyses based on a sample of 33 red howler monkeys from the region of Santa Cruz de la Sierra, Bolivia, and concluded that their karyotype differed considerably from those of Colombian red howlers (*A. s. seniculus*), and therefore should be considered a different species. Similarly, comparative cytogenetic analyses by Stanyon et al. (1995) demonstrated karyotype differences between *A. sara* and *A. arctoidea* congruent with typical differences observed between species belonging to different genera. Groves (2001) considered *sara* to be a full species. Cortés-Ortiz et al. (2003) and Perelman et al. (2011) included mitochondrial and nuclear sequence data of *A. sara* individuals in their phylogenetic analyses, but only the former authors also included samples from *A. seniculus* from Colombia. Phylogenetic analyses based on mitochondrial DNA data show that *A. sara* and *A. seniculus* are sister taxa that diverged approximately 2.4 MA (Cortés-Ortiz et al. 2003). Based on cytogenetic and molecular data, the recognition of *A. sara* as a full species is strongly supported. Nonetheless, further studies are needed to understand the actual borders of its geographic range, its relationships with other howler species, and the levels of genetic variation across the distribution of this taxon.

3.3.4.8 *Alouatta nigerrima* Lönnberg, 1941

Type: Originally in the Stockholm Museum (none of the seven specimens was designated as holotype in the original description [da Cruz Lima 1945]). Lectotype in the Swedish Museum of Natural History NRM A63 3316 (indicated by Cabrera [1957], and officially designated by Gregorin [2006]).
Type locality: The left margin of the Rio Tapajós (restricted by Cabrera [1957] to Patinga, state of Pará, Brazil).
Common name: Amazonian black howler.

Alouatta nigerrima is endemic to Brazil, with a geographic range that extends between the rios Madeira and Tapajós, north to the Rio Amazonas (Fig. 3.1). A few specimens have also been collected in the northern margin of the Rio Amazonas, in the regions of Oriximiná and Obidos, in the state of Pará (Gregorin 2006).

Lönnberg (1941) described *A. nigerrima* as a full species, distinct from its neighbor *A. belzebul tapajoensis* (here *A. discolor*, see above), and considered that these two forms were phylogenetically close. One of the most important distinctive characters described by Lönnberg (1941) as diagnostic of *A. nigerrima* is related to the morphology of the hyoid bone, which clearly distinguishes it from *A. discolor* (Gregorin 2006). Cruz Lima (1945) also considered *A. nigerrima* to be a distinct species, but Hershkovitz (1949) placed it as a subspecies of *A. belzebul* (although recognizing that the morphology of the hyoid bone could place it closer to *A. seniculus* than to *A. belzebul*). Cabrera (1957) and Hill (1962) followed Hershkovitz in listing *nigerrima* as a subspecies of *A. belzebul*.

Armada et al. (1987) studied the karyotypes of 10 *A. belzebul* individuals captured on the left margin of the Rio Tocantins, state of Pará, Brazil, and of one captive individual of unknown origin tentatively identified as *A. belzebul nigerrima*, based on pelage coloration. They found considerable differences in the karyotypes of these two forms, and suggested a taxonomic reevaluation of these taxa. Oliveira (1996) noted that the g-banding pattern of *A. b. nigerrima* presented by Armada et al. (1987) was more similar to the one observed in *A. seniculus* than in *A. b. belzebul*. Bonvicino et al. (2001) analyzed mitochondrial sequence data of seven Brazilian *Alouatta* species, including a sample from the same individual identified as *A. belzebul nigerrima* by Armada et al. (1987), and found that it was phylogenetically closer to *A. macconnelli* and *A. seniculus* than to *A. belzebul*.

Gregorin (2006) analyzed the pelage coloration and cranial morphology of 98 specimens of *nigerrima*, and found that the distinctive black pelage was invariable across most of the specimens he analyzed. He also noticed that the morphology of the hyoid bone was distinct from any other Brazilian howler (confirming the observations previously made by Cruz Lima [1945]), but that it is more similar to the hyoid of *A. macconnelli* than to that of *A. belzebul*.

These morphological and genetic studies have supported the early recognition of *A. nigerrima* as a distinct species from *A. belzebul* and phylogenetically closer to the *seniculus* group. The genetic analyses have, however, been based on a single individual of unknown origin. Given its proximity to *A. macconnelli* and the fact that this latter taxon presents great variation in pelage coloration that includes individuals that are completely black (see Gregorin 2006), the question arises as to whether this specimen really originates from the range of *A. nigerrima* or is in fact a dark phase individual of *A. macconnelli*. Further genetic studies from individuals of known origin are needed to discard this possibility and validate the status of *A. nigerrima*.

3.4 Concluding Remarks

This review of the taxonomic history of the howler monkeys allows us to recognize nine distinct species: *A. palliata*, *A. pigra*, *A. seniculus*, *A. arctoidea*, *A. belzebul*, *A. caraya*, *A. guariba*, *A. sara*, and *A. macconnelli*. Three other taxa are tentatively considered here as species: *A. discolor*, *A. ululata*, and *A. nigerrima*, but their full validation as species still requires thorough genetic and/or morphological studies. Furthermore, we include *puruensis* and *juara* as subspecies of *A. seniculus*, as there is no data available to strongly support their taxonomic position as distinct species. The possibility remains that *A. guariba* is composed of two or more subspecies or even species. We recognize *A. pigra* and *A. palliata* as the only howler species present in Mesoamerican, with *A. palliata* including *coibensis* and *trabeata* as subspecies (besides *palliata*, *mexicana*, and *aequatorialis*) given that molecular data does not support the separation of these two taxa as distinct species from *A. palliata*.

Throughout this review, it should be evident that we still have a long way to go to fully resolve the taxonomy of *Alouatta*. This is not surprising given the wide distribution of the genus—the largest of any Neotropical genus—and the long history of diversification of the living taxa, which started about 7 MA. Particular efforts should be made to understand the distributions of the different forms and the genetic and morphological variation within taxa. Ideally, studies should use specimens from known geographical locations, and include individuals from as many localities as possible within the known range of the taxa, ensuring the inclusion of individuals from or near the type locality and from locations near the known or presumed boundaries. They also should include representatives of closely related taxa, not only those from geographic neighbors, but also those that are considered phylogenetically closest. This endeavor requires collaboration among researchers from different countries or geographical regions, and across different disciplines.

Our ability to properly identify and classify different taxa that represent distinct evolutionary units requires integrated taxonomic, biogeographic, and evolutionary studies (i.e., addressing the Linnean, Wallacean, and Darwinian shortfalls in biodiversity conservation; Diniz-Filho et al. 2013), and has immediate implications for the long-term survival of these taxa. Most species of howlers and other Neotropical primates face great and varied threats to their survival, and our ability as scientists to properly portray the extent of diversity within this group will contribute to the public understanding of the importance of maintaining this diversity. As a first step in this direction, we need to be able to clearly distinguish the different forms based on strong biological (genetic and morphological) evidence. As such, the taxonomy that prevails in a particular moment is a scientific hypothesis based on current knowledge, and changes are to be expected as more knowledge is acquired.

Taxonomic instability due to rapid changes in taxonomic arrangements may produce confusion at the moment of identifying proper units for conservation. However, these changes help to identify meaningful evolutionary lineages that require immediate conservation attention. In this respect, what is worrisome is not that the taxonomy of a group changes over time, but whether or not the changes made (or proposed) are supported by thorough and solid scientific evidence. When changes in taxonomic arrangements arise due to a better understanding of the evolutionary relationships within a group, they must be accepted as part of the development of science and should not be considered fickle and inconvenient to conservation efforts. Rather, they should be seen as elements to consider that strengthen our efforts to conserve biological diversity and meaningful evolutionary units.

As studies of howler monkeys in new geographical areas and using new genetic and morphological technique increase, it is likely that the taxonomic arrangement proposed here will change. Our responsibility lies in ensuring that the information used to make the decisions to do these changes is solid and comprehensive before these changes are accepted.

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