

Notes on the taxonomy and distributions of the tufted capuchin monkeys (*Cebus*, Cebidae) of South America

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Abstract

A good understanding (categorization) of the diversity and distribution of the tufted capuchin monkeys (*Cebus*) has proved to be extraordinarily intractable. Its lack is now hampering conservation efforts, for, despite them being, in general, wide-ranging and adaptable, their forests are being destroyed to the extent that many populations are now evidently seriously threatened. Conservation measures require that we know better their diversity not only to protect them in the wild but also to establish captive breeding programs. In this paper, we present some notes which resulted from our analysis of a recent published hypothesis regarding their systematics by C. P. Groves, in his influential synthesis *Primate Taxonomy* (2001). We are *not* presenting another hypothesis (taxonomy), but review aspects of some of the names and synonyms of Groves' taxonomy, and briefly discuss its concordance with the results of a largely unpublished PhD thesis of tufted capuchin systematics completed by Cecília Torres de Assumpção in 1983.

Keywords: Primates, taxonomy, Platyrrhini, Cebidae, *Cebus*, tufted capuchin monkeys

Introduction

The division of a group of organisms into component species, their evolutionary relationships to each other, and the mapping of their geographic distributions are all essentially hypotheses, albeit based to a greater or lesser degree on factual information. A taxonomic arrangement is a hypothesis, just as is the distribution map of the component taxa. Getting the right hypothesis is of course fundamental for all aspects of the study of organisms but, most urgently today, is crucial for the conservation of biological diversity, which requires, above all, categorizing living beings and knowing where they live.

One can test and modify an existing hypothesis or one can start afresh with a new analysis and interpretation of the relevant information and construct an entirely new hypothesis. The latter is generally the preferred option when the existing hypothesis is believed or shown to be, if not entirely wrong, irrevocably flawed. In this situation the old hypothesis can supposedly be discarded. It is possible to start afresh. In the case of taxonomy, however, the old hypotheses should never be discarded because a fundamental and vital element of taxonomy is consistency and stability in attributing names to organisms. The sacred rule of "first author preference" is not merely a guarantee for credit to be given where credit is due, but essential for scientific progress.

A morphological monograph, the result of years of careful dissection and analysis, maintains its usefulness only in so far as it can be attributed to an organism which can be identified over the centuries that follow. Taxonomy is the filing system which allows us to accumulate knowledge of the living world, and, in the case of conserving it, allows for quantification and delineation of the massive task at hand. What is it exactly that humans are destroying and what is that we need to save?

Synonyms are not just the flotsam of hypotheses which have been discarded, either as a result of new information or techniques in systematics or, regrettably, in many cases due to aspects of human nature and circumstance which so often result in poor science. They are, most importantly, a record of hypotheses—names and their authors—and for this reason always require consideration in any situation where taxonomy is being investigated with a view to revision. The history of a biological name carries with it vital information for building new hypotheses. Giving a new name to an organism demands that all previous names which could possibly have been given to the very same organism be considered, investigated and discarded. The multidisciplinary nature of systematics today—including such as morphology, physiology, molecular genetics, karyology, behaviour and biogeography—means that scholars in these disciplines regularly throw up new hypotheses, and yet often without due consideration given to the rules of zoological nomenclature, and what to many is a tedious task of unraveling the past—old and rare documents and registers, and biological specimens and their labels, in diverse and distant museums and libraries. It is necessary to have a thorough knowledge of the taxonomic history of the organism or group of organisms in question.

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The group of organisms in question here is the tufted capuchin monkeys of the genus *Cebus*. A good understanding (categorization) of their diversity and distribution has proved extraordinarily intractable over the centuries, and its lack is now beginning to hamper conservation efforts, for, despite them being, in general, wide-ranging and adaptable, their forests are being destroyed to the extent that many populations are now evidently seriously threatened. We do not know what we might be losing. Conservation measures require that we know better their diversity not only to protect them in the wild but also to establish captive breeding programs. In this paper, we present some taxonomic notes which resulted from our analysis of, and attempts to fully understand, a recent published hypothesis regarding their systematics: that of Groves in his influential synthesis *Primate Taxonomy* (2001). We stress (perhaps strangely, but not without reason) that we are *not* presenting another hypothesis (taxonomy). We examine here aspects of some of the names and synonyms of Groves' arrangement, reviewing the origin and use of the principal names ascribed to the tufted capuchin monkeys since Elliot's revision published in 1913, and briefly discuss a most important study of tufted capuchin systematics carried out by Torres (1983).

The tufted capuchin monkeys

In a taxonomic key to species and subspecies of the genus *Cebus*, Elliot (1913, p.77) separated the capuchin monkeys into those with "heads without tufts on male" (Group A) and those with "heads with tufts or ridges on male" (Group B). Hershkovitz (1949, 1955) adopted this species group separation, while pointing out that although all Elliot's Group B capuchins were indeed tufted, the Group A capuchins included three truly tufted capuchins: *Cebus apella*, *C. frontatus* and *C. variegatus*. While Elliot (1913) recognized 12 species of tufted capuchin (including the three from his untufted group), Cabrera (1957) and Hill (1960) reduced them all to just one, *Cebus apella*, with 11 (Cabrera) and 16 (Hill) subspecies. The taxonomy of Hill (1960) was based on the work of Remington Kellogg who was revising the tufted capuchins at the time. Despite the plethora of names available and his detailed and scholarly treatment, the synthesis of Hill (1960) raised so many uncertainties that it failed to encourage any further research and a consolidation of the taxonomy and systematics of the group (see for example, Hernández-Camacho & Cooper, 1976). As a result, for most of the last 30 years, all Amazonian tufted capuchin monkeys have been ascribed to just one form *Cebus apella apella*. Only in 1994 did Aquino and Encarnación venture further subspecific rankings for the tufted capuchins in the Peruvian Amazon (*C. apella pallidus*, *C. a. peruanus*, *C. a. maranonis* and an undescribed form). Their taxonomy was influenced by Philip Hershkovitz of the Chicago Field Museum, who was working on the group in the early 1990's for the second volume of his major treatise on the New World monkeys (Hershkovitz, 1977). Unfortunately Hershkovitz died in 1997 without publishing his findings.

Meanwhile, a revision of the non-Amazonian forms by Kinzey (1982) brought the names of three of the Brazilian Atlantic forest capuchin monkeys, *xanthosternos*, *nigritus* and *robustus*, into common usage; all as subspecies of *Cebus apella* (see Coimbra-Filho, 1990; Mittermeier & Coimbra-Filho, 1981

and Mittermeier et al., 1988;). Although not recognized by Kinzey (1982), the names *pallidus*, *vellerosus* and *paraguayanus* were also being kept alive by Argentinean research groups who were studying the capuchin monkeys from the *yungas* of the eastern slopes of the Andes in Argentina and the Atlantic forest of Argentina and Paraguay (Brown, 1989, 1990; Brown & Colillas, 1984; Brown & Rumiz, 1986; Chalukian, 1985; Mantecon et al., 1984 and Mudry de Pargament & Slavutsky, 1987).

Cecília Torres de Assumpção (Torres, 1983, 1988) initiated a major systematic revision of the tufted capuchin monkeys which unfortunately was not completed due to her untimely death in 1985. Using multivariate analyses of pelage and cranial characters she identified five "core areas" of phenotypes with relatively consistent characters. In his book on primate taxonomy, Groves' (2001) proposed a scheme based on his examination of skins and skulls in a limited number of museums. Discussion of his taxonomy takes up the majority of this paper. Finally, José de Sousa e Silva Jr. of the Goeldi Museum in Belém, Brazil, recently completed a doctoral thesis (2001) on the systematics of capuchin monkeys which will undoubtedly contribute enormously too to our understanding of this group. His findings have yet to be published, however.

Of the revisions mentioned above (see also Table 1), only Hill (1960) and Sousa e Silva Jr. (2001) mapped the distributions of the taxa they identified as valid. Distribution maps are available for Peru (Aquino & Encarnación, 1994), Venezuela (Bodini & Pérez-Hernández, 1987 and Linares, 1998), Bolivia (Anderson, 1997), and Colombia (Hernández-Camacho & Cooper, 1976 and Defler, 2003). Groves (2001) gave cursory descriptions of the ranges of the tufted capuchins he listed but, with the insufficient information available, understandably did not attempt to map them. In order to map the limits of the ranges of his four species, it is still necessary to formulate some sort of hypothesis as to the ranges of the subspecies of each. To do this requires collating what is known of the ranges of the subspecies and their synonyms and, like a jigsaw puzzle, put them together to provide at least a reasonable estimate as to the geographical limits of the species that Groves (2001) proposes (see Fragaszy et al., 2004).

The thesis of Cecília Torres de Assumpção (1983)

Fully recognizing the extraordinary variability of the tufted capuchins, and the confusion of names and synonyms, Cecília Torres de Assumpção (Torres, 1983, 1988), courageously tackled the problem of their systematics for her Doctoral degree at the University of Edinburgh. Of 42 named tufted capuchin monkeys, she found that 19 had no type locality. Specimens she examined from three type localities did not agree with the original descriptions (*tocantinus* Lönnberg, 1939, *cucullatus* Spix, 1823 and *xanthocephalus* Spix, 1823). Of the 20 remaining, she found that in 13 the type specimen represented just one of various phenotypes found in the area, such that if the characters used to identify them were valid for distinguishing subspecies, there would be two or three at each locality. Due to the confusion of names and synonyms, and the high degree of individual variation, Torres attempted a statistical approach, which effectively was "starting from scratch." Her objectivity, purposely untrammelled by the weighty and confused baggage of

Table 1 - A comparison of the classifications of the tufted capuchins (*sensu* Hershkovitz, 1949) of the genus *Cebus*, by Elliot (1913), Lönnberg (1939: only some of the forms were discussed), Cruz Lima (1945: only Amazonian forms), Vieira (1955: only Brazilian forms), Cabrera (1957), Hill (1960) and Groves (2001).

Elliot (1913)	Vieira (1955) (Brazil)	Hill (1960)
<i>C. apella</i> (Linnaeus, 1758)	<i>C. nigrinus</i> (Goldfuss, 1809)	<i>C. apella apella</i> (Linnaeus, 1758)
<i>C. frontatus</i> Kuhl, 1820	<i>C. frontatus</i> Kuhl, 1820	<i>C. apella margaritae</i> (Goldfuss, 1809)
<i>C. variegatus</i> É. Geoffroy, 1812	<i>C. vellerosus</i> I. Geoffroy, 1851	<i>C. apella fatuellus</i> (Linnaeus, 1766)
<i>C. libidinosus</i> Spix, 1823	<i>C. robustus</i> Kuhl, 1820	<i>C. apella tocantinus</i> Lönnberg, 1939
<i>C. fatuellus</i> (Linnaeus, 1766)	<i>C. variegatus</i> É. Geoffroy, 1812	<i>C. apella macrocephalus</i> Spix, 1823
<i>C. fatuellus peruanus</i> Thomas, 1901	<i>C. libidinosus libidinosus</i> Spix, 1823	<i>C. apella magnus</i> von Pusch, 1941
<i>C. macrocephalus</i> Spix 1823	<i>C. libidinosus versutus</i> Elliot, 1910	<i>C. apella juruanus</i> Lönnberg, 1939
<i>C. versuta</i> Elliot, 1910	<i>C. libidinosus paraguayanus</i> Fischer, 1829	<i>C. apella maranonis</i> von Pusch, 1941
<i>C. azarae</i> Rengger, 1830	<i>C. libidinosus pallidus</i> Gray, 1865	<i>C. apella peruanus</i> Thomas, 1901
<i>C. azarae pallidus</i> Gray, 1865	<i>C. libidinosus juruanus</i> Lönnberg, 1941	<i>C. apella pallidus</i> Gray, 1865
<i>C. cirrifer</i> É. Geoffroy, 1812	<i>C. apella apella</i> (Linnaeus, 1758)	<i>C. apella cay</i> Illiger, 1815
<i>C. crassiceps</i> Pucheran, 1857	<i>C. fatuellus macrocephalus</i> Spix, 1823	<i>C. apella libidinosus</i> Spix, 1823
<i>C. caliginosus</i> Elliot, 1910	<i>C. fatuellus tocantinus</i> Lönnberg, 1939	<i>C. apella robustus</i> Kuhl, 1820
<i>C. vellerosus</i> I. Geoffroy, 1851	<i>C. fatuellus peruanus</i> Thomas, 1901	<i>C. apella frontatus</i> Kuhl, 1820
	<i>C. fatuellus trepidus</i> (Linnaeus, 1766)	<i>C. apella nigrinus</i> (Goldfuss, 1809)
Lönnberg (1939) (only some forms)¹		<i>C. apella xanthosternos</i> Wied, 1820
<i>C. fatuellus macrocephalus</i> Spix, 1823	Cabrera (1957)	
<i>C. fatuellus peruanus</i> Thomas, 1901	<i>C. apella apella</i> (Linnaeus, 1758)	Groves (2001)
<i>C. fatuellus tocantinus</i> new subspecies	<i>C. apella libidinosus</i> Spix, 1823	<i>C. apella apella</i> (Linnaeus, 1758)
<i>C. libidinosus pallidus</i> Gray, 1865	<i>C. apella macrocephalus</i> Spix 1823	<i>C. apella fatuellus</i> (Linnaeus, 1766)
<i>C. libidinosus juruanus</i> new subspecies	<i>C. apella margaritae</i> (Goldfuss, 1809)	<i>C. apella macrocephalus</i> Spix, 1823
	<i>C. apella nigrinus</i> (Goldfuss, 1809)	<i>C. apella peruanus</i> Thomas, 1901
Cruz Lima (1945) (Amazonia)	<i>C. apella pallidus</i> Gray, 1865	<i>C. apella tocantinus</i> Lönnberg, 1939
<i>C. libidinosus libidinosus</i> Spix, 1823	<i>C. apella paraguayanus</i> Fischer, 1829	<i>C. apella margaritae</i> Hollister, 1914
<i>C. libidinosus juruanus</i> Lönnberg, 1941	<i>C. apella robustus</i> Kuhl, 1820	<i>C. libidinosus libidinosus</i> Spix, 1823
<i>C. fatuellus macrocephalus</i> Spix, 1823	<i>C. apella vellerosus</i> I. Geoffroy, 1851	<i>C. libidinosus pallidus</i> Gray, 1866)
<i>C. fatuellus trepidus</i> (Linnaeus, 1766)	<i>C. apella versutus</i> Elliot, 1910	<i>C. libidinosus paraguayanus</i> Fischer, 1829
<i>C. fatuellus tocantinus</i> Lönnberg, 1939	<i>C. apella xanthosternos</i> Wied, 1820	<i>C. libidinosus juruanus</i> Lönnberg, 1939
<i>C. fatuellus peruanus</i> Thomas, 1901		<i>C. nigrinus nigrinus</i> (Goldfuss, 1809)
<i>C. apella apella</i> (Linnaeus, 1758)		<i>C. nigrinus robustus</i> Kuhl, 1820
		<i>C. nigrinus cucullatus</i> Spix, 1823
		<i>C. xanthosternos</i> Wied-Neuwied, 1826

¹ Analysis of material collected by Alfonso Maria Olalla, obtained by Count N. Gyldenstolpe and presented to the Natural History Museum, Stockholm.

the systematic treatments of the past, makes this study of particular interest. I review her findings in some detail due to the fact that her study, which comprised a doctoral thesis of 337 pages (nearly 200 of them devoted to the systematics of capuchins monkeys), was never published. A summary paper, written by her, was published posthumously in Portuguese in the *Revista Nordestina de Biologia* in 1988.

Torres examined 750 specimens of tufted capuchins from 163 localities. She recorded cranial characters and pelage color

and patterns (15 characters overall) of 260 skins and skulls of adult individuals (130 of each sex), most of them from Brazil, for which complete locality data were available. Age was estimated by tooth eruption and wear, and the degree of closure of the espheno-occipital suture at the base of the cranium. The localities, wherever possible including those of the types, covered the ranges of 13 of the 16 forms recognized by Hill (1960). Torres took into account the possibilities of sexual dimorphism and also changes with age. Some of the cranial

measures were sexually dimorphic, and she analyzed males and females separately. No clear sexual dichromatism was evident. She found that a number of cranial characters and the form of the tufts changed with age, even when adult. The age changes in tuft shape and size she illustrated with drawings of two series of specimens, one from Fernandópolis, western São Paulo (within the range of Groves' [2001] *C. nigrurus cucullatus*) and the other from Linhares, Espírito Santo (within the range of Groves' [2001] *C. nigrurus robustus*). For the cranial measures, she found that there was a tendency to continue increasing in size during adulthood, while diminishing in the oldest individuals.

Univariate statistical analyses indicated geographical patterns for each character, but due to the limitations of the methods used, Torres (1988) summarized only three tendencies which she considered valid: in the upper Amazon (specimens from the Rio Juruá) the majority of the characters showed particularly high averages; in central Brasil (Mato Grosso, specimens from the Rio Aricá and Serra da Chapada), south-east Brazil (state of São Paulo, western Minas Gerais) and the east and north-east of the state of Maranhão, the majority of the qualitative characters had particularly low values; and in the east of the state of Santa Catarina, the north of Rio Grande do Sul, and central Bolivia (Buena Vista, Santa Cruz) the characters again showed high averages. Torres indicated that the Santa Catarina and Rio Grande do Sul specimens (with some affinity to those in São Paulo) may be a distinct local form.

Torres' multivariate analysis demonstrated five clusters, differing slightly between males and females. In the males, these were: 1) Upper Amazon to central Bolivia; 2) upper Rio Juruá; 3) a large area from the central to eastern Amazon, central, eastern and southeastern Brazil to eastern Paraguay and extreme northeastern Argentina; 4) a small area of the upper Rio Araguaia; and 5) a small area of coastal Santa Catarina and Paraná. For the females they were: 1) upper Rio Juruá; 2) a large central Brazilian center with similar proportions to that of the males; 3) a connection between animals from the lower Rio Tapajós and Mato Grosso; 4) south-east Brazil, including Espírito Santo, Rio de Janeiro, and eastern Minas Gerais; 5) a small area of coastal Santa Catarina and Paraná. The analysis separated particularly the specimens from the following areas: the upper Rio Juruá; southern Brazil (eastern Santa Catarina, and northern Rio Grande do Sul); Central Brazil (for example, São Domingos, Rio das Mortes in Mato Grosso); and eastern Brazil (for example Linhares, northern Espírito Santo, and Matias Barbosa, Minas Gerais).

Overall, Torres (1983, 1988) identified a certain consistency in characters from five major regions.

1. *Western Amazonia, centered on the upper Rio Juruá.* In these capuchin monkeys one can expect: poorly developed sagittal crests; relatively large crania, the ventral hairs reddish or brownish in most specimens; a generally distinct dorsal stripe, darker than the flanks; hairs on the flanks generally reddish brown as in the shoulders.

2. *Middle and lower Rio Amazonas and the Guianas, centered on French Guiana.* In these capuchin monkeys one can expect: poorly developed sagittal crests; dark ventral hairs; a generally distinct dorsal stripe which is darker than the flanks; variably brown colors of the hairs on the flanks, with the shoulders lighter; and a group of dark hairs on the forehead above each eye; a dark cap (that is not light brown) forming a

"V" on the forehead; and the females are more likely to form tufts than the males.

3. *Eastern Bahia, centered around Ilhéus and Belmonte (mouth of the Rio Jequitinhonha).* In these capuchin monkeys one can expect: ventral hairs which are brownish-red or reddish; sagittal crests which are apparently delayed in their development; a consistent color pattern for the hairs of the flanks, including black, yellow and light brown; the cap is frequently pale (light brown); tufts of long hairs can be present but in general lie back on the head; a stripe of pale hairs or a mixture of pale and dark hairs between the eyes and the cap.

4. *Eastern Minas Gerais and Espírito Santo to the north of the Rio Doce, centered on the north bank of the Rio Doce.* In these capuchin monkeys one can expect: ventral hairs reddish brown; sagittal crests generally well-developed; a dark cap (not light brown); absence of a dorsal stripe which is darker than the flanks; hairs of the flanks reddish brown; presence of two tufts of long hairs on the head which converge giving the appearance of just one tuft.

5. *Coastal areas of São Paulo, Paraná, and Santa Catarina, centered on the vicinities of Corupá and Joinville.* In these capuchin monkeys one can expect: conspicuous sagittal crests; dark ventral hairs; dark cap (not light brown); hairs on the flanks black or blackish brown; well-developed tufts of hairs on the cap, which are either erect or oriented to the sides or front of the head; white hairs mixed with dark hairs on the anterior dorsum and flanks (more frequent in adult females).

Despite considerable variation in the specimens from these five areas, Torres (1988) was able to identify characters which were exclusive of each. She concluded (p.25) that "the populations in each [...] appear to be differentiated and one could say that they have suffered a certain degree of speciation." In her summary (1988) she indicated that these preliminary findings suggest subspecies. A sixth area identified by Torres, was not as clear cut. All but the last character (listed below) could also be found in other areas, and Torres concluded that "it would appear that none of the characters examined give strong evidence that the populations have undergone differentiation."

6. *A broad area which includes central and north-east Brazil (states of Goiás, Sergipe and eastern Mato Grosso, Maranhão, western Pernambuco, western Bahia, northeastern São Paulo and Paraná, western Minas Gerais.* In these capuchin monkeys one can expect: ventral hairs occasionally yellowish brown; flanks occasionally grayish brown, cap occasionally brown; a diffuse dorsal stripe; crania relatively small.

Torres offered four explanations for the confusion in this sixth, central area: 1) that the characters studied were not appropriate; 2) that the characteristics of the region (seasonal, open vegetation rather than closed rain forests) were influencing phenotypic variation; 3) hybridization is extensive with the surrounding, more distinct forms; and 4) speciation is occurring but is not as advanced as in the other areas. She gave preference to the latter two, with many of the phenotypes she observed having the appearance of transitional forms with the other five areas.

The taxonomic arrangement of Colin P. Groves (2001)

As we will discuss below, the findings of Torres (1988), which stopped short of applying names to the capuchin monkeys

of her six regions or “core areas,” conform well with the independent findings of Groves (2001). Groves (2001) hypothesis for the taxonomy and diversity of the tufted capuchin monkeys, which he refers to as the ‘*Cebus apella* group,’ was based on the examination of skins and skulls in a few museums, most importantly the US National Museum in Washington, DC, and the American Museum of Natural History in New York. Although he did not have access to her thesis, he was able to surmise that there was concordance through the brief summary of Torres (1983) provided in Mittermeier et al. (1988), and remarked that “The main divisions are so impressive that, despite the undeniable evidence of some natural interbreeding in intervening areas, I propose to recognize them as full species (four in number; the characters of *nigritus* and *robustus* seem to overlap...” (Groves, 2001; p.152). Groves resurrected a number of tufted capuchin names, and divided them into four species and 14 species and subspecies. His taxonomy includes six forms recognized by Elliot (1913), a further three recognized by Lönnberg in 1939 (two described by him), two recognized by Vieira (1955), and another two recognized by Cabrera (1957). Groves also distinguished the form *cucullatus* Spix, 1823, which was not considered a valid name in any of these previous revisions (see Table 1). The following discusses the four species, their subspecies, and some of the names which Groves (2001) lists as junior synonyms.

***Cebus libidinosus* Spix, 1823**

Cebus libidinosus (*sensu* Groves, 2001) includes the following four subspecies: *Cebus libidinosus libidinosus* Spix, 1823; *Cebus libidinosus pallidus* Gray, 1866; *Cebus libidinosus paraguayanus* Fischer, 1829; and *Cebus libidinosus juruanus* Lönnberg, 1939.

Cebus libidinosus libidinosus Spix, 1823

Bearded capuchin monkey, Spix’s capuchin monkey

Type locality: Rio Carinhanha, a left bank tributary of the Rio São Francisco, eastern Brazil (according to Hill [1960] and Cabrera [1957]), but given by Vieira (1955) as Cuiabá, Mato Grosso.

According to Hill (1960), *C. a. libidinosus* has a longer pelage than *cay* (= *paraguayanus*), and lacks the white hairs on the hands and feet. The crown patch is composed of hairs of more uniform length, which show no tendency to form lateral tufts or crests. The face is adorned with a short erect beard, which is not confined to the chin, but encircles the face from the temples downwards. Coloration varies little from *cay*. Hill (1960) described the range of this subspecies as east central Brazil along the left bank of the Rio São Francisco, which separates its range from the form *xanthosternus* (Wied, 1820). This range includes western Minas Gerais and part of western Bahia, and extends north through the north-eastern states of Sergipe, Piauí, Pernambuco, Natal, and Ceará to Maranhão. Hill (1960) indicated that it intergrades with *Cebus apella apella* in the vicinity of Miritiba, on the evidence of skins collected by F. Schwanda, now in the Edinburgh University Anatomical Museum. Vieira (1955) also listed *C. libidinosus libidinosus* for Miritiba, on the evidence of Pinto (1941). Mysteriously, Lönnberg (1939) described a young male (No. 7446) collected

from Prainha, Rio Tapajós, in central Amazonia as *Cebus libidinosus*, and Cruz Lima (1945) included *C. libidinosus libidinosus* in his treatise on the primates of Amazonia on the basis of this specimen.

Cebus libidinosus pallidus Gray 1866

Pale capuchin monkey

Type locality: Bolivia, restricted by Cabrera (1957) to the Rio Beni, Bolivia.

This form was considered to be a subspecies of *C. azarae* Rengger, 1830 by Elliot (1913). Lönnberg (1939) discussed the name *azarae* and concluded that it was preceded by *paraguayanus* Fischer, 1829. Because *paraguayanus* was already considered by Lönnberg to be a subspecies of *libidinosus* Gray, 1865, he placed *pallidus* as a subspecies of *libidinosus* as well. It is known from Bolivia and Peru. Lönnberg (1939) described seven specimens from Pto. Salinas, Río Beni in Bolivia. Aquino & Encarnación (1994) placed *Cebus apella pallidus* in south-west Peru, south of the Ríos Madre de Dios and Inambari in the Department of Puno. They gave the name of *Cebus apella paraguayanus* to the tufted capuchins north of the Madre de Dios. Anderson (1997), on the other hand, attributed all northern and central Bolivian tufted capuchin monkeys to *Cebus apella pallidus*, even those in the Pando region north of the Madre de Dios. Anderson (1997) identified *C. a. paraguayanus* as restricted to the south-east of Bolivia. As discussed above, Mantecon *et al.* (1984) and Brown & Colillas (1984) indicated *paraguayanus* for northern Bolivia and south-east Peru. If, as Aquino & Encarnación (1994) suggested, *pallidus* is restricted to the south of the Río Madre de Dios, and that *C. apella peruanus* is the form to the north, with *C. apella macrocephalus* occurring north of the Río Purús, then there is a troublesome anomaly of Groves’ (2001) *C. libidinosus juruanus* being isolated from other *libidinosus* subspecies.

Cebus libidinosus paraguayanus Fischer, 1829

Paraguayan capuchin monkey, Azara’s capuchin monkey

Type locality: Paraguay, restricted by Cabrera (1957) to Brazo Norte del Pilcomayo, due to its proximity to Asunción, where Azara resided.

Vieira (1955) placed this form as a subspecies of *Cebus libidinosus* Spix, 1823, following Cabrera and Yepes (1940). Hill (1960), however, gave preference to the name *Cebus apella cay* Illiger, 1815, with the common name of Azara’s capuchin, and a type locality of “Paraguay, left bank of the Rio Paraguay”. Hill (1960) also considered *Cebus versuta* Elliot, 1910, recognized by Vieira (1944) and given as a subspecies of *Cebus libidinosus* by Vieira (1955), as a junior synonym. There is considerable confusion on the definition of the forms *paraguayanus* and *pallidus* and their ranges, which cover eastern Paraguay, part or all of the Pantanal of Mato Grosso, into Bolivia and the north-west of Argentina.

Hill (1960) described *C. a. cay* as similar to *C. a. pallidus* Gray, 1865 (of central Bolivia and northern Mato Grosso) but darker in general coloration and differing in the form of the black cap (black, sometimes with a chestnut-brown tinge) and in the coloration of the hands, feet and digits (covered with whitish hairs). Hill (1960) describes *C. a. pallidus* as like a pale

libidinosus, with a small crown patch which is blackish or brown, often with a short lateral ridge or crest each side. The forearms and shanks, and hands and feet are black, but with some grayish-white hairs mingled with the black on the fingers and toes.

The distribution of *C. a. paraguayanus* is described by Cabrera (1957) as the south of the state of Mato Grosso (now the states of Mato Grosso and Mato do Grosso do Sul) and extreme south-east of Goiás, Brazil, through Paraguay, to south-east Bolivia, to northern Argentina, including the provinces of extreme south-east Jujuy, Salta, Formosa, and Chaco. In Paraguay, Hill (1960) restricted *C. a. cay* to the west of the Río Paraguai.

Brown & Colillas (1984) and Mantecon et al. (1984) recorded that *C. a. paraguayanus* occupies semideciduous forests in northwestern Argentina in the extreme south-west of the Province of Jujuy, and the Province of Salta, in the phytogeographic province of the *Yungas*, the populations of which are very similar to those occupying eastern Paraguay (Fragaszy et al., 2004). Mantecon et al. (1984) concluded that the standard karyotypes of the forms *vellerosus* and *paraguayanus* from Argentina and *paraguayanus* from Paraguay were similar in chromosomal size and morphology. Mudry de Pargament & Slavutsky (1987), studying the chromosomes of the Paraguayan capuchin monkeys and those in northwest Argentina, also concluded that they “constituted a single karyomorph population, in spite of the phenotypic differences observed.” Brown & Colillas (1984) and Mudry de Pargament et al. (1987) provided distribution maps in which *C. a. paraguayanus* occurred in eastern Paraguay, extending north to the Pantanal of Mato Grosso, and also in the northwestern Argentina, extending just a little way into southern Bolivia. The map of Mudry de Pargament et al. (1987) shows *C. apella vellerosus* restricted to the Province of Misiones, while in neighbouring Brazil they followed Kinzey (1982) in naming the tufted capuchins as *C. apella nigritus*. Brown & Colillas (1984) placed *C. a. vellerosus* north as far as western São Paulo. Capuchin monkeys are not found in the *chaco* region of the Provinces of Formosa and Chaco in northern Argentina. So the distribution of *C. apella paraguayanus* would form a horseshoe shape, bordering the xerophytic *chaco* of Argentina, Bolivia, and Paraguay. In the west, the limits are defined by the Andes in Argentina and Bolivia, and in the east it is confined to eastern Paraguay, east of the Río Paraguai. Probably its southernmost limit in the east is defined by the confluence of the Ríos Paraguai and Paraná, about 27°15'S.

The range of *C. apella paraguayanus* would appear as such to be fairly well-resolved. However, Brown (1986) indicated *C. a. pallidus* for Bolivia and south-east Peru, and mentioned that the northwestern Argentinean *Cebus* is very similar to the form *pallidus*. Discussing the historical biogeography of the *Yungas* region of north-west Argentina, he concludes that this population of *Cebus* has been repeatedly connected and separated from Paraguayan *C. a. paraguayanus* and the Bolivian *C. a. pallidus*. Brown (1986, p.81), significantly, indicated the Argentinean *Yungas Cebus* merely as “*Cebus apella* ssp.,” and restricted *C. a. paraguayanus* to Paraguay, making no connection through Brazil and south-east Bolivia to the forms in Salta and Jujuy provinces.

Stallings (1985, 1989) confirmed the absence of *Cebus* in the Paraguayan *chaco*. According to Brown & Colillas (1984) and

Mantecon et al. (1984), the distribution of *C. a. paraguayanus* extends into south-east Peru, and northern Bolivia, south of the Río Madre de Dios, extending east into Brazil through the part of the state of Mato Grosso do Sul, to the Río Paraná. Although these authors leave a large lacuna covering the Pantanal region in the state of Mato Grosso do Sul, Cabrera (1957) indicates that the region is also occupied by *C. a. paraguayanus*.

While not shown in his distribution map, Hill (1960) gave the range for *C. a. cay* as the “territory between the Río Paraná and Río Paraguay in southern Mato Grosso, southern Goiás and Paraguay”, and listed the following localities: Corumbá, Miranda, Salobra, Rio Piquiri (right-bank affluent of R. Paraguay), Chapada, Urucum, Aricá and São Lourenço. As pointed out by Hill (1960), Aricá was listed by Vieira (1955) for *C. libidinosus pallidus* (a form also recognized by Hill for northern Bolivia), and Hill concluded that the ranges of the two forms meet somewhere in central Mato Grosso, possibly along the watershed between the streams draining into Paraguai-Paraná system on the south and those forming the headwaters of the Tocantins, Xingu and Tapajós to the north. Hill (1960) substantiated his description of the range by mentioning examples obtained by Krieg along the right bank affluents of the Río Paraná, Rio Ivinhema, Rio Taquaraçu, and Rio Samambaia (according to Kuhlhorn, 1955), and also a series in the American Museum of Natural History from Anápolis, Goiás, 1000 m altitude, south-west of Brasília, collected by R. M. Gilmore. Hill (1960) argued that the Anápolis series, although variable, resemble more closely *cay* than any other race of *Cebus apella*.

Aquino & Encarnación (1994) and Anderson (1997) consider the tufted capuchin of central and northern Bolivia and southeast Peru to be the form *pallidus* (see below). The extension of *C. a. paraguayanus* to northern Bolivia and south-east Peru argued by Mantecon et al. (1984) and Brown & Colillas (1984), therefore, invades the range of this form as given by Cabrera (1957), Hill (1960), Aquino & Encarnación (1994), Anderson (1997) and Vieira (1955).

Cebus libidinosus juruanus Lönnberg, 1939

Juruá capuchin monkey

Type locality: Brazil: Frente a João Pessôa, Rio Juruá.

Cebus libidinosus juruanus is known from its type locality on the right bank of the Juruá near the mouths of the Ríos Tarauacá and Eiru. João Pessôa is now called Eirunepe. Besides the type locality, Lönnberg listed specimens collected by Alfonso Maria Ollala in 1936 from Igarapé do Gordão and Igarapé Grande (*igarapé* is a stream or creek) both on the Rio Juruá, and Santo Antônio, Rio Eiru, a south bank affluent of the Rio Juruá. He stated that they occur on both banks of the Rio Juruá. Overall, Lönnberg described *juruanus* as darker than the nominate *C. libidinosus* and *C. libidinosus pallidus*. The darker color (general color of upper parts is dark rufescent brown, somewhat resembling “auburn”) Lönnberg associated with heavier rainfall (also his explanation for the dark *tocantinus*). Cruz Lima (1945) and Vieira (1955) listed this form, but provided no information beyond that already given by Lönnberg.

Hill (1960) suggested a distribution between the upper Rio Juruá and the Rio Envira. Enigmatically, Groves (2001) indicated that material from the British Museum (Natural History) from Mato Grosso, far to the south and east of the Rio

Juruá, is referable to this subspecies. *Cebus apella* from Mato Grosso listed in Napier (1976) is from the Serra da Chapada (now Chapada dos Guimarães), which is a little north-east of Cuiabá, and was identified by Thomas (1904) as *Cebus azarae* Rengger 1830, given as a junior synonym of *C. libidinosus paraguayanus* by Groves (2001). Torres (1983, 1988) identified the upper Rio Juruá as a core area for a very distinct group of tufted capuchins, principally in terms of flank color (generally reddish brown, as in the shoulders) and in their relatively large skulls (see below). She found that the color of the ventral hairs (reddish or red in most specimens she examined) is similar to specimens from the Rio Tapajós, and that the cap shape does not distinguish them from tufted capuchins in Peru and Bolivia. As mentioned above, *C. libidinosus juruanus* would be completely isolated from other *libidinosus* subspecies if the capuchins to the north of the Río Madre de Dios in Bolivia and Peru are considered to be *C. apella peruanus*, and north of the Rio Purus, *C. apella macrocephalus*, as suggested by Aquino & Encarnación (1994).

Cebus nigrinus (Goldfuss, 1809)

Cebus nigrinus (*sensu* Groves, 2001) includes the following three subspecies: *Cebus nigrinus nigrinus* (Goldfuss, 1809); *Cebus nigrinus robustus* Kuhl, 1820; and *Cebus nigrinus cucullatus* Spix, 1823.

Cebus nigrinus nigrinus (Goldfuss, 1809)

Black-horned capuchin

Type locality: Brazil, restricted to Rio de Janeiro by Vieira (1944).

Cebus a. nigrinus is a large dark colored race, very dark brown to black, with long hair, and in adults two elongated lateral frontal tufts or ridges on the crown which contrast with the whitish superciliary areas and cheeks (Hill, 1960). It is the form recognized south of the Rio Doce, in the states of Minas Gerais and Espírito Santo, Brazil. The type locality is Rio de Janeiro (= Serra dos Órgãos), although no type is preserved (Hill, 1960). Hill (1960) regarded the form *vellerosus* I. Geoffroy, 1851 from northern Argentina as a synonym. Vieira (1955) recognized *C. vellerosus*, but listed *Cebus cirriifer* E. Geoffroy, 1812 and *Cebus caliginosus* Elliot, 1910, as synonyms of *C. nigrinus* as did Hill (1960), and gave the distribution as southern Brazil, in the state of Rio de Janeiro (Serra dos Órgãos), south to the state of São Paulo and the north of the state of Paraná. One presumes that he was referring to regions inland, as he put *frontatus* occurring in the Serra do Mar and coastal region to the east, and *C. vellerosus* evidently occurring to the west in São Paulo and Paraná, east of the Rio Paraná, extending into northern Argentina.

Hill (1960, p.489), who regarded *vellerosus* as a synonym, gives the following distribution: "Eastern Brazil from the Serra dos Órgãos in Rio de Janeiro state, southwards through the states of São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul; range inland limited on the west by the Rio Paraná which separates the territory of *nigrinus* from that of *cay* (Kuhlhorn, 1939). Westwards range extending into Argentine territory of Misiones. Mountainous areas of São Paulo and other southern states presumably excluded from the range of *nigrinus* as *Cebi* of

these comprise the subspecies *frontatus*. Vieira (1955) restricts the southern range of *nigrinus* to northern Paraná and records material from more southerly localities [see *C. a. vellerosus*]... under *vellerosus*, which he treats as a distinct race." Neither *C. a. vellerosus* nor *C. a. frontatus* were recognized by Kinzey (1982), who indicated on his map a distribution for *C. a. nigrinus* which extended south from the Rio Doce in Minas Gerais and Espírito Santo, and south from the Rio Grande in Minas Gerais and São Paulo, throughout the states of Rio de Janeiro, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul, east of the Rio Paraná. He included the locality Alto da Serra, cited by Hill (1960) as occupied by *C. a. frontatus*, along with others nearby such as Ubatuba, Ilha de São Sebastião, and Boracéia, and those listed for *C. a. vellerosus* by Vieira (1955), such as Presidente Epitácio, Lins, and Valparaíso in São Paulo, and Porto Camargo, Paraná.

Cebus nigrinus robustus Kuhl, 1820

Crested capuchin monkey, robust tufted capuchin monkey, white-shouldered capuchin monkey

Type locality: Morro da Arara, north of the Rio Mucurí, Minas Gerais, Brazil.

Hill (1960) refers to this form as the crested or white-shouldered capuchin. It is distinguishable from all other forms by the median conical crest on the crown. The general color is bright red-brown. Hill (1960) described the distribution as eastern Brazil, from southern Bahia (Rio Jucuruçú), through Espírito Santo (Colatina, Rio Piracicaba, Rio Sussuú, Rio Doce) to Rio de Janeiro and westwards into Minas Gerais (Rio Matipó). Kinzey's (1982) analysis placed the form *C. a. nigrinus* to the south of the Rio Doce in Minas Gerais and Espírito Santo, extending into Rio de Janeiro and São Paulo; a scheme followed by Oliver & Santos (1991). Torres (1983, 1988) also identified clearly different forms either side of the Rio Doce. The Rio Matipó locality cited by Hill (1960) is south of the Rio Doce (above the confluence with the Rio Piracicaba), and Kinzey (1982) regarded skins collected from there by José Pinto da Fonseca in 1919 as hybrids between *C. a. nigrinus* and *C. a. robustus*.

It would seem that the range of *C. a. robustus* extends north of the Rio Jucuruçú in Bahia, as far as the Rio Jequitinhonha (Rylands et al., 1988; Oliver & Santos, 1991). The westernmost locality in the state of Minas Gerais is given by Pinto (1941), who argued vehemently for the validity of the form, and obtained specimens from the headwaters of the Rio Pissarão, in a mountainous region north of the Rio Piracicaba, not far from the town of Presidente Vargas. It is possible that the Serra do Espinhaço of Minas Gerais, running north-south and defining the transition from the Atlantic forest to bush savanna (*cerrado*) in the west, marks the western limits of the distribution of this form. Further west (and west of the Serra do Espinhaço), Kinzey (1982) recorded a specimen from Tomas Gonzaga, near Corinto, which he listed as *C. a. robustus* (= *C. a. robustus* x *C. a. libidinosus*).

Cebus nigrinus cucullatus Spix, 1823

Type locality: Brazil, São Paulo Province.

Elliot (1913) listed *Cebus cucullatus*, *C. xanthosternos* Kuhl 1820 and *C. robustus* Kuhl, 1820, as junior synonyms of *C.*

variegatus E. Geoffroy, 1812). Curiously, Vieira (1955) and Hill (1960) listed *cucullatus* as a junior synonym of *robustus*, even though they did not include São Paulo as part of its range. *Cebus apella vellerosus* I. Geoffroy, 1851 (Type locality: Brazil, São Paulo, further restricted by Cabrera (1957) to Porto Cabral) was listed as a junior synonym of *Cebus apella nigrinus* (Goldfuss, 1809) by Hill (1960), and as a junior synonym of *Cebus nigrinus cucullatus* by Groves (2001), although he noted (p.156) a communication from Ignacio Avila that the name *cucullatus* may not be applicable under the *International Code of Zoological Nomenclature*, Article 23(b) (concerns the advisability of maintaining long-standing names, in which case *vellerosus* might be considered to take preference). Groves (2001, p.152) also indicated that the name *cirrifer* E. Geoffroy in Humboldt, 1812, from “Brazil”, the type of which is in Paris, is almost certainly a senior synonym of *C. nigrinus cucullatus*, but he refrained from using the name, evidently not being certain enough.

Vieira (1944), who listed the form *vellerosus* as a full species, described it as very similar to *C. a. nigrinus*. It has tufts similar to those of *nigrinus*, but is smaller, and the principal distinguishing characteristic is the presence of long white hairs mixed with the dark gray-brown (*pardo*) fur on the body, especially on the back. Although Vieira (1944) indicated that it was restricted to the Rio Tietê valley and the banks of the Rio Paraná in the state of São Paulo, he later (1955) included the north of Argentina (Misiones), and in Brazil, the west of the state of Paraná (Porto Camargo, Rio Paraná, east bank, mouth of the Rio Ivaí) as well as western São Paulo (Valparaiso, between the Rios Tietê and Paranapanema), Lins (middle Rio Tietê), Presidente Epitácio (Rio Paraná, south of the Rio Tietê), and Porto Cabral (Rio Paraná, Pontal do Paranapanema), east of the Rio Paraná. Coimbra-Filho (1976) recorded that *C. a. vellerosus* was quite common in the Morro do Diabo State Park, São Paulo, on the north bank of the Rio Paranapanema near the Rio Paraná. Mantecon et al. (1984), Brown & Colillas (1984), Brown (1986) and Mudry de Pargament et al. (1987) discussing Argentinean *Cebus apella*, recognized *C. a. vellerosus* in northeastern Argentina, Province of Misiones, occupying evergreen forests of the Paranaense phytogeographical province from Santa Ana, through Iguazú and between the Rios Uruguai and Paraná, and extending north into Brazil, east of the Rio Paraná, in the west of the states of Santa Catarina, Paraná and São Paulo (Cabrera, 1957). Mudry de Pargament et al. (1987) pointed out that, although limited to the east of the Rio Paraná in Brazil, there are no ecological or physical barriers which could define the range limits of this subspecies with that of *C. a. nigrinus* (here *C. nigrinus cucullatus*), and they proposed that the two will intergrade. Groves (2001) implied his agreement with the Argentinean distribution of *cucullatus* stating that it is “the most southerly capuchin, from about 24 to 30°S.” Hill (1960) and Groves (2001) regarded *Cebus caliginosus* Elliot, 1910 (type locality: Colônia Hansa (now Corupá), Santa Catarina, Brazil) to be a junior synonym of *nigrinus* and *cucullatus*, respectively.

Cebus versuta Elliot, 1910

Type locality: Araguary, Rio Jordão, western Minas Gerais, Brazil.

Cebus versuta was described from five specimens procured by Alphonse Robert (now in the British Museum of Natural

History) from the Rio Jordão, an affluent of the Rio Paranaíba in 1901. Kinzey (1982) considered it a synonym of *C. libidinosus libidinosus*, with the area south of the Rio Grande in the state of São Paulo as occupied by hybrids between *C. a. nigrinus* and *C. a. libidinosus*. Groves (2001) synonymized this name with *Cebus apella paraguayanus*, which is problematic in geographic terms. The type locality is north of the range of *C. nigrinus (nigrinus and cucullatus)* and east of the range of *C. libidinosus libidinosus*, and there is no evident point of contact with the form *paraguayanus*.

Hill (1960) regarded it to be a junior synonym of *Cebus apella cay* Illiger, 1815, which other authors recognize as *Cebus apella paraguayanus*. His distribution map shows a range for *C. apella cay* which is limited to Paraguay and part of the Pantanal of Mato Grosso, although his written description of the range extends it right up into Goiás. Western Minas Gerais was left blank in the distribution map provided by Hill (1960), and in this case it would be possible for his *cay* to insinuate itself between the northern limits of his range for *C. apella nigrinus* and the southern limit to the range of *C. apella libidinosus*. Vieira (1944) regarded this form as distinct on the basis of six skins from Franca, northern São Paulo, and considered it a subspecies of *Cebus libidinosus* which, geographically, would make sense. He described it as having black/chestnut general color, a black head to the nape (with two tufts like those of *C. a. nigrinus*), the temporal region, face and forehead yellowish-white, the tail dark chestnut at the base and black at the tip, and the throat and chest grayish brown, becoming darker on the ventrum. The arms, thighs, legs are chestnut brown washed with yellow, hands and feet nearly black, toes and fingers yellowish. Cabrera (1957) listed *Cebus apella versutus* and described it as having a limited distribution in the south-west of the state of Minas Gerais and the north-east of the state of São Paulo (copying Vieira [1955]).

Cebus frontatus Kuhl, 1820

White cheeked capuchin

Type locality: Unknown.

Groves (2001) was unable to allocate this name to any of the subspecific forms he recognized, although he suggested it might be a poorly preserved specimen of a subspecies of *Cebus nigrinus*. The description of *Cebus frontatus* Kuhl, 1820 was based on captive animals of unknown provenance. Pinto (1941) and Vieira (1944) identified five specimens in the São Paulo Museum as *C. frontatus* (see Torres, 1983). Pinto (1941) provided a drawing of the face, but Hill (1960) illustrated it with a drawing of a sketch of the holotype in the Paris museum made by P. Dandelot, which Torres (1983) found bore no resemblance to the type. The description by Hill (1960) was as follows: “Pelage long, uniformly dark brown, with the hairs of the crown radiating from a centre on the vertex and elongated anteriorly to form a transverse frontal diadem on both sexes; lateral frontal tufts present and said by Vieira (1944) to differentiate this race from *cirrifer* (= *nigrinus*)”.

Vieira (1944) pinpointed the lack of distinct tufts and a longer pelage in the form *frontatus* to distinguish it from *C. a. nigrinus*. Although lacking a type locality, Vieira (1944, 1955), listing it as a full species, with *Cebus lunatus* Kuhl 1820 as a synonym (as argued by Elliot, 1913), gave the distribution as the

mountainous coastal region of southern Brazil, in the state of São Paulo (Alto da Serra, Serra de Paranapiacaba, Cananéia), extending south into the states of Paraná, and north-east Santa Catarina (Colônia Hansa [now Corupá]: type locality of *Cebus caliginosus* Elliot, 1910). This would restrict *C. a. nigrinus* to the states of Espírito Santo and Rio de Janeiro, and northern São Paulo, perhaps to the north of the Rio Tietê, or Rio Paranapanema, although Vieira (1955) also records the north of the state of Paraná for this species. The distribution given by Hill (1960) repeats *verbatim* that provided by Vieira (1955). Interestingly Hill (1960) gives the locality of São Sebastião for *C. a. nigrinus*. This island is off the São Paulo coast, east of Alto da Serra, and Hill's distribution map for *Cebus apella* (between pages 462 and 463) gives the two subspecies as sympatric. Torres (1983) argued that Pinto (1941) incorrectly identified the São Paulo specimens as *frontatus* and, relating various other confusions, misidentifications and anomalies, concluded that "this form is better considered unidentifiable." (p.239).

Cebus xanthosternos Wied, 1820

Cebus xanthosternos Wied, 1820

Yellow-breasted capuchin, buff-headed capuchin monkey

Type locality: Boca d'Obu, Belmonte, Bahia

Elliot (1913) considered the name *xanthosternos* to be a junior synonym of *C. variegatus* E. Geoffroy, 1812. His description of *variegatus* is indeed close to that of *xanthosternos*, while he also includes as synonyms *robustus* and *cucullatus*, in which case he is right in asserting that "this is an exceedingly variable species." *Cebus xanthosternos* is a very distinct form because of the large, round head, with smooth forehead and crown, the hairs being short and adpressed and not tending to form tufts or crests laterally. The black area on the crown is reduced to a small rounded spot, leaving a large area of yellowish tinge on the forehead and temples. The shoulders, front of arms, and chest or entire underparts, are pale yellow to orange.

Vieira (1955) regarded *Cebus xanthosternos* Kuhl, 1820 to be a junior synonym of *Cebus variegatus* E. Geoffroy, 1812, and gives the distribution as Bahia (Belmonte, Vila Nova); Espírito Santo (Colatina); Rio de Janeiro. Vieira also recognized *C. robustus*, describing a sympatric distribution in southern Bahia and Espírito Santo. Hill (1960) also incorrectly extended the distribution south through the range of *robustus* and part of *nigrinus* into Rio de Janeiro. Pinto (1941) argued for the validity of the form *xanthosternos* (as a distinct species) on the basis of skins collected by Ernst Garbe from Vila Nova (now Senhor do Bonfim) in the north-west of Bahia, near the headwaters of the Rio Itapicurú. The validity of *C. a. xanthosternos* as distinct from *C. a. robustus*, has been argued by a number of recent authors (Coimbra-Filho, 1986; Kierulff et al., 2004; Oliver & Santos, 1991; Rylands et al., 1988; Seuánez et al., 1986; see also Torres, 1983, 1988). The distribution of this form was reviewed by Coimbra-Filho et al. (1991, 1991/1992), and Oliver & Santos (1991), and extends throughout the region north of the Rio Jequitinhonha north and west to the Rio São Francisco in Bahia, southern Sergipe, and parts of northern Minas Gerais, wherever suitable habitat is available. In large areas of this dry xerophytic thorn scrub where the deciduous caatinga forests have been

decimated, it is not. A record from the Rio Jucurucú, to the south of the Rio Jequitinhonha (C. A. Camargo in 1932; see Kinzey, 1982) is enigmatic, being the domain of *C. a. robustus*, also collected from this locality. This locality is listed by Vieira (1955) and might be the reason for the confusion in the distributions. One supposes it might have been a pet animal taken from southern Bahia north of the Rio Jequitinhonha.

Cebus apella (Linnaeus, 1758)

Cebus apella (*sensu* Groves, 2001) includes the following six subspecies: *Cebus apella apella* (Linnaeus, 1758); *Cebus apella fatuellus* (Linnaeus, 1766); *Cebus apella margaritae* Hollister, 1914; *Cebus apella macrocephalus* Spix, 1823; *Cebus apella peruanus* Thomas, 1901; and *Cebus apella tocantinus* Lönnberg, 1914.

Cebus apella apella (Linnaeus, 1758)

Brown capuchin monkey, tufted capuchin monkey

Type locality: "America," restricted to French Guiana by Humboldt (1812) (Groves, 2001).

Type locality: "Guiana", restricted by E. Geoffroy (1812) to Cayenne, by Thomas (1911) to Suriname (Dutch Guiana), and by Tate (1939) to Guyana (British Guiana) (Hill, 1960).

Only one Amazonian tufted capuchin monkey has been recognized over the last 30 years: *Cebus apella apella* (for example, Eisenberg, 1989; Eisenberg & Redford, 1999; Emmons & Feer, 1997; Nowak, 1999 and Wolfheim, 1983;): an uncomfortable situation considering the degree of speciation that has evidently occurred in other primates of the region. It would seem that the stronghold of *Cebus apella apella* is the Guianas, and Brazil, at least east of the Rio Negro. Boher-Bentti & Cordero-Rodríguez (2000) extended it to the southern extreme of the Orinoco Delta (the village of Curiapo), although it is otherwise not recognized as occurring in eastern Venezuela (Bodini & Pérez-Hernández, 1987; Linares, 1998). Its northern limit in Venezuela is in the Federal Territory of Amazonas, where it occurs along both sides of the upper Rio Orinoco, with its precise range being limited by savannas.

In the scheme of Groves (2001), the range limits to the west and the south of the Rio Amazonas are constrained by *C. apella macrocephalus* and *C. a. tocantinus* respectively. Hill (1960) indicated that *C. apella apella* occurred south of the Rio Amazonas from the Rio Xingu east to the Rio Maruim in Maranhão, excluding in his map (between pp.462 and 463) the lower Rio Tocantins, domain in his view of *C. apella tocantinus*. In his text on the distribution of *Cebus apella apella*, Hill (1960) also attributed the Rio Iriri a west bank tributary of the Rio Xingu to the form *tocantinus*. In the southern Amazon, *C. apella apella* would be restricted by the transition to *Cerrado*, the bush savanna of central Brazil, where *C. libidinosus libidinosus* occurs. Groves (2001) gave the range of *C. apella macrocephalus* as extending east to the Rio Tapajós, south of the Rio Amazonas, and mentioned material from Itacoatiara on the north bank, also listed as a locality for *macrocephalus* by Cruz Lima (1945) and Vieira (1955). Itacoatiara is east of Manaus, and would therefore be an incursion into the Guianan range of *Cebus apella apella*. Vieira (1955) gives the locality of Manaus for *C. apella apella*, and Itacoatiara, about 100 km east, for *C. fatuellus*

macrocephalus. Vieira (1955) placed *C. fatuellus macrocephalus* throughout the middle Amazon of Brazil, east as far as the Rio Xingu (Redenção), and listed localities such as Codajáz (north of the Rio Solimões, west of the Rio Negro), Jaburú on the Rio Purús, and south through Rondônia to the Rio Guaporé and northern Mato Grosso, north of Cuiabá. Consensus on the range of *C. apella apella* is only on the Guiana Shield east of the Rio Negro and south of the Rio Amazonas, east of the Rio Xingu.

Simia trepida Linnaeus, 1766

Type locality: Suriname, Dutch Guiana.

This Linnaean capuchin monkey from the Guianas was listed by Tate (1939), Cruz Lima (1945) and Vieira (1955). Tate (1939) attributed material from French Guiana and from Brazil (a series from Faro, Rio Jamundá [= Nhamundá]) to this form. Although Cruz Lima (1945) indicated that he was inclined to “filiate to it the representatives of the group *fatuellus* from the left bank of the lower Amazon to the Guianas” (p.146), the capuchin monkey that he placed in the Guianas was *Cebus apella apella*. Vieira (1955) listed it as the form of the “Guianas; Brazil: Amazonas (left bank of the lower Amazonas.” Hill (1960) and Groves (2001), considered it a junior synonym of *Cebus apella apella*, named by Linnaeus himself eight years earlier.

Cebus apella fatuellus (Linnaeus, 1766)

Colombian brown capuchin, brown horned capuchin, hooded capuchin

Type locality: Unknown, but assigned by Tate (1939) as the “Forests of the Upper Magdalena valley with Tolima, from “5000 to 7000 feet” (Elliot)”

Hernández-Camacho & Cooper (1976) discussed the type locality assigned by Tate (1939), indicating the probability that it was in the Department of Huila, which prior to 1900 was known as the State of Tolima. According to Hill (1960) the range of this form is eastern Colombia, possibly extending southwards along the lower slopes of the Andes into Peru, where it would meet the range of *C. a. peruanus*. Groves (2001) added that he had seen specimens from Villavicencio and other localities on the Río Guaviare in Colombia, and on the Rio Negro. Hernández-Camacho & Cooper (1976) mapped the distribution of *Cebus apella* in Colombia in some detail, although they made no attempt to apply subspecific names. It occurs throughout the Colombian Amazon and foothills of the Andes (to at least 1,300 m). There is also an isolated population in upper Río Magdalena in the Department of Huila up to 2,700 m in the region of San Agustín and a small part of the Department of Cauca (Tierradentro) at altitudes of up to 2,500 m near Inzá. It extends north as far as the Río Arauca on the Venezuelan border. Hill (1960) indicated a range for *C. apella fatuellus* which included eastern and north-central Colombia, along with a large part of western Venezuela up to Lake Maracaibo. According to Bodini & Pérez-Hernández (1987) and Linares (1998) *Cebus apella* occurs only in southern Venezuela. Although Hernández-Camacho and Cooper (1976, p.59) did not attempt to distinguish subspecific forms in Colombia, they stated that “We remain unconvinced, on the basis of examinations of over 120 widely distributed museum specimens, that *Cebus apella* north of the Amazon from

Colombia eastward exhibit phenotypic distinctions that would justify the recognition of more than one subspecies throughout this large region”. Presuming that Colombian populations are those which Groves (2001) is recognizing as *C. apella fatuellus*, the question remains as to the southern limits (Río Putumayo?) where it would meet *C. apella peruanus*, and western limits, where it would meet *C. apella macrocephalus*, or *C. apella apella* if *macrocephalus* were to be restricted to the south of the Río Amazonas, as indicated by Aquino & Encarnación (1994).

Cebus apella macrocephalus Spix, 1823

Large-headed capuchin

Type locality: Brazil, forests of Lago Catuá, Rio Solimões, Amazonas.

Recognized by Hill (1960) and Groves (2001), this is the form occurring in the upper Amazon, east of the Río Ucayali (Aquino & Encarnación, 1994). According to Hill (1960), from there it ranges east, traversing the lower and middle stretches of the southern tributaries of the Rio Solimões-Amazonas as far as the Rio Tapajós. The distribution given by Groves (2001, p.153) is as follows: “This subspecies ranges widely through the middle Amazon: Lönnberg (1939) recorded it from Codajáz, Itacoatiara and Lago Cuitena north of the Amazon, the Rio Purús and Prainha [Rio Madeira] and other localities east of the Rio Tapajós.” Cruz Lima (1945), following Lönnberg (1939), listed a specimen from Prainha as *C. libidinosus libidinosus*. Vieira (1955), besides listed localities on the Rios Purús, Amazonas-Solimões (including Itacoatiara, invading the range of *C. apella apella*), Guaporé (Rondônia), Tapajós, and Xingu. There is a conflict in this case as to the identity of the tufted capuchin in the interfluvium of the lower Rios Madeira and Tapajós, with both *C. a. tocantinus* and *C. macrocephalus* being candidates (see below).

Cebus apella peruanus Thomas, 1901

Peruvian tufted capuchin

Type locality: Peru: Huaynapata, Maracapata, 760 m, Cuzco.

Aquino & Encarnación (1994) gave a distribution for *C. apella peruanus* as north of the Ríos Madre de Dios and Inambari to the right (south) bank of the Río Purús to its headwaters. Moving north, Aquino & Encarnación (1994) indicated an unknown, but distinct *Cebus apella* subspecies for the Río Pachitea basin, “The specimens from the montane forests between 800 m and 1000 m a.s.l. from the Departments of Huanáco, Pasco and Junín show distinct phenotypical characters and might belong to a fifth subspecies.” (p.36). North of there and west of the Río Ucayali, is the form *maranonis*, extending across the Río Marañón basin to the Río Putumayo. *Cebus apella maranonis* Pusch, 1941, from “Peru: Hamburgo 5°S, 75°W”, was recognized by Aquino & Encarnación (1994), but considered a junior synonym of *peruanus* by Groves (2001). Aquino & Encarnación (1994) placed *C. a. macrocephalus* east of the Río Ucayali and north of the Río Purús in Peru. If Groves (2001) is correct in synonymizing *C. a. maranonis* with *C. a. peruanus*, this implies that the unidentified form from the Pachitea basin, separating as it does the distributions of the two, is also attributable to *C. a. peruanus*.

Cebus apella tocantinus Lönnberg, 1939

Tocantins tufted capuchin

Type locality: Brazil: Cametá, Rio Tocantins.

This form was first described as a subspecies of *Cebus fatuellus*, and listed as such by Cruz Lima (1945) and Vieira (1955). Lönnberg (1939) described it as a dark race (general body color is dark, chestnut brown, becoming rufous towards the flanks), very similar to *peruanus*. He associated this with the fact the two forms occurred in areas of particularly high rainfall. These *peruanus* and *tocantinus* were recognized as distinct taxonomic entities by both Lönnberg (1939) and Groves (2001) due to their geographic separation south of the Rio Solimões-Amazonas by the forms *macrocephalus* and *apella*. The range given by Hill (1960) was a small blob around the type locality at the mouth of the Rio Tocantins, otherwise entirely surrounded by *Cebus apella apella*. Groves (2001) stated that he had seen specimens from the south bank of the lower Amazon as far west as the Rio Madeira. This would take in part of Hill's (1960) ranges for *C. apella apella* (between the Rios Tocantins and Xingu) and *C. a. macrocephalus* (between the Rios Tapajós and Madeira). Lönnberg (1939) indicated that it occurs some way to the southwest of the type locality, presumably between the Tocantins and Xingu at least.

Cebus magnus von Pusch, 1941

Type locality: Peru: Rio Putumayo, N. 1°, W. 76°.

This form was recognized by Hill (1960), who described it as "much resembling *macrocephalus*" but larger, due chiefly to longer fur, and having light-colored bases to the dorsal hairs. The distribution given by Hill (1960) is the western Colombian Andes (Putumayo Department), in a small range of the uppermost reaches of the Rios Caquetá, Putumayo and Napo. This is contiguous with the northern part of the range of *C. apella maranonis* postulated by Aquino & Encarnación (1994). Groves (2001) considered it a junior synonym of *C. apella peruanus*.

Cebus apella margaritae Hollister, 1914

Margarita Island capuchin

Type locality: Venezuela, Margarita Island.

Today restricted to the highlands of the island of Margarita, Venezuela (Sanz and Marques, 1994), Groves (2001) had reservations of the taxonomic status of this subspecies. It is darker than the *Cebus apella* in the Federal Territory of Amazonas, on the upper Orinoco in Venezuela (Linares, 1998). It is well separated geographically from all other tufted capuchin monkeys, the nearest population being the southern extreme of the Río Orinoco delta (Boher-Bentti & Cordero-Rodríguez, 2000). Groves (2001; see also Linares, 1998) supposed that it was introduced in Pre-Columbian times, and found it to be more closely allied to *C. a. fatuellus* than with *C. a. apella*.

Discussion

Although Torres (1983) explicitly avoided applying names, the species, and in some cases the subspecies, recognized by Groves (2001), can be roughly ascribed to the

six areas she identified (in parentheses are other forms discussed here):

1. Western Amazonia – *C. libidinosus pallidus*, *C. libidinosus juruanus*, *C. apella macrocephalus*, *C. apella peruanus*, (*C. magnus*)
2. Middle and lower Rio Amazonas and the Guianas – *C. apella apella*, *C. apella tocantinus*, (*Simia trepida*)
3. Eastern Bahia – *C. xanthosternus*
4. Eastern Minas Gerais and Espírito Santo, north of the Rio Doce – *C. nigrurus robustus*
5. Coastal areas of São Paulo, Paraná, and Santa Catarina – *C. nigrurus nigrurus*, *C. nigrurus cucullatus*, (*C. frontatus*)
6. Central and north-east Brazil – *C. libidinosus libidinosus*, *C. libidinosus paraguayanus*, (*C. versuta*)

The next task is to ground-truth the hypothesis of Groves (2001), and our aim in this short review was to provide a geographical basis to begin doing so. Here we summarize some of the major issues in defining the boundaries of the ranges of the species and subspecies, the resolution of which will undoubtedly reflect back on, and probably modify, the taxonomy that Groves (2001) proposed.

Cebus libidinosus pallidus and *C. libidinosus paraguayanus* have both been identified as the tufted capuchin of Paraguay (east of the Rio Paraguai), the Pantanal of Mato Grosso, in Bolivia and north-west Argentina. A key area is the Río Madre de Dios. If, as postulated by Anderson (1997), *C. libidinosus pallidus* occurs in central and northern Bolivia through the Pando region to the north of the river, then where does its range stop to meet that of *C. apella peruanus*? If *C. apella peruanus* is the form occurring to the north of Bolivia in Brazil, then this would isolate the form *C. libidinosus juruanus* from its conspecifics. If we follow Aquino & Encarnación (1994), *C. apella peruanus* occurring along the right bank of the Rio Purus would clearly separate the upper Juruá tufted capuchins from any other subspecies of *libidinosus* (see maps, figure 1.4 & 1.5 of Fragaszy et al., 2004). Groves (2001) considered *C. apella maranonis* of Aquino & Encarnación (1994) to be a synonym of *peruanus*, and this would place *peruanus* as the form in the Andean foothills through most of Peru, and presumably Ecuador extending to Colombia. Although Colombian tufted capuchins were well-mapped by Hernández Camacho & Cooper (1976), the question remains as to the range limits defining *peruanus* and *fatuellus*, perhaps the Río Putumayo, and *fatuellus* with *C. apella apella* (perhaps the Rio Negro) and *C. apella macrocephalus* to the east, although Aquino & Encarnación (1994) restrict *macrocephalus* to the south of the Río Amazonas. Going east thorough the Amazon basin, Aquino & Encarnación (1994) clearly place *C. apella macrocephalus* east of the Río Ucayali, but where this form meets *C. apella apella* (somewhere along a north-south trajectory through the middle Amazon it seems) or perhaps *C. apella tocantinus* (unless its range really is just a blob or a sliver otherwise surrounded by *C. apella apella*) is not known. *C. apella* seems to have been firmly identified for the Guaiana Shield at least east of the Rio Negro, as well as east from the Rio Tocantins.

Central Brazil is complicated, as indicated by Torres (1988), both in terms of taxonomy and distributions. The enormous variability may be due to natural climate and vegetation changes

in landscapes of forest patches, *cerrado* forest, dry forests, and gallery forest where one can imagine that the tufted capuchins are often “living on the edge”, and which have also suffered widespread decimation even since Pre-Columbian times (Coimbra-Filho & Câmara, 1996). To understand the inland range of *Cebus xanthosternos*, for example, one is first challenged to even find them. As Torres (1988) pointed out, another aspect which has confused, perhaps irreparably, our attempts to understand the diversity and ranges of tufted capuchins, in central and particularly north-east Brazil, is the widespread trafficking and mixing of the monkeys as animals are transported as pets. *Cebus apella robustus* is a well-defined taxon, with it seems a well-defined range, although the western limits, probably marked by the Serra do Espinhaço in Minas Gerais are poorly known, and perhaps never will be with the loss of its forests. What are the range limits defining the boundaries of *C. libidinosus libidinosus* with *pallidus/paraguayanus*? Which tufted capuchins occur in northern Minas Gerais, east of the Rio São Francisco? The type locality of *Cebus versuta* is listed by Groves (2001) as a junior synonym of *C. apella paraguayanus*, while its type locality is eastern Minas Gerais (in the Triângulo Mineiro, north of the Rio Grande). This could only be within the range of *C. libidinosus libidinosus* or *C. nigrinus cucullatus*. Field surveys should help in identifying the boundaries where *C. nigrinus cucullatus* ranging along the right bank of the Rio Paraná and *C. nigrinus nigrinus* of the coastal Atlantic forest meet in the states in southern Brazil.

Groves' (2001) taxonomy of the tufted capuchins is a most interesting and challenging hypothesis. The broad variation in pelage patterns is disconcerting, and clearly evident even amongst individuals of the same group in such as *C. libidinosus* from central Brazil and *C. xanthosternos* from the state of Bahia (see, for example, Kierulff et al., 2004). An understanding of this variation will require attentive and careful documentation of wild populations in key areas of their ranges, armed with a good understanding of what to look for and the range of characters which are beginning to allow for some notion as to their classification into geographic groups to which names can be applied. The aim, above all, is to be aware of their diversity so that it can be conserved. If we can make sense of it—all the better.

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