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NEW SERIES, NO. 55

Titis, New World Monkeys of the Genus *Callicebus* (Cebidae, Platyrrhini): A Preliminary Taxonomic Review

Philip Hershkovitz

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Titis, New World Monkeys of the Genus *Callicebus* (Cebidae, Platyrrhini): A Preliminary Taxonomic Review

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Titis, New World Monkeys of the Genus *Callicebus* (Cebidae, Platyrrhini): A Preliminary Taxonomic Review

Abstract

Tropical American titis, genus *Callicebus* (Cebidae, Callicebinae), are described in terms of external, cranial, postcranial, dental, and cerebral characters. Comparisons are made with other platyrrhines, including all other nonprehensile-tailed cebids. As presently constituted, the genus consists of 13 species and 16 included subspecies, each described and defined here. The systematic arrangement, in four species-groups roughly equivalent to size groups from smallest to largest, is based on trenchant morphological characters. The *modestus* group consists of a single species which appears to be the most primitive living cebid. The *donacophilus* group, comprised of three species, is nearer the *moloch* group, the latter with eight species including *dubius*, and *personatus*, largest of the genus. The geographic ranges of several species of the *moloch* group overlap those of others. The *torquatus* group contains a lone species that differs grossly from all other cebids in its combination of external, skeletal, and cytogenetic characters.

I. Introduction

This is the sixth and last of a series of preliminary and abridged taxonomic reviews of six genera of the nonprehensile-tailed New World monkeys of the family Cebidae, comprising Volume 2 of *Living New World Monkeys* (*Platyrrhini*) (Hershkovitz, in prep.). Preceding reviews by this author were of *Aotus* (1983), *Saimiri* (1984), *Chiropotes* (1985), *Cacajao* (1987a) and *Pithecia* (1987b).[1]

Callicebus proves to be the most complex and diversified genus of the platyrrhine group. In my earlier review (1963a), only three species were recognized; the number now is 13. The earlier study was based on little more than 100 specimens, all but a few in the collection of Field Museum of Natural History. The present account results from the study of nearly 1,200 specimens of *Callicebus* preserved in 22 North American, South American, and European natural history collections. No less important than the greater number of specimens available for the present study was newly gained cytological information, and insights into evolutionary pathways in tegumentary coloration.

This preliminary report as in the case of the earlier ones is intended to give advice of revised taxonomic arrangements, descriptions of new species and subspecies, and changes in scientific nomenclature. Where appropriate, new ideas are broached and controversial subjects explored. Because of limitations of time and space, the synonymies are abridged and the taxonomic accounts are reduced to the minimum required for accurate identifications. A short article on titi behavior has been published elsewhere (Hershkovitz, 1987c). Studies on the origin, dispersal, and differentiation of the species and subspecies of *Callicebus* have been incorporated in an independent article

[1] The dedication of *Pithecia irrorata vanzolinii* to Dr. Paulo E. Vanzolini was inadvertently omitted from the *Pithecia* revision (Hershkovitz, 1987). The naming is in recognition of one of the most preeminent Brazilian scientists, who has accorded unstinted attention and assistance to me and every other scientist making use of the natural history material preserved in the Universidade de São Paulo Museu de Zoologia.

(Hershkovitz, 1988). This and many other topics of *Callicebus* biology not mentioned here, and an exhaustive bibliography, are included in expanded form in Volume 2 of *Living New World Monkeys* (*Platyrrhini*) (in prep.).

II. Material

A total of 1,188 specimens of *Callicebus,* including extant types, were examined. Nearly all are represented by skin and respective skulls. The available 14 complete or nearly complete postcranial *Callicebus* skeletons represent *C. donacophilus* (6), *C. cupreus* (5), and *C. torquatus* (3). Comparisons were routinely made with skins and skeletal material of remaining nonprehensile-tailed genera and other platyrrhines. Results of continuing studies of hard and soft anatomical parts are included in Volume 2 of the monograph in preparation.

III. Methods

Culled and abridged synonymies are used here under the generic and specific or subspecific names. Full synonymies, in effect a complete chronological bibliography of each taxon, are given in Volume 2 of *Living New World Monkeys* (*Platyrrhini*) (in prep.).

Significant differences in color or color pattern between individuals and taxa are described and interpreted in terms of metachromism (p. 40).

Symbols for teeth are the first letter, in lower case, for each kind (example, i for incisor, but pm for premolar). A tooth of the upper jaw is indicated by a superscript (example, m^2 for second upper molar); a tooth of the lower jaw is indicated by a subscript (example, m_2 for second lower molar). This simple method is used uniformly throughout, irrespective of the symbol's positions in the text. Other symbols such as an upper case letter for upper teeth, and lower case letter for lower teeth (examples, M^1, m_1) are redundant, and self defeating if the letter, uppercase or lower, is the first in a sentence, paragraph, phrase, table, or key.

Summaries only of standard external, osteological, and dental measurements are given here. Other measurements are included where deemed necessary. In all cases, individual measurements, means, extremes, and ratios prove sufficient for due assessment or resolution of size-related problems of taxonomy or phylogeny.

IV. Abbreviations

The specimens of titis recorded here are preserved in the institutions listed as follows with their abbreviations.

AMNH = American Museum of Natural History, New York
BM(NH) = British Museum (Natural History), London BM only used for "Specimens examined"
EPNQ = Escuela Politécnica Nacional, Quito
INDERENA = Instituto de Desarrollo de los Recursos Renovables, Bogotá
INPA = Instituto Nacional de Pesquisas Amazônicas, Manaus
FMNH = Field Museum of Natural History, Chicago
LSUMZ = Louisiana State University Museum of Zoology, Baton Rouge
MHNM = Muséo de Historia Natural, Madrid
MNHNP = Muséum National d'Histoire Naturelle, Paris
MNHU = Museum für Naturkunde der Humboldt-Universität, Berlin
MNR = Museu Nacional, Rio de Janeiro
MPEG = Museu Paraense Emilio Goeldi, Belém
MVZ = Museum of Vertebrate Zoology, University of California, Berkeley
NHMW = Naturhistorische Museum, Wien
PPP = Proyecto Peruano de Primatología, Iquitos
RMNH = Rijksmuseum van Natuurlijke Historie, Leiden
RNHMS = Royal Natural History Museum, Stockholm
SEPSFA = Serviço do Estudos e Pesquisas Sôbre a Febra Amarela, Rio de Janeiro (most specimens deposited in MNR)
SNG = Senckenbergische Naturforschende Gesellschaft, Frankfurt
ULSM = Museo de la Universidad de La Salle, Bogotá
UMMZ = Museum of Zoology, University of Michigan, Ann Arbor
UNICN = Universidad Nacional, Instituto de Ciencias Naturales, Bogotá

USNM = National Museum of Natural History, Washington, D.C.

USPMZ = Universidade de São Paulo Museu de Zoologia, São Paulo

ZSM = Zoologische Staatssammlung, München

V. Genus *Callicebus* Thomas

Callitrix Hoffmannsegg, 1807: 86—type species, *Callitrix torquata* Hoffmannsegg by monotypy; generic name preoccupied by *Callitrix* Desmarest 1804, a synonym of *Cebus* Erxleben.

Callithrix É. Geoffroy, 1812a: 357—included species *Simia sciurea*, [= *Saimiri sciureus* Linnaeus], *S. personata* [here designated type], *S. lugens, S. torquata, S. amicta, S. moloch*; generic name a homonym of *Callithrix* Erxleben, 1777, for marmosets.

Saguinus Lesson, 1827: 56—included species, *Simia sciureus* [= *Saimiri sciureus* Linnaeus], *personatus, lugens, amictus, torquatus, moloch, melanochir, infulatus* [= *Aotus infulatus* Kuhl]; name preoccupied by *Saguinus* Hoffmannsegg 1807, a genus of tamarin.

Callicebus Thomas, 1903: 457—new name for *Callithrix* É. Geoffroy, preoccupied by *Callithrix* Erxleben, 1777, for marmosets.

Type species—*Callithrix personata* É. Geoffroy (= *Callicebus personatus* É. Geoffroy), by original designation (Thomas, 1903, p. 457).

VI. Geographic Distribution (figs. 1, 2)

The genus occurs throughout most of the tropical zone forests of the Amazon and Orinoco basins, parts of the Atlantic and Paraná forests of southeastern Brazil, and Paraná forests of Bolivia and Paraguay. In Venezuela, it occurs in the state of Amazonas south of the Río Ventuari and in the state of Bolívar between the Ríos Caura and Caroni; in Colombia, east of the Andes and south of the Río Tomo and upper Río Meta; in Ecuador, east of the Cordillera Oriental; in Amazonian Peru, from below 1000 m altitude; in Bolivia, the departments of Pando, northern La Paz, Beni, eastern Cochabamba, and Santa Cruz to about 18° south; in Paraguay, the Chaco between the Ríos Paragua and Pilcomayo; in Amazonian Brazil, west of the Rio Tocantins-Araguaia, south bank Rio Amazonas, and west of the Negro-Branco on the north bank, in the states of Roraima, Pará, Amazonas, Rondônia, and Acre; in the Atlantic forest of Brazil, east of the Rio São Francisco basin and the Rio Paraná-Paraiba, then south to the Rio Tietê, in the states of Bahia, Minas Gerais, Espírito Santo, Rio de Janeiro, and São Paulo.

Callicebus distribution is disrupted by the Brazilian *cerrado* which extends from the Rio Tocantins-Araguaia and Rio Paraguay-Taquari Novo on the west, to the Rios São Francisco and Paraná-Paraiba on the east, south into the States of Rondônia and Mato Grosso. The distributional lacuna between the Rios Aripuanã and Madeira (fig. 1) in central Brazil may be real and not because of neglect by investigators. Other large areas within the generic range with apparently suitable habitats are also without titis.

Apparently suitable titi habitats exist in *cerrado* gallery forests but the monkeys are not present. They must have lived there when forests were more extensive, interconnected, and communicating with Amazon and Atlantic coast rain forests. When *cerrado* gallery forests contracted into small isolated valley tracts with resources probably too limited to sustain titis, these monkeys, without haven in surrounding *cerrado*, disappeared. Now, *Callithrix jacchus, Cebus apella*, and *Alouatta caraya* are the only nonhuman primates in *cerrado* gallery forests. These generalist species also foray and forage widely in *cerrado*.

VII. Dispersal and Speciation

Centers of origin of the ancestral forms of each of the four species groups of *Callicebus* were probably the highlands on the western border of the present range of the genus (fig. 1). As habitats at lower elevations became available with receding rivers and retiring floodplains during Quaternary climatic changes, titi dispersal was downstream through gallery forests. Fragmentations and interruptions of dispersal routes by shifting and dividing riverbeds, and river bend cutoffs, separated and isolated populations. The longer and more effective the isolation, the greater the differentiation of the separated populations from each other and parental stocks. Reshuffling of river channels could have resulted in mutual absorption of erstwhile isolated populations, or sympatry between populations that attained species grade.

The concept of centripedal dispersal, with fluvial dynamics providing the isolated arenas for establishment of founder populations, was introduced by me (1963a,b) on the basis of an inade-

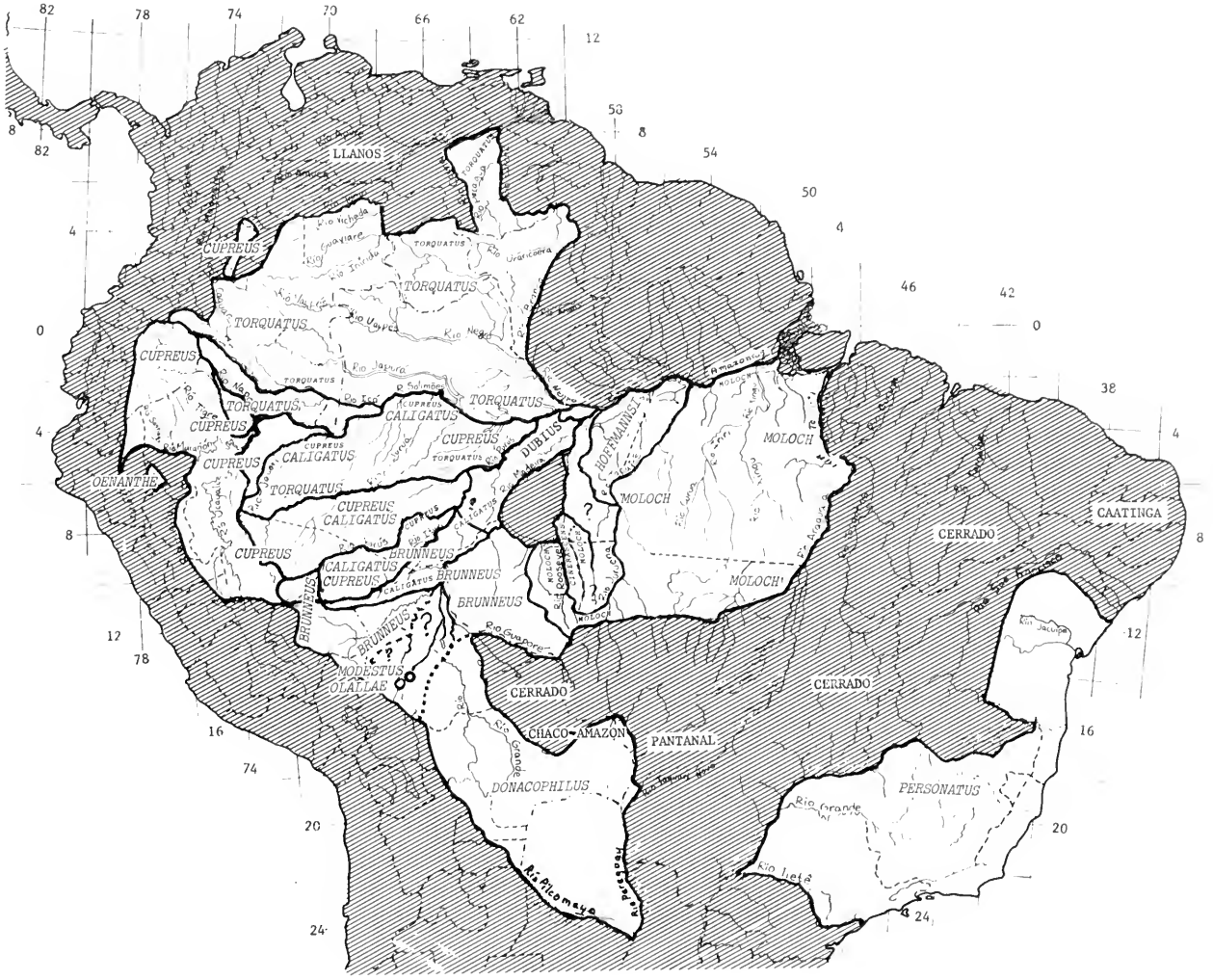

FIG. 1. Geographic distribution of the species of *Callicebus*. Names of sympatric species repeated where range boundaries overlap. Range maps of individual species are included in species accounts.

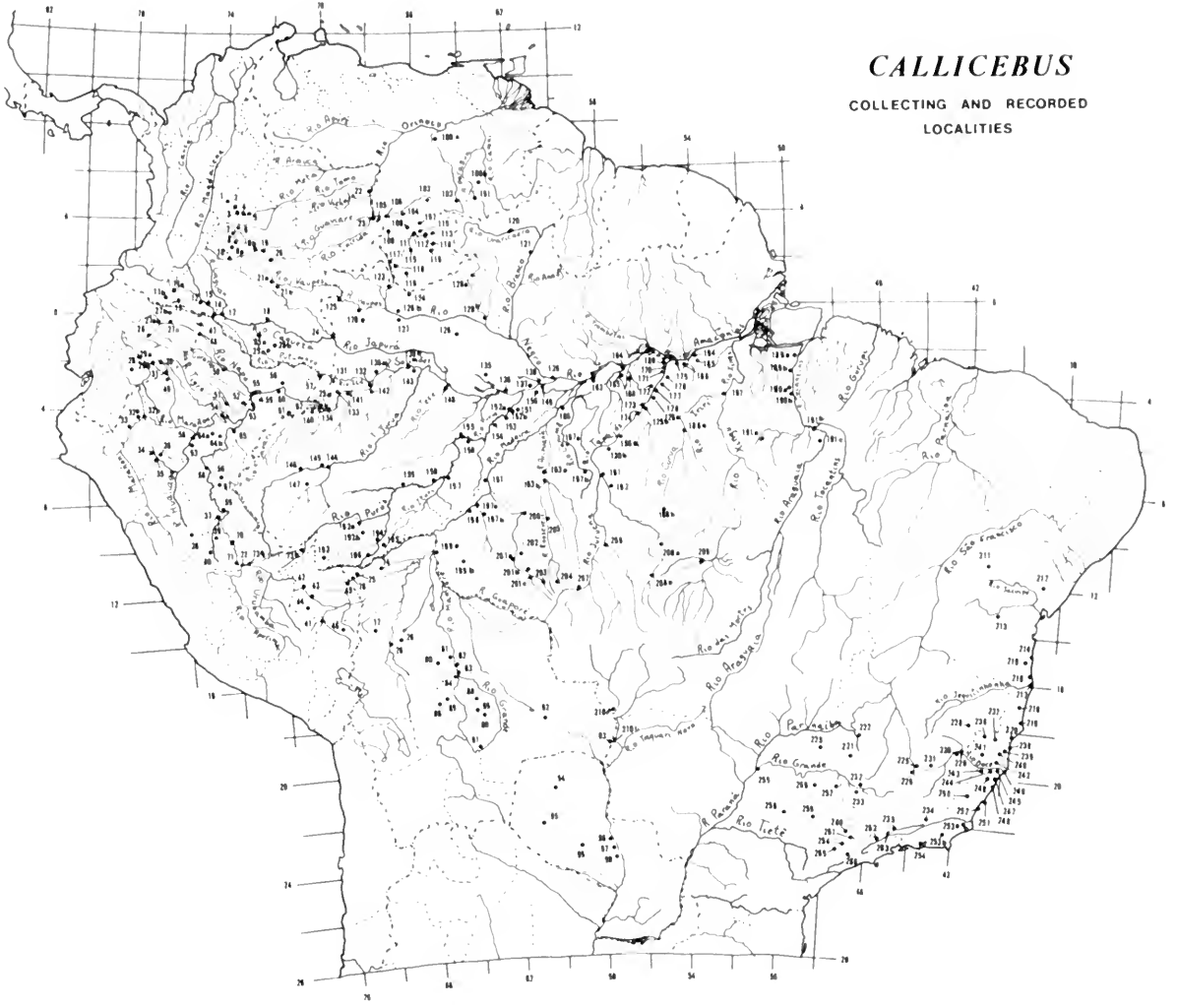

FIG. 2. Localities (numbered dots) where titis have been collected or recorded. Geographically clustered localities are indicated by the same numbered dot. See Gazetteer for names of numbered localities.

quate three-species taxonomy of *Callicebus*. The concept was somewhat refined (1972b, p. 395), expanded (1977, p. 413), and drastically revised (1988) with the benefit of critical zoogeographic data not previously consulted, and new morphological information.

An alternative explanation to the centripedal/fluvial dynamics concept of titi speciation was the hypothesis of forest refuges put forward by Kinzey (1982). His presentation was premised on the untenable three-species taxonomy of *Callicebus,* and a fancied correlation of the titi distributional pattern with mooted Pleistocene forest refuges postulated by others on the basis of taxonomic revisions of living insects, birds, and lizards. As shown by Hershkovitz (1988, pp. 248, 269), Kinzey's reconstructions are inconsistent with available data and mostly irrelevant.

Recent studies of past and present formation and ecology of the Amazonian basin support the hypothesis that river dynamics may be the major factor in creating and maintaining high species diversity (Salo et al. 1986, p. 254; Räsäner et al., 1987). In a review of the fluvial geomorphology of the Amazon basin, Salo (1987, p. 203) declared that "geomorphological barriers which could explain the observed distribution patterns [of biota] on the basis of present and past edaphic differences, rendering the Pleistocene forest refuge theory implausible and unnecessary." As for primates, Salo (1987, p. 208) noted that "Hershkovitz (1968, 1969, 1977) . . . has the merit of being the first author to clearly distinguish flood plain dynamics from the isolation effects of the river channels alone. He states that the shifting of river courses and, to a minor degree, waifing, where unoccupied territory was involved, was [sic] probably more effective in promoting speciation among Amazonian callitrichids during any one climatic regime than shifting climates during the entire Pleistocene (Hershkovitz 1977, p. 413)."

VIII. External Characters

Diagnostic

Titis are small rabbit-sized, nonprehensile-tailed, thickly furred or shaggy, somberly to brightly colored monkeys; visage tamarin-like, eyes not unusually enlarged, without whitish "spectacles" or circumocular band; overall size between that of tamarins and pitheciines, combined head and body length 270–450 mm, tail from about 10% to nearly 50% longer, average hind foot length about 95 mm (80–113), ear from notch about 32 mm (28–40); weight from 1 to 2 kilos; pedal digit I with tegula or nail, all remaining digits including manual I with short claws; muzzle comparatively short, narrow, nose not bulbous; face bare or moderately hirsute, the hairs short or long but not concealing skin; blackish supraorbital tufts well developed; forehead like crown or contrastingly blackish or whitish; crown uniformly colored like nape or contrasting, never striped, coronal hairs never tufted or whorled, always directed back and usually cresting against raised nuchal hairs; sideburns usually prominent, like crown or contrastingly colored; terminal half of hairs of back multibanded, sometimes faintly so, less frequently uniformly colored; tail either variegated but not distinctly banded, or uniformly colored with undersurface like upper, if nearly entirely or dominantly blackish with pencilled tip same or buffy; skin of face, ears, external genitalia blackish.

IX. Cranial Characters (figs. 3–7, 43)

Diagnostic

Greatest skull length (GSL) between 55 and 80 mm; basicranial index (condylobasal length, CBL: GSL) between 73 and 88; cerebral index (braincase volume, BCV:GSL) between 20 to 30; supraorbital ridges well defined, frontal bone above and between ridges (glabella) depressed or flattened; orbits with dorsoventral diameter slightly greater than mediolateral diameter, biorbital breadth less than zygomatic breadth; interorbital septum broad, pneumatized, not perforated; inferior orbital fissure nearly entirely closed; dental (palatal) arcade more nearly V-shaped than U-shaped; interpterygoid fossa reduced, compressed, or vestigial; frontal, maxillary, and ethmoidal sinuses greatly enlarged; mandibular angle broadly expanded.

Descriptive

Viscerocranium orthognathous, sometimes with muzzle produced forward (*C. modestus*), neurocranium dolichocephalic; premaxillae not forward projecting or markedly elongate; dorsal and lateral sutures, except interpremaxillary, obliterated in old individuals; contact between ascending or lateral

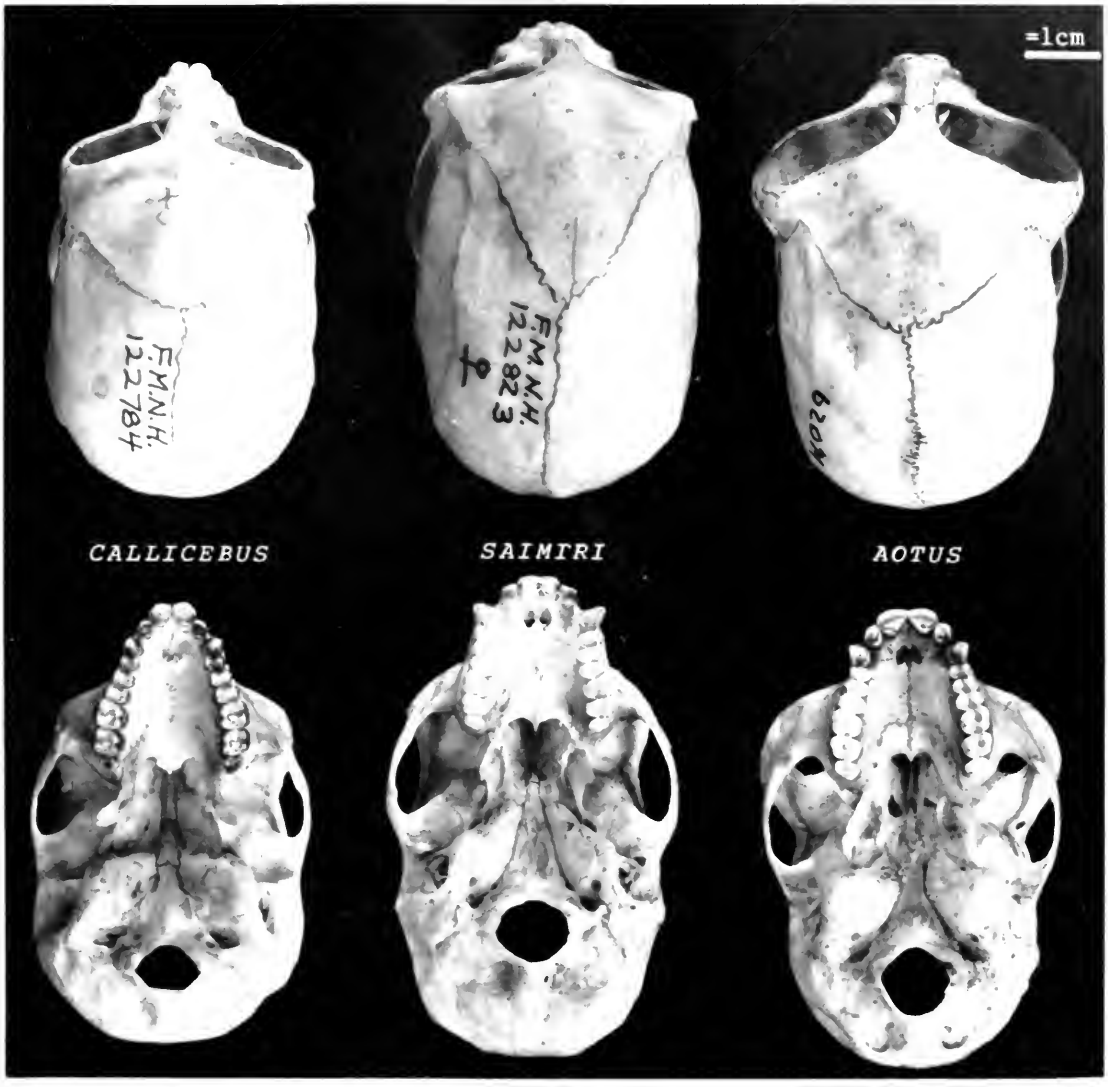

FIG. 3. *Callicebus, Saimiri, Aotus:* dorsal and ventral views of skulls of *Callicebus cupreus* (FMNH 122784 ♂), *Saimiri sciureus* (FMNH 122823 ♀), *Aotus nigriceps* (FMNH 62074).

process of premaxillary and nasal bones minimal or absent.

Dorsal outline of combined nasals narrowly subrectangular with slight expansion in front, square to bluntly pointed behind, the frontonasal sutures, however, becoming obliterated with age; dorsal contour of nasals plane to moderately concave, tips not extending beyond plane of acanthion perpendicular to Frankfurt horizontal; greatest combined width of nasals approximately equal to greatest width across unworn i^{1-1}, or less than half distance across outer alveolar borders of canines; nasofrontal region between nasion and glabella inflated.

Frontal bone behind supraorbital ridges depressed or flattened before rising to apex at midfrontal-parietal suture (bregma); metopic suture closed after eruption of m^1; longitudinal axis between parietal bones usually about 10% to 15% shorter than longitudinal axis between frontal bones, sometimes as long or up to 11% longer; superior temporal lines (ridges in old individuals) convergent across frontals but not meeting, distance between them at frontoparietal sutures at

FIG. 4. *Callicebus, Saimiri, Aotus:* left sides of crania and mandibles; same shown in Figure 3.

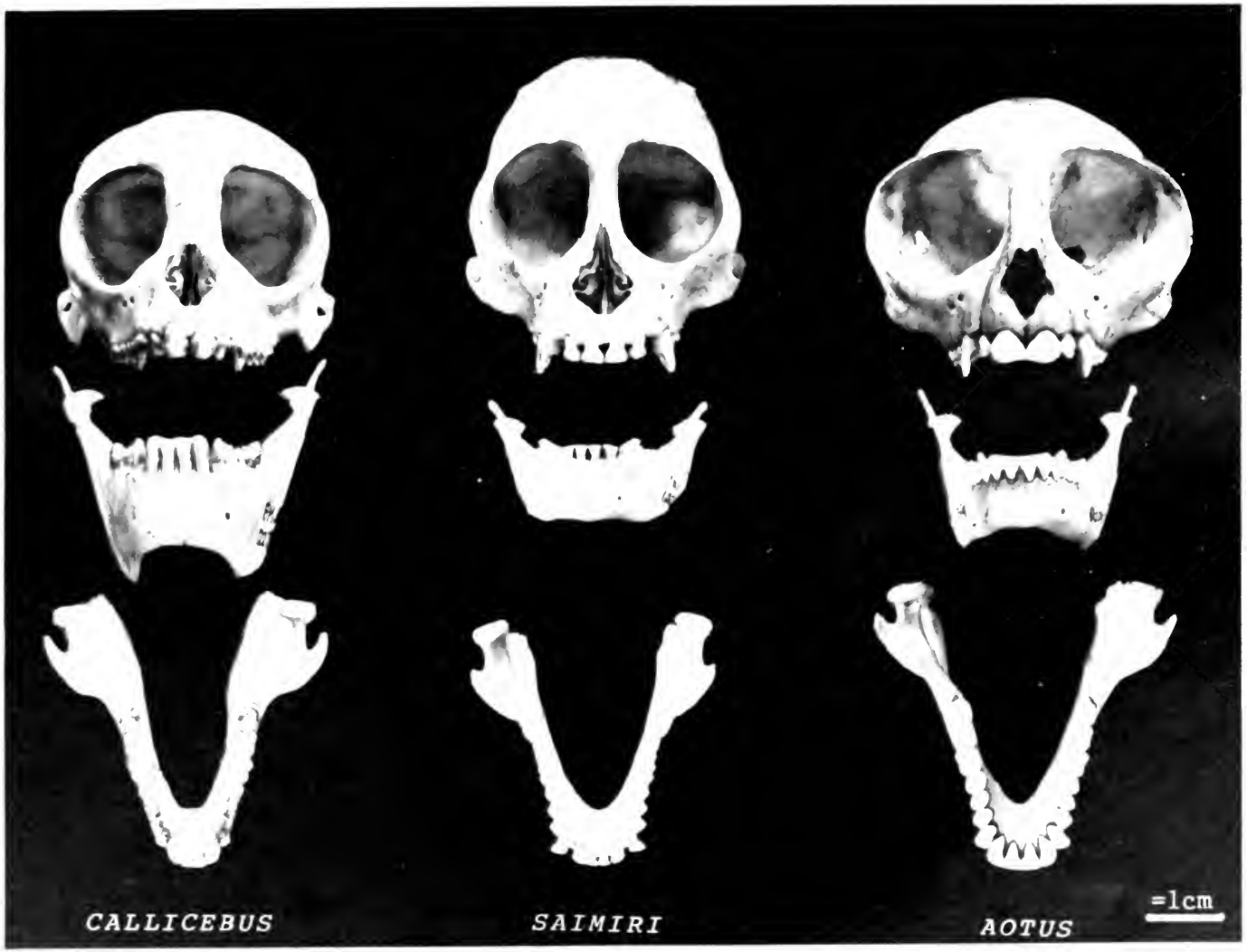

FIG. 5. *Callicebus, Saimiri, Aotus:* frontal views of crania, frontal and dorsal views of mandibles; same shown in Figure 3.

FIG. 6. Pterygoid processes of *Rousettus* (Pteropidae, Chiroptera), *Pteropus* (Pteropidae, Chiroptera), and *Aotus* (Cebidae); **a**, primitive pterygoid process, **b**, lateral or parapterygoid process (neomorphic).

least half greatest width of braincase, roughly parallel-sided or slightly convergent on parietal bones, then divergent, sometimes convergent but not meeting at junction with parieto-occipital suture; sagittal crest absent; distinct mastoid process absent, styloid process if present fused to ventral crest of tympanic bulla; frontal and maxillary sinuses enlarged.

Orbits well separated; interorbital septum at ethmoid bone extremely pneumatized, least interorbital width greater than greatest width across nasals and greater than combined width across crowns of inner pair of incisors (i^{1-1}); biorbital breadth slightly more or less than mastoidal breadth but greater (ca. 5%) than width of braincase; inclination of lateral orbital border about 65° to 75° relative to Frankfurt horizontal plane; lacrimal bone and fossa contained entirely within orbit, contact between nasals and lacrimals absent; infraorbital foramina (1–4) smaller than malar foramen, diameter of each 1 mm or less; inferior orbital (sphenomaxillary) fissure reduced, nearly completely concealed by surrounding orbital bones; postglenoid foramen small, obsolete, or absent.

Ethmoturbinal bone II vestigial or absent; communication present between orbitosphenoidal cells or sinus with ethmoidal sinus and nasal cavity; ostium between frontal sinus and nasal cavity large (fig. 45); auditory bulla comparatively large, anterior fourth subsquare, flattened, posterior two-thirds bilobed; dorsoventral axis of meatus nearly perpendicular to basicranial axis; carotid foramen exposed to view on ventral surface.

Upper dental arcade more nearly V-shaped than U-shaped, i^2 staggered behind i^1; diastema between canine and outer incisor small or absent; posterior borders of small incisive foramina prolonged to behind posterior plane of canines; palate extended behind to anterior plane of last molars or slightly beyond posterior plane; mesopterygoid fossa more nearly U-shaped than V-shaped; interpterygoid fossa greatly reduced, vestigial or virtually absent, the hamular process correspondingly small or vestigial but present; distance between pterygoid plates measured from base to base of hamular processes equal to or greater than distance across tips of canines; border of incisura Civini from nearly fully excised to nearly entirely closed; width of basioccipitobasisphenoidal suture about half or less the least median basioccipital length; presphenoid bone exposed on basicranial surface between vomerine plates.

Mandibular angle broadly expanded, produced well behind condylar-basal axis; coronoid process elongate, pointed, hooklike, produced well above condylar process; extremes of symphyseal angle 29°–65°. For additional description, illustrations, and comparative cranial characters consult Hershkovitz (1977, pages in subject index under *cranium*).

Pterygoid Processes (figs. 6, 7)

Variation in the structure of the pterygoid processes of the sphenoid bone may display distinctive characters in mammals generally; their evo-

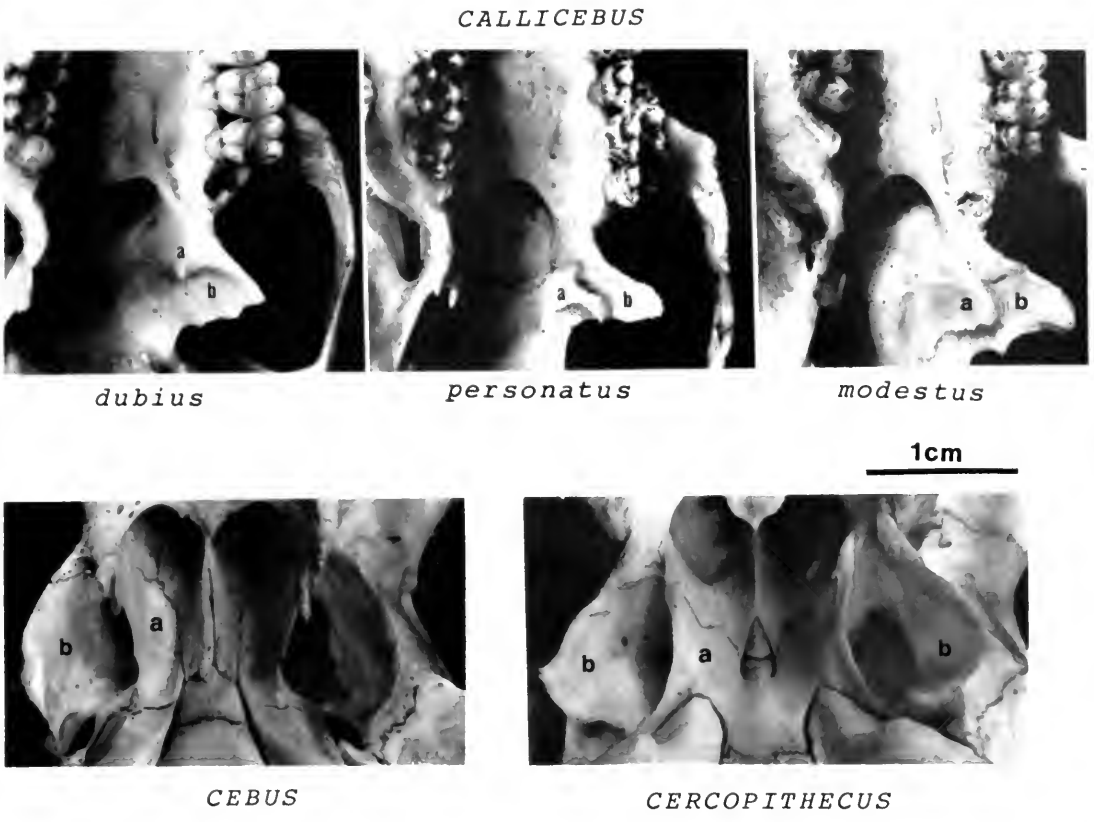

FIG. 7. Pterygoid processes of *Callicebus dubius* (holotype, FMNH 38886); *Callicebus personatus* (FMNH 61539); *Callicebus modestus* (lectotype, RHNMS 135); *Cebus albifrons* (FMNH 18867); *Cercopithecus kandti* (FMNH 27531); **a,** primitive pterygoid process, **b,** lateral or parapterygoid process (neomorphic).

lutionary history and differentiation in selected taxa have been described by Hershkovitz (1977, pp. 161–166). In primates, each pterygoid process consists of a pair of more or less divergent plates. The flaring lateral process or wing of the pterygoid plate is larger than the medial. Separation between them varies from a narrow slit to a large, deeply excavated bowl-shaped fossa. Whatever the degree of differentiation, the complex pterygoid system with lateral and medial plates appears to be primitive for primates. This is not true for all mammalian orders.

The pterygoid process in most marsupials, insectivores, bats, edentates, and carnivores is a relatively simple undivided vertical plate, continuous with and, except for the suture, hardly distinguishable from the sphenoidal process of the palatine bone. In more derived groups a ridge appears on the lateral surface of the primitive plate. With increasing differentiation the lateral ridge expands into a flaring triangular wing or plate, horizontal in some forms, canted to a nearly vertical position in others. The general trend appears to be toward greater expansion and complication of the lateral pterygoid wing or parapterygoid process with concomitant reduction of the primitive or medial pterygoid process. In fruit bats (Pteropidae) for example, the original pterygoid process persists as a simple plate in the genus *Rousettus.* In the larger *Pteropus* a well-developed neomorphic wing appears as a lateral horizontal process derived from the primitive pterygoid process (fig. 6).

In primates, the lateral process has attained greater size than the medial process, but both plates are well developed in catarrhines. In platyrrhines the overall evolutionary trend has been toward dominance of the lateral processes and, ostensibly, ultimate displacement of the original process as a functional and structural unit. The lateral process attains maximum expansion in *Cebus,* where the primitive or medial process is little more than a third the size but otherwise similar to that of most

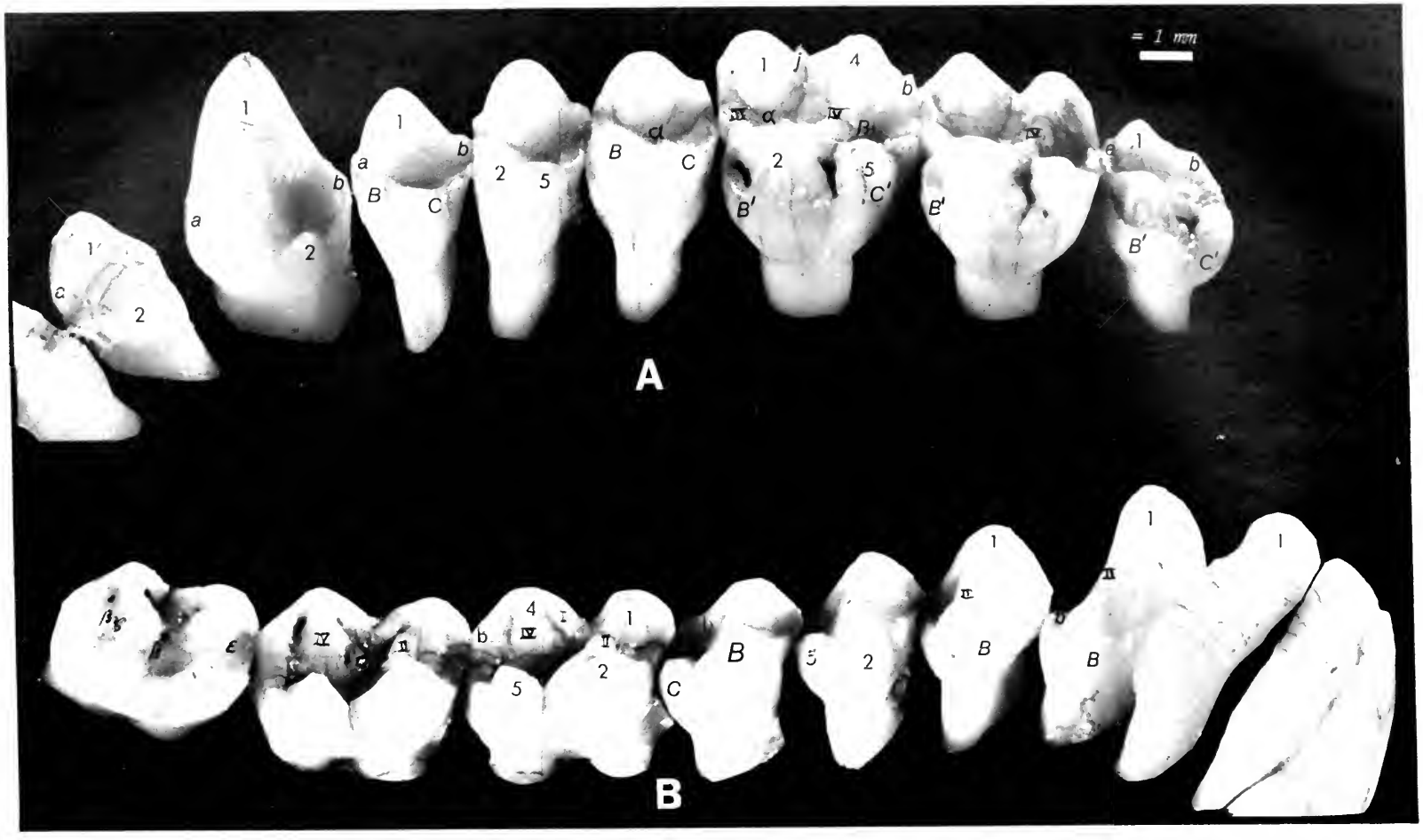

FIG. 8. **A**, Left upper and **B**, lower dental arcades of *Callicebus torquatus* (FMNH 70700) (distomedial portion of i^1 missing). Explanation of symbols, the homologues of lower teeth in parentheses: ***1***, eocone or paracone (eoconid or protoconid); ***2***, protocone (metaconid); ***4***, metacone (hypoconid); ***5***, hypocone (entoconid); ***a***, mesiostyle or parastyle (mesiostylid or parastylid); ***b***, distostyle; metastyle; hypoconule (distostylid, hypoconulid); ***d***, plagioconule or metaconule; ***j***, ectostyle or stylocone; ***I***, (centrocristid); ***II***, epicristid; ***III***, protoloph or protocrista; ***IV***, plagiocrista or metaloph (plagiocristid); ϵ, pretrigon basin or fossa; α, trigon basin or fossa; β, talon basin (talonid basin); $B\delta$, (pretalonid basin); ***B***, anterolingual or primary lingual cingulum; ***B'***, neoanterolingual or secondary lingual cingulum; ***C***, posterolingual cingulum or posterior shelf; ***C'***, neoposterolingual or secondary posterior cingulum. For description of symbols and figures of all dental types see Hershkovitz (1977, pp. 276–337).

catarrhines. In remaining platyrrhines, the medial process is comparatively degenerate. In most species of *Callicebus* it approaches obsolescence, its appearance that of a small hamular process of the lateral process. In *Callicebus modestus,* however, the medial process is better preserved than in congeners and nearly as large as that of *Aotus* or *Saimiri.*

X. Dental Characters (figs. 8, 9)

(For terminology and symbols, see p. 12; Hershkovitz, 1977, pp. 276–301)

Diagnostic

i^1 with cutting edge bluntly pointed, protocone present on lingual cingulum; i^2 staggered behind i^1; canine low, that of male not visibly larger than that of female, and with little or no separation from i^2; pm^2 lower than pm^3 on lingual aspect; molars heavy, brachyodont, cusps high, sharp, buccal and secondary lingual cingula usually well developed, often crenulated and marked with styles and accessary conules; m^1 largest; m^2 wider than any premolar; m^3 about as large as pm^2 or pm^3; lower canine usually lower in profile than i_2, without separation by diastema; pm_2 not differentiated as honing tooth, molarized like pm_3 but smaller; coronal outline of pm_4 roughly elliptical, not square; m_2 as large or slightly larger than m_1, much larger than any premolar; unworn molar basins deep, the talonid basin wrinkled, one or more conulids present.

Upper Tooth Row (fig. 8A)

Middle incisor (i^1) about as high as long but slightly narrower (front to back), tips broadly pointed becoming plane with wear, terminal styles (*a, b*) greatly reduced, not evident in worn tooth, lingual cingulum with well-formed protocone (*2*); outer incisor (i^2) about half bulk of i^1, staggered behind, approximately as long as wide or as high, crown pointed, terminal styles indicated, protocone present.

Canine, measured from cingulum, half again to two times higher than i^2, and pm^2, slightly separated from the first, touching the second; terminal styles weakly defined, the distostyle (*b*) usually

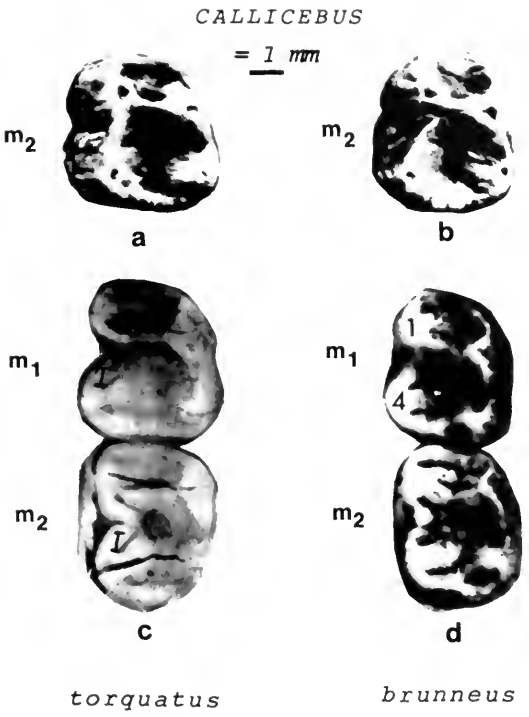

FIG. 9. Lower molars of *Callicebus torquatus* and *Callicebus brunneus*: **a, b** from Kinzey, 1978 (**a,** moderately worn, **b,** little worn); **c,** FMNH 70693, unerupted m_2 cracked; **d,** LSUMZ 12289, little worn.

stronger than mesiostyle (*a*); lingual cingulum well defined, protocone incipient or absent.

Premolars seen in profile from buccal aspect appear to increase or decrease in height from first to last, from lingual aspect decrease appears less; pm^2 with protocone well defined, hypocone incipient, secondary anterior lingual cingulum absent or incipient, distostyle when present slightly better defined than mesiostyle when present; pm^3 more molarized than pm^2, distostyle and secondary anterior cingulum (B′) more or less defined; molarization of pm^4 more advanced, coronal fossae usually well excavated, secondary anterior cingulum broader.

Molars heavy, brachyodont, cusps thick, pointed; m^1 largest, from as high to slightly lower than pm^4 but nearly three times its bulk, higher than m^2 and about a third to half again larger; metacone about as large as paracone to distinctly larger; protoconule poorly defined or absent, plagioconule (metaconule) present, absent, or more likely fused with metaloph, protocone about as large as either outer cusp but lower, hypocone from one-third to nearly as large as protocone, labial shelf (A) with

well defined ectostyle *j* (stylocone), ectostyles *k* and *l* minute or absent, terminal styles present or undefined, lingual shelf well defined and usually crenulated; m^2 essentially like m^1 but smaller; m^3 about half or third bulk of m^2, paracone and metacone relatively small, connecting eocrista without deep incisure, hypocone often absent, plagioconule usually present.

Lower Tooth Row (fig. 8B)

Cutting edge of incisive row plane or slightly concave (fig. 5), inner incisor half or less bulk of outer, body tapered to thick base without definite cingulum or terminal stylids; outer incisor subfalcate, cutting edge pointed, base thickened, anteroposterior length about equal to crown height, cingulum poorly defined in unworn tooth, metaconid absent, weak distostylid usually present.

Canine functionally an element of incisive field, subequal in height to outer incisor, sometimes higher, without diastema in front; lingual cingulum with or without metaconid, epicristid present or absent, distostylid present.

Premolars increasing in bulk, decreasing in height from first to last, male pm_2 like that of female, not differentiated as honing tooth; epicristids well defined; metaconid incipient to large in pm_2, well defined in pm_{3-4}; entoconid small or absent in pm_2, small to large in pm_{3-4}; terminal stylids (*a, b*) usually present; hypoconid absent.

Molars thick, brachyodont, quadritubercular; cusps high, pointed; m_1 smaller to sometimes as large as m_2; m_3 smaller than m_1, sometimes as large; epicristids sharp-edged; plagioconulid present, accessory conulids present or absent; terminal stylids present.

Variation

Dental characters of the species are essentially those described for the genus. Certain variables, however, particularly stylar and other supplementary elements of the upper cheek teeth of *Callicebus torquatus,* are more persistent and better defined than in congenerics. Differences are enumerated in box below. For terminology and symbols see Hershkovitz (1977, pp. 276–301).

The teeth of *Callicebus personatus* are generally more robust than those of most individuals of other species, but *C. personatus* is also more robust.

Centrocristid (Cristid Obliqua) (fig. 9)

Differences between *Callicebus torquatus* and *C. brunneus* in length and angle of the molar centrocristid, or cristid obliqua, described by Kinzey (1978), do not hold in material at hand. According to Kinzey, the cristid in *C. torquatus* is shorter, less sharply curved inward than in *C. brunneus.* This is thought to be correlated with a high ratio of insectivory (20% feeding time) and low folivory (4% feeding time) in *C. torquatus,* compared with lesser insectivory (1%) and greater folivory (26%) in *C. brunneus.* The different dental morphology of these species, however, is found in unworn or worn molars of each species. Structure of unworn m_2 of *C. torquatus* (FMNH 70693) and worn m_2 (MNR 2467) agrees with that of Kinzey's figured m_2 of *C. brunneus*; cristid of *C. torquatus* (FMNH 78582) matches that of Kinzey's *C. torquatus*; its talonid basin, however, appears to agree with that of his *C. brunneus.* A m_2 of a young *C. brunneus* (LSUMZ 12289) resembles that of Kinzey's *brunneus,* whereas an m_2 of an old *brunneus* (MNR 19234, FMNH 78673) concords with Kinzey's *torquatus.*

Callicebus torquatus (fig. 8)	**Other *Callicebus* species**
1. pm^{2-4}: Mesostyle (*a*) and distostyle (*b*) well defined.	1. pm^{2-4}: Styles *a, b,* absent in pm^2; absent, obsolete, or weakly defined in pm^{3-4}.
2. m^1: Mesostyle and distostyle well defined to absent (in well-worn teeth); metaloph (*IV*) well defined; metaconule (*d*) present or absent; protoloph (*III*) present; protoconule present or absent; stylocone (*j*) present or absent.	2. m^1: Styles weakly defined or absent; metaloph well defined; metaconule present or absent; protoloph rarely present; protoconule rarely present; stylocone absent.
3. m^3: Stylocone present or absent.	3. m^3: Stylocone absent.
4. m_{1-2}: Styloconid sometimes present.	4. m_{1-2}: Styloconid absent.

Variables of the sort described, including intermediates at all grades, are demonstrable in *all* species of *Callicebus*. Furthermore, the enamel pattern is not consistently the same in m_1 and m_2 of the same tooth row, or opposite tooth rows of the same individual. The differences may be partly genetic and partly caused by wear. They do not appear to be correlated with dietary preferences. According to Wright (1984, p. 65), *Callicebus brunneus* may be much more insectivorous during some parts of the year than indicated by Kinzey's studies. Milton and Nessimian (1984) also suggest seasonal variation in food preferences in titis. In any event, the slightly higher canines (table 12) and greater persistence of cutting edged premolar styles of *Callicebus torquatus*, as compared with those of congenerics, may contribute to greater success in snagging, biting, and chopping hard-coated insects.

Cheek Tooth Size

Size of individual cheek teeth follows the same order from largest to smallest in all species and both sexes. The gradation in upper and lower cheek teeth is formulated as follows on the basis of visual estimates of bulk, and measurements where necessary. Size of teeth in parenthesis appears to be the same.

$$\frac{m1\text{–}m2\text{–}(m3\text{–}pm4)\text{–}pm3\text{–}pm2}{(m2\text{–}m1)\text{–}m3\text{–}pm4\text{–}pm3\text{–}pm2}$$

In general, the lower premolars are wider than long but in the single, available specimen of *C. modestus*, they are longer than wide, and relatively even narrower in the single specimen of *C. olallae*. Infrequent exceptions include the following:

- pm_3 about as large as m_3 in single specimen at hand of *C. oenanthe* and one specimen of *C. discolor*.
- m_3 larger than m_1 in a few specimens of *C. personatus*, *C. donacophilus* and *C. moloch*; m_3 larger than m_2 in a few specimens of *C. moloch*.

Canines

Canines of *Callicebus* are smallest and possibly least derived of haplorhines. The upper tooth most nearly resembles the first premolar (pm^2) and functions in the same field. The lower canine is smaller than the upper, less specialized, inclined forward, and functionally a part of the incisor field.

A slightly greater average canine crown height in males is correlated with a comparably greater average body size (table 10). Kinzey (1978) measured upper and lower canines of most of the same specimens with similar findings. He concluded that sexual dimorphism is lacking in *Callicebus*, but the data including the slightly greater body size in males, suggest a trend in that direction.

Sequence of Dental Succession

The order of eruption of the permanent dental suite, determined from 20 juvenals representing species *brunneus, caligatus, cupreus, donacophilus, personatus*, and *torquatus*, follows. The order of teeth shown in parentheses is interchangeable.

$$i^1\text{–}(i^2\text{–}m^1)\text{–}m^2\text{–}pm^4\text{–}pm^3\text{–}pm^2\text{–}(c^1\text{–}m^3)$$

Lower teeth exhibit the same sequence.

Metaloph

The *Callicebus* metaloph or plagiocrista (IV) is bulbous. In unworn molars, the lingual element (IV′) and labial element (IV″) appear more or less separated. A metaconule, when or if present, is usually not recognizable as such. Della Serra and Picosse (1951), nevertheless, identified a metaconule in all first and second molars and about 57% in third molars of 98 specimens representing various species of *Callicebus*. In the more than 300 dental suites of *Callicebus* I examined, a definable metaconule was rarely or questionably present. The lingual crest (IV′) of the metaloph, however, could be mistaken for a metaconule. The metaloph of m^3 was absent in about the same frequency as the element Della Serra and Picosse identified as a metaconule.

Enamel Prism Patterns

A study of the enamel prisms in platyrrhine molariform teeth by Gantt (1980) revealed that in transverse section those of *Callicebus, Aotus, Saimiri*, and *Cebus* are C-shaped and tightly packed. In *Alouatta* and *Ateles*, they are also C-shaped but widely separated by interprismatic enamel. Prisms

in the callitrichids *Cebuella, Callithrix,* and *Saguinus* are circular or polygonal with wide interprismatic regions. The three patterns recognized by Gantt are broad modifications of those of Boyde (1971).

Nogami and Yoneda (1983) recognized two enamel prism patterns based on the presence or absence of Schreger's bands, as follows.

Nonserial Pattern—Schreger's bands absent; nearly all rows of enamel prisms straight to slightly curved and nearly uniformly oriented from dentinoenamel junctions to the tooth surface; interprismatic material between adjacent rows well developed; observed in *Saimiri sciureus, Callicebus "moloch", Aotus "trivirgatus", Alouatta seniculus, Saguinus oedipus, S. labiatus, Leontopithecus rosalia.* The pattern was also observed in the lorisoid *Nycticebus coucang,* and in *Tupaia gracilis* (Scandentia).

Multiserial Pattern—Schreger's bands present; the pattern consists of a few to several uniformly oriented, closely packed rows of enamel prisms angled in position to the adjacent pack of straight rows in a herringbone design; interprismatic regions of crystallites well developed; observed in *Callithrix jacchus, Cebuella pygmaea, Cebus apella, Pithecia monachus, Cacajao melanocephalus, Ateles belzebuth, Lagothrix lagothricha, Brachyteles arachnoides.* The same pattern is said to occur in Cercopithecoidea "without exception" (Nogami & Yoneda, 1983, p. 572).

The cited authors infer taxonomic and phylogenetic significance from their respective prism patterns. However, none of the proposed patterns (Boyde, 1971; Gantt, 1980; Nogami & Yoneda, 1983) agree in substance and all include contradictions of relationships based on dental gross morphology and evolutionary sequences. That the structures of enamel prism patterns are variable has been admitted by all authors. As noted by Boyde (1971, p. 85), "examples of all the basic arrangements . . . will usually be found in any enamel sample."

In their review of scanning electron microscope studies of primate enamel, Martin et al. (1988, p. 1523) conclude that "in every case, the initial description of the enamel type which characterizes any higher taxonomic group has required modification in the light of subsequent studies of larger samples of taxa from within that group." In this connection they recommend a "survey of more tooth types per individual at a range of depths within the enamel, and of more species representative of higher taxa." My reviews of the literature on enamel prisms, and my studies of the gross morphology of thousands of dental systems of living forms representing all families of mammals, all genera of primates, all species of platyrrhines, and many extinct taxa, lead to two conclusions. 1) Differences in enamel prism structure of taxonomic significance at any systematic level has not been demonstrated, and may not exist; and 2) Gross topography of the superficial enamel layer exhibits all that is or may be of consistent taxonomic significance at any if not every phylogenetic level.

Crazing

The term crazing was proposed by Hershkovitz (1977, p. 327) for the fine brown line fracture pattern of the dental enamel because of its resemblance to the superficial crack pattern of porcelain, glazed, varnished, or enameled surfaces.

Crazing in susceptible, fully erupted mammalian teeth varies from presence in a single tooth, usually incisor or canine, to a few or all teeth of the dental arcade. Crazing is distinctive of some taxa, absent in others. It is normally absent in the unerupted and often the erupting tooth of those individuals or species where crazing is present in the fully erupted or worn tooth. In morphologically (or genetically?) susceptible teeth, crazing increases and spreads through the arcade with the ongoing impact of biting or chewing.

Among platyrrhines, cebid teeth are more heavily crazed than those of callitrichids and callimiconids. Those of *Callicebus* are among the most heavily crazed, whereas those of *Alouatta* are the least crazed and the arcade of some individuals of *A. seniculus* noncrazed (3 of 10 examined). Among callitrichids, tamarin teeth are more crazed than those of marmosets, but with those of the pygmy marmoset, *Cebuella pygmaea* (12 specimens), noncrazed. Teeth of all catarrhines are crazed throughout most or all of the arcade except the noncrazed arcade of the smallest species, *Miopithecus talapoin* (6 specimens). Dental enamel susceptibility, not size of the animal, however, is the crazing factor.

Crazing usually begins with a wavy transverse line that multiplies into many that become crisscrossed with increasing use of the tooth. They are distinguishable from usually vertical cracks or lamellae that penetrate the dentine and from such internal structures as perikymata, striae of Retzius, and Schreger's bands. The latter, said to prevent

TABLE 1. Postcranial elements of three species of *Callicebus*; sample number in parentheses.

Name	Incisura scapulae	Long axes, obturator foramen	Entepicondylar foramen	Third trochanter
Callicebus				
donacophilus (7, incl. 2 subadults)	deep (4) widely open (1)	anteroposterior (3) equidistant (1)	absent (7)	absent (2) rudimentary (3) developed (1)
cupreus (5)	enclosed (4) deep (1)	anteroposterior (5)	absent (5)	rudimentary (1) developed (4)
torquatus (4)	enclosed (3)	anteroposterior (4)	enclosed (2)	rudimentary (3)

enamel cracking (Koenigswald & Pfretzschner, 1987), is present in crazed and noncrazed teeth.

In an ongoing survey of crazing in mammalian teeth, the full report to be published in Volume 2 of *Living New World Monkeys*, it was found that crazing is virtually absent in all Insectivora; absent in Macroscelididea, all New World Marsupialia except the three known species of *Caluromys* (Didelphidae), and the vast majority of Australian marsupials, and Chiroptera; mixed in Strepsirhini among primates; and consistently present in Haplorhini but absent in the samples examined of *Tarsius, Cebuella,* and *Miopithecus*. Crazing may be correlated with the loss or absence of Nasymph membrane.

Given the systematic position of each of the above taxa, noncrazing must be the primitive condition, crazing the derived. In no case is a consistent relationship between crazing and enamel prism pattern evident.

XI. Postcranial Skeletal Characters

Third Trochanter (table 1, figs. 10–11)

In *Callicebus cupreus* (5 specimens) the third trochanter varies from a small conspicuous flange (AMNH 211478) to rudimentary or nearly absent. In *C. donacophilus* (7) variation also ranges from a flange (FMNH 121659) to absent; in available femurs of *C. torquatus* (3) the trochanter is obsolete or absent. Variation in *Saimiri* (9) is comparable. The same is true of *Aotus* (30), but the larger number of samples shows a wider range of variation.

Variation of the third trochanter as an evolutionary marker in mammals generally has been discussed elsewhere (Hershkovitz, 1987b, p. 402).

Lesser Trochanter (figs. 10–11)

The feature appears to be well developed in all *Callicebus* examined. The same is true for *Saimiri, Aotus,* and other nonprehensile-tailed cebids. Variation in size of lesser trochanter among these genera is not great but nevertheless approximates the entire range depicted by Ford (1980, p. 322), with "primitive primate femur" to "primitive platyrrhine femur" and "primitive catarrhine femur." Nearly the full "evolutionary change" from primitive to derived, as interpreted by Ford, is found in *Pithecia monachus* alone.

According to Ford (1980, p. 323), the larger the lesser trochanter the more primitive. Hence, she argued, that of *Cebuella pygmaea,* the smallest living platyrrhine with proportionately largest lesser trochanter, is either most primitive or "secondarily derived." No evidence was proffered that this or any other character of *Cebuella* is optionally either "primitive" or "secondarily derived." Actually, the size of the *Cebuella* lesser trochanter may be no larger than that of others if allowance is made for allometric change from small to large femurs. The lesser trochanter in the larger, nearest-related *Callithrix jacchus,* for example, is about the same size as that of *Cebuella* but more robust. Insofar as I can determine, the lesser trochanter is an accommodation for the variably sized muscles *psoas major, m. iliacus,* and *m. quadratus* which insert on it, and not the reflection of a dim ancestry.

Distal Femoral Epiphysis (fig. 12, table 2)

Two character states in the morphology of the distal femoral epiphysis were described and figured by Ford (1980, p. 324). The first is termed

FIG. 10. Femurs, left, proximal: *Aotus azarae*: **a,** AMNH 21515, third trochanter absent; **b,** AMNH 122721, third trochanter (3tr) moderately developed; **c,** AMNH 211457, third trochanter greatly expanded; *Callicebus donacophilus*: **d, f,** FMNH 121659, third trochanter present; **e, g,** FMNH 121660, third trochanter absent.

"squared" with "the ratio of anteroposterior depth to mediolateral width approaching one." This state was regarded as primitive. The figured model (Ford, 1980, fig. 3) is the distal femoral epiphysis of *Lemur mongoz*. Included among "squared" is the epiphysis of "*Tarsius, Hemiacodon, Galago, Lichanotus* (*Avahi*), *Lemur, Smilodectus, Northarctus,* and *Plesiadapis,*" and to a lesser degree that of *Daubentonia* and *Arctocebus*.

The second distal femoral epiphyseal state found in all platyrrhines and catarrhines is the "derived condition which is compressed anteroposteriorly (or elongated mediolaterally)." The figured model (Ford, 1980, fig. 3) is the distal femoral epiphysis of the platyrrhine *Callicebus* [*donacophilus*] *pallescens*. Both types are reproduced here (fig. 12). The difference between them is accurate. However, no measurements, evidence of other kind, or argument is presented for distinguishing the "squared" epiphysis as primitive, and the "compressed" as derived.

Measurements of the distal femoral epiphysis of skeletons of modern primates and nonprimates in Field Museum collections are shown in Table 2. The data and other available information indicate that "squared" and "compressed" distal epiphyses are both independently derived and no less derived than the respective locomotor systems to which they belong. The measurements suggest that the greater the deviation of the mean proportion

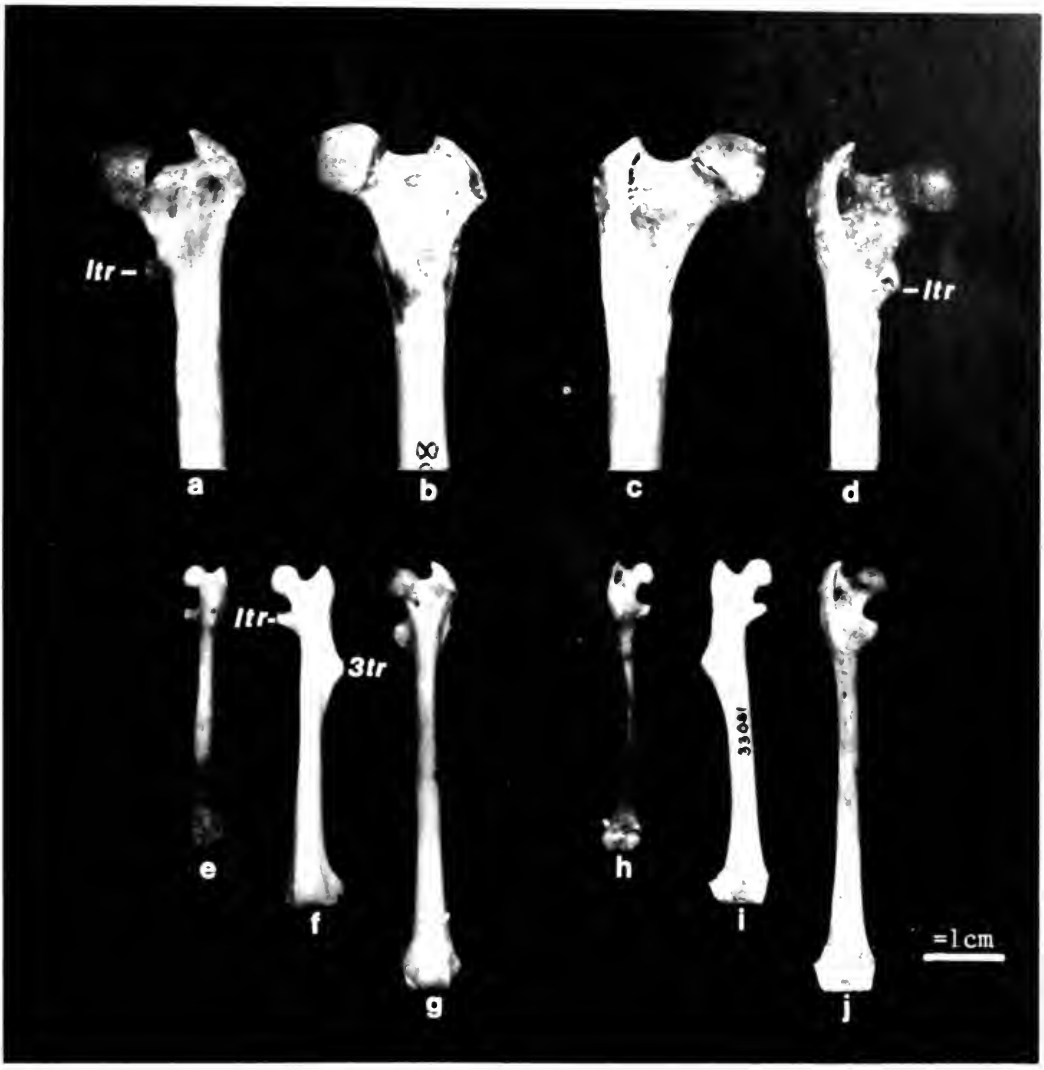

FIG. 11. Femurs, left, proximal: **a, d,** *Pithecia pithecia* (FMNH 95504) with lesser trochanter present; **b, c,** *Pithecia pithecia* (FMNH 95508) with lesser trochanter obsolete; **e, h,** *Cebuella pygmaea* (FMNH 60454); **f, i,** *Tupaia* sp (FMNH 33031); **g, j,** *Callithrix jacchus* (FMNH 53735), all with lesser trochanter; **ltr** = lesser trochanter, **3tr** = third trochanter.

of depth to width either positively or negatively from ca. 90 of a hypothetical structural (ancestral?) model, the more derived the epiphysis. The mean ratio of all lemuroids and of the lorisoid *Galago* exceeds .9, whereas those of all platyrrhines and catarrhines and some lorisoids are less. The mean ratio of the haplorhine tarsier, *Tarsius bancanus,* is highest, whereas that of the nonprimate tree shrew *Tupaia glis* with primate-like distal femoral epiphysis coincides with the ratio of the hypothetical structural model. Overlapping individual ratios occur among platyrrhines, catarrhines, lorisoids, lemuroids, and tupaiids, but the ratios by themselves imply neither locomotor similarities nor phylogenetic relationships.

Morphologically, the bulging external epicondyle exaggerates the mediolateral width of the "compressed" epiphysis. The less the bulge, the greater the mean (table 2).

The intercondylar fossa of the distal femoral epiphysis describes a Roman arch in most strepsirhines, all catarrhines, and most cebids examined. The arch is Gothic, often grading into the Roman, in remaining cebids, all callitrichids, *Tar-*

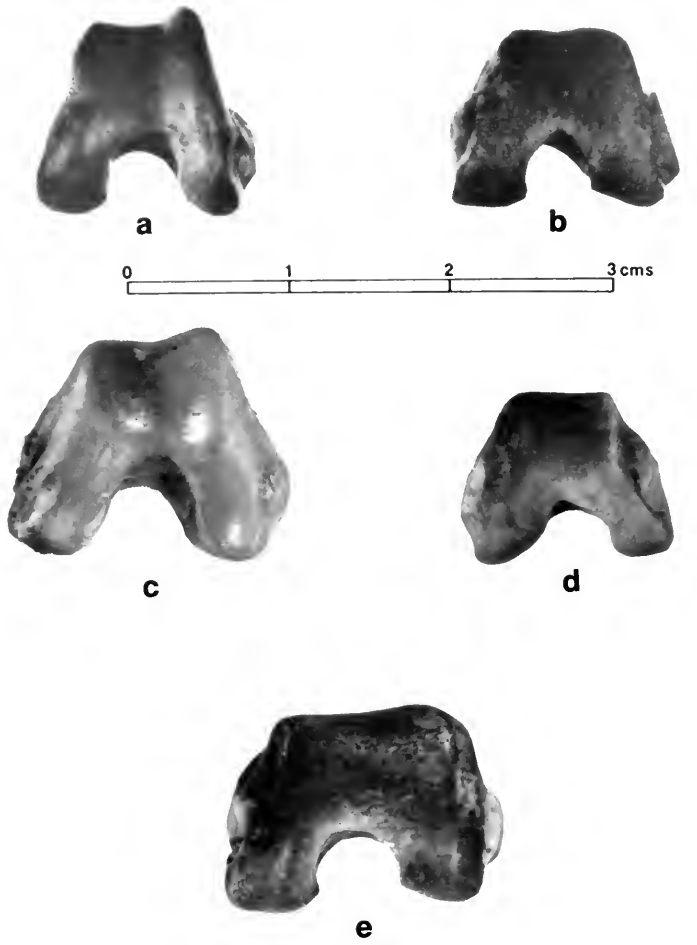

FIG. 12. Left distal femoral epiphysis, inferior view: **a,** *Lemur mongoz* (USNM 337946); **b,** *Callicebus donacophilus pallescens* (USNM 269827); **c,** *Cercopithecus albogularis* (FMNH 35129); **d,** *Callicebus torquatus* (FMNH 70691); **e,** *Pithecia pithecia* (FMNH 95504). Figures **a** and **b,** scale included, from Ford (1980, p. 324); **a** = "squared" type; **b-e** = "compressed" type; intercondylar fossa "Gothic" in *Callicebus* (**b, d**), "Roman" in remaining.

sius, and tupaiids. The direction of variation suggests that the Roman arch may be derived from the Gothic. The distal femoral epiphysis of the comparatively generalized marsupial *Didelphis* closely resembles the "compressed" or Gothic type in *Callicebus.* It is clear that the significance of the variation in the form of the distal femoral epiphysis depends on more than is apparent in the bone itself.

Distal Tibial Epiphysis (fig. 13, table 3)

The bone does not lend itself well to diagnostic distinctions between nonprehensile-tailed cebid genera on the basis of characters adduced by Ford (1986). Her study of the tibia, particularly the elements of the epiphysis, embraced all platyrrhines and selected catarrhines. Few of her characterizations, however, are clear. Notwithstanding, shape of the distal tibial epiphysis proves meaningful, to a limited extent, for sorting genera and in some cases indicating phylogenetic relationships. The most useful measurements of the epiphysis, those which can be repeated with reasonable accuracy, are greatest anteroposterior depth to greatest lateromedial width; the smaller the ratio the more nearly rectangular the epiphysis. Ratios of the selected sampling of tibias shown in Table 3 are roughly divisible into five size groups as sorted in Table 3. Species of each of the three strictly platyrrhine groups are strongly size-related, the larger

TABLE 2. Distal femoral epiphysis: Ratio of anteroposterior depth to mediolateral width (×100). For four or more specimens of a taxon only the mean is given, followed by extremes (in parentheses) and number of samples. Shape of intercondylar fossa, anterior view (fig. 12) is indicated in column 3. The systematic arrangement within major groups is not intentionally phylogenetic where it may appear so.

Taxon	Anteroposterior mediolateral	Intercondylar arch
Platyrrhini		
Pithecia monachus	71 (69–72) 6	Roman
Pithecia pithecia	73 (69–78) 12	Gothic to Roman
Chiropotes satanas	74 (70–77) 7	Gothic to Roman
Cacajao calvus	74 (72–77) 7	Gothic to Roman
Cebus apella	77 (70–85) 15	Roman
Callicebus donacophilus	77 (73–83) 5	Gothic to Roman
Callicebus cupreus	79 (76–85) 4	Gothic to Roman
Callicebus torquatus	77, 85	Gothic
Saimiri sciureus	82 (80–83) 4	Gothic
Leontopithecus rosalia	82 (78–85) 10	Gothic to Roman
Saguinus oedipus	84 (78–89) 18	Gothic
Saguinus leucopus	85 (81–89) 8	Gothic
Cebuella pygmaea	85 (79–89) 9	Gothic
Aotus azarae	86 (82–91) 22	Gothic
Saguinus fuscicollis	88 (83–93) 4	Gothic
Callithrix jacchus	89 (84–96) 11	Gothic
Catarrhini		
Macaca fascicularis	85 (80–89) 8	Roman
Cercocebus torquatus	86 (77–96) 14	Roman
Lorisoidea		
Loris tardigradus	74, 82	Gothic
Perodicticus potto	79 (76–80) 4	Gothic
Nycticebus coucang	80 (75–84) 10	Gothic
Galago crassicaudatus	101 (96–104) 6	Roman
Lemuroidea		
Microcebus sp.	92	Gothic
Cheirogaleus sp.	87, 91, 95	Gothic
Lemur catta	96 (94–101) 6	Roman
Lemur rubriventer	96	Roman
Varecia variegata	99 (93–105) 4	Roman
Propithecus verrauxi	106	Roman
Lemur mongoz	106 (103–108) 6	Roman
Avahi laniger	111, 117	Roman
Lemur fulvus	101 (95–104) 5	Roman
Tarsioidea		
Tarsius bancanus	122 (120–125) 7	Gothic
Tupaioidea (nonprimate)		
Tupaia glis	92 (87–91) 11	Gothic

cebids having smaller ratios or rectangular epiphyses. The ordering of atelines, pithecines, and to a lesser extent marmoset-like cebids (*Aotus, Callicebus, Saimiri*) and callitrichids, reflects phylogenetic relationships within each group. The clustered ratios of tree shrews (Scandentia) and of catarrhine monkeys are clearly independent of the platyrrhine groupings. The same applies to *Callimico.*

Entepicondylar Foramen (fig. 14)

The entepicondylar (supracondylar) foramen of the distal portion of the humerus is an ancient reptilian and mammalian character persistent in some living mammals, completely lost, obliterated, occasionally vestigial, rarely atavistic in the remaining. The foramen, for passage of brachial artery and median nerve, pierces the internal su-

FIG. 13. Distal epiphysis of right tibia, medial and ventral (articular) views of **a,** *Aotus azarae boliviensis* (AMNH 211462); **b,** *Callicebus torquatus* (FMNH 70691); **c,** *Callicebus cupreus* (FMNH 122786); **d,** *Cacajao calvus* (RHNMS 040140); **e,** *Lagothrix lagothricha* (FMNH 70584); **f,** *Brachyteles arachnoides* (USPMZ 6482).

TABLE 3. Ratios (×100) of greatest length (anteroposterior) to greatest width (lateromedial) of inferior epiphyseal surface of right and left tibia in selected primate taxa; means are followed by extremes (in parentheses) and number of sample. Actual measurements of sexually dimorphic species may differ but ratios remain about the same. Specimens in FMNH collection except the Hispaniolan monkey tibia (USNM 254682).

Taxon	Anteroposterior	Lateromedial	Ratio (×100)
Tupaia sp.	3.1	4.7	66
Tupaia glis	3.6, 3.7	6.2, 6.0	58, 62
Urogale everetti	3.7 (3.5–3.8) 4	5.5 (5.0–6.1) 4	67 (62–76) 4
Cebuella pygmaea[1]	3.0 (2.8–3.1) 14	3.9 (3.7–4.2) 14	76 (70–82) 14
Callithrix jacchus	4.5 (4.1–4.9) 11	5.5 (5.1–6.2) 11	81 (77–91) 11
Callithrix argentata	4.6 (4.3–4.9) 4	6.1 (5.7–6.3) 4	76 (75–79) 4
Saguinus leucopus	5.6 (5.4–5.8) 9	7.2 (6.3–7.7) 9	77 (74–79) 9
Saguinus fuscicollis	5.6 (5.4–5.7) 4	6.5 (6.3–7.0) 4	86 (80–90) 4
Saguinus imperator	5.6 (5.5–5.6) 4	6.9 (6.6–7.1) 4	81 (79–85) 4
Saguinus oedipus	5.7, 5.8	7.5, 7.3	76, 79
Saguinus labiatus	5.9 (5.4–6.4) 4	7.1 (6.6–7.7) 4	83 (77–88) 4
Leontopithecus rosalia	5.9 (5.5–6.6) 11	7.6 (7.1–8.3) 11	77 (70–88) 11
Callimico goeldii	5.7 (5.4–5.8) 5	7.4 (6.9–7.5) 5	77 (77–78) 5
Saimiri sciureus	6.3 (5.9–7.4) 20	8.0 (7.3–9.1) 20	83 (78–89) 20
Callicebus donacophilus	6.8 (6.3–7.1) 8	8.9 (8.0–9.3) 8	77 (73–82) 8
Callicebus cupreus	7.3 (6.4–8.0) 8	9.0 (8.3–9.7) 8	81 (71–91) 8
Callicebus torquatus	7.5, 7.5, 7.5	8.7 8.7, 9.9	86, 86, 76
Aotus nigriceps	6.6, 6.6	8.5, 9.2	77, 72
Aotus lemurinus	7.1 (7.0–7.3) 4	8.8 (8.3–9.1) 4	81 (78–88) 4
Aotus azarae	7.9 (6.9–9.0) 30	9.3 (8.1–10.8) 30	85 (76–93) 30
Miopithecus talapoin	7.3 (6.5–8.3) 4	9.5 (8.2–10.7) 4	78 (75–81) 4
Pithecia pithecia	9.4 (8.4–10.2) 9	12.4 (11.7–13.8) 9	76 (69–80) 9
Pithecia monachus	9.7 (8.6–10.6) 7	13.2 (11.5–15.0) 7	73 (65–79) 7
Chiropotes satanas	9.6 (9.1–10.3) 8	13.7 (13.2–14.1) 8	70 (67–73) 8
Cacajao calvus	10.6 (10.3–11.2) 6	15.7 (14.0–16.7) 6	68 (66–74) 6
Cebus nigrivittatus	10.8 (9.8–11.9) 4	14.3 (13.6–15.1) 4	76 (70–83) 4
Cebus apella	11.1 (9.4–11.8) 40	14.1 (12.0–16.0) 40	75 (68–83) 40
Cebus albifrons	11.3 (10.6–11.9)	14.0 (13.4–14.9) 9	81 (77–86) 9
Cebus capucinus	11.4 (10.7–12.4) 15	15.2 (14.5–16.4) 15	75 (71–79) 15
Alouatta seniculus	11.5 (9.9–13.9) 12	19.4 (17.7–23.0) 12	59 (53–71) 12
Lagothrix lagothricha	12.0 (11.1–12.5) 10	20.6 (18.9–21.3) 10	59 (55–61) 10
Presbytis cristata	12.0, 12.3	15.2, 16.0	79, 77
Ateles sp.	13.7 (13.4–14.2) 4	25.8 (25.5–26.1) 4	54 (52–56) 4
Brachyteles arachnoides	13.9 (13.6–14.2) 4	25.8 (25.5–26.1) 4	54 (52–56) 4
Macaca fascicularis	13.9 (13.1–14.7) 4	16.8 (16.2–18.3) 4	82 (81–86) 4
Cercopithecus l'hoesti	10.6, 10.7	13.7, 13.1	77, 82
Cercopithecus neglectus	12.5 (11.3–13.6) 5	15.4 (13.9–17.1) 5	81 (79–85) 5
Cercopithecus mitis	14.1 (12.7–15.3) 4	16.5 (13.9–19.0) 4	85 (80–86) 4
Cercopithecus albogularis	14.7 (12.0–16.6) 4	17.9 (14.4–20.1) 4	82 (80–86) 4
Cercocebus torquatus	14.7 (13.9–15.6) 5	18.5 (18.2–18.9) 5	79 (76–83) 5
Erythrocebus patas	15.5 (15.2–15.7) 4	18.3 (16.9–19.6) 4	85 (79–93) 4
Colobus guereza	16.1 (14.0–17.6) 7	20.1 (17.1–22.9) 7	81 (75–91) 7
Presbytis entellus	16.2 (13.1–18.4) 6	21.6 (15.7–25.6) 6	76 (71–83) 6
Theropithecus	16.2	20.8	78
Papio cynocephalus	18.1 (15.6–20.8) 4	23.6 (20.6–26.6) 4	76 (73–78) 4
Nasalis larvatus	20.1, 19.8	26.5, 26.1	76, 76
Hylobates moloch	11.1 (10.8–11.3) 6	16.1 (14.8–17.4) 6	69 (65–75) 6

[1] One specimen (FMNH 60799) with distal synostosis of fibula and tibia; left synostosis 7.5 mm, right 8.0 mm; fibular length 37 mm. No other case of limb bone fusion was observed in specimens examined. Fleagle and Simons (1983, p. 239, fig. 2) record comparable degrees of synostosis of tibia and fibula in an individual each of platyrrhines *Callithrix jacchus, Saimiri sciureus,* and *Pithecia pithecia.*

pracondylar ridge which provides surface for origin of forearm supinator muscles.

The outer border, or supracondylar arch, of the entepicondylar foramen is usually stout. In some taxa it appears to have expanded medially without formation of a foramen. In other taxa, the arch appears as a thin slip or spinous process projecting from upper, lower, or both outer margin(s) of the incompletely formed foramen.

Presence or absence of the entepicondylar fo-

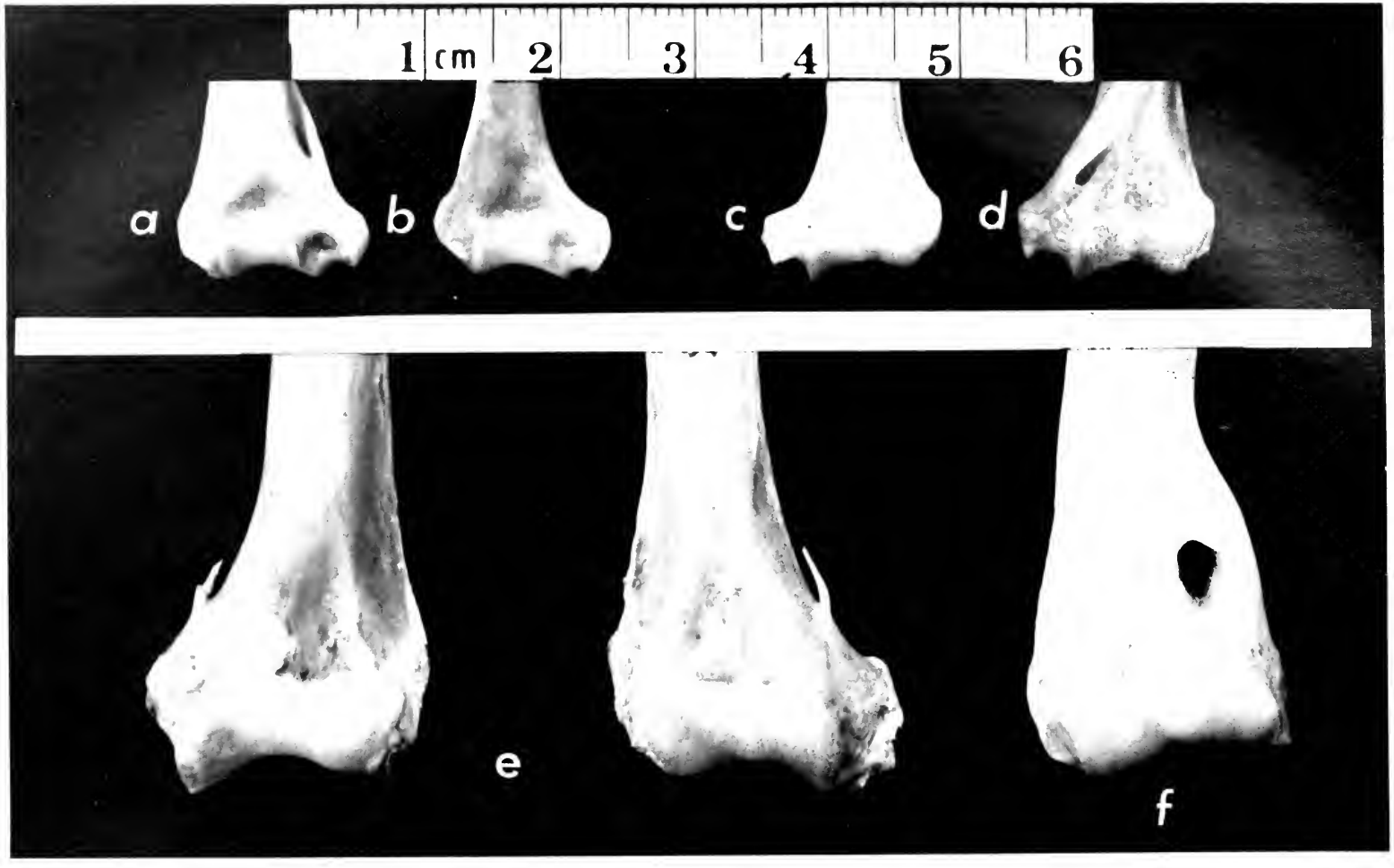

FIG. 14. Distal portion of humerus: **a,** *Callicebus torquatus* (FMNH 70691 ♀), left, posterior aspect, entepicondylar foramen present; **b,** *Callicebus donacophilus* (FMNH 121659 ♂), left, posterior aspect, entepicondylar foramen absent; **c,** *Aotus lemurinus griseimembra* (FMNH 68858 ♀), left anterior aspect, entepicondylar foramen absent; **d,** *Aotus azarae* (AMNH 211483 ♂), entepicondylar foramen present; **e,** *Cebus albifrons* (FMNH 61858 ♂), left and right anterior aspect, entepicondylar foramen incomplete; **f,** *Cebus albifrons* (FMNH 70633 ♂), right anterior aspect, entepicondylar foramen complete.

ramen in *Callicebus* and other mammals appears to be consistent at the species grade with individual variation limited to infrequent abnormalities. Within a genus it may be consistently present in one species, consistently absent in another. The same appears to be true of entire mammalian orders, or only of families of an order, subfamilies of a family, and genera of a subfamily or family.

Orders lacking the entepicondylar foramen include Monotremata, Chiroptera, Artiodactyla, Perissodactyla, and Proboscidea. In the order Carnivora, with seven living families, the aperture is absent in the Canidae, Ursidae, and all Mustelidae except all species of Mephitinae (skunks, genera *Conepatus, Mephitis, Spilogale*). Within the Scandentia, the family Tupaiidae includes the monotypic genus *Urogale* with foramen present, and genus *Tupaia* with foramen present in species *T. tana* (FMNH 33031) and absent in species *T. glis* (FMNH 46642). I have not investigated other species of the order. Rodentia, insofar as known, lacks the foramen with notable exception of the approximately 60 species of the cricetine genus *Peromyscus* (cf. Manville, 1961, p. 103; Hall, 1981).

Among living Primates, the entepicondylar foramen is present in most strepsirhines, absent in others. In haplorhines, it is present in *Tarsius*, absent in catarrhines. Among platyrrhines (table 4), the foramen is absent in callitrichids *Cebuella* and *Callithrix*, present in *Leontopithecus* and seven species of *Saguinus*, but not in *S. imperator*. The foramen is retained in *Callimico* (Callimiconidae). In cebids, the aperture is absent in two of three species examined of *Callicebus* and present in the third, *C. torquatus*, on other grounds the most derived of 13 recognized species of the genus. In *Aotus* for which humeri are available, *A. lemurinus* has the foramen and *A. azarae* is without. The squirrel monkey (*Saimiri*), all species of pitheciines (*Pithecia, Chiropotes, Cacajao*), and *Cebus* exhibit well-defined foramina. In contrast, all large prehensile-tailed cebids (*Alouatta, Lagothrix, Ateles, Brachyteles*) lack the foramen. The same applies to all living Old World monkeys, apes, and man, albeit a vestige may be present as a rare individual anomaly.

The entepicondylar foramen is present in the humerus of the extinct *Cebupithecia sarmientoi* of the La Venta fauna of the Colombian Miocene (Stirton, 1951). No other intact humerus of extinct New World platyrrhines is known. The Oligocene *Aegyptopithecus zeuxis*, from the Fayum of Egypt, characterized by Fleagle and Simons (1982, pp. 175, 192) as a "primitive anthropoid" and "hominoid," has a well-developed entepicondylar foramen, as does the European Miocene hominoid *Pliopithecus* (Fleagle & Simons, 1982, p. 190). The humerus of *Aegyptopithecus* is not much larger than that of *Cebus*, which also retains the foramen and is smaller than those of the four large prehensile-tailed cebid genera which lack it (table 4). Primitive characters obvious in the published

TABLE 4. Entepicondylar (supracondylar) foramen: Presence or absence in Platyrrhini. N = number of specimens examined, all in FMNH.

	N	Absent	Present
Callitrichidae			
Cebuella pygmaea	7	7	0
Callithrix jacchus	11	11	0
Callithrix argentata	2	2	0
Saguinus fuscicollis	4	0	4
Saguinus midas	6	0	6
Saguinus leucopus	5	0	5
Saguinus oedipus[1]	23	0	23
Saguinus labiatus	4	0	4
Saguinus mystax	7	0	7
Saguinus imperator	5	4½	½
Leontopithecus rosalia[2]	9	0	9
Callimiconidae			
Callimico goeldii	3	½[3]	2½
Cebidae			
Callicebus donacophilus	7	7	0
Callicebus cupreus	5	5	0
Callicebus torquatus	2	0	2
Aotus lemurinus	3	3	0
Aotus azarae	30	30	0
Saimiri spp.	11	0	11
Pithecia pithecia	11	0	11
Pithecia monachus	4	0	4
Chiropotes satanas	11	0	11
Cacajao calvus	4	0	4
Cebus nigrivittatus	1	0	1
Cebus capucinus	7	0	7
Cebus albifrons[4]	4	0	4
Cebus apella	20	0	20
Alouatta palliata	2	2	0
Alouatta seniculus	4	4	0
Lagothrix lagothricha	18	18	0
Ateles spp.	15	15	0
Brachyteles arachnoides	2	2	0

[1] Includes 9 *S. o. oedipus*, 14 *S. o. geoffroyi* (10 captive).

[2] Given in error as 4 absent, 3 present, in Hershkovitz (1977, p. 811).

[3] Right humerus, FMNH 57999.

[4] Supracondylar process is vestigial on both humeri, FMNH 61858.

TABLE 5. Summary of skeletal measurements and limb bone ratios (×100) of *Callicebus, Aotus,* and *Saimiri.*

Name	Pelv. sup. diam. / Pelv. inf. diam.	Radius	Humerus	Radius / Humerus
Callicebus				
donacophilus ♂♂	103	62	73	86
donacophilus ♀♀	107	56	70	80
donacophilus –	103	60, 62	73, 74	82, 85
cupreus ♂♂	103 (93–111) 4	66 (57–71) 4	77 (68–80) 4	86 (84–89) 4
cupreus ♀♀	103	64	77	83
torquatus ♀♀	—	64, 94	79, 102	81, 92
Aotus				
azarae ♂♂[1]	105 (94–106) 9	73 (70–77) 11	79 (75–83) 11	91 (90–94) 11
azarae ♀♀[1]	102 (97–109) 6	72 (69–76) 11	79 (69–83) 11	91 (88–93) 11
nigriceps ♂♂	90	—	—	—
infulatus ♀♀[2]	—	68	73	93
lemurinus ♀♀[3]	113	66 (63–68) 3	73 (72–74) 3	90 (87–93) 3
Saimiri				
sciureus ♂♂	84, 89	67	74	91 (87–93) 3
sciureus ♀♀	84	62, 61	70, 74	82, 89

[1] *A. azarae boliviensis.*
[2] *A. azarae infulatus.*
[3] *A. lemurinus griseimembra.*

photographs of the complete humeri of two individuals of *Aegyptopithecus* (Fleagle & Simons, 1982, pp. 178, 179) include the nearly straight long axis of the bone with plane of distal base at right angles to it.

The irregular distribution of the entepicondylar foramen in the Mammalia with constancy of presence or absence certain only at species grade endows the element with taxonomic or diagnostic significance at that grade. Logically, all descendants of the prototype of an order or of a family or genus without the foramen should lack it. Presence of the foramen in the genus *Peromyscus* only amidst the vast polytypic order of rodents without it is enigmatic. Inconstancy of the character among the generic or family groupings of New World monkeys (table 4) provides more examples of phylogenetic variability. Only in the largest platyrrhines and all living catarrhines is absence, actually nondevelopment of the foramen, a constant. There can be no certainty that the large, extinct *Aegyptopithecus zeuxis* with entepicondylar foramen present may not have an as yet undiscovered sister species or near relative, without the foramen. Among living primates, a morphological ancestral model for the Hominoidea as conceived by Fleagle and Simons (1982) but possessing more primitive characters, including smaller size than *Aegyptopithecus,* could be a species of *Callicebus.* Yet here, the foramen is known to be present in one species, absent in two. Presumably, the absence or vestigial state of the foramen represents an arrested developmental stage or a secondary ossification of the area where the aperture had been.

Limb Bone Proportions (table 5)

Fore- and hind limb bones are longer relative to trunk (first cervical to last sacral) in *Callicebus torquatus* than in *C. donacophilus* and *C. cupreus.* A comparable relationship exists between *Pithecia monachus* and the longer-limbed *P. pithecia* (Hershkovitz, 1987b, p. 400, tables VI, VII; note misplacement of first caption of last grouping).

Sternum (figs. 15–16)

Size and shape of the primate sternum is highly variable. The manubrium, however, appears to have some qualified systematic importance. In certain primate groups, the manubrium is goblet-shaped, in others it is double cruciform. A few intermediates occur among both groups. In the goblet-shaped manubrium, the ratio of the greatest anterior width to greatest breadth between anterior lateral incisures is slightly less than to more

TABLE 5. Continued.

Tibia	Femur	Radius + humerus / Tibia + femur	Trunk	Radius + humerus / Trunk	Tibia + femur / Trunk
89	94	77	253	53	72
86	88	75	240	52	72
89, 89	89,94	75, 74	250, 234	53, 58	71, 78
93 (85–97) 4	97 (87–101) 4	75 (73–77) 4	242 (220–264) 4	59 (57–61) 4	79 (77–81) 4
93	96	75	264	53	72
93	99	74	214, 262	67, 73	90
101 (95–106) 13	103 (97–109) 13	74 (73–76) 11	266 (217–295) 13	56 (52–67) 11	77 (70–90) 11
99 (89–103) 11	101 (89–105) 12	76 (74–78) 10	261 (227–286) 12	58 (55-60) 10	75 (72–80) 10
93	96	—	249	—	76
94	93	75	241	58	78
91 (89–93) 3	94 (92–95) 3	76 (74–77) 3	232 (216–266) 4	62 (58–65) 3	82 (77–87) 3
90	91	78 (76–79) 3	216 (206–232) 3	65 (62–89) 3	83 (81–87) 3
84, 85	88, 86	77, 79	223, 240	56, 59	71, 77

than 100%. In the double cruciform manubrium, the ratio is less than 100%, rarely more.

The species of *Callicebus* and other nonprehensile-tailed cebids are arranged below according to shape of manubrium. Ratios (×100) described above are shown in brackets followed by sample number.

Goblet-shaped manubrium

Aotus nigriceps [94] 1
Aotus azarae [105 (96–124)] 10
Aotus lemurinus [100; 109] 2
Pithecia monachus [119 (109–130)] 4
Pithecia pithecia [107 (94–127)] 8
Cacajao [112; 118] 2

Double cruciform manubrium

Callicebus donacophilus [91] 1
Callicebus cupreus [92 (83–104)] 4
Callicebus torquatus [79, 83, 84] 3
Saimiri sciureus [74 (71–79)] 4
Saimiri? (Zoo) [85 (80–92)] 5
Chiropotes satanas [89 (81–96)] 4

Vertebral Formulae

See Table 6 for vertebral formulae of *Callicebus*, *Saimiri*, and *Aotus*.

Caudal Vertebrae (fig. 17, table 7)

Structure of the first few postsacral vertebrae is complex. They are followed by one or two less complex vertebrae transitional to the comparatively simple caudal vertebrae. The number of complex sacral-like caudal vertebrae varies from two to four. The first transitional is distinctive but more nearly like a sacral than a simple caudal vertebra. The second transitional, if present, is more nearly caudal than sacral in form but supports a more or less developed dorsal crest, the vestige of the spinous process.

The complex and transitional postsacral vertebrae were described in terms of "caudal vertebral crests" in previous publications (Hershkovitz, 1985, p. 10; 1987a, p. 19; 1987b, p. 400). The sequentially numbered transitional and crested (pre-simple caudal) vertebrae for nonprehensile-tailed cebids are listed in Table 7.

Incisura Scapulae

Described and compared in Table 1 for *Callicebus donacophilus*, *C. cupreus*, and *C. torquatus*.

TABLE 6. Vertebral formulae of *Callicebus, Saimiri,* and *Aotus.*

Taxon	Cervical	Thoracic	Lumbar	Sacral	Caudal	Source
Callicebus						
donacophilus (7)	7	12 (7)	7 (7)	3 (7)	23+ (1); 26 (2); 27 (1)	FMNH (7)
cupreus (5)	7	12 (5)	7 (5)	3 (5)	26 (4)	AMNH (3); FMNH (2)
torquatus (4)	7	12 (2); 13 (2)	7 (2); 6 (2)	3 (4)	27 (3)	FMNH (4)
sp. (3)	7	12 (2); 13 (1)	7 (2); 8 (1)	3 (3)	—	Schultz, 1961
Saimiri						
sciureus (5)	7	13 (5)	6 (2); 7 (3)	3 (5)	27 (1); 29 (1); 30 (1)	FMNH (7)
sciureus (2)[1]	7	13 (2)	7 (2)	3 (2)	24, 27	Flower, 1863
sp. (16)	7	13 (16)	6 (2); 7 (14)	3 (16)	—	Schultz, 1961
Aotus						
lemurinus (4)	7	12 (1); 13 (2); 14 (1)	7 (3); 8 (1)	3 (4)	26 (1); 27 (1)	AMNH (1); FMNH (3)
nigriceps (1)	7	14	7	3	—	FMNH (1)
azarae (27)	7	12 (3); 13 (2); 14 (18); 16 (1)	7 (3); 8 (19); 9 (4)	2 (1); 3 (24); 4 (2)	26 (3); 27 (9); 28 (1); 29 (1)	AMNH (27)
sp. (2)	7	13, 15	6, 7	3 (2)	18, 27	Flower, 1863
sp. (15)	7	13 (3); 14 (12)	7 (13); 8 (2)	3 (13); 4 (2)	24 (24–31) 14	Schultz, 1961

[1] Zoo specimen.

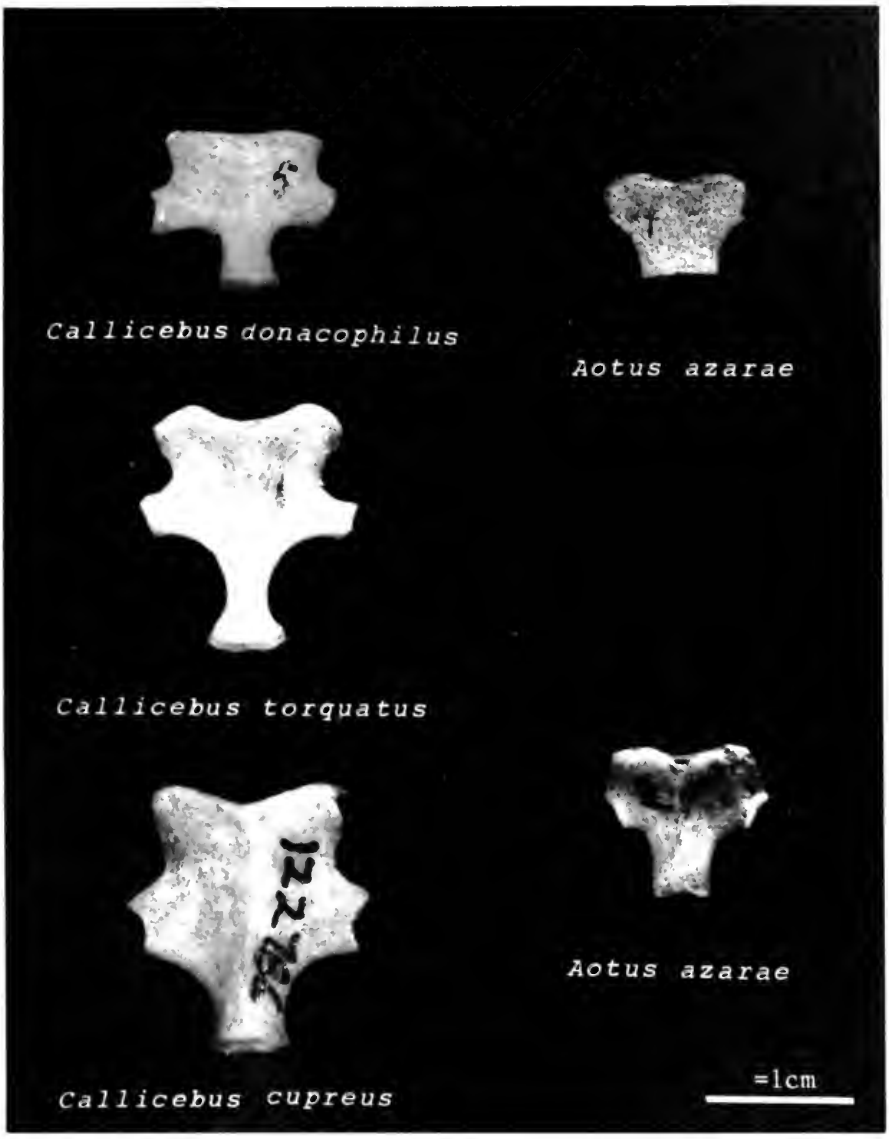

FIG. 15. Sternal manubria: double cruciform manubrium of *Callicebus cupreus* (FMNH 122786), *Callicebus torquatus* (FMNH 70692), *Callicebus donacophilus* (FMNH 121659); goblet-shaped manubrium of *Aotus azarae* (AMNH 211479), *Aotus azarae* (AMNH 211469).

Pelvic Dimensions

Ratios of superior to inferior pelvic diameters are summarized and compared in Table 5 for *Callicebus, Aotus,* and *Saimiri.*

Obturator Foramen

Described and compared in Table 1 for *Callicebus donacophilus, cupreus,* and *torquatus.*

XII. Cerebral Characters

Brain Mass and Body Size

The correlation between increasing brain mass or weight with increasing body mass or weight in primates has been demonstrated by indices of encephalization devised by Stephan (1967a,b), Stephen and Andy (1969), Bauchot (1978), Stephan et al. (1981), and others. Their findings were based on serial sections of brains of 24 species of Insec-

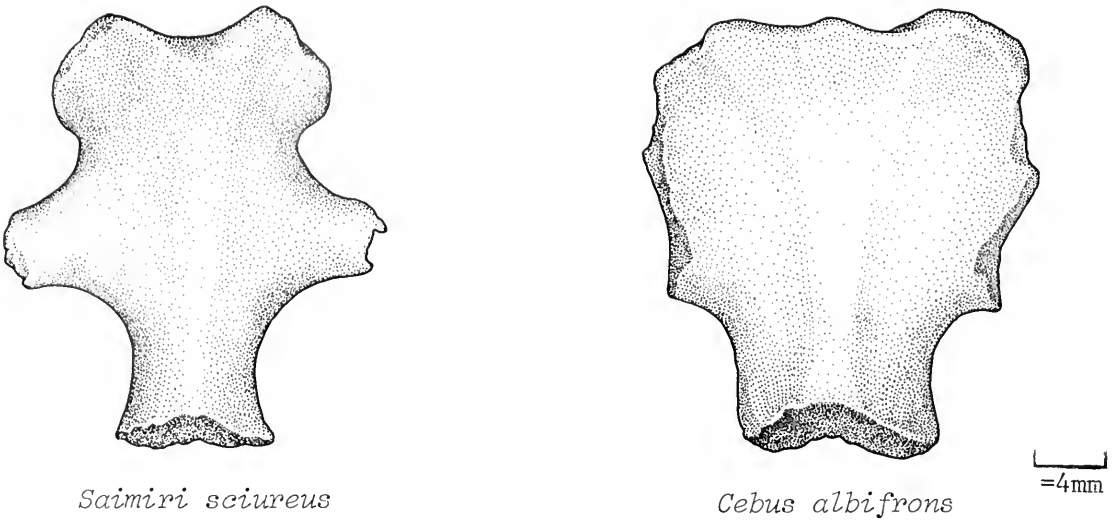

FIG. 16. Sternal manubria: double cruciform manubrium of *Saimiri sciureus* (FMNH 70668); goblet-shaped manubrium of *Cebus albifrons* (FMNH 98043).

tivora (sensu lato), regarded by them as most primitive of living mammals and basal for comparative purposes. The primates included 18 Strepsirhini and 21 Haplorhini. Two species of Tupaiidae, grouped with "Prosimians" in works cited above, are here counted with Insectivora (sensu lato).

The extremely complex, time-consuming, painstakingly controlled preparations of the brains, constructions of formulae, and procedures for evaluations have been described by the cited authors. The derived numerical index of encephalization they calculated for each primate species is an estimate of the number of times or multiple each brain, or part thereof, is larger than those of a basal insectivore species of approximately the same body weight. Their progressive arrangement of the indices purports to show the increased encephalization and evolutionary distance of each primate species from basal insectivores. The values are admittedly not precise but esteemed accurate enough for these types of comparisons (Stephan & Andy, 1969, p. 373).

The progressive platyrrhine indices of encephalization as classified by Bauchot and Stephan (1969, p. 260) are summarized below. The progression by subfamily includes (in parentheses) the representative species and particular index of encephalization of each (values of synonyms averaged).

Alouattinae (*Alouatta* sp., 476).
Callimiconinae (*Callimico goeldii,* 576).
Callitrichinae (*Saguinus oedipus,* 531; *Callithrix jacchus,* 574; *S. midas,* 608; *Leontopithecus rosalia,* 608).
Aotinae (*Aotus,* sp., 532; *Callicebus moloch,* 610; *C. cupreus,* 640).
Pitheciinae (*Pithecia pithecia,* 764; *P. monachus,* 815).
Atelinae (*Ateles geoffroyi,* 876; *A. fusciceps,* 859; *A. paniscus,* 943; *Lagothrix lagothrica,* 1075).
Cebinae (*Saimiri sciureus,* 842; *S. oerstedi,* 865; *Cebus capucinus,* 1038; *C. apella,* 1090).

The above systematic arrangement or phylogeny conforms, with minor exceptions, to those of others (Schultz, 1941; Hershkovitz, 1977) who employed simpler methods. Questionable hierarchical positions, particularly those of *Alouatta, Saimiri, Callimico,* and *Saguinus* in the above summary, may result from insufficient material or the authors' uncritical use of data borrowed from literature, errors of transliteration, or the combination of weights of sexually dimorphic individuals. A basic methodological weakness of their entire work is the uncritical factoring of brain weights, which attain relative stability in subadults and often in juvenals (fig. 18, table 8), against body weights, which vary with age, sex, health, visceral content, habitat, and season in and between in-

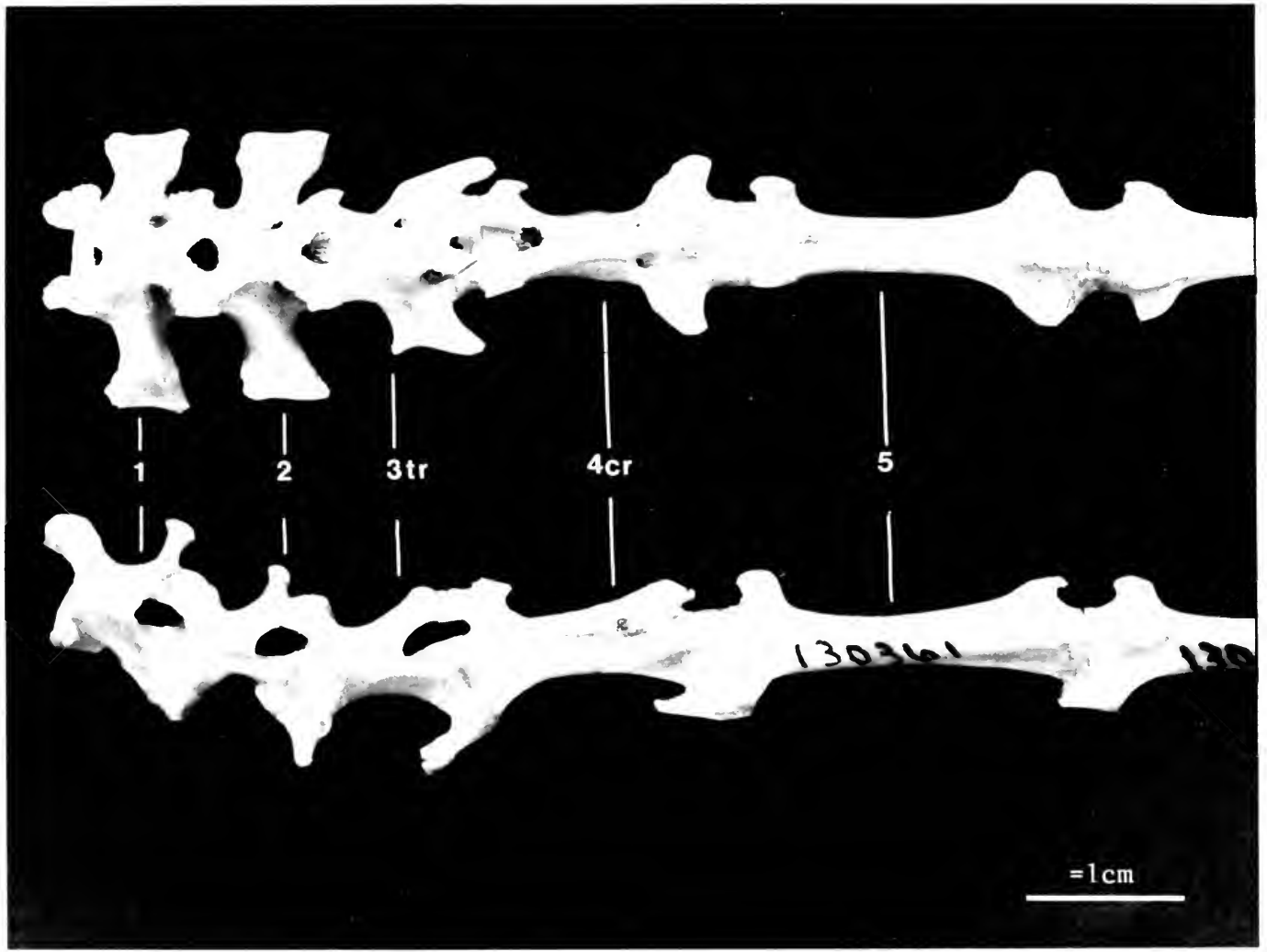

FIG. 17. Caudal vertebrae **1–5** (6 incomplete) of *Callicebus cupreus* (FMNH 130361), dorsal and left side views; vertebra number **3** transitional (**tr**), number **4** crested (**cr**).

TABLE 7. Sequence number of transitional and crested postsacral (or presimple caudal) vertebrae of nonprehensile-tailed cebids; sample number shown in parentheses.

Taxon	Transition vertebra number	Crested vertebra number
Callicebus donacophilus (6)	3rd (5); 4th (1)	4th (5); 5th (1)
Callicebus cupreus (5)	3rd (5)	4th (5)
Callicebus torquatus (3)	4th (3)	5th (3)
Aotus lemurinus (4)	3rd (1)	4th (1)
	4th (2)	4th (2)
	5th (1)	5th (1)
Aotus azarae (26)	3rd (7)	4th (3); 5th (4)
	4th (19)	5th (19)
Saimiri sciureus (4)	5th (4)	6th (4)
Saimiri sp. (Zoo) (5)	4th (1)	5th (1)
	5th (3)	5th (1); 6th (2)
	6th (1)	7th (1)
Pithecia monachus (3)	4th (3)	5th (3)
Pithecia pithecia (10)	3rd (5)	4th (4); 5th (1)
	4th (5)	5th (5)
Chiropotes satanas (5)	4th (5)	5th (5)
Cacajao calvus (1)	5th (1)	6th (1)

dividuals. The cited authors corrected for slight differences between the fresh and preserved brains they weighed, yet accepted body weights indiscriminantly from the literature. That the systematic arrangement of their indices of encephalization is not more skewed than appears attests to the reality, with few exceptions, of a general correlation between increasing brain weight or volume and increasing body size in primates.

Increasing fissuration or cerebral complexity is also correlated with increasing cerebral weight or neurocranial volume and body size (Hershkovitz, 1977, pp. 354–366). The relationship, however, is not purely allometric in platyrrhine ontogeny or phylogeny. Nonallometric trends also characterize other primate phyletic lines with different relationships between body size and cerebral complexity.

The arrangement in Table 9 of the species of *Callicebus* based on the ratio of braincase capacity (indicator of brain weight) to greatest skull length (indicator of body mass) reveals that the indices of encephalization (BCV/GL) expressed by the number 20 for *C. modestus* and 21 for *C. olallae* are minimum for cebids and rank with that of

TABLE 8. Juvenal and adult braincase volumes and encephalization indices in *Callicebus* and *Aotus*.

	BCV[1]	GL[2]	$\frac{BCV^3}{GL}$ (×100)
Callicebus torquatus medemi			
[4]Juvenal m^1 (FMNH 70695)	19.5	55.5	35
[5]Adults	20 (19–21) 8	69.3 (62.5–74.3) 52	29
Callicebus cupreus ornatus			
Juvenal m^1 (FMNH 87812)	17	54.1	31
Adults	17 (15–18) 9	62.8 (60.5–64.5) 21	27
Aotus vociferans			
[6]Juvenal m^0 (FMNH 41490)	21	58.2	36
[6]Adult m^3 (FMNH 41492)	19	63.6	30
Adults	17.6 (14–20) 22	62.6 (57.7–66.4) 53	28
Aotus azarae boliviensis			
Juvenal m^0 (FMNH 68861)	22	58.8	37
Adults	17 (15–21) 18	68.0 (60.4–66.6) 32	27

[1] BCV = Braincase volume.

[2] GL = Greatest length of skull (= indicator of body mass or weight).

[3] BCV/GL = Ratio of braincase volume to greatest length of skull (= index of encephalization; mean only given for adults).

[4] First upper molar (m^1) only erupted.

[5] Males and females with complete, fully erupted permanent dentition in all species listed. Figures are means, extremes (in parentheses), sample number.

[6] From Montalvo, Ecuador (fig. 18).

FIG. 18. *Aotus vociferans:* **upper,** juvenal cranium (FMNH 41490), front and left side; **lower,** adult cranium (FMNH 62074). See Table 7 for braincase volumes and encephalization indices.

TABLE 9. Cerebral and cranial indices of the species of *Callicebus*. Figures are ratios (×100) of single specimens or means of ratios (×100) of two or more specimens (number in parentheses).[1]

Species	BCV[2] / GL	CB[3] / GL	BW[4] / BL
Callicebus modestus	20 (1)	86 (1)	62 (1)
Callicebus olallae	21 (1)	84 (1)	67 (1)
Callicebus donacophilus	25 (5)	82 (20)	65 (13)
Callicebus oenanthe	24 (1)	81 (2)	68 (3)
Callicebus hoffmannsi	26 (12)	82 (41)	67 (43)
Callicebus moloch	26 (12)	81 (45)	66 (42)
Callicebus caligatus	27 (15)	80 (17)	67 (18)
Callicebus ornatus	27 (16)	81 (16)	69 (16)
Callicebus cupreus	28 (64)	80 (165)	67 (67)
Callicebus dubius	28 (1)	78 (3)	66 (4)
Callicebus brunneus	28 (12)	81 (21)	67 (18)
Callicebus cinerascens	28 (2)	81 (10)	67 (10)
Callicebus torquatus	29 (19)	81 (82)	68 (10)
Callicebus personatus	29 (22)	81 (20)	64 (18)
(Totals)	(180)	(444)	(264)
Mean	27	81	67
Extremes	20–29	78–86	62–69

[1] Cranial measurements of males and females combined; the differences between them are not significant (tables 8–10).

[2] Cerebral or encephalization index: Braincase volume (BCV) to greatest skull length (GL).

[3] Cranial index: Condylobasal length (CB) to greatest skull length (GL).

[4] Braincase index: Braincase width (BW) to braincase length (BL).

TABLE 10. Primate cerebral and cranial indices: Cerebral index (BCV/GL); cranial index (CB/GL); braincase index (BW/BL). Figures are ratios (×100) of single specimens or means of ratios (×100) of two or more specimens (sample number in parentheses).

Taxon	Sex	BCV[1] / GL	CB[2] / GL	BW[3] / BL
Lemuridae[4]				
Microcebus murinus		6 (1)	89 (1)	77 (1)
Galagidae[4]				
Galago demidovi		7,8	87, 88	73, 80
Tarsiidae[4]				
Tarsius philippinensis		9 (10)	79 (10)	75 (10)
Callitrichidae[5]				
Cebuella pygmaea		13 (19)	78 (34)	68 (61)
Callithrix humeralifer		18 (57)	81 (7)	64 (109)
Saguinus nigricollis		20 (102)	79 (17)	62 (494)
Leontopithecus rosalia		23 (4)	81 (13)	60 (13)
Callimiconidae[5]				
Callimico goeldii		22 (6)	74 (10)	65 (11)
Cebidae[4]				
Callicebus[6]	♂♂, ♀♀	27 (178)	81 (444)	67 (264)
Aotus l. griseimembra	♀♀	25 (8)	78 (25)	66 (26)
Aotus l. griseimembra	♂♂	26 (2)	78 (27)	66 (28)
Aotus a. boliviensis	♀♀	28 (10)	79 (26)	65 (24)
Aotus a. boliviensis	♂♂	29 (7)	80 (20)	65 (20)
Saimiri boliviensis peruviensis	♀♀	38 (6)	67 (17)	68 (18)
Saimiri boliviensis peruviensis	♂♂	39 (14)	69 (23)	67 (26)
Saimiri sciureus macrodon	♀♀	40 (26)	69 (41)	67 (42)
Saimiri sciureus macrodon	♂♂	40 (30)	69 (48)	66 (49)
Pithecia pithecia	♀♀	38 (5)	79 (8)	70 (8)
Pithecia pithecia	♂♂	39 (7)	80 (16)	68 (16)
Pithecia monachus	♀♀	44 (5)	82 (39)	70 (26)
Pithecia monachus	♂♂	43 (16)	83 (39)	70 (38)
Alouatta seniculus	♀♀	52 (5)	93 (5)	68 (5)
Alouatta seniculus	♂♂	52 (5)	87 (5)	70 (5)
Chiropotes albinasus	♀♀	59, 62	79 (7)	74 (7)
Chiropotes albinasus	♂♂	60 (4)	81 (7)	75 (7)
Chiropotes satanas	♀♀	65 (3)	78 (35)	74 (15)
Chiropotes satanas	♂♂	63 (8)	80 (29)	73 (14)
Cacajao melanocephalus	♀♀	67 (3)	77 (13)	71 (20)
Cacajao melanocephalus	♂♂	67 (8)	78 (12)	70 (22)
Cacajao calvus	♀♀	71 (14)	79 (30)	73 (30)
Cacajao calvus	♂♂	73 (10)	80 (29)	72 (32)
Cebus apella	♀♀	77 (5)	77 (5)	72 (5)
Cebus apella	♂♂	77 (5)	78 (5)	70 (5)
Cebus albifrons	♀♀	80 (4)	73 (4)	69 (4)
Cebus albifrons	♂♂	85 (5)	77 (5)	68 (5)
Lagothrix lagothricha	♀♀	91 (5)	81 (5)	73 (5)
Lagothrix lagothricha	♂♂	86 (5)	82 (5)	70 (5)
Ateles paniscus chamek	♀♀	99 (5)	78 (5)	71 (5)
Ateles paniscus chamek	♂♂	98 (5)	81 (5)	69 (5)
Brachyteles arachnoides	♀	94 (1)	81 (1)	73 (1)
Brachyteles arachnoides	♂♂	93, 101	81 (2)	73 (2)
Brachyteles arachnoides	?	104(juv.)	90 (1)	77 (1)

[1] Cerebral (Encephalization) Index: Braincase volume (BCV) to greatest length of skull (GL).
[2] Cranial Index: Condylobasal length (CB) to greatest length of skull (GL).
[3] Braincase Index: Braincase width (BW) to braincase length (BL).
[4] Raw data from FMNH specimens.
[5] Basic data from Hershkovitz (1977, table 2, p. 946, unnumbered).
[6] See Table 5 for cranial indices of individual species of *Callicebus*.

callitrichids such as *Saguinus* with ≈ 20. Indices of the remaining species of *Callicebus* are higher and coincide with those of *Aotus* (25–29). Differences in brain capacity between *Callicebus modestus* and *C. olallae* from that of congenerics may be narrowed by more samples. The greater difference between *Aotus* (25–29) and *Saimiri* (39–40) (table 10), however, is significant not only as to their respective grades of cerebral evolution but also to a multitude of morphological and behavioral characters, as well. It may well mark a watershed between the marmoset-like cebids *Callicebus* and *Aotus* and remaining forms of the family Cebidae (table 10).

The otherwise progressive relationship between increasing brain size and increasing body size, as indicated by skull length, is disrupted by *Alouatta* (column 1, table 10). Howlers with middleweight or pithecine-sized brains, and heavyweight or ateline-sized bodies (cf. Hershkovitz, 1977, table 30) are phyletic giants unrelated to pithecines, atelines, or other living or known extinct platyrrhines. Alouattine peculiarities have been discussed elsewhere (Hershkovitz, 1977, pp. 364-5).

The figures in column 2, Tables 9, 10, headed CB/GL or ratio of condylobasal length to greatest skull length, are suggestive of the position of the foramen magnum. The higher the ratio the more posteriorly or backwardly-directed the foramen, and the more primitive the braincase morphology. The highest strepsirhine ratio shown is that of *Microcebus murinus*; the highest platyrrhine ratios are those of *Alouatta* species and *Callicebus modestus*. The figures of the third column BW/BL, or braincase width to braincase length, suggest braincase shape. The higher the ratio, the more brachycephalic the braincase. Only the first column, the ratio of encephalization to body size or skull length, shows a consistent progression from lowest to highest with heavy body *Alouatta* the only significant exception.

Brain Mass and Age

The full-sized brain, determined by braincase capacity, may be attained in cebids before eruption of the first molar (m^0). Braincase length and width at the m^0 or m^1 stage, however, are usually less than average for a full-sized adult skull (fig. 18, table 8; see also Schultz, 1941, p. 277). The discrepancy between braincase capacity and apparently smaller external braincase dimensions of young animals is due to their relatively small, shallow orbits, near 0° basicranial flexure or kyphosis, and loosely fitted or open cranial sutures of the incompletely developed neurocranium. In the adult braincase, with capacity reduced by enlarged, deeply set orbits, fully flexed basicranium, and completely closed immovable sutures, accommodation of the larger brain is made possible by fissuration of the cerebral surface area (cf. Hershkovitz, 1977, p. 364, fig. VI.14).

XIII. Craniocerebral Size Classes (tables 11, 13)

Criteria used for body size or mass and brain weight are my uniformly measured greatest skull length, condylobasal length, and braincase volume. The few trustworthy body weights available co-vary directly with cranial dimensions (table 11). External measurements for most specimens examined were recorded by scientifically untrained hunters or commercial collectors and are not entirely reliable.

The species of *Callicebus* are roughly grouped in three size classes. The size range is from *C. donacophilus* with greatest skull length about 63 mm, condylobasal length about 53 mm, to *C. personatus*, with the greatest cranial lengths about 78 and 64 mm. Size overlap between the species is broad. The arrangement of species by size classes follows.

Class I—Small (figs. 19–21, tables 11, 13)

Callicebus donacophilus
Callicebus olallae
Callicebus modestus

Callicebus modestus, known from lectotype and subadult paralectotype, stands apart from all congenerics by its elongate skull and extremely small braincase. The greatest skull length (64.7 mm), places *modestus* squarely within the intermediate size class (II). The condylobasal length (55.9), measured from the extreme posterior position of the occipital condyles to tip of pointed muzzle, locates *modestus* high in the large size class (III). Notwithstanding, other cranial measurements, particularly the small braincase volume, smallest for cebids, and size of tanned hide, indicate that *modestus* is a small-bodied titi, like *C. donacophilus*.

TABLE 11. Craniocerebral-canine size relationships between species and sexes of *Callicebus*.

Callicebus	Greatest skull length	Weight (g)	Braincase volume	Canine height
d. donacophilus ♂♂	60.5 (57.8–63.0) 8	—	14, 15	3.5 (2.8–4.2) 10
d. donacophilus ♀♀	60.0 (58.2–61.7) 7	—	15, 15, 15	3.3 (2.7–4.1) 6
d. pallescens ♂♂	59.9 (58.0–62.2) 5	800	—	3.7 (3.2–4.1) 5
d. pallescens ♀	56.6	—	—	3.2
olallae ♂	60.2	—	12.5	2.8
modestus ♂	64.7	—	13	3.6
oenanthe ♂	64.6	—	—	4.0
oenanthe ♀♀	62.3, 63.5	—	15.5	2.7, 3.0
brunneus ♂♂	64.7 (60.1–68.1) 14	845	18 (16–21) 11	3.2 (2.5–3.7) 13
brunneus ♀♀	64.8 (60.1–68.1) 15	850	17.5	2.5, 3.0, 2.5
h. hoffmannsi ♂♂	64.0 (60.5–66.7) 14	—	18	3.1 (2.2–3.9) 13
h. hoffmannsi ♀♀	63.3 (60.1–66.8) 15	—	15, 17.5	3.0 (2.4–3.4) 13
h. baptista ♂♂	63.1 (60.6–67.2) 6	—	16.5 (16–17) 4	3.2 (2.6–3.9) 6
h. baptista ♀♀	62.7 (59.9–66.1) 9	—	16 (16–17) 5	3.0 (2.6–3.4) 8
moloch ♂♂	64.1 (61.9–66.4) 24	850, 1,000, 1,200	16, 17, 18	3.1 (2.3–3.8) 22
moloch ♀♀	63.3 (59.7–66.3) 32	877 (700–1,020) 6	16 (15–19) 9	3.1 (2.4–3.7) 29
dubius ♂	68.8	—	17	3.0
dubius ♀♀	60.9, 65.1	—	—	—, 3.1, 3.5
c. ornatus ♂♂	63.2 (60.9–64.5) 13	1,178	17 (15–18) 9	3.5 (2.8–4.1) 11
c. ornatus ♀♀	62.3 (60.5–63.7) 8	1,163	18 (17–19) 6	3.5 (3.1–3.8) 7
c. discolor ♂♂	64.1 (60.1–68.8) 54	845, 950, 1,010	18 (14–21) 29	3.7 (2.3–4.2) 54
c. discolor ♀♀	63.9 (59.9–67.5) 36	1,075	17 (16–19) 4	3.1 (2.0–4.2) 34
c. cupreus ♂♂	65.5 (62.4–68.9) 36	1,106 (1,000–1,175) 4	17, 18	3.8 (2.3–4.2) 35
c. cupreus ♀♀	63.9 (60.0–66.8) 30	—	—	3.2 (2.3–4.4) 29
caligatus ♂♂	65.1 (61.8–68.7) 12	—	17 (15–21) 11	3.3 (2.8–4.2) 13
caligatus ♀♀	63.9 (62.5–66.0) 8	—	18 (17–19) 4	2.9 (2.3–3.5) 9
cinerascens ♂♂	63.1, 65.7	—	19	2.8, 4.1, 3.0
cinerascens ♀♀	65.1 (62.1–67.8) 7	—	18	2.9 (2.5–3.4) 5
t. medemi ♂	69.1	1,100	21	4.1
t. medemi ♀♀	68.5 (65.5–70.5) 8	1,310 (1,151–1,462) 6	20 (18–25) 7	3.7 (2.9–4.2) 5
t. lugens ♂♂	68.4 (60.4–72.8) 41	—	21 (20–22) 5	3.8 (3.1–4.7) 27
t. lugens ♀♀	67.1 (61.8–71.5) 30	—	21, 21	3.6 (3.0–4.1) 21
t. torquatus ♂♂	69.3 (67.1–70.5) 6	—	—	3.7 (3.1–4.3) 6
t. torquatus ♀♀	68.8 (66.0–71.5) 5	—	—	3.6 (3.0–4.1) 4
t. lucifer ♂♂	69.7 (65.8–74.3) 13	1,500	19	3.7 (3.1–4.5) 11
t. lucifer ♀♀	69.7 (67.8–73.2) 7	—	—	3.6 (2.8–4.2) 4
t. regulus ♂♂	72.0, 67.5	—	21	3.5
t. regulus ♀♀	65.6, 71.9, 71.3	—	20	—, 3.4, 3.8, 3.8
t. purinus ♂♂	70.7, 70.0, 73.4	—	20	4.6, —, —, 3.4
t. purinus ♀♀	71.1 (69.0–73.6) 5	—	21	4.6, 2.9, 3.6
p. melanochir ♂	66.3	—	22	3.4
p. melanochir ♀♀	65.7, 66.4, 71.1	1,370	—	3.2 (2.5–3.8) 4
p. nigrifrons ♂♂	67.8 (65.5–72.4) 7	—	19	2.8 (2.2–3.2) 5
p. nigrifrons ♀♀	69.9 (68.1–72.0) 4	—	—	2.6, 2.9, 3.5
p. personatus ♂♂	71.7 (70.3–78.3) 10	1,270 (1,050–1,650) 5	—	3.3 (2.6–4.0) 10
p. personatus ♀♀	68.9 (64.7–72.7) 10	1,378 (970–1,600) 6	20, 21	3.3 (2.8–3.9) 7

Class II—Medium (figs. 19–21)

Callicebus oenanthe
Callicebus brunneus
Callicebus moloch
Callicebus hoffmannsi
Callicebus dubius
Callicebus cupreus
Callicebus caligatus
Callicebus cinerascens

All members of this class are closely related inter se, but with a greater distance between *oenanthe* and the rest.

TABLE 12. Summary of known karyotypes of *Callicebus*.

Callicebus	Sex	2n	Bia[1]	A[2]	X	Y(X)	Source
cupreus cupreus	♂	46	20	24	Bia	A	Bender & Mettler, 1958, p. 187, fig. 1
cupreus cupreus	♀	46	—	—	—	—	Benirschke & Brownhill, 1963, p. 338.
cupreus cupreus	♂	46	20	24	Bia	Bia	Egozcue et al., 1969, p. 17, fig. 2.
cupreus cupreus	♀	46	20	24	Bia	(Bia)	Benirschke & Bogart, 1976, p. 27, fig. 5.
cupreus discolor	♀	46	20	24	Bia	(Bia)	de Boer, 1974, p. 29, fig. 6.
cupreus ornatus	♂	46	20	24	Bia	Bia	de Boer, 1974, p. 32, fig. 7.
moloch	♂	48	20	26	Bia	?[3]	Pieczarka & Nagamachi, 1988, p. 653, figs. 1–4.
moloch	♀	48	20	26	Bia	(Bia)	Pieczarka & Nagamachi, 1988, p. 653, figs. 1–4.
brunneus	♂	48	20	26	Bia	Bia[3]	Minezawa *et al.*, 1989, p. 81, fig. 2
brunneus	♀	48	20	26	Bia	(Bia)	Minezawa *et al.*, 1989, p. 81, fig. 2
d. donacophilus	♂	50	22	26	Bia	Bia	de Boer, 1974, p. 30, fig. 6.
torquatus subsp.[4]	♀	20	10	10	?	?	Egozcue *et al.*, 1969, p. 21, fig. 3.
torquatus subsp.	♀	20	10	8	Bia	(Bia)	Benirschke & Bogart, 1976, p. 25, fig. 1–4.

[1] Biarmed automosomes.
[2] Acrocentric autosomes.
[3] "Minute."
[4] Sex chromosomes included in autosome count.

Class III—Large (figs. 19–21)

Callicebus torquatus
Callicebus personatus

Callicebus torquatus averages slightly smaller than *C. personatus*, but in other respects differs widely from it and other species. The nearest affinities of *C. personatus* appear to be with *C. cinerascens*, whereas *C. torquatus*, like *C. modestus*, is not closely related to any other species of *Callicebus*.

XIV. Sexual Dimorphism

Apart from those of the reproductive system, there are no appreciable morphological differences between the sexes at comparable ages (table 13). However, a trend toward greater body size and correspondingly longer canines in males is detectable.

XV. Karyotypes and Taxonomy (table 12)

Recent discoveries of distinctive karyotypes among some erstwhile "subspecies" of *Callicebus* "*moloch*" cast doubt on the validity of the components of the species as proposed in 1963 by Hershkovitz.

The first known titi karyotype, that of a male *Callicebus cupreus cupreus* with the diploid number 46, was reported by Bender and Mettler (1958, p. 187; see also Chu & Bender, 1961, p. 1401; Bender & Chu, 1963, p. 284). The female of *Callicebus cupreus cupreus* was also shown to have the chromosomal complement $2n = 46$ (Benirschke & Brownhill, 1963, p. 338).

Egozcue *et al.* (1969, p. 17, fig. 2) confirmed the diploid chromosome number for *Callicebus cupreus* but used the blanket name "*C. moloch*" following the dictum of Hershkovitz (1963). The X and Y chromosomes were described as submetacentric. The next advance in *Callicebus* cytogenetics, made by the same team of Egozcue *et al.* (1969, p. 21, fig. 3), was the discovery of the diploid chromosome number 20, for *Callicebus torquatus*, the lowest known for primates.

Studies of platyrrhine cytogenetics by de Boer (1974) brought to light the diploid number 50 in a male *Callicebus* "*moloch*" *donacophilus* and raised questions regarding the correct systematic position of the taxon. As viewed by de Boer (1974, p. 35), "*cupreus* and *ornatus* (possibly together with *discolor* and *brunneus*, all of which were included in a separate species, *C. cupreus* by Hill) on the one hand, and *donacophilus* (possibly together with *moloch* and *hoffmansi*) on the other, may be more than only subspecially distinct. The karyotypic dif-

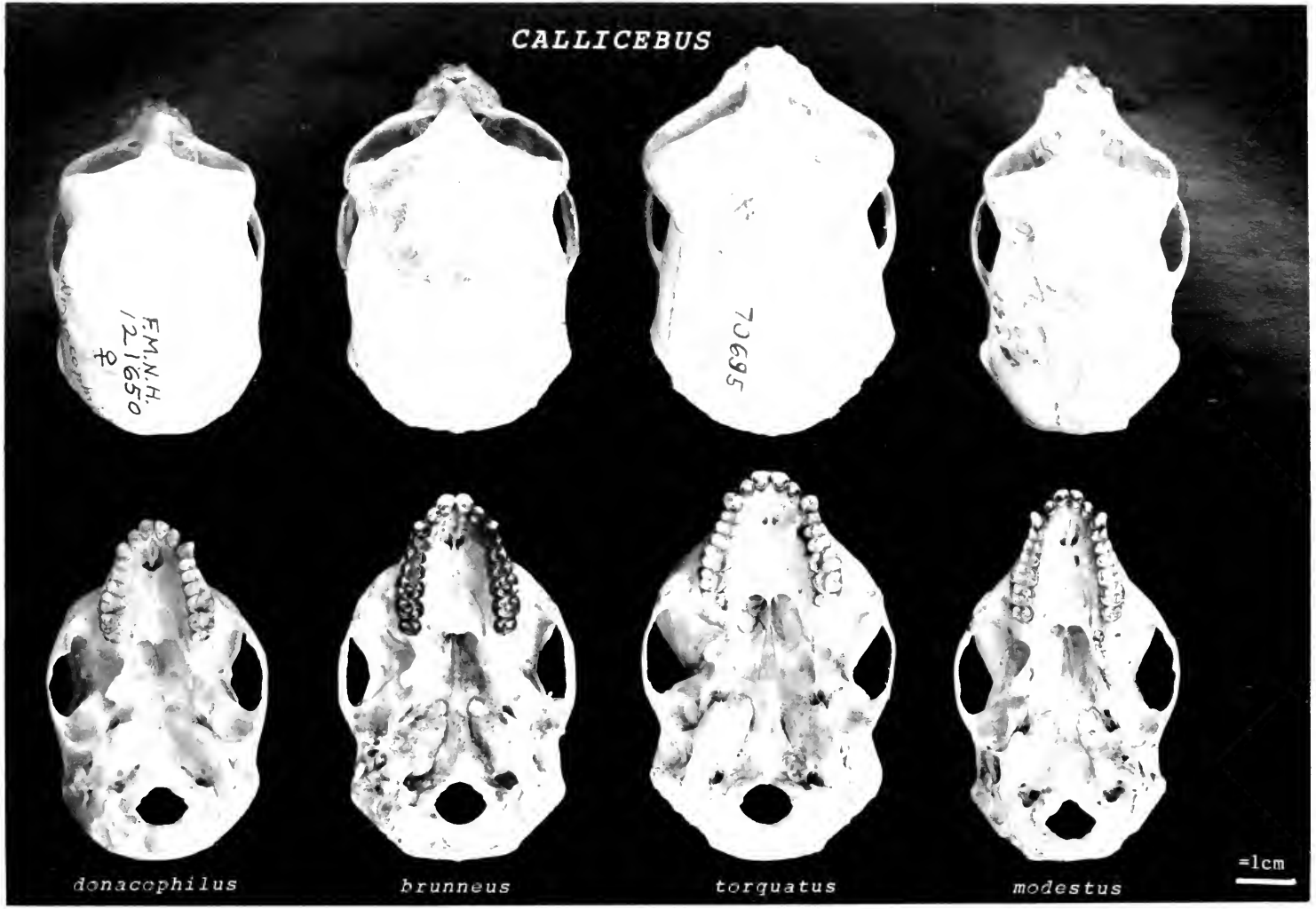

FIG. 19. *Callicebus*, dorsal and ventral views of skulls of *Callicebus brunneus*, FMNH 14338; *C. donacophilus*, FMNH 121650; *C. torquatus*, FMNH 70695; *C. modestus*, RNHMS 135 (lectotype).

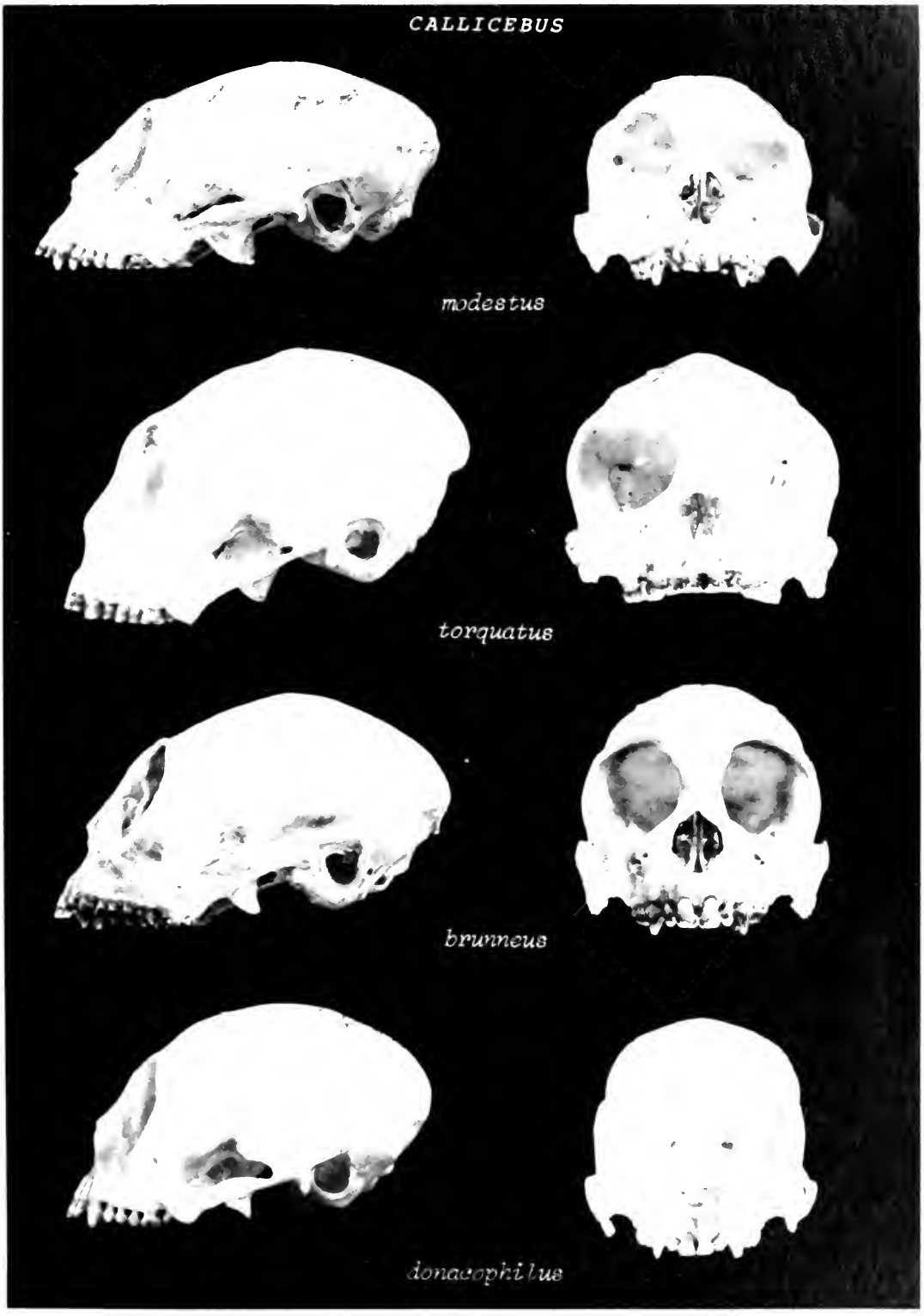

FIG. 20. *Callicebus*, left side and frontal views of crania; same skulls shown in Figure 19.

ferences probably form a solid barrier which prevents intergradation."

Benirschke and Bogart (1976, p. 32) remarked on the "unusually dissimilar numbers (50, 46, 20), found in the very few specimens examined." They observed that Giemsa-banded and radioautographed chromosomes of two female *Callicebus torquatus* and one *C. cupreus cupreus* examined by them exhibited few comparable chromosome segments. Koiffman and Saldanha (1981, p. 669) also commented on the chromosomal differences which "cannot be explained by processes of centric fusion or fission."

Finally, Pieczarka and Nagamachi (1988) showed that the chromosome complement of the real or restricted *Callicebus moloch,* determined from 22 males and 17 females from the left bank of the lower Rio Tocantins, Pará, Brazil, was 48. This number effectively separated true *Callicebus moloch* from all other titis previously treated as subspecies of *C. moloch.* The same diploid number, 48, discovered by Minezawa et al. (1989) in 2 males and 2 females of a northern Bolivian *Callicebus* "*moloch*" *brunneus,* exhibits certain morphological differences from the karyotype of *C. moloch.* The two species are parapatric.

Chromosomal heterogenecity, as observed by Marks (1987, p. 148), may be common in genera like *Callicebus* which is "characterized by monogamy and territoriality, and lives in very small social groups." The genus *Aotus,* composed of at least 9 monogamous species, each distinguished from the others by its karyotype, is another case in point.

XVI. Metachromism: Evolutionary Change of Mammalian Tegumentary Coloration (fig. 22)

Geographic variation among the subspecies of *Callicebus* is apparent in coat color (Hershkovitz, 1988). The process of evolutionary change in tegumentary coloration has been termed metachromism (Hershkovitz, 1968; 1970; 1977, pp. 99–101). Its essential features, all relevant to *Callicebus,* are summarized below.

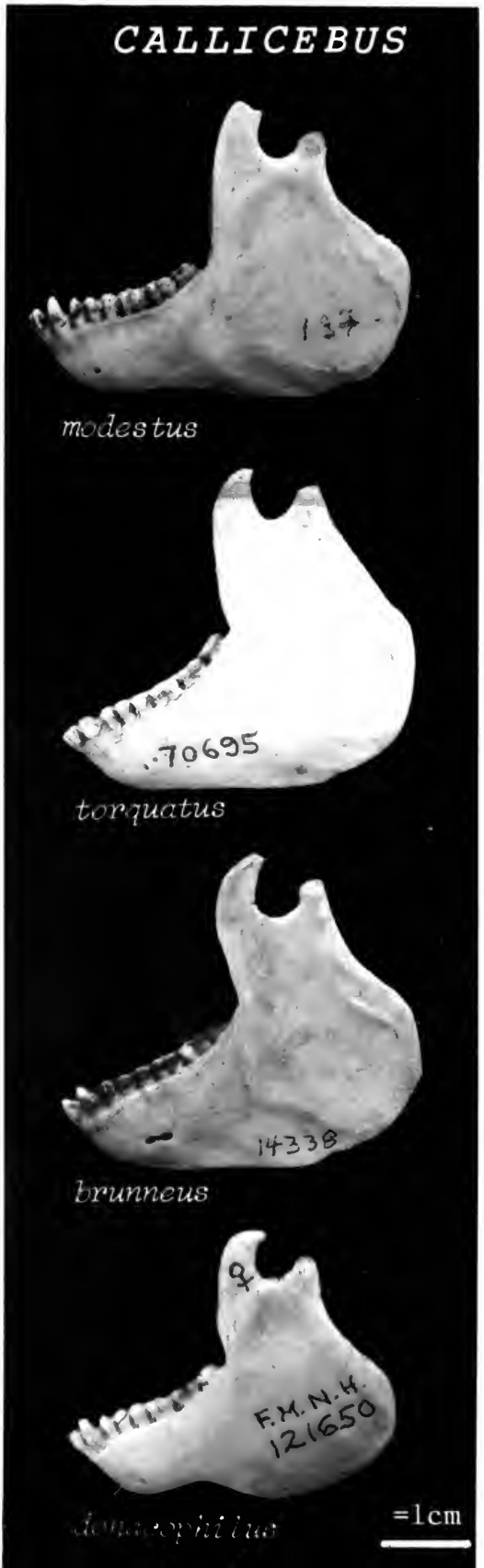

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FIG. 21. *Callicebus,* right side of mandibles of crania shown in Figure 19. *C. modestus* mandible, RNHMS 135 (misnumbered "137").

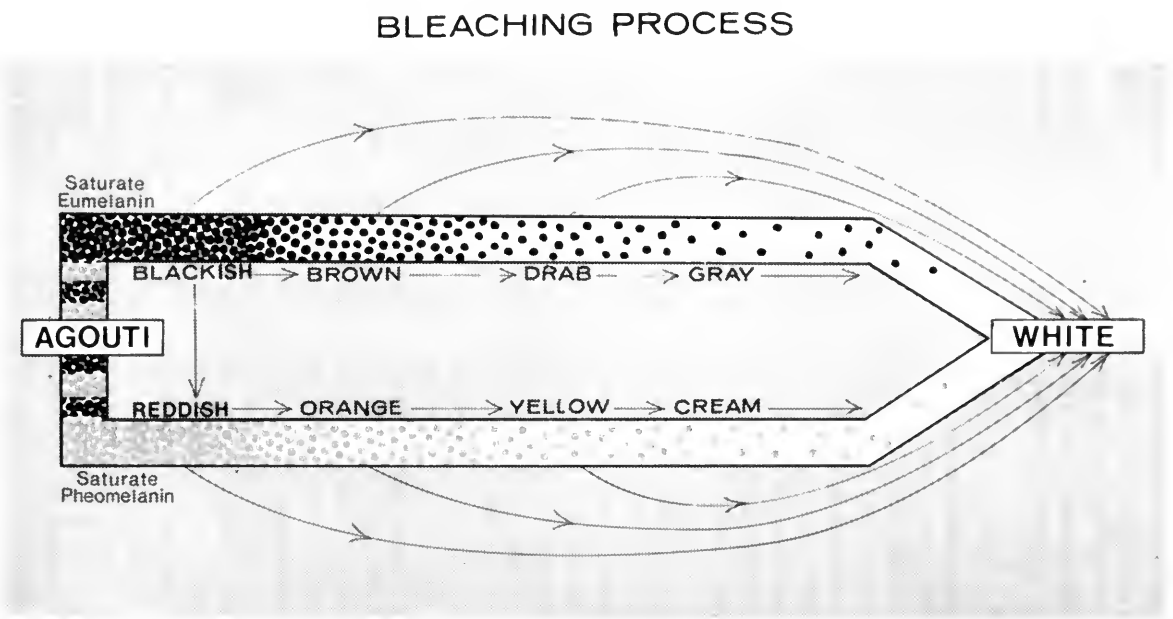

FIG. 22. Metachromism summarized: The evolutionary change in pelage coloration from the primitive agouti hair pattern of alternating bands of eumelanin (blackish) and pheomelanin (reddish) to saturation of either pigment, followed by bleaching or dilution of the monochromatic hair to colorless or white. The bleaching process may be gradual or abrupt (figure modified from Hershkovitz, 1968, 1977).

The two pigments of mammalian tegumentary coloration are eumelanin (dark brown or "blackish"), found in hair, skin, and iris; and pheomelanin ("reddish"), in hair only. The pigments are produced by melanocytes which deposit them as granules into the medulla of the growing hair. The primitive pilary color pattern from which all other patterns can be derived is agouti. In the individual hair the agouti pattern is characterized by alternation of eumelanin and pheomelanin bands over at least the terminal half; the pigment of the basal or hidden portion of the hair is typically eumelanin.

Divergence of coloration from the primitive agouti pattern of individual hairs (usually the "cover hairs"), pilary fields (chromogenetic fields), or the entire coat to either uniformly eumelanin or uniformly pheomelanin is caused by a breakdown or hobbling of the switching mechanism which controls the deposition of the two pigments in alternation. As change progresses each monochromatic or saturate hair of a chromogenetic field appears to fade or bleach by gradual reduction of the amount of pigment granules deposited in each hair. The process is, as a rule, correlated with clinal geographic variation. The eumelanic bleaching process or pathway is brown → drab → gray → white or colorless; the pheomelanic pathway is reddish → orange → yellow → buff or cream → white. Gradation from saturate to colorless may also be abrupt, with omission of one or more intermediate tones of the chromatic scale. Reversals of saturation or bleaching (dilution) have not been observed. Once lost, the agouti pattern is not known to reappear in phylogeny. Nevertheless, genetic recombination in experimentally produced hybrids of saturate parents may restore the agouti pattern in the offspring (Hershkovitz, 1977, p. 721, figs. X.52, X.53).

Elaboration and deposition of eumelanin pigment in the *saturate* hair may switch back to elaboration and deposition of pheomelanin pigment. This is not a reversal to the agouti pattern of alternating color bands. The initial effect of the pigmentary replacement is a bicolored hair with varying amounts of the basal portion pheomelanin, sometimes with a slight mixture of eumelanin, and the terminal portion eumelanin. Ultimately, the entire hair except the very fine blackish tip is replaced by pheomelanin which in turn tends to bleach to blond or near white (fig. 22). Examples of the ongoing replacement process among primates are found in lion tamarins, most notably in the dominantly eumelanin *Leontopithecus rosalia chrysopygus* and *L. r. chrysomelas,* with replacement nearly or virtually complete in the reddish *L. r. rosalia.* The chromatic change is similar in uacaries, genus *Cacajao* (Hershkovitz, 1987a, p. 50). In extremes of both genera, the replacement pheomelanin bleaches to nearly white. Other examples include the dominantly to completely eumelanin howler, *Alouatta belzebul,* that grades into the dominantly to completely pheomelanin *Alouatta seniculus.*

Metachromatic change, or phylogenetic breakdown of tegumentary pigment production and deposition, appears accelerated in small geographically isolated populations where no outbreeding can occur, at least initially, and inbreeding is essential for survival. Constraints on change include assortative mating in established populations and continuous or sporadic gene flow between neighboring populations.

Precise or standardized terms for each of the myriad tones of eumelanin or pheomelanin do not exist. Tones of the eumelanin scale may be seen as blackish with dilution to grayish or nearly white. Those of the pheomelanin scale may be viewed as reddish with dilution to orange, buffy, or cream to nearly white. True black or red is not found in hair. The nearest approach to black is the eumelanin dark brown. "Red" hair is actually the pheomelanin orange or a more saturate "reddish." In albinos, the unpigmented skin permits the true red of the blood's hemoglobin to show through. White is colorless. The colorless portion of a hair appears translucent to the eye or under the microscope. The seeming whitish or grayish hair, or band, is dilute or bleached pheomelanin or eumelanin.

Misrepresentation of color terms in the following descriptions of taxa is avoided by use of blackish, reddish, grayish, whitish, buffy, and similarly modified adjectives for what to the uncritical eye appears black, red, gray, white, buff, and others of the sort.

Monochromic hairs of either eumelanin or pheomelanin may contain a slight mixture of the other pigment. The dominant pigment is referred to in the color descriptions, qualified where necessary.

Species of *Callicebus* characterized by dominance of eumelanin on forehead, crown, and cheiridia are *hoffmannsi, brunneus, caligatus, personatus,* and *torquatus.* Species characterized by dominance of pheomelanin on the same parts are *modestus, donacophilus, olallae, oenanthe, moloch,* and *cupreus.*

Callicebus cinerascens tends toward pheomela-

nization but forehead and crown remain agouti. *C. dubius* is dominantly eumelanic like *caligatus* but with forehead pheomelanic as in *C. cupreus discolor.*

XVII. Systematic Arrangement of the Species and Subspecies

***modestus* Group** (figs. 19–21)

Callicebus modestus Lönnberg, 1939

NOTES—Known only from the adult lectotype skin and skull and those of a subadult paralectotype; among smallest species of genus; externally most similar to members of the *moloch* group; cranially most distinctive and probably most primitive among cebids and higher primates; the mandibular angle, however, is extremely derived; braincase volume smallest for cebids.

***donacophilus* Group** (figs. 19–21)

Callicebus donacophilus d'Orbigny, 1836
C. d. donacophilus d'Orbigny, 1836
C. d. pallescens Thomas, 1907
Callicebus olallae Lönnberg, 1939
Callicebus oenanthe Thomas, 1924

NOTES—Comprised of smaller species; morphologically intermediate between the *modestus* and *moloch* groups but nearer latter; diploid chromosome number for *C. d. donacophilus* = 50; unknown for remaining taxa.

***moloch* Group** (figs. 19–21)

Callicebus cinerascens Spix, 1823
Callicebus hoffmannsi Thomas, 1908
C. h. baptista Lönnberg, 1939
C. h. hoffmannsi Thomas, 1908
Callicebus moloch Hoffmannsegg, 1807
Callicebus brunneus Wagner, 1842
Callicebus cupreus Spix, 1823
C. c. cupreus Spix, 1823
C. c. discolor I. Geoffroy and Deville, 1848
C. c. ornatus Gray, 1870
Callicebus caligatus Wagner, 1842
Callicebus dubius Hershkovitz, 1988
Callicebus personatus É. Geoffroy, 1812
C. p. melanochir Wied-Neuwied, 1820
C. p. nigrifrons Spix, 1823
C. p. personatus É. Geoffroy, 1812
C. p. barbarabrownae

NOTES—All species save the last are typical titis, once regarded conspecific (Hershkovitz, 1963a). Diploid chromosome number for *C. c. cupreus, C. c. discolor, C. c. ornatus* = 46; for *C. moloch* = 48; for *C. brunneus* = 48. *C. personatus,* known only from skins and skulls, is largest species of genus, its systematic position uncertain.

***torquatus* Group** (figs. 19–21)

Callicebus torquatus Hoffmannsegg, 1807
C. t. medemi Hershkovitz, 1963a
C. t. lugens Humboldt, 1811
C. t. torquatus Hoffmannsegg, 1807
C. t. lucifer Thomas, 1914
C. t. regulus Thomas, 1927
C. t. purinus Thomas, 1914

NOTES—Distinguished from all other titis by blackish coat color and by cranial and postcranial skeletal characters; average size nearly that of *C. personatus*; diploid chromosome number = 20 (subspecies ?), lowest for primates and among lowest for mammals.

XVIII. Geographic Size Variation

Species of *Callicebus* with smallest individuals (*donacophilus, modestus, olallae*) are clustered at the southwestern corner of the geographic range of the genus. Those with largest individuals occur in or are centered at the eastern (*personatus*) and northwestern (*torquatus*) extremes of the range. Species with middle-sized (*cupreus, caligatus, brunneus, dubius, cinerascens, moloch, hoffmannsi*) and small (*oenanthe*) individuals occupy the middle ground, between the others.

XIX. Geographic Relationships

Allopatric Species (fig. 1)

Callicebus personatus, largest-bodied species of the genus with a geographic range greater than that

of other species except *C. torquatus,* inhabits coastal and inland forests of eastern Brazil. The species is separated by about 1,000 km from nearest related *Callicebus moloch* to the northwest, and about 500 km from distantly related but nearest neighbor *C. donacophilus* to the southwest. It is unlikely that titis of any kind will be discovered within the extensive geographic gap. The Atlantic forest subregion occupied by *C. personatus* is also inhabited by such noteworthy primate endemics as the woolly spider monkey (*Brachyteles arachnoides*) and lion tamarin (*Leontopithecus rosalia*).

Callicebus oenanthe (fig. 1) is isolated in the Peruvian montane forest at the western extreme of the generic range. The original description of *oenanthe* and its geographic position suggest close affinities, if not identity, with nearest neighbor *Callicebus cupreus discolor.* Notwithstanding, *Callicebus oenanthe* most nearly resembles *C. donacophilus* of the Bolivian highlands about 2,000 km to the south. The geographic gap between *C. oenanthe* and *C. cupreus discolor* may be less than 100 km. Additional collecting may reduce or even eliminate the hiatus. The morphological gap between the taxa, however, is too great to be bridged by presumptive geographically intermediate populations. Sympatric endemics include the night monkey (*Aotus miconax*) and yellow tail woolly monkey (*Lagothrix flavicauda*).

Parapatric Species (fig. 1)

Parapatric species of *Callicebus* live on opposite sides of rivers or watershed divides. Passive transfer of titi populations of one side of the river to the other by river bend cutoffs must occur frequently. Equivocal locality records on the east bank of the Rio Tapajós suggest enclave populations of *C. hoffmannsi* in the range of *C. moloch.* These enclaves of one species in the territory of the other are usually ephemeral. This is not sympatry, but may become so with establishment and geographic spread of the enclave population. The parapatric species of *Callicebus* are *C. donacophilus, C. hoffmannsi, C. moloch, C. brunneus,* and perhaps *C. modestus* and *C. olallae.*

The geographic range of the Bolivian and Paraguayan *Callicebus donacophilus* (fig. 4) includes part of the upper Río Beni drainage basin which also supports *Callicebus brunneus, C. olallae,* and *C. modestus* (fig. 1). Probable contact between the species is not indicated by present information. Boundaries between them are drawn arbitrarily or left open. The Bolivian highland *Callicebus modestus* and *C. olallae,* known only from type localities hardly 50 km apart in the upper Río Yaruma-Mamoré basin, differ widely from each other and all others. In the absence of contrary evidence, each may also be regarded as an isolated relic species despite the geographic proximity to each other and to populations of *C. brunneus* and *C. donacophilus.* Their geographic position may be analogous to that of the Peruvian *Callicebus oenanthe* and perhaps should be classified with it as essentially insular.

Sympatric Species (fig. 1)

Species sharing part or all of their geographic range are sympatric. The sympatric forms of *Callicebus* are the following, the degree of sympatry from coextensive to slight overlap in range or marginal indicated in parentheses and shown on map (fig. 1).

Callicebus moloch with *C. cinerascens* (partial)
Callicebus brunneus with *C. caligatus* (partial)
Callicebus brunneus with *C. cupreus cupreus* (partial)
Callicebus brunneus with *C. donacophilus* (possibly partial)
Callicebus caligatus with *C. cupreus cupreus* (partial)
Callicebus caligatus with *C. dubius* (questionably marginal)
Callicebus caligatus with *C. torquatus purinus* (coextensive)
Callicebus caligatus with *C. torquatus regulus* (coextensive)
Callicebus torquatus purinus with *C. cupreus cupreus* (*C. c. egeria*?) (coextensive)
Callicebus torquatus regulus with *C. cupreus cupreus* (*sensu stricto*) (coextensive)
Callicebus torquatus lucifer with *Callicebus cupreus discolor* (partial)
Callicebus torquatus lugens with *Callicebus cupreus ornatus* (slight overlap)

XX. Key To Species of *Callicebus* Based on Coloration

1. Forehead whitish, buffy or grayish agouti to brownish agouti not demarcated from crown, fine blackish superciliary line often present 2
1′. (a) Forehead grayish, brownish or blackish agouti, or entirely blackish, hands or feet, or both, blackish or brownish; or (b) forehead whitish to grayish, well demarcated from crown 6
2. Sideburns buffy, yellowish, orange, or reddish brown sharply contrasting with agouti crown ... 3
2′. Sideburns grayish or brownish agouti hardly or not demarcated from agouti crown 4
3. Outer surface of forearms, part or all of forelegs, and cheiridia uniformly reddish in marked contrast with grayish agouti or buffy upper arms and thighs ..... *C. cupreus* (p. 60)
3′. Outer surface of forearms and forelegs grayish agouti, buffy agouti, or brownish agouti like upper arms and thighs; cheiridia like outer side of limbs 14
4. Grayish malar stripe conspicuous; cheiridia grayish, buffy, or tawny more or less like outer side of arms and legs; whitish ear tufts present 13
4′. Malar stripe absent; cheiridia brownish or blackish brown like outer side of arms or legs; pale ear tufts present or absent 5
5. Whitish or grayish ear tufts conspicuous, pelage of dorsum and sides of trunk brownish agouti, the pilary banding conspicuous ..... *C. modestus* (p. 46)
5′. Ear tufts absent or inconspicuous; pelage of dorsum and sides of trunk nearly uniform reddish brown, the pilary banding inconspicuous ..... *C. olallae* (p. 49)
6. Forehead with well-defined whitish or grayish frontal band or blaze 7
6′. Forehead grayish or blackish agouti to entirely blackish, without frontal blaze 9
7. Sideburns agouti like crown; face framed whitish or grayish; cheiridia and outer side of forearms and legs agouti ..... *C. oenanthe* (p. 51)
7′. Sideburns reddish contrasting with agouti crown; face framed reddish, cheiridia mostly to entirely reddish, whitish or blackish 8
8. Crown blackish; cheiridia mostly to entirely blackish agouti ..... *C. dubius* (p. 66)
8′. Crown buffy agouti to reddish or reddish brown agouti; cheiridia entirely reddish or partly to entirely whitish ..... *C. cupreus* (p. 60)
9. Throat whitish, buffy, yellowish, or orange, sharply defined from chin and chest; sideburns blackish ..... *C. torquatus* (p. 78)
9′. Throat like sideburns or chest 10
10. Tail reddish orange, grayish, blackish, or mixed; sideburns blackish, reddish brown, reddish, or grayish 11
10′. Tail blackish or grayish; sideburns, chest and belly grayish or whitish .... *C. cinerascens* (p. 51)
11. Sideburns reddish, sharply demarcated from blackish crown; underparts and inner side of limbs sharply defined reddish; tail marbled ..... *C. caligatus* (p. 66)
11′. Sideburns blackish or reddish brown, like crown; underparts and inner side of upper arms and thighs not sharply defined from sides of trunk; tail variable 12
12. Upper parts of body dark brown, the hairs finely banded, pelage thick but not shaggy, tail dominantly blackish or blackish brown, the hairs finely banded; underparts brownish, arms, legs, cheiridia blackish ..... *C. brunneus* (p. 59)
12′. Upper parts of body dominantly grayish, buffy, or orange, the hairs coarsely banded, pelage shaggy, underparts grayish or buffy; tail buffy, orange, reddish, grayish, or coarsely mixed; cheiridia and distal parts of outer surface of forearms and legs blackish, remainder of limbs agouti like sides .. .. *C. personatus* (p. 69)
13. Whitish ear tufts conspicuous, whitish frontal blaze absent ..... *C. donacophilus* (p. 46)
13′. Whitish ear tufts absent or inconspicuous, whitish frontal blaze present, inconspicuous or absent ..... *C. oenanthe* (p. 51)
14. Cheiridia like outer side of limbs or darker ..... *C. hoffmannsi* (p. 54)
14′. Cheiridia contrastingly paler than outer side of limbs ..... *C. moloch* (p. 56)

XXI. Species and Subspecies Accounts

Callicebus modestus Lönnberg

Callicebus modestus Lönnberg, 1939: 17.

LECTOTYPE—Adult male, skin and skull, Royal Natural History Museum, Stockholm, no. A612105, collected 28 December 1937, by A. M. Olalla, original number 135; lectoparatype, subadult male, skin and skull RNHMS, collected by A. M. Olalla, 28 December 1937, original number 136.

TYPE LOCALITY—El Consuelo, Río Beni, Beni, Bolivia; altitude, 196 m above sea level.

DISTRIBUTION (fig. 23)—Known only from the upper Río Beni basin in the upper Río Madeira watershed, Beni, Bolivia.

DIAGNOSTIC CHARACTERS—All upper and outer parts brownish or reddish agouti except whitish ear tufts, forehead reddish brown agouti, like crown, the thin blackish superciliary fringe excepted; outer surface of limbs reddish brown agouti; hands, toes blackish or mixed blackish and reddish; sideburns not contrasting in coloration with forehead and crown; whitish malar stripe absent, whitish ear tufts present; tail dominantly blackish agouti, darker than dorsum.

Skull (figs. 5, 7, 19–21) elongate, comparatively low-slung, greatest height perpendicular to Frankfurt plane about 51% greatest skull length; condylobasal length about 86% greatest skull length; braincase extremely narrow, greatest width about 48% greatest skull length (50%–59% in other species); postorbital constriction about 41% greatest skull length (43%–53% in other species); posterior palatal border behind posterior plane of m^{3-3}; superior temporal ridges extremely approximated, distance between them at frontoparietal sutures about 50% greatest braincase width, about 22% at lambdoidal crest between parieto-occipital sutures; hamular process of pterygoid plate least reduced, the interpterygoid fossa widest and deepest of genus.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *Callicebus brunneus* by generally paler coloration, forehead reddish brown agouti, ear tufts whitish, outer surface of limbs not blackish; from *C. caligatus* by sideburns not sharply defined from coloration of crown, forehead, and crown agouti, ear tufts whitish, tail dominantly blackish throughout; from *C. cupreus discolor* and *C. c. ornatus* by absence of pale frontal blaze, dominantly brownish outer surface of limbs; from *C. oenanthe* by forehead-like crown, facial border blackish; from all other species of *Callicebus* by one or more of above characters and most cranial characters detailed above.

SPECIMENS EXAMINED—Total 2. **BOLIVIA. Beni:** El Consuelo, Río Beni, 2 (RNHMS, including lectotype and subadult lectoparatype).

Callicebus donacophilus d'Orbigny

DISTRIBUTION (fig. 23)—Upper basins of Ríos Mamoré and Grande in Bolivia, west bank of upper Río Paraguay basin in Paraguay, Bolivia, and Brazil.

DIAGNOSTIC CHARACTERS—Average size smallest; pelage thick, long; head, upper, and outer sides of body and limbs buffy or "grayish" agouti to dominantly orange agouti; whitish ear tufts conspicuous; forehead like crown, blackish superciliary fringe incipient or absent; buffy malar stripe well developed; sideburns agouti like crown; throat agouti, most of chest, belly uniformly orange; upper surface of hands dominantly buffy or buffy agouti, paler than forearms; tail mixed buffy and blackish, base contrastingly buffy; skull essentially like those of the *moloch* group but muzzle slightly more elongate.

COMPARISONS—Distinguished from *Callicebus brunneus* by paler coloration throughout; from *C. caligatus, C. cupreus, C. moloch,* and all other species of *Callicebus* except *C. oenanthe,* by well-developed malar stripe and near uniformity or lack of marked contrasts in agouti coloration of crown, forehead, sideburns, outer side of limbs, cheiridia, back, and tail; from *cinerascens* by whitish ear tufts, malar stripe, uniformly buffy to orange underparts; from *oenanthe* by conspicuous whitish ear tufts and absence of whitish facial fringe.

Key to Subspecies of *Callicebus donacophilus*

1. Outer surface of limbs dominantly orange agouti; back buffy to orange agouti ..... *donacophilus*
1′. Outer surface of limbs dominantly buffy agouti; back buffy or "grayish" agouti ..... *pallescens*

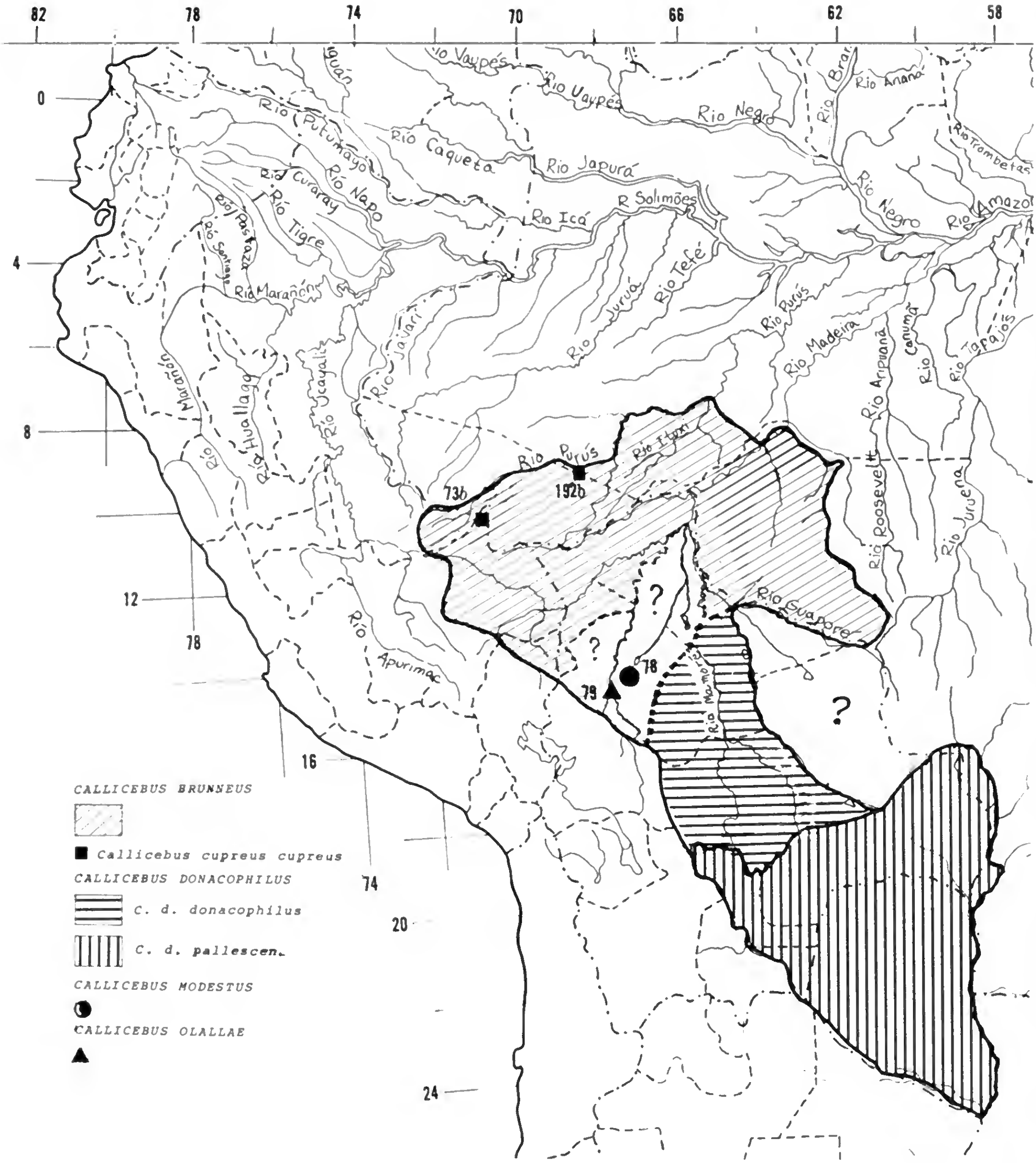

FIG. 23. Geographic distribution of *Callicebus brunneus, C. donacophilus donacophilus, C. d. pallescens, C. modestus* (circle no. 78, only known locality), and *C. olallae* (triangle no. 79, only known locality), in shaded parts of Peru, Brazil, Bolivia, and Paraguay. Squares show localities where both *C. brunneus* and *C. cupreus cupreus* have been recorded. See Figure 1 for overlap of species ranges and Gazetteer (p. 104) for explanation of numbers.

Callicebus donacophilus donacophilus D'Orbigny (fig. 24)

Callithrix donacophilus d'Orbigny, 1836: Atlas, pl. 5 (animal and name).

HOLOTYPE—Represented by a colored figure of animal captioned "CALLITHRIX donacophilus, d'Orb[igny]" in the "Atlas" of the Mammals of the "Voyage dans l'Amérique Méridionale", issued 1836 as a separate folio without text.

FIG. 24. *Callicebus donacophilus donacophilus* d'Orbigny. Photograph courtesy Dr. Russell A. Mittermeier.

The holotype, apparently an adult, sex unknown, was presumably preserved mounted, perhaps with skull in skin, in the exhibition galleries of the Muséum National d'Histoire Naturelle, Paris. I did not find the specimen in the museum collection.

TYPE LOCALITY—"Dans les bois et parmi les roseaux qui bordent les rivières de la province de Moxos [Beni], dans le république de Bolivia [In the woods and among the reeds bordering the rivers [of the Río Mamoré basin] in the province of Moxos, Republic of Bolivia] (d'Orbigny & Gervais, 1847, p. 10).

DISTRIBUTION (fig. 23)—West central Bolivia in the upper Ríos Mamoré-Grande and San Miguel basins, Beni and Santa Cruz provinces; altitudinal range between 100 and 500 m above sea level.

DIAGNOSTIC CHARACTERS—Upper and outer parts of head, body, outer, and inner sides of forelimbs buffy to orange agouti, the parts not contrasting; cheiridia like arms and legs or slightly paler; underparts of body uniformly orange or brownish orange; tail mixed blackish and buffy with base distinctly paler, pencil undistinguished; ears hairy, conspicuously tufted whitish.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *Callicebus donacophilus pallescens* by more saturate coloration throughout, pelage less shaggy; from *Callicebus moloch* by agouti sideburns not contrasting with agouti parts of head and trunk; from *brunneus* by pale agouti forehead, forearms, legs, and paler underparts; from *C. cupreus discolor* by absence of whitish frontal blaze, sideburns agouti like crown; from *C. oenanthe* by conspicuous whitish ear tufts and absence of whitish facial fringe or suborbital tufts; from *C. personatus* and *C. torquatus* by buffy or brownish agouti forehead, cheiridia grayish agouti, tail mixed buffy and blackish, and whitish ear tufts.

SPECIMENS EXAMINED—Total 38. **BOLIVIA. Beni:** Camiaco, 3 (AMNH); **Cochabamba:** Misión San Antonio, 2 (AMNH); San Antonio, 5 (AMNH); Todos Santos, 2 (AMNH; FMNH); "Yungas", 1 (BM); **Santa Cruz:** Bella Esperanza, Cercado, 1 (MNR); Buenavista, 8 (AMNH; BM, 6; FMNH); Camino de Santa Cruz a Clara, Cercado, 1 (MNR); Cupesi, Cercado, 1 (MNR); El Valle, Cercado, 1 (MNR); Río Surutú, 1 (AMNH); Santa Cruz de la Sierra, 1 (AMNH); Sara 2 (BM); Locality unknown, 3 (BM, Bridges collector); 6 (FMNH, Lincoln Park Zoo, Chicago).

Callicebus donacophilus pallescens Thomas (fig. 25)

Callicebus pallescens Thomas, 1907: 161.

HOLOTYPE—Adult male, skin and skull, British Museum (Natural History) no. 94.3.6.1; collected October 1893 by J. Bohls.

TYPE LOCALITY—Thirty miles north of Concepción, Chaco, Paraguay.

DISTRIBUTION (fig. 23)—West of the Río Paraguay in the Gran Chaco of Paraguay, and Pantanal of Mato Grosso do Sul, Brazil.

DIAGNOSTIC CHARACTERS—Upper and outer sides of head and body and outer sides of limbs pale buff agouti, pelage extremely long, trunk shaggy; facial hairs nearly concealing skin, malar stripe well defined, blackish superciliary line weakly defined or absent.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from other titis by extreme pallor and shagginess of agouti coat; sideburns, cheiridia, forehead, and outer side of extremities uniformly agouti, the parts not contrastingly colored, the conspicuous whitish ear tufts excepted.

SPECIMENS EXAMINED—Total 19. **BRAZIL. Mato Grosso:** Corumbá, 5 (USPMZ); Fazenda Acurizal, Pantanal, 1 (AMNH). **PARAGUAY. Alto Paraguay:** Puerto Casado, 1 (AMNH); **Chaco:** Fortín Madpejón, Cerro León, 50 km WNW, 1 (UMMZ); San Salvador, opposite, 1 (BM); **Nueva Asunción:** Trans-Chaco Road, 19 km WSW km 588, 1 (UMMZ); **Presidente Hayes:** Concepción, 30 km N, holotype (BM); Fort Wheeler, 7 (AMNH); Puerto Pinasco, 1 (USNM).

Callicebus olallae Lönnberg

Callicebus olallae Lönnberg, 1939: 16.

HOLOTYPE—Adult male, skin and skull, Royal Natural History Museum, Stockholm, no. A632187, collected 12 February 1938, by A. M. Olalla, original no. 187.

TYPE LOCALITY—La Laguna, 5 km from Santa Rosa, Beni, Bolivia; altitude, ca. 200 m above sea level.

DISTRIBUTION (fig. 23)—Known only from the

FIG. 25. *Callicebus donacophilus pallescens* Thomas. Photograph by B. A. Luscombe; courtesy Dr. Russell A. Mittermeier.

type locality in the upper Río Beni drainage basin, Beni, Bolivia.

DIAGNOSTIC CHARACTERS—Face framed with blackish, forehead reddish brown agouti; outer surface of limbs reddish brown; cheiridia dominantly blackish; sideburns not markedly contrasting in coloration with crown and forehead; blackish suborbital vibrissae conspicuous; back and sides dominantly orange, hairs with extremely broad orange median band; tail entirely dark agouti in sharp contrast with back; whitish ear tufts weak; skull as in the *C. moloch* group but hamular process and interpterygoid fossa less reduced than usual.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *Callicebus brunneus* by dominantly orange coloration throughout; from *C. modestus* and all species of *Callicebus* except *C. oenanthe,* by individual hairs of back with broad orange median band; from *C. oenanthe* by blackish rimmed face and absence of whitish frontal blaze; from *C. donacophilus* by dominantly brownish or blackish cheiridia and lack of sharp contrast between coloration of underparts and sides of body; from *caligatus* by orange agouti forehead, from *C. moloch* and *C. hoffmannsi* by absence of sharp contrast between sideburns and forehead and crown; from all other species by one or more of above characters.

SPECIMENS EXAMINED—Total 1. **BOLIVIA. Beni:** La Laguna, near Santa Rosa, Río Beni, 1 (RNHMS, the holotype).

Callicebus oenanthe Thomas (fig. 26)

Callicebus oenanthe Thomas, 1924: 286.

HOLOTYPE—Adult male, skin and skull, British Museum (Natural History) no. 24.7.11.1; collected 14 January 1924 by Latham Rutter.

TYPE LOCALITY—Moyobamba, San Martín, Peru, altitude ca. 840 meters.

DISTRIBUTION (fig. 27)—Northern Peru; known only from the upper Río Mayo valley in the department of San Martín; altitudinal range 750–950 m.

DIAGNOSTIC CHARACTERS—Frontal blaze usually present, the buffy or whitish color continuous with long cresting hairs bordering face; pale malar stripe present; sideburns, outer surface of limbs, and upper surface of cheiridia dominantly to entirely agouti; inner surface of limbs, chest, belly orange; entire tail dominantly dark brown agouti; body pelage thick, facial pelage longer than usual but not concealing skin; skull like those of the *moloch* group.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *Callicebus cupreus* by whitish or buffy facial fringe or ruff of crested hairs, malar stripe, outer surface of limbs and upper surface of cheiridia agouti; from *C. caligatus* and *C. brunneus* by pale frontal blaze usually present; from *donacophilus* by larger size, frontal blaze usually present, whitish ear tufts inconspicuous or absent, tail base dark brown agouti; from all other species of *Callicebus* by one or more of above characters.

SPECIMENS EXAMINED—Total 6. **PERU. San Martín:** Moyobamba, 4 (BM, including holotype of *oenanthe* Thomas); Río Seco, 1 (AMNH); Yurac Yacu, 1 (BM).

Callicebus cinerascens Spix (fig. 28)

[?]*Simia Cineracia* Griffith, 1821: 92, and colored plate opposite—name based solely on colored figure of a New World monkey.

Callithrix cinerascens, Spix, 1823: 20, pl. 14 (animal).

HOLOTYPE—Male, skin mounted with skull in, No. 3, Zoologische Staatssammlung, München, collected by J. von Spix, who gives no date.

TYPE LOCALITY—Said to be the forests of the Ríos Putumayo or Içá at the Peruvian border, Amazonas, Brazil. Spix was in the area during January 1820, but there is no evidence that he or anyone else ever collected the species there.

DISTRIBUTION (fig. 29)—Brazilian specimens from parts of southeastern Amazonas, Rondônia, and Mato Grosso in the upper Rio Madeira basin agree with *cinerascens* and nothing else. The only *Callicebus* known from the stated type region between the Ríos Putumayo or Içá and the Rio Solimões, are *C. cupreus discolor* and *C. torquatus lucifer* (fig. 27). It is unlikely that *Callicebus cinerascens* would occur here on the north bank of the Rio Solimões, and also in the Rio Madeira basin on the south bank of the Rio Amazonas. Either the type locality given by Spix is wrong, or the south bank titis are not *C. cinerascens.*

DIAGNOSTIC CHARACTERS—Forehead, crown, sides of body, chest, belly, limbs, and tail grayish to blackish agouti, all contrasting with tawny agouti middorsum; largest species of *moloch* group.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from all other

FIG. 26. *Callicebus oenanthe* Thomas. Skin of referred specimen from Río Seco, San Martín, Peru (AMNH 73226).

species of *Callicebus* by grayish agouti forehead, crown, sides of body, chest, belly, and limbs except sometimes digits; sideburns and throat usually grayish agouti but sometimes yellowish approaching condition in *C. hoffmannsi hoffmannsi*; the contrastingly colored reddish brown agouti dorsum is as in *C. moloch,* from which it is readily distinguished by grayish agouti chest, belly, inner

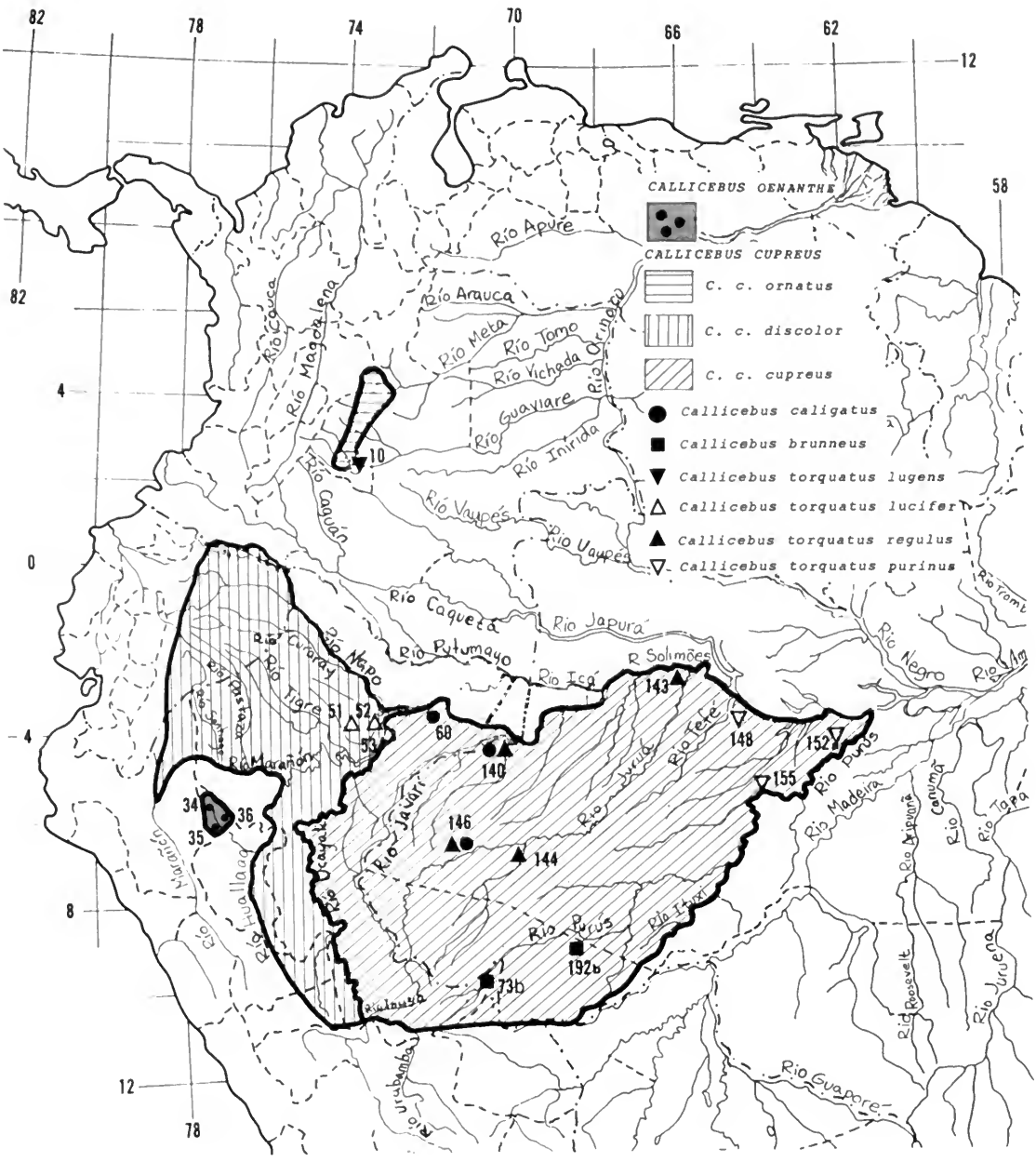

FIG. 27. Geographic range of *Callicebus cupreus cupreus* (shaded parts of Brazil, Peru), *C. c. discolor* (shaded parts of Peru, Ecuador), isolated *C. c. ornatus* (shaded parts of Colombia), and isolated *C. oenanthe* (shaded circles, Peru; known localities numbered); numbered symbols are of localities shared with sympatric species. See Gazetteer (p. 104) for explanation of numbers.

surface of limbs, and inconspicuously colored sideburns. Nearest resemblance in size and coloration is with the dominantly blackish agouti *C. personatus melanochir*, but the grayish agouti limbs, forehead, and pelage surrounding face and ears of *C. cinerascens* are distinctive.

SPECIMENS EXAMINED—Total 10. **BRAZIL. Amazonas:** Prainha, 7 (USPMZ); **Mato Grosso:** São

João, Aripuanã, 1 (MPEG); **Rondônia:** Otoho, Rio Jiparaná, 2 (MNR).

Callicebus hoffmannsi Thomas

DISTRIBUTION (fig. 29)—South bank lower Amazonian region, Brazil, from west bank lower Rio Tapajós to east bank lower Rio Madeira; south to Rio Canumã, states of Pará and Amazonas.

DIAGNOSTIC CHARACTERS—Upper and outer surface of head, trunk, and limbs grayish to blackish agouti; forehead like crown, whitish ear tufts absent; sideburns, underparts of body, and inner side of limbs sharply contrasted yellowish or reddish; tail dominantly blackish agouti to nearly entirely blackish, tail tip sometimes entirely buffy.

COMPARISONS—Distinguished from *Callicebus moloch* and *C. cupreus* by upper surface of hands blackish agouti; from *C. cinerascens* by chest, belly, and inner side of limbs uniformly buffy to reddish; from *C. caligatus* by outer surface of forelimbs agouti; from *C. brunneus* by forehead and crown grayish or blackish agouti; from *C. donacophilus, C. modestus, C. olallae,* and *C. personatus* by sharply contrasted bright yellowish or reddish sideburns and absence of conspicuous whitish ear tufts; from *C. dubius, C. discolor, C. ornatus,* and *C. oenanthe* by absence of frontal blaze; from other species by one or more of above characters.

FIG. 28. *Callicebus cinerascens* Spix. Copy of original color plate of holotype (Spix, 1823, pl. 14) in Zoologische Staatssammlung, München.

Key to Subspecies of *Callicebus hoffmannsi*

1. Sideburns, underparts, and inner side of limbs pale orange or yellowish ..... *hoffmannsi*
1′. Sideburns, underparts, and inner side of limbs bright reddish or reddish brown ..... *baptista*

Callicebus hoffmannsi baptista Lönnberg

Callicebus baptista Lönnberg, 1939: 7, pl. 1 (animal)—BRAZIL: *Amazonas* (Lago do Baptista; Lago Tapaiuna).

TYPES—None specified; 17 syntypes of original description, all in the Royal Natural History Museum, Stockholm, include 5 males, 6 females from Lago do Baptista, collected 24 January–27 March, 1936, 3 males, 3 females from Lago do Tapaiuna collected 4–9 May 1936, all by A. M. Olalla. An adult male, skin and skull, no. A611510, of the Lago do Baptista series, collected 28 February 1936, is here designated lectotype; the syntypes become lectoparatypes.

TYPE LOCALITY—Originally unspecified, restricted to Lago do Baptista by Hershkovitz (1963a, p. 29).

DISTRIBUTION (fig. 29)—Known only from the type locality and the nearby Lago do Tapaiuna, both localities on Isla Tupinambaranas of the lower Rio Madeira. The range may actually extend from between east bank lower Rio Madeira and west bank Rio Canumã from about 5°16′S, 59°45′W, northward through the chain of paranás to Rio Amazonas near Parintins, Amazonas, Brazil.

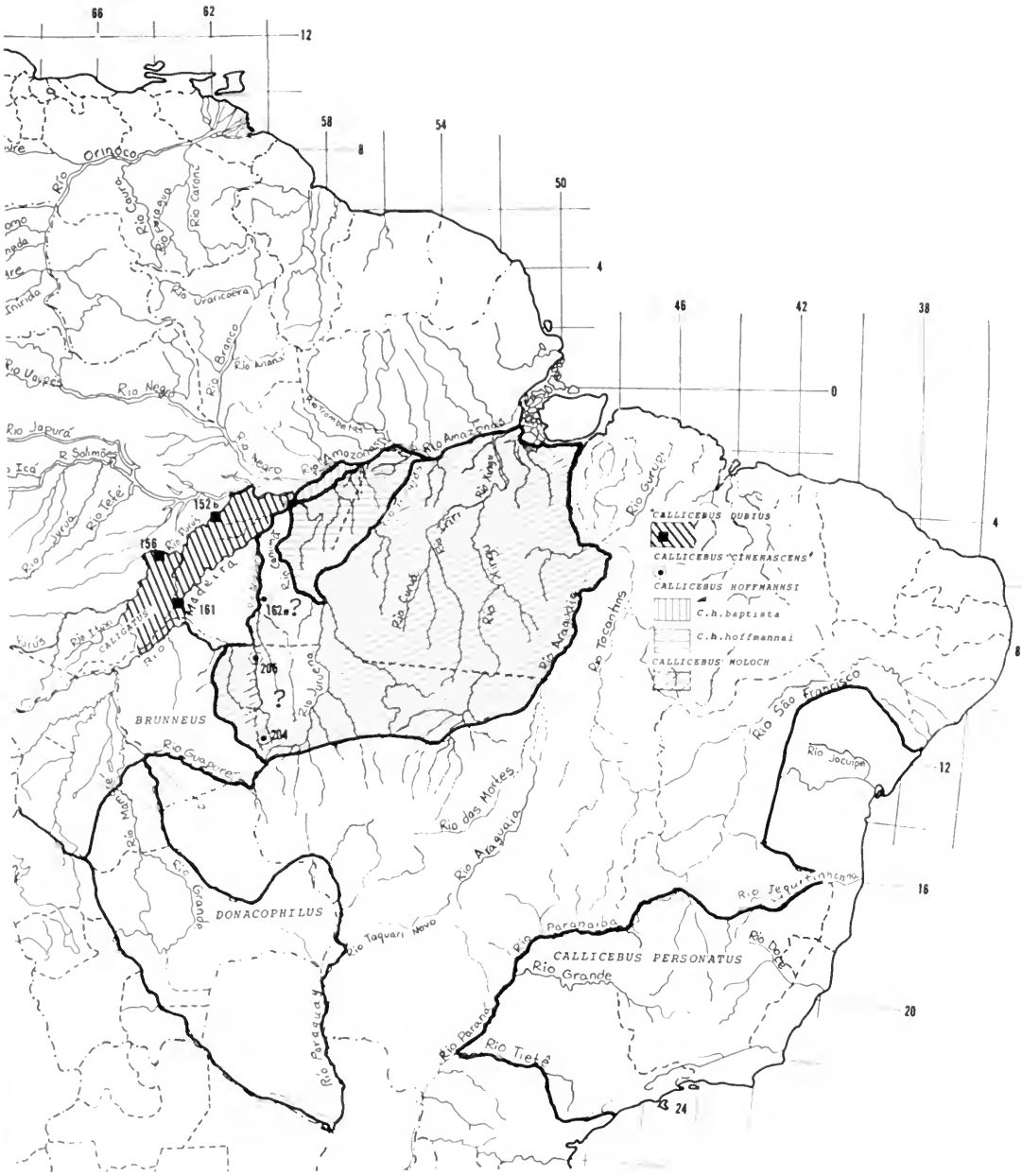

FIG. 29. Geographic distribution (shaded) of Brazilian *Callicebus hoffmannsi hoffmannsi, C. h. baptista, C. moloch,* and *C. cinerascens* (known localities numbered), and *C. dubius* (known localities numbered). See Figure 1 for overlap of geographic ranges and Gazetteer (p. 104) for explanation of numbers.

DIAGNOSTIC CHARACTERS—See Key to Subspecies.

MEASUREMENTS—See Table 13.

COMPARISONS—Underparts and sideburns most saturate pheomelanin of *moloch* group, distinguished from *Callicebus h. hoffmannsi* and all other species by dark brownish or "grayish" agouti upper and outer parts of trunk, limbs, crown, and forehead, undifferentiated cheiridia, sharply contrasted dark reddish sideburns, and underparts and inner surface of limbs.

SPECIMENS EXAMINED—Total 45. **BRAZIL.**

FIG. 30. *Callicebus hoffmannsi hoffmannsi* Thomas (young animal). Sideburns, beard, underparts, inner side of limbs yellowish. Photograph courtesy Dr. Russell A. Mittermeier.

Amazonas: Lago do Baptista, 38 (FMNH, 14; MNR, 4; RNHMS, 10; USPMZ, 10); Lago Tapaiuna, 6 (RNHMS); locality unknown, 1 (AMNH).

Callicebus hoffmannsi hoffmannsi Thomas (fig. 30)

Callicebus Hoffmannsi Thomas, 1908: 89.

HOLOTYPE—Adult male, skin and skull, British Museum (Natural History) no. 1908.5.9.11, collected 13 February 1906 by W. Hoffmanns.

TYPE LOCALITY—Urucurituba, Rio Tapajós, Pará, Brazil. The type locality was originally given as "Urucurituba, Santarém." Santarém, on the right bank of the lower Rio Tapajós, is type locality of *Callicebus remulus* (= *C. moloch*). Urucurituba at 3°30'S on the opposite bank of the Rio Tapajós is in the area whence nearly all titis examined agree with the holotype of *hoffmannsi*. Nevertheless, other east (right) bank Rio Tapajós specimens (Fordlandia, 2) are either mislabelled or had been transferred in an oxbow cutoff from west to east bank. Although west bank *hoffmannsi* and east bank *moloch* are specifically distinct (Hershkovitz, 1988), specimens of the first may be enclaves within the range of the second rather than true sympatriots.

DISTRIBUTION (fig. 29)—Central Brazil south of the Rio Amazonas, from left bank Rio Tapajós-Juruena in the states of Pará and Amazonas, west to right bank Rio Canumã-Sucunduré in Amazonas.

DIAGNOSTIC CHARACTERS—See key to subspecies of *Callicebus hoffmannsi* (page 54).

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *Callicebus moloch* by blackish agouti upper surface of cheiridia, by blackish tail usually without contrastingly pale pencil, and pale orange or yellowish underparts, inner side of limbs, and sideburns; from *C. hoffmannsi baptista* mainly by pale orange or yellowish, not bright reddish or mahogany, underparts and sideburns; from all other species with which comparisons need be made by agouti forehead undifferentiated from crown, agouti outer side of arms, legs, and upper side of cheiridia contrasted with pale orange or yellowish sideburns and underparts.

SPECIMENS EXAMINED—Total 61. **BRAZIL. Pará:** Arapiuns, Rio, 1 (MPEG); Arara, 1 (FMNH); Aruã, 1 (USPMZ); Brasília Legal, Rio Tapajós, 3 (USPMZ); Casa Nova, 1 (RNHMS); Fordlandia, 2 (USPMZ); Igarapé Amorim, 2 (AMNH); Igarapé Bravo, 6 (AMNH); Irocanga, 1 (RNHMS); Itaituba, 2 (USPMZ); Patinga, 1 (RNHMS); Santa Rosa, Ilha Urucurituba, 3 (USPMZ); Sumauma, Rio, 2 (USPMZ); Urucurituba, 6 (BM, holotype of *hoffmannsi*; 5, USPMZ); Vila Bella, Boca Andirá, 12 (AMNH); Vila Bella Imperatriz, 10 (AMNH); Vila Braga, Rio Tapajós, 7 (BM, 3; MPEG, 2; MNR; AMNH).

Callicebus moloch Hoffmannsegg (fig. 31)

Callicebus moloch Hoffmannsegg, 1807: 97; local name, *oiabussá*.

[*Callithrix*] *hypoxantha* Illiger, 1815: 107—nomen nudum.

[*Callithrix*] *hypokantha* Olfers, in Eschwege, 1818: 201—new name for *moloch* Hoffmannsegg; male and female syntypes in Berlin Museum; characters.

Simia sakir, Giebel, 1855: 1036, footnote—name erroneously attributed to Spix, 1813 (Denkschr., pl. 19) and cited in synonymy of *Callithrix moloch*.

Callicebus remulus Thomas, 1908: 88—BRAZIL: *Pará* (type locality, Santarém, Rio Tapajós); holotype, female, skin and skull, British Museum (Natural History) no. 76.6.19.1, collected 3 July 1912, by Mr. Wickham.

Callicebus emiliae Thomas, 1911: 606—BRAZIL. *Pará* (type locality, lower Rio Amazonas). Napier, 1976: 55—holotype, female, skin and skull, British Museum (Natural History) no. 1911.4.28.1.

Callicebus geoffroyi Miranda Ribeiro, 1914: 19—BRAZIL: Renaming of figured individual identified as *Callithrix moloch* by I. Geoffroy (1844, pl. 3, a zoo animal without locality data).

SYNTYPES—Several male and female individuals, two of which are or have been in the Zoologisches Museum der Humboldt-Universität, Berlin, and an adult, mounted with skull in skin, Muséum National d'Histoire Naturelle, Paris, no. 687(522), all collected by Herr Sievers and donated by Count von Hoffmannsegg, March 1808.

TYPE LOCALITY—"Unweit der Stadt Para," (Hoffmannsegg, 1807, p. 100), or near the town of Belém, Pará, Brazil.

DISTRIBUTION (fig. 29)—Amazonian Brazil south of the Rio Amazonas in the states of Pará, Mato Grosso, and neighboring parts of Amazonas and Rondônia. In Pará from the west bank of Rio Tocantins-Araguaia west to the east bank of the Rio Tapajós, south to the headwaters of the Rios Araguaia, Xingu, and Tapajós in northern Mato Grosso, west to the east bank of the Rio Jiparaná in Rondônia and east bank of the Rio Aripuanã in Amazonas.

DIAGNOSTIC CHARACTERS—Upper and outer surface of head, trunk, and limbs buffy or "grayish" agouti to pale brown agouti; forehead not

FIG. 31. *Callicebus moloch* Hoffmannsegg. Sideburns, beard, underparts, inner side of limbs orange. Photograph courtesy Dr. Russell A. Mittermeier.

sharply defined from grayish crown to distinctly paler, whitish ear tufts inconspicuous or absent; sideburns, underparts of body, and inner side of limbs sharply contrasted orange; hairs of tail dominantly blackish agouti terminally, orange or buffy basally, terminal portion including pencil buffy.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *C. cupreus* and *C. caligatus* by outer surface of forelimbs agouti; from *cinerascens* by uniformly orange inner sides of limbs, chest, and belly; from *C. brunneus* by forehead and crown grayish agouti; from *C. dubius, C. cupreus discolor, C. c. ornatus,* and *C. oenanthe* by absence of frontal blaze; from *C. donacophilus, C. modestus,* and *C. olallae* by sharply contrasted bright orange sideburns and absence of conspicuous whitish ear tufts; from *donacophilus* by absence of malar stripe; from *C. hoffmannsi* by upper surface of hands buffy and usually paler than outer side of arms, pencilled tip of tail consistently buffy; from other species by one or more of above characters.

SPECIMENS EXAMINED—Total 184. **BRAZIL. Amazonas:** Castanhos, Foz do, 3 (MNR); São João, Rio Jamarí, 1 (MNR); Tamaruri, 1 (MNR); **Mato Grosso:** Arinos, Rio, 3 (MNR, 2; USPMZ, 1); Fazenda São José, Rio Peixoto de Acevedo, 1 (MNR); Rio Arraios, alto Rio Xingu, 1 (MNR); Rio Teles Pires, 1 (MRN); Locality unknown, 1 (MNR); **Pará:** Aramanaí, Igarapé, 3 (AMNH); Arumateua, Rio Tocantins, 2 (AMNH; BM); Aveiros, 6 (RNHMS); Baião (opp.), 1 (AMNH); Belterra, 1 (MNR); Bom Jardim, 2 (USPMZ); Cachimbo, 1 (USPMZ); Carajas, Serra, 5 (MPEG); Caxiricatuba, 27 (AMNH, 9; USPMZ, 16; NHMW, 2); Cuiabá-Itaituba, 1 (MPEG); Cuçari, 1 (BM); Curuatinga, 2 (MNR); Cururú, Rio, 1 (MNR); Curuá, Foz do, 3 (USPMZ); Fordlândia, 36 (FMNH, 5; USPMZ, 31); Ipanema, 4 (MNR); Iriri, Rio, 1 (MPEG); Itaituba-Jacareacanga, km 14, 3 (USNM, 2; USPMZ); Itapuama, 6 (RNHMS, 5; USPMZ); Lucilândia-Xinguara, 3 (MPEG); Maica, 1 (USNM); Marucá, 2 (USPMZ); Monte Cristo, 3 (USPMZ); Mundo Novo, Igarapé, Rio Iriri, 2 (MPEG); Piquiatuba, 11 (FMNH; MNR, 3; USPMZ, 7); Santarém, 7 (BM, 2; MNR, 3; MPEG; NHMW); Santarém-Cuiabá, km 82, 1 (USNM); Santarém-Cuiabá, km 212, 4 (MPEG, 2; USNM, 2); Santarém-Cuiabá-Itaituba, BR 165, 1 (MPEG); Santo Antonio, Rio Tocantins, 1 (USPMZ); São João, Rio Araguaia, 1 (MPEG); Saúde, 2 (MPEG); Tamaruri, Rio Cuçari, 1 (MNR); Tapaiuna, 2 (FMNH); Taperinha, 2 (NHMW; USPMZ); Tauary, 9 (AMNH, 8; FM); Tavio, 4 (FMNH 3; USPMZ); Tucuruí, Rio Tocantins, 1 (MPEG); **Rondônia:** Alvorado d'Oeste, Linha 64, BR 429, Km 87, 5 (MPEG). Nova Brasilia, 4 (USPMZ); Nova Colonia, 1 (USPMZ).

Callicebus brunneus Wagner (fig. 32)

Callithrix brunea [sic] Wagner, 1842: 357.
Callithrix brunnea Wagner, 1848: 455—BRAZIL: *Amazonas* (type locality, Rio Madeira); 4 syntypes in Naturhistorische Museum, Wien; specific name emended.

LECTOTYPE—Adult male, skin and skull, Naturhistorische Museum, Wien no. 3454, selected by Elliot (1913, p. 257; cf. Hill, 1960, p. 126, for sex); lectoparatypes, 1 young male (mounted, in exhibition hall), 2 females (NHMW 3453, skin only; the other mounted in exhibition hall), all collected September 1829 by Johann Natterer.

TYPE LOCALITY—Brazil, subsequently specified by Pelzeln (1883, p. 20) as Cachoeira da Bananeira, Rio Guaporé, upper Rio Madeira, Rondônia.

DISTRIBUTION (figs. 23, 27)—Middle and upper Rio Madeira basin in Rondônia and Acre, Brazil, the departments of Madre de Dios, Puno, and Cusco in Peru; west into the upper Rio Purús basin in Amazonas, Brazil, and Ucayali, Peru; altitudinal range about 100–650 m above sea level.

The actual provenance of the AMNH specimens of *Callicebus brunneus* labeled "Río Inuya" and "Río Urubamba", upper Río Ucayali valley, Ucayali, Peru, by "collectors" Olalla Hijos, is questionable.

DIAGNOSTIC CHARACTERS—Duskiest species of *moloch* group; forehead, forearms, legs, cheiridia, and two-thirds to entire tail blackish but with pencilled tip often contrastingly pale; sideburns reddish brown or blackish, not sharply defined from forehead and crown; upper parts and sides of body brownish agouti, underparts brownish or reddish brown, not sharply defined from sides of body. Cranial characters like those of the *moloch* group.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *Callicebus modestus* and *C. olallae* by generally blackish or dark brown forehead and outer surface of limbs, chest, and belly, ears not tufted whitish; from *caligatus* by blackish or reddish brown sideburns, underparts not sharply defined from crown and sides of body, tail entirely or dominantly blackish except often tip; from *C. cupreus* by blackish of forehead usually extending to crown, brownish or

blackish not reddish or whitish cheiridia, tail mostly to entirely blackish; from all other species of *Callicebus* by one or more of above characters.

SPECIMENS EXAMINED—Total 36. **BRAZIL. Acre:** Sena Madureira, 1 (MNR). **Mato Grosso:** Unknown locality, 1 (MR); **Rondônia:** Cachoeira da Bananeira, 4 (NHMW); Cachoeira Nazaré, 3 (USPMZ); Finca Rio Candeia, 2 (MPEG); Porto Velho, 4 (FMNH, 2; MPEG; USPMZ); Rio Jamari, 1 (MNR); Santa Barbara, Jamari, 1 (USPMZ). **PERU. Cuzco:** Huajllumbe, 2 (FMNH); **Puno:** Candamo, 1 (FMNH); **Madre de Dios:** Altamira, 1 (FMNH); Itahuania, 1 (FMNH); nr. Santa Rosa, 1 (LSUMZ); **Ucuyali:** Balta, 3 (LSUMZ); Río Curanja, 1 (LSUMZ); **?Ucayali:** "Boca Río Urubamba," 7 (AMNH); "Río Inuya," 2 (AMNH).

FIG. 32. *Callicebus brunneus,* skin of FMNH 75985; head, limbs blackish, dorsum dominantly brownish agouti.

Callicebus cupreus Spix

DISTRIBUTION (fig. 27)—Upper Amazonian regions of Brazil, Ecuador, and Colombia, and upper Orinocan region of Colombia; in Brazil from left bank of the Rio Madeira west into Peru to the Río Huallaga; upper Río Madre de Dios basin in Bolivia and Peru; north of the Río Marañón-Amazonas and west of the Río Aguarico-Napo to the base of the Eastern Cordillera in Peru and Ecuador; in eastern Colombia between the left bank of the Ríos Guamués and Putumayo in the Amazonian watershed, absent northward about 350 km, then in the upper Río Orinoco basin along the eastern Andean base to the Sierra de la Macarena between the Ríos Guayabero and Upía. Amazonian and Orinoco populations are separated by a distributional hiatus of about 350 km.

The hiatus between Amazonian and Orinoco populations of *Callicebus cupreus* may be attributed to climatic changes during the latest interglacial. At that time the cooler, drier climate may have promoted replacement of the sylvan link between northern and southern populations by a pastoral barrier, remnants of which still stand. The more humid Sierra de la Macarena retained the forest habitat where the northern population evolved into *C. c. ornatus.*

DIAGNOSTIC CHARACTERS—Forehead, exclusive of blackish superciliary fringe (if present), buffy to reddish brown agouti like crown or with contrastingly pale buffy or whitish tuft, transverse band or blaze; sideburns reddish or orange; sides of neck, throat, chest, and belly reddish or orange, sharply contrasted with buffy brown agouti of back and sides of body; inner surface of forearms and legs reddish or orange, outer surface like inner, or mostly agouti like sides of body; cheiridia reddish or mostly to entirely buffy to whitish; tail mixed or roughly marbled or annulated blackish and buffy agouti for entire length and/or with variable portions of distal half of pencilled tip dominantly buffy; cranial characters like those of the *C. moloch* group; diploid number of chromosomes = 46 (*C. c. cupreus*; *C. c. discolor*; *C. c. ornatus*).

COMPARISONS—Distinguished from all other species of *Callicebus* by one or more of the following: back and sides agouti, underparts and inner side of limbs contrastingly reddish orange; crown buffy to brownish agouti; forehead with or without buffy or whitish tuft, frontal blaze or transverse band; outer surface of lower arms and legs uniformly reddish or dominantly agouti, upper surface of cheiridia similar or paler, never blackish, the digits often paler than metapodials, side-

burns uniformly orange or reddish and not contrasted with color of inner surface of forearms; whitish ear tufts absent or when present correlated with buffy or whitish frontal tuft or transverse blaze; tail mixed blackish and buffy, marbled or with terminal half or less dominantly buffy, pencil like remainder of tail or buffy.

Key to Subspecies of *Callicebus cupreus*

1. Forehead with buffy or whitish transverse band or blaze; or midfrontal mark a whitish tuft only, hairs of tuft with single pheomelanin annulation 2
1'. Forehead without buffy or whitish transverse band; or midfrontal mark a whitish tuft, hairs of tuft with two pheomelanin annulations ..... *cupreus*
2. Upper surface of cheiridia (hands and feet) mostly to entirely reddish, not contrasting with reddish of forearms ..... *discolor*
2'. Upper surface of cheiridia partly (digits) to entirely buffy or whitish contrasting with reddish of forearms ..... *ornatus*

Callicebus cupreus cupreus Spix (figs. 33, 37)

Callithrix cuprea Spix, 1823: 23, pl. 17 (animal)—BRAZIL: local name *yapusa*.

Callicebus egeria Thomas, 1908: 89—BRAZIL: *Amazonas* (type locality, Teffe [= Tefé], Rio Solimões); holotype, male, skin and skull, British Museum (Natural History) no. 8.5.9.10, collected 7 June 1906, by W. Hoffmanns.

[?]*Callicebus toppini* Thomas, 1914: 480—PERU: *Madre de Dios* (type locality, Río Tahuamanu, about 12°20'S, 68°45'W); holotype, female, skin and skull, British Museum (Natural History) no. 14.3.3.3, collected by Capt. H. H. Toppin. Thomas, 1918: 241, colored pl. (holotype)—reprint of original text of description, color plate added.

Callicebus cupreus acreanus Vieira, 1952: 23—BRAZIL: *Acre* (type locality, Iquiri, upper Rio Purús); holotype, female, skin and skull, USPMZ No. 7332, collected September 1951 by Paulo E. Vanzolini.

C[*allithrix*]. *discolor*, I. Geoffroy (part, not I. Geoffroy and Deville), 1851: 41—part, BRAZIL *Amazonas* (Rio Amazonas [= Solimões]); PERU: *Loreto* (Río Amazonas).

TYPE—Lectotype, adult female, mounted with skull in skin, Zoologische Staatssammlung, München, no. 10, selected by Osman Hill (1960, p. 122); lectoparatypes in Munich are no. 24, adult mounted, without skull; no. 89a, adult male, mounted without skull; no. 89b, adult mounted without skull; all collected January 1820 by J. B. von Spix.

TYPE LOCALITY—Rio Solimões, Brazil, near the Peruvian boundary; restricted to Tabatinga by Hershkovitz (1963a, p. 36), but should be Rio Solimões opposite Tabatinga because the species does not occur on the north bank or Tabatinga side of the Solimões. Restriction of the type locality of *Callicebus cupreus* Spix to the "Peruvian Amazonas" by Thomas (1908, p. 90) is not valid. The types originated in Brazil.

DISTRIBUTION (figs. 23, 27, 36, 42)—South bank of the Amazonas-Solimões from the left bank of the Rio Purús, Amazonas, Brazil, west to the east bank of the Río Ucayali, in Loreto and northern Ucayali, Peru, south in the Rio Purús basin in Acre, Brazil, Loreto, and Madre de Dios, Peru; altitudinal range to approximately 200 m above sea level. Specimens in the American Museum of Natural History from Río Urubamba (75986–75988, possibly 75991) and from Sarayacu (76504, 76419–76422) may have been collected elsewhere.

DIAGNOSTIC CHARACTERS—Sideburns, legs, and underparts uniformly reddish contrasting with buffy agouti of upper and outer sides of trunk and crown; forehead like crown but usually with blackish fringe formed by superciliary vibrissae and bases of marginal hairs.

MEASUREMENTS—See Table 13.

COMPARISON—Distinguished from *Callicebus cupreus ornatus* and nearly all *C. c. discolor* by absence of contrastingly pale transverse frontal blaze; however, a few dominantly whitish frontal hairs sometimes present; from *C. c. ornatus* and *C. oenanthe* by uniformly reddish arms and cheiridia; from *C. caligatus* and *C. brunneus* by entire crown buffy to orange agouti, cheiridia reddish; from all other forms of *Callicebus* by one or more of the above characters.

SPECIMENS EXAMINED—Total 130. **BRAZIL. Acre:** Iquiri, 1 (USPMZ, holotype of *acrensis* Vieira);

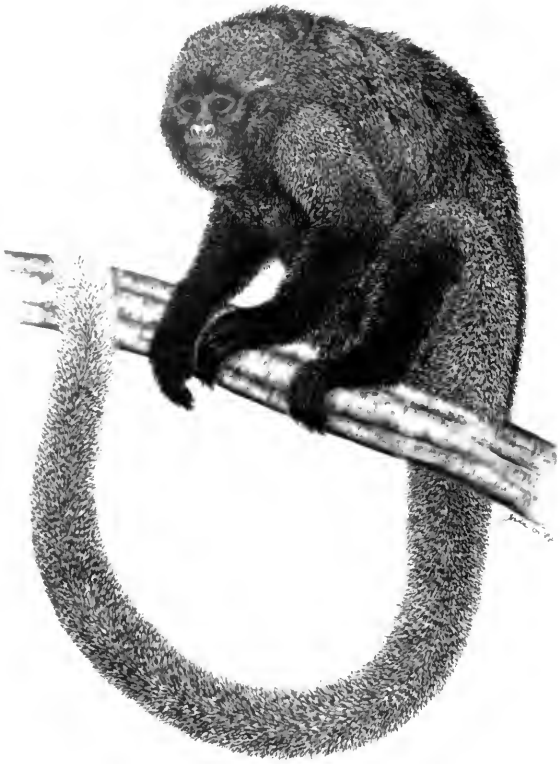

FIG. 33. *Callicebus cupreus cupreus* Spix. From color portrait by Zorica Dabich (from Hershkovitz, 1987c). Sideburns, throat, arms, legs, and underparts are reddish orange.

Manoel Urbano, 2 (USPMZ); São Luiz da Mamoria, 1 (MPEG); Sena Madureira, 1 (MNR); **Amazonas:** Aiapuá, 14 (BM, 10; MNR, 3; RNHMS); Eirunepé, 17 (USPMZ); Fonte Boa, 2 (MNR); Igarapé Gordão, 1 (RNHMS); Itaboca, 1 (RNHMS); Jaburú, 3 (RNHMS); João Pessõa, 9 (1, MNR; 8, RNHMS); Pauini, 2 (USPMZ); Porta da Castanha, Tefé, 3 (MPEG); Rio Juruá, 3 (BM, 1; USPMZ, 2); Santa Cruz, 25 (USPMZ); Santo Antonio, 13 (RNHMS, 11; USPMZ, 2); Tefé, 3 (BM, holotype of *egeria* Thomas; MPEG; USNM); "upper Amazon," 1 (BM). **PERU. Loreto:** Balta, 2 (LSUMZ); Cashiboya, 3 (BM); Cerro Azul, 2 (BM; FMNH); Orosa, 6 (AMNH, 5; PPP); Pavas, 2 (AMNH); **Madre de Dios:** Río Inuya, 1 (AMNH); Río Tapiche, 2 (AMNH); Río Yavarí, 1 (MNHNP); "Sarayacu," 4 (AMNH); Tahuamanu, 1 (BM, holotype of *toppini* Thomas); **Ucayali:** "Río Urubamba," 4 (AMNH).

Callicebus cupreus discolor
I. Geoffroy and Deville (fig. 34)

Callithix discolor I. Geoffroy and Deville, 1848: 498. *C[allithrix]. cuprea leucometopa* Cabrera, 1900: 83, pl. 1 (animal, male)—PERU: *Loreto* (type locality, junction of Ríos Napo and Aguarico); syntypes, no. 535, old male, skin and skull, subadult female, skin and skull, Museo Nacional de Historia Natural, Madrid; collected between 1862 and 1865 by Marcos Jiménez de la Espada; local name, *tzocallo* [sic].

Callicebus subrufus Elliot, 1907: 192—PERU: *Loreto* (type locality, Pachitea, Río Ucayali, altitude 400–500 ft); holotype, skin and skull, British Museum (Natural History), no. 4.7.7.2.

Callicebus paenulatus Elliot, 1909: 244—ECUADOR: *Pastaza* (type locality, Andoas, Río Pastaza); holotype, skin and skull, British Museum (Natural History), no. 80.5.6.14, collected September 1878 by Clarence Buckley.

Callicebus cupreus napoleon Lönnberg, 1922: 3—ECUADOR: *Napo* (type locality, Río Napo, altitude 2500 ft); syntypes, 2 skins and skulls, Royal Natural History Museum, Stockholm, collected 1920 and 1921 by Ludovic Söderström. Hill, 1960: 116, 131—characters; distribution.

Callicebus rutteri Thomas, 1923: 692—PERU: *Pasco* (type locality, Puerto Leguía, Río Pachitea, upper Río Ucayali, altitude 1500 ft); holotype, skin only, British Museum (Natural History), no. 23.10.16.1; collected 31 May 1923 by Latham Rutter.

HOLOTYPE—Skin and skull originally in the Muséum National d'Histoire Naturelle, Paris, col-

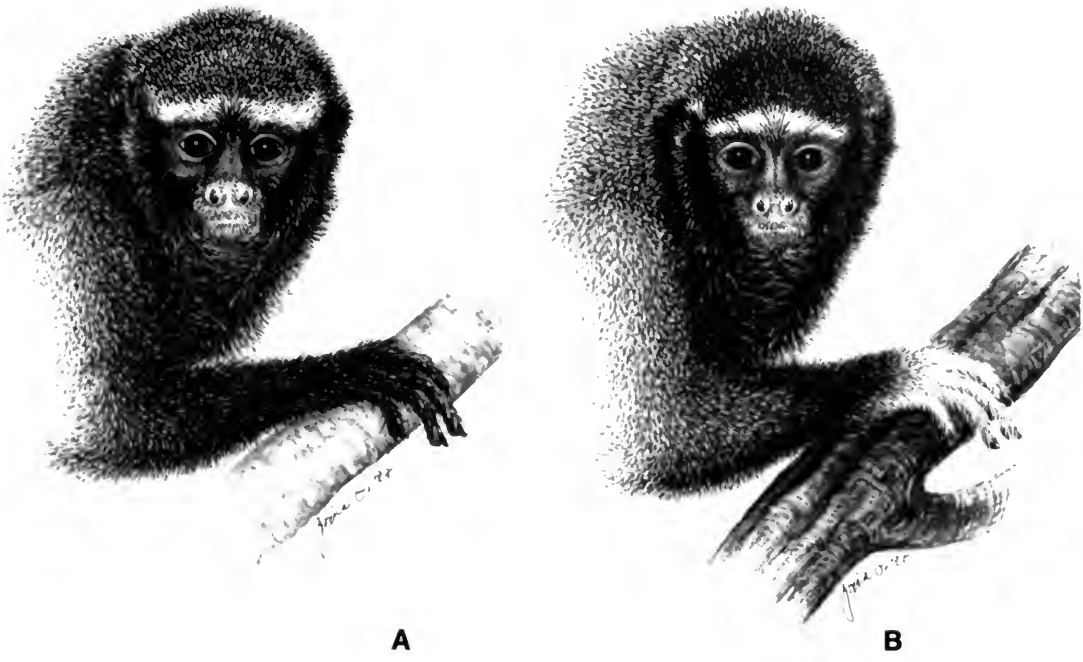

FIG. 34. **A,** *Callicebus cupreus discolor* I. Geoffroy and Deville; **B,** *Callicebus cupreus ornatus* Gray. From color portraits by Zorica Dabich (from Hershkovitz, 1987c). Color as in *C. c. cupreus* except forehead with whitish blaze; in *ornatus,* forearms partially agouti and hands tending to whitish.

lected 1847 by Comte Francis de Castelnau and Emile Deville. The holotype is no longer in the museum collection.

TYPE LOCALITY—Sarayacu, Río Ucayali, Ucayali, Peru.

DISTRIBUTION (figs. 27, 42)—Upper Amazonian region, in Peru between the Ríos Ucayali and Huallaga south of the Río Marañón, and between the Ríos Napo and Santiago north of the Marañón; in Ecuador from east of the Andean foothills to the Río Napo-Aguarico basin, north to the Río Putumayo and across into Colombia to the south bank of the Río Guamués.

According to Soini (1982, p. 40), *Callicebus c. discolor* is absent from the lower Río Ucayali basin and the Samiria-Pacaya watershed. I observed no titis in the region during fieldwork in 1980. Hernández-Camacho and Cooper (1976, p. 49) speculated on the possible occurrence of *C. c. discolor* between the east bank of the Río Napo-Aguarico and the right bank of the Río Putumayo south of the Río Guamués.

True provenance of the specimens of *Callicebus c. discolor* in the American Museum of Natural History "collected" by the Olallas at "Boca Río Inuya, Río Urubamba" and "Lagarto, Alto Ucayali" requires confirmation. The Río Inuya is on the east bank or wrong side of the Río Ucayali boundary of the *discolor* range, as here understood. The specimens from Lagarto, Río Ucayali, Alto may actually have been taken at or near that place on the west bank of the Río Ucayali. They agree with specimens from lower down the river at Yurimaguas and the Río Pachitea region.

DIAGNOSTIC CHARACTERS—Forehead, as a rule, with whitish or buffy tuft or transverse band or blaze sharply contrasted with agouti of anterior portion of crown; sideburns, side of neck, lower arms, legs, cheiridia, chest, and belly reddish, sharply contrasted with agouti crown, back, sides of body, and tail; tail mixed brownish and buffy agouti but often with pencilled tip to as much as terminal third dominantly buffy.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *Callicebus cupreus ornatus* and *C. oenanthe* by entirely reddish forearms and cheiridia; from *C. caligatus* and *C. brunneus* by whitish or buffy frontal tuft or

transverse band; from *C. caligatus, C. brunneus,* and *C. dubius* by buffy, orange, or reddish agouti anterior portion of crown, upper surface of cheiridia reddish; from all other forms of *Callicebus* by one or more of above traits.

The sole feature that almost consistently separates *Callicebus cupreus discolor* from *C. c. cupreus* is the buffy or whitish tuft or transverse frontal blaze. In one of 5 specimens from Río Tigrillo, Peru, the *discolor* blaze consists of a few dominantly whitish hairs (FMNH 122783); in another (Andoas, BM 80.5.6.14) it is absent. In other samples from the same localities the blaze is well developed. In *C. c. cupreus* the blaze is normally absent, but in two individuals from Cerro Azul (BM 28.5.2.44; FMNH 64288) a small tuft of midfrontal hairs are dominantly whitish. The blaze effect is created here by two narrow subterminal pheomelanin bands of frontal hairs; in *discolor,* the effect is produced by a single wide subterminal pheomelanin band of frontal hairs.

SPECIMENS EXAMINED—Total 133. **ECUADOR. Napo:** Río Coca, mouth, 1 (EPNQ); Río Napo, 4 (BM; FMNH; MHNM, 2 syntypes of *leucometopa* Cabrera); Río Payamino, 3 (FMNH); Río Suno, mouth, 1 (EPNQ); San Francisco, 3 (UMMZ); **Pastaza:** Andoas, 2 (BM, holotype of *paenulatus* Elliot; AMNH); Montalvo, 1 (FMNH); Río Copataza, 4 (BM); Río Pindo, 1 (EPNQ); **Not located:** Río Liguino, 2 (EPNQ). **PERU. Amazonas:** Bushimkin, 4 (MVZ); Ciudad Constitución, Río Palcazu, 1 (PPP); Kusu, 5 (MVZ); Pagaat, 4 (MVZ); Río Marañón, 1 (FMNH); Río Santiago, 1 (AMNH); Shimpunts, 1 (MVZ); Tseasim, 1 (MVZ); **Huánuco:** Tingo María, 13 (BM, 8; FMNH, 5); **Loreto:** Boca Río Curaray, 22 (AMNH); Iquitos, 10 (BM, 2; AMNH, 8); Lagartococha, 2 (AMNH); Mishana, Río Nanay, 1 (PPP); Mucha Vista, Río Curaray, 1 (PPP); Puerto Indiana, 6 (AMNH); Río Tigrillo, 5 (FMNH); Santa Luisa, Río Nanay, 10 (FMNH); **Pasco:** Puerto Leguía, 1 (BM, holotype of *rutteri* Thomas); Puerto Victoria, 4 (FMNH); Río Pachitea, 1 (BM, holotype of *subrufus* Elliot); **Ucayali:** Cumaría, 4 (BM); Lagarto, 6 (AMNH); "Río Inuya," 2 (AMNH); Yarinacocha, 5 (FMNH).

Callicebus cupreus ornatus Gray (fig. 34)

Callithrix ornata Gray, 1866: 57.

HOLOTYPE—Skin and skull, British Museum (Natural History), no. 1859.7.9.4, purchased from Maison Verraux, Paris.

TYPE LOCALITY—"Nouvelle Grenade," now Colombia, restricted to the Villavicencio region, Río Meta, Meta, by Hershkovitz (1963a, p. 44).

DISTRIBUTION (figs. 27, 42)—Eastern Colombia from extreme southeastern Cundinamarca (Medina) south, into the department of Meta, along the base of the Cordillera Oriental and the Sierra de Macarena to the Río Guayabero, upper Río Guaviare.

Hernández-Camacho and Cooper (1976, p. 49) give the northern limits of the range as the lower Río Upía, a tributary of the Río Meta, in Meta department. Two Medina specimens in the British Museum (Natural History) were subsequently recorded by Napier (1976, p. 56). At the southern extreme of the range *Callicebus cupreus ornatus,* according to Hernández-Camacho and Cooper (1976, p. 56), "is marginally sympatric with *C*[*allicebus*]. *lugens* along both banks of the Guayabero River." Olivares (1962, p. 307) observed the two species on the left bank of the Guayabero but did not mention them living on the right bank. This bank of the Guayabero is largely savanna bordered by gallery forests.

Callicebus cupreus ornatus and *C. torquatus* are the only forms of the genus known to occur in the upper Río Orinoco basin. The geographic gap of approximately 350 km separating *C. c. ornatus* from its nearest relative, *C. c. discolor,* is occupied by *Callicebus torquatus medemi.*

DIAGNOSTIC CHARACTERS—Pale frontal blaze or transverse band present; crown reddish brown to nearly blackish, hair bases buffy or whitish; sideburns, underparts, and inner side of limbs reddish; outer side of thighs and upper arms buffy agouti like sides of body; outer side of legs and lower part of forearms reddish, digits contrastingly pale.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *C. cupreus discolor, C. c. cupreus,* and *C. dubius* by pale or whitish digits contrasting with reddish ankles and wrists; from *C. oenanthe* by uniformly reddish sideburns, crown dominantly reddish to reddish brown; from *C. brunneus* and *C. caligatus* by buffy or whitish frontal transverse blaze; from other forms of *Callicebus* by one or more of the preceding characters.

SPECIMENS EXAMINED—Total 99. **COLOMBIA. Cundinamarca:** Medina, 2 (BM); locality unknown, (BM, type of *ornatus* Gray); **Meta:** Agua Clara (Caño), 9 (UNICN); Barbascal, 2 (MVZ); Barrigon, 6 (AMNH); Los Micos, 14 (FMNH); Río Guapayo, La Macarena, 19 (AMNH, 11; FMNH, 8); Río Guayabero, 3 (UNICN); Restrepo, 13 (AMNH); San Martín, 4 (FMNH); Villavicencio, 27 (AMNH, 16; ULSM, 3; USNM, 8).

FIG. 35. *Callicebus caligatus* Wagner. New York Zoological Society Photo. Coloration as in *C. cupreus cupreus* (fig. 33) except forehead, crown, arms, and legs eumelanized.

Callicebus caligatus Wagner (figs. 35, 37)

Callithrix caligata Wagner, 1842: 357—BRAZIL: *Amazonas* (Borba, Rio Madeira; Manaqueri, Rio Solimões). Wagner, 1843: 42—English translation of original description.
Callicebus caligatus Thomas, 1908: 90—BRAZIL: part, *Amazonas* (type locality restricted to Borba).
Callithrix castaneoventris Gray, 1866: 58—"BRAZILS" (type locality); holotype, skin and skull, BM 44.5.14.20/45.6.17.10, purchased from Parzudaki.
Callicebus usto-fuscus Elliot, 1907: 191—BRAZIL: (precise type locality unknown); holotype, skin and skull, British Museum (Natural History), no. 51.7.3.1.

LECTOTYPE—The skin with skull from Borba, by restriction of type locality (Thomas, 1908); 2 lectoparatypes, including 1 skin only (NHMW) from Borba, collected May 1832, one skin and skull (NHMW 7546/112) from Manaquiri, collected December 1832, all by J. Natterer.

TYPE LOCALITY—Borba, Rio Madeira, restricted by Thomas (1908, p. 90). Borba is on the east bank of the Rio Madeira where the species is otherwise unknown. Presumably, the type was collected on the west bank of the river opposite Borba, or possibly elsewhere than in the Rio Madeira basin itself.

DISTRIBUTION (figs. 27, 36, 44)—Western Brazil, south of the Rio Solimões, presumably from the west bank of the Rio Madeira west to the Río Ucayali-Tapiche in Loreto, Peru, and the Río Javarí (Yavarí), south to the Río Tahuamanu, Pando, Bolivia; recorded from the States of Amazonas and Acre in Brazil and bordering Loreto department in Peru. Except for the original Natterer specimens labelled "Borba" and "Manaquiri," the species is unknown from the Rio Madeira watershed or east of the Rio Purús in Brazil. Specimens of *C. caligatus* in the American Museum of Natural History, collected by the Olallas, are mislabelled "Boca Rio Inuya" and "Sarayacu."

DIAGNOSTIC CHARACTERS—Blackish of forehead continuing over anterior portion of crown; forearms dark reddish to mostly blackish; cheiridia blackish to reddish brown or reddish; tail mixed buffy and grayish (marbled) for entire length or becoming dominantly to entirely buffy distally; sideburns, underparts, and inner sides of limbs reddish contrasting with dusky upper and outer parts; cranial characters like those of the *moloch* group.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *C. brunneus* by arms, legs, and sideburns more reddish, reddish underparts contrasting markedly with brownish agouti sides, tail mixed or somewhat annulated, at least on proximal half, the hairs banded buffy and grayish but with terminal fifth to half often dominantly buffy, the entire tail contrasting markedly with coloration of upper and underside of body; from *cupreus* by forehead entirely blackish, cheiridia blackish or dark reddish brown; from *C. cupreus discolor, C. cupreus ornatus,* and *C. dubius* by blackish forehead and absence of contrastingly pale or whitish frontal tuft or transverse band, forearms and legs reddish, brown, or blackish, cheiridia notably darker; from all other species of *Callicebus* by one or more of the above characters.

SPECIMENS EXAMINED—Total 54. **BOLIVIA. Pando:** Río Nareuda, 1 (FMNH). **BRAZIL. Acre:** Rio Branco, 2 (MPEG); Xapuri, 1 (MNR); **Amazonas:** Arumã, 3 (RNHMS); Canabuoca, 6 (BM, 4; MNR, 1; RNHMS, 1); Estirão do Equador, 7 (MPEG); Itaboca, 2 (RNHMS); Labrea, 1 (RNHMS); Manaqueri, 1 (NHMW); "Manaus," 1 (RNHMS); Paraná do Jacaré, 3 (SNG); Redempção, 2 (RNHMS); Rio Jaquirana, 1 (MPEG); opposite Tabatinga, 1 (FMNH); locality unknown, 1 (BM, holotype of *castaneoventris* Gray); "Orinoco," 1 (BM). PERU. **Loreto:** "Boca Río Inuya," 1 (AMNH 98384); "Iquitos," 1 (AMNH); Orosa, 6 (AMNH); Quebrada Esperanza, 3 (FMNH); Río Tapiche, 2 (AMNH); San Fernando, 2 (FMNH); Santa Cecilia, Río Manití, 2 (FMNH); "Sarayacu," Río Ucayali, 2 (AMNH). **LOCALITY UNKNOWN:** 1 (BM, holotype of *ustofuscus*).

Callicebus dubius Hershkovitz (fig. 37)

[?]*Callithrix caligata* Pelzeln (part not Wagner), 1883: 9—BRAZIL: specimen with whitish frontal blaze from unknown locality purchased 1840 from H. Parreyss.
Callicebus caligatus Thomas (not Wagner), 1908: 90—BRAZIL: part, *Amazonas* (Humaitá, Rio Madeira).
Callicebus cupreus caligatus Hill (part, not Wagner), 1960: 125–126—BRAZIL: *Amazonas* (individuals with "central white spot or star" only).
Callicebus moloch cupreus Hershkovitz (part, not Spix), 1963a: 37, 64—BRAZIL: *Amazonas* (Lago do Aiapuá).
Callicebus moloch Napier (part not Hoffmannsegg), 1976: 55—BRAZIL: part *Amazonas* (Lago do Mapixi with reference to *C. subrufus*).
C[*allicebus*]. *castaneoventris* Napier (not Gray), 1976: 56—skin and skull, BM, 1970. 381, listed as a syntype.
Callicebus dubius Hershkovitz, 1988:264 (fig. 13, with figures for *dubius* and *caligatus* transposed).

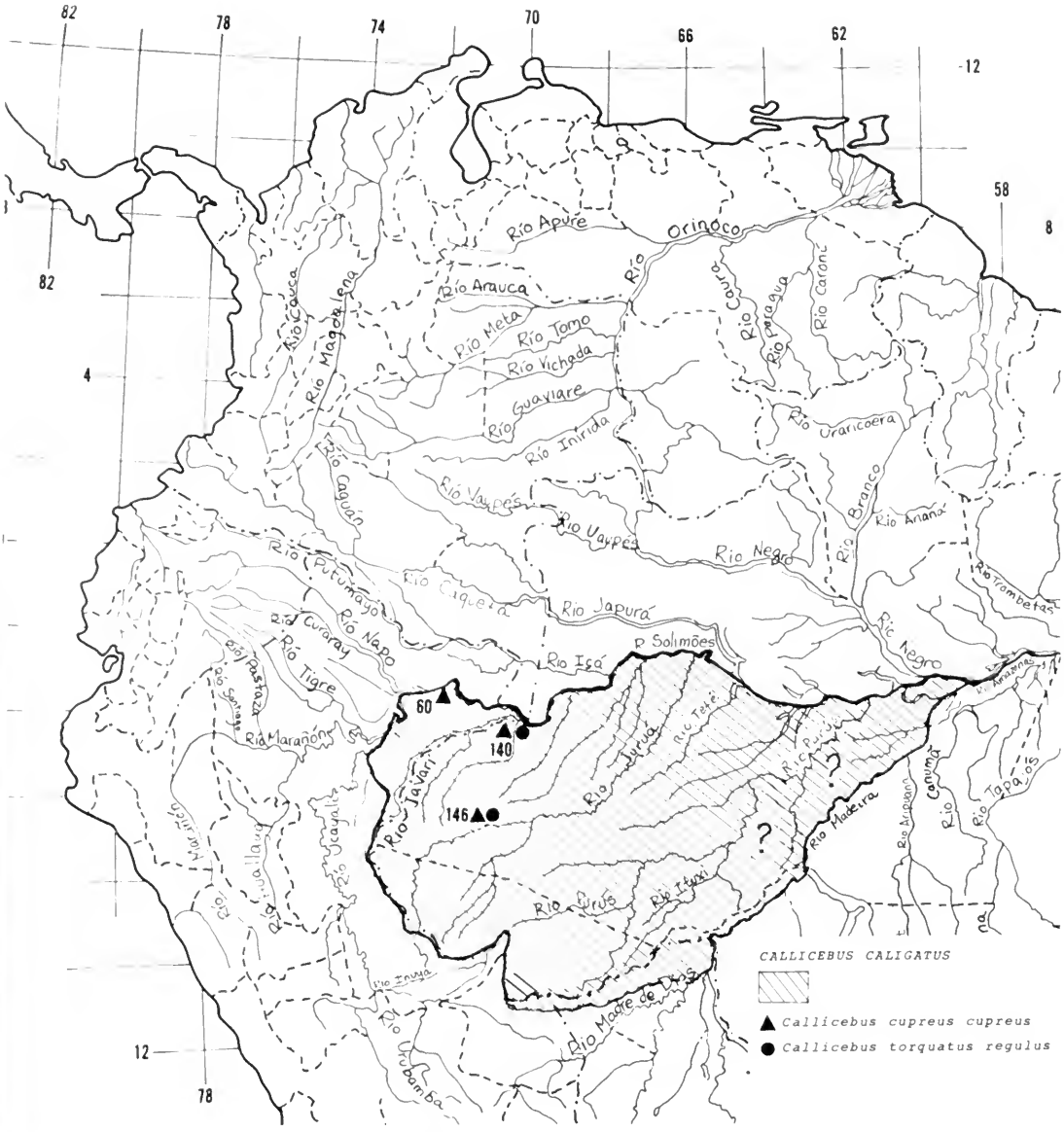

FIG. 36. Geographic distribution of *Callicebus caligatus* in Peru and Brazil. Triangles show localities where *C. caligatus* has been recorded with *C. cupreus cupreus*, numbered circles with *C. torquatus regulus*. See Figure 1 for overlap of geographic ranges, and Gazetteer (p. 104) for explanation of numbers.

HOLOTYPE—Adult female, skin and skull, FMNH 38886, collected June 1931 by Carl Lako.

TYPE LOCALITY—Said to be Lago do Aiapuá, west bank lower Río Purús. Distributional records and geographic relationships of *Callicebus dubius* indicate that the holotype more likely originated on the east bank of the lower Río Purús, probably opposite Lago do Aiapuá. The collector, Carl Lako, purchased from native hunters most of the specimens he sold to museums or dealers. The information he received regarding place and date of capture, usually days to months after the event, depended on the testimony of his agents. Measurements given on his labels are approximations in cm, some grossly inaccurate.

DISTRIBUTION (fig. 29)—Between west bank of Rio Madeira and east bank of lower Rio Purús, Amazonas, Brazil.

Proc. Acad. Nat. Sci. Phil. 140(1), 1988. In the original plates white-browed *C. Dubius* and the dark-browed *C. Caligatus* were incorrectly transposed.

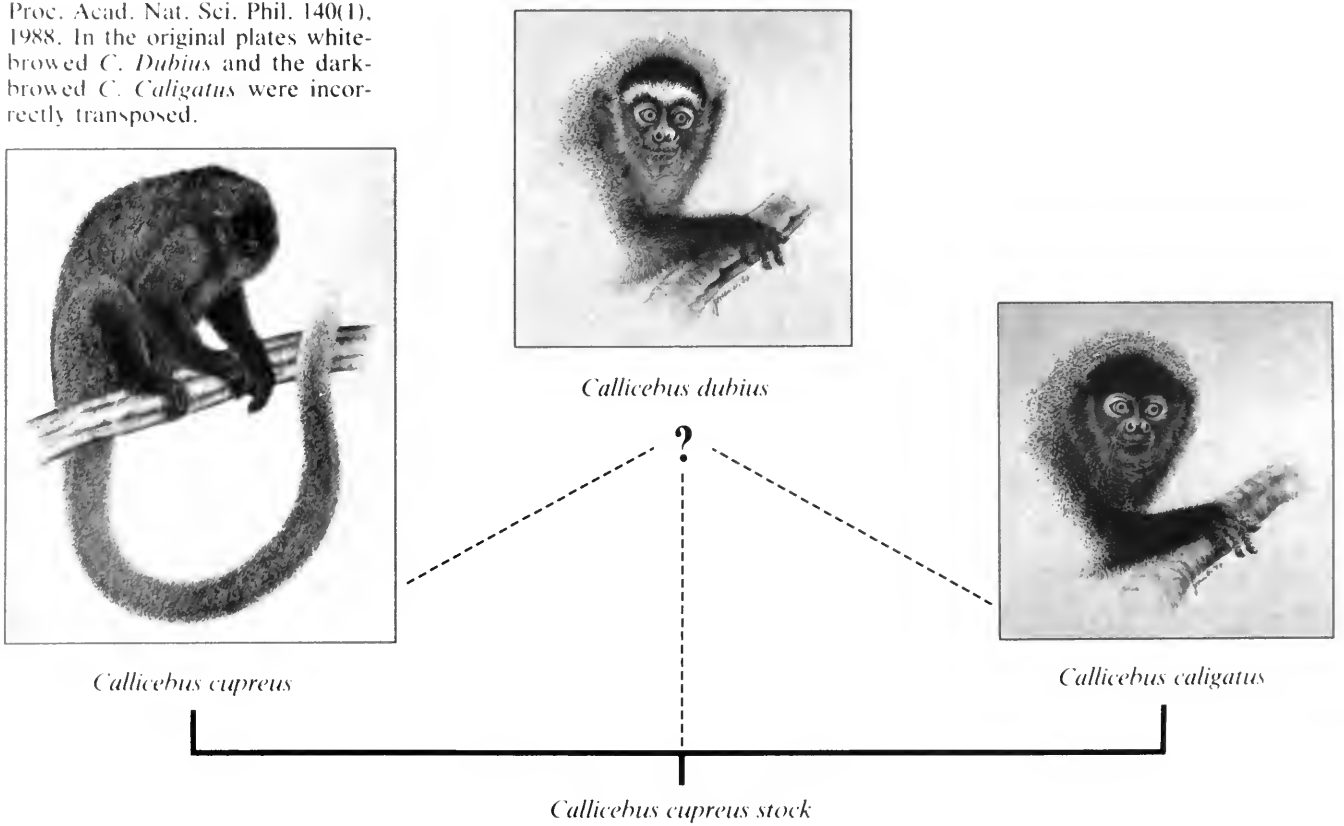

FIG. 37. *Callicebus dubius* has the eumelanin crown of *C. caligatus,* the bleached frontal pheomelanin blaze common to *C. cupreus discolor* and *C. c. ornatus* (fig. 34), whereas the outer side of limbs presents a mosaic of the pheomelanin of *C. cupreus* and eumelanin of *C. caligatus. C. dubius* may have evolved independently from an unknown titi stock perhaps near *C. cinerascens,* or by hybridization between *C. cupreus* and *C. caligatus.* (Reproduced from Hershkovitz, 1988, p. 267, in black and white from the corrected color plate which was distributed by the author as an offprint.)

DIAGNOSTIC CHARACTERS—Buffy or whitish frontal tuft or transverse blaze present, crown anterior to ears blackish; sideburns, most of outer surface of forearms, and legs reddish; cheiridia blackish or reddish brown; skull essentially as in the *moloch* group, but with line between frontal bones about as long as straight line between parietals, palate across molars extremely wide.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *Callicebus cupreus discolor, C. c. ornatus,* and *C. oenanthe* by pronounced blackish coronal band bordering whitish frontal blaze and dominantly blackish or reddish brown cheiridia; from *C. c. cupreus* by frontal blaze and dark cheiridia; from *C. caligatus* by whitish frontal tuft or blaze; from all other species of *Callicebus* by one or more of the foregoing characters.

EXTERNAL CHARACTERS OF HOLOTYPE—Forehead with pale buffy blaze, the hairs with narrow blackish bases and tips, radiating from center, the whole bordered by a thin line of blackish hairs including superciliary vibrissae in front and sides and a broad blackish coronal band behind; remainder of crown brownish agouti, the lax hairs cresting against shorter blackish hairs in front and longer raised agouti nuchal hairs behind; hairs of nape, back, rump, and cover hairs of midback with 4 or 5 narrow pheomelanin bands, each alternating with a eumelanin band; sides of trunk like back but hairs longer, 5- to 6-banded; outer side of thighs and upper arms brownish agouti like back; lower arms and legs reddish, upper surface of tail dominantly blackish agouti on proximal third, mixed blackish and grayish agouti on remainder, pencilled tip missing, underside like upper but with base dominantly blackish agouti; blackish face naked except for fine buffy hairs surrounding lips and between nostrils; sideburns, sides of head, and beard uniformly deep reddish; hairs of sides directed forward and upward, of neck forward and laterally, the reddish coloration sharply contrasted with that of forehead and crown; hairs of throat, chest, belly, and inner side of limbs unbanded reddish or reddish brown with those of throat whorled; cheiridia dominantly blackish agouti; length of gular and pectoral glands combined about 6 or 7 cm; blackish ears with buffy agouti hairs on outer (medial) side, reddish brown on inner.

VARIATION—Distinction of *C. dubius* from *C. caligatus* is based on its pale frontal tuft or blaze. This character, however, is tenuous. The blaze occupies nearly the entire forehead in the holotype and the Lago do Mapixi specimen. It is equally conspicuous in one of two skins (BM 8.5.9.8) from Humaitá, Rio Madeira, but represented by a few whitish banded hairs in the second (BM 8.5.9.9); blaze of so-called cotype of *castaneoventris* (BM 70.381) no better developed than that of second Humaitá specimen with which it agrees in all other respects; blackish superciliary fringe absent or poorly defined; tail marbled or dominantly blackish for most of length, pencilled tip buffy, but in the Lago do Mapixi specimen terminal fifth dominantly buffy.

TAXONOMY—Relationship between *Callicebus dubius* and *C. caligatus* recalls those between an odd specimen of *Callicebus cupreus cupreus* with an incipient pale frontal tuft and two odd specimens of *C. cupreus discolor* without frontal tuft or blaze. With exception noted, the normally blazeless *C. c. cupreus* and normally blazed *C. c. discolor* are each well defined allopatric subspecies. *Callicebus dubius* and *C. caligatus* likewise distinguishable, the one by presence and the other by absence of frontal tuft or blaze, but in this case may be sympatric. In general, the coloration of *C. dubius* appears to be a mosaic of that of *C. cupreus* and *C. caligatus,* suggesting that this species may be a hybrid of the other two.

The hypothetical origin and possible relationship between *C. dubius, C. caligatus,* and *C. cupreus* have been discussed elsewhere (Hershkovitz, 1988, p. 24) and illustrated here (fig. 37). In the original publication (Hershkovitz, 1988, fig. 13), the colored figures of *Callicebus dubius* and *Callicebus caligatus,* but not the binomials, were transposed by the printer. The author was not shown proofs. Fortunately, the journal editor supplied 200 corrected figures for distribution with the reprints of the article. The promised corrigendum for volume 140 of the Proceedings of the Academy of Natural Sciences, Philadelphia, has not yet been honored.

Representatives of *C. cupreus, C. caligatus,* and *C. torquatus* are sympatric in the Lago do Aiapuá region, on the left (west) bank of the Rio Purús. It is unlikely that a fourth species, *C. dubius,* occurs with them.

SPECIMENS EXAMINED—Total 5. **BRAZIL. Amazonas:** Humaitá, 2 (BM); "Lago Aiapuá", 1 (FMNH, holotype of *dubius*); Lago Mapixi, 1 (BM); locality unknown, 1 (BM 70.381).

Callicebus personatus É. Geoffroy

DISTRIBUTION (fig. 38)—Southeastern Brazil, in the states of Bahia, Espírito Santo, Minas Gerais,

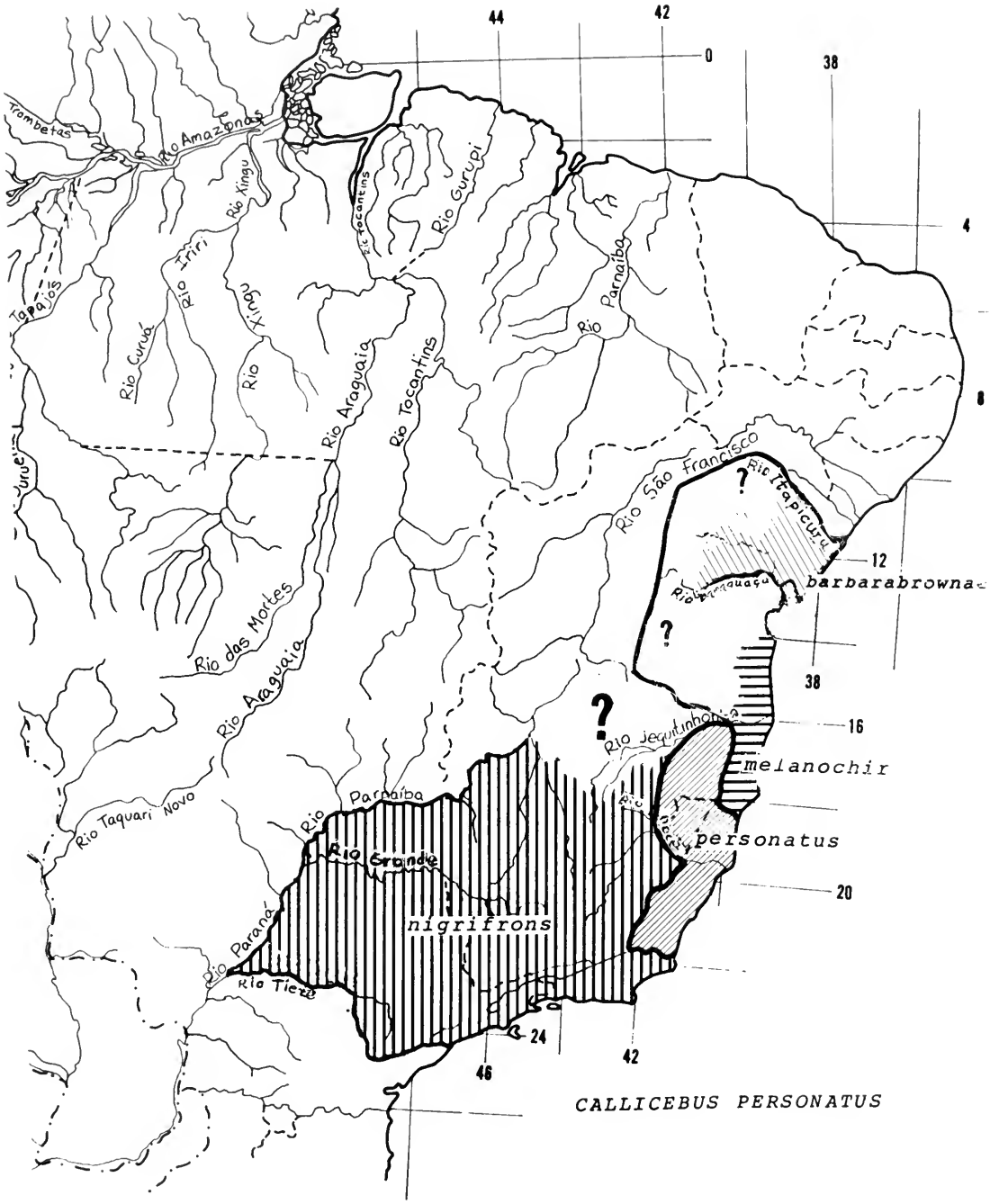

FIG. 38. Geographic distribution in remnants of Atlantic forest, eastern Brazil, of *Callicebus personatus barbarabrownae, C. p. melanochir, C. p. nigrifrons,* and *C. p. personatus.*

Rio de Janeiro, and São Paulo; from about 11° S on the coast, west to about 41°W in Bahia, south through Espírito Santo and Rio de Janeiro, southwest into Minas Gerais and São Paulo between the Rios Parnaíba-Paraná and Tietê.

DIAGNOSTIC CHARACTERS—Average size largest (tables 11, 13); cranial characters essentially as in *moloch* group except average cerebral index greater, average braincase index less (table 9); pelage coarse, shaggy with full coat of hidden brownish

wool hairs; color of trunk variable, cover hairs with 2 or 4 pheomelanic bands sharply defined to shadowy, or uniformly, pheomelanin; cheiridia blackish, the blackish often extending proximally as a tapered band to mid-arm or mid-foreleg, remainder of limbs grayish, buffy, yellowish or orange, the hairs banded or unbanded; facial hairs long, often comparatively thick but not concealing skin; forehead blackish with or without fine buffy banding; sideburns and ear tufts blackish; tail orange, reddish, mahogany, or mixed with blackish, never entirely blackish.

COMPARISONS—Distinguished from all other titis by larger average size; from *C. torquatus*, by cheiridia blackish (except *C. t. medemi*), throat not whitish or buffy and not sharply contrasted with chest or sideburns, tail not blackish; from *C. moloch* and *C. hoffmansi* by forehead and sideburns dominantly or entirely blackish or brownish; from *C. brunneus* by tail reddish, orange, or not blackish, blackish cheiridia sharply defined from grayish, buffy, or orange agouti of arms and forelegs; from *C. dubius* and *C. cupreus discolor* by forehead blackish; from remaining species by one or more of preceding characters.

Key to Subspecies of *Callicebus personatus* (fig. 39)

1. Forehead, entire crown, throat dominantly grayish agouti, buffy agouti or pale brownish agouti, the hairs finely banded ..... *melanochir*
1′. Forehead, crown halfway or quite to plane of ears blackish or buffy, the hairs mostly to entirely blackish or buffy 2
2. Forehead, crown, throat dominantly brownish (eumelanin) agouti or entirely brownish, the pheomelanin subterminal band of hairs narrow or absent 3
2′. Forehead, crown, throat, dominantly buffy (pheomelanin), the hairs except fine blackish tips almost or entirely pheomelanin ..... *barbarabrownae*
3. Forehead, crown blackish to about halfway plane of ears, remainder of crown grading into coarsely banded buffy or orange of nape; throat pale like chest ..... *nigrifrons*
3′. Forehead, crown blackish to plane of ears, remainder sharply defined buffy or orange, like nape; throat blackish ..... *personatus*

Callicebus personatus melanochir
Wied-Neuwied (fig. 40)

Callithrix melanochir Wied-Neuwied, 1820: 258 (footnote).
Callithrix incanescens Kuhl, 1820: 40—Lichtenstein manuscript name for syntype of *Callithrix melanochir* in Berlin Museum.
Callithrix gigot Spix, 1823: 22—BRAZIL: part, *Bahia* (Ilheus; type description in text, not plate 16); Kraft, 1983: 432—BRAZIL: part, *Bahia*, holotype adult female, mounted without skull, no. 26, Zoologische Staatssammlung, München; not the color figure by Spix (1823, p. 22, pl. 16).

TYPES—Adult female, mounted, Zoologische Staatssammlung, München. Syntypes in the natural history museums of Leiden (2), of Berlin (1), of Paris (1), and of Prince Maximilian von Wied-Neuwied museum (1); all types mounted with skull in skin, collected between February and middle April 1816. The Maximilian museum no longer exists. According to Avila-Pires (1965, p. 10) the Paris museum type has been lost, but it seems to have reappeared (skin no. 505, skull A2.815); one of the two Leiden specimens registered 17690 (mounted skin with skull) is here designated *lectotype*, the paralectotype is a skin and skull.

TYPE LOCALITY—Morro d'Arara or Fazenda Arara, Bahia, Brazil (Wied-Neuwied, 1820, p. 258). Subsequent restriction to the lower Rio Belmonte (= Rio Jequitinhonha) by Avila-Pires (1965, p. 10), was unnecessary.

DISTRIBUTION (fig. 38)—Eastern Brazil, in the state of Bahia from the Rio Mucuri north to the Rio Itapicurú, west to the divide between coastal streams and Rio São Francisco; the area north of the Rio Paraguaçu supports the extremely pale *C. p. barbarabrownae*.

DISTRIBUTION (fig. 38)—Atlantic coastal forests of eastern Brazil, in the state of Bahia from the Rio Mucuri north to the Rio Contas.

DIAGNOSTIC CHARACTERS—See key to subspecies and Fig. 39.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *C. person-*

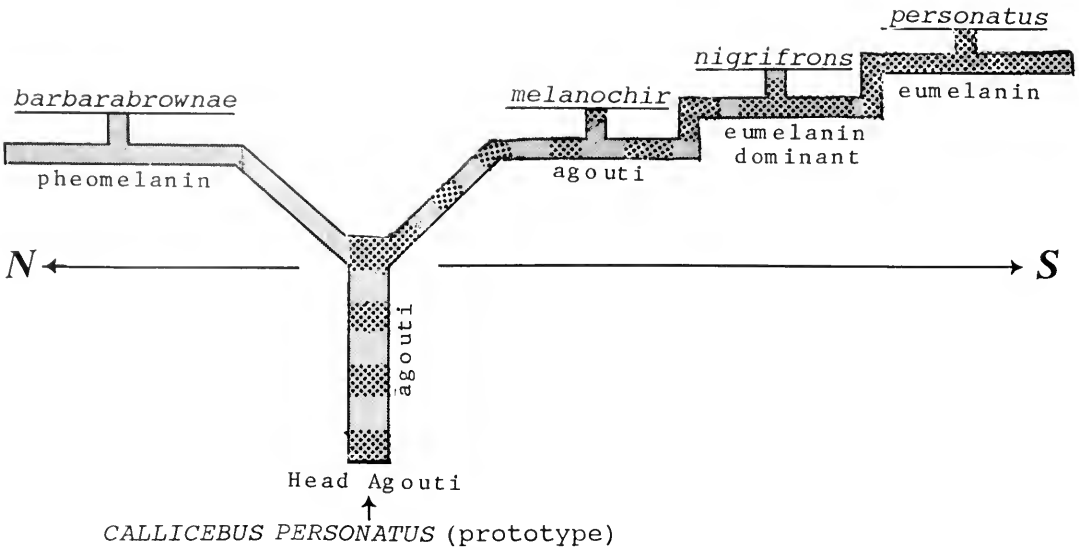

FIG. 39. Geographic differentiation of the agouti-headed prototype of *Callicebus personatus,* a dichotomous metachromic cline (cf. p. 40). Southward (***S***) the agouti patterned forehead of *C. p. melanochir* and part of crown becomes dominantly eumelanin in *C. p. nigrifrons,* then most of crown and cheeks become entirely eumelanin in *C. p. personatus*; northward (***N***) the agouti head pattern has become dominantly to entirely pheomelanin in *C. p. barbarabrownae.* (Monkey tree modified with additions from Hershkovitz, 1988, color fig. 15, p. 267.)

atus nigrifrons and *C. p. personatus* by forehead not sharply defined blackish, entire crown blackish agouti or grayish agouti like nape, sides of neck and throat grayish agouti or blackish agouti; from *C. p. barbarabrownae* by darker coloration, head dominantly eumelanin, not pheomelanin; from *C. cinerascens* by cheiridia and facial fringe blackish.

SPECIMENS EXAMINED—Total 6. **BRAZIL. Bahia:** Ilheus, 2 (ZSM, holotype of *gigot*; MNR); Rio Doce, 1 (Senckenberg); locality unknown, 3 (BM; MNHNP, syntype of *melanochir*; USPMZ).

Callicebus personatus nigrifrons Spix (fig. 41)

Callithrix nigrifrons Spix, 1823: 21, pl. 15 (animal).

Pithecia melanops Vigors, 1829: 14—"Black-faced Pithecia" [entire description], "Mexico." Gray, 1870: 56—cited in synonymy of *Callithrix personatus.*

Callithryx [sic] *chloroenemis* Lund, 1840: 313—nomen nudum.

Callithrix chlorocnemis [sic] Lund, 1842: 135, 200—BRAZIL: *Minas Gerais* (type locality, Pleistocene cave deposits, Lagoa Santa); a nomen nudum. Winge, 1895: 33–34—said to be identical with *Mycetes crinicaudus* Lund and *C. personata* É. Geoffroy, without other indication, description, or designation of type specimen (Hershkovitz, 1963b, p. 397).

Callithrix crinicaudus Lund, 1841a: 110—BRAZIL: *Minas Gerais* (type locality, Lagoa Santa); name based on the *guigó* of natives.

Jacchus grandis Lund, 1841b: 290, 295, pl. 27, fig. 5 [sic = 8] (proximal portion of femur)—BRAZIL: *Minas Gerais* (type locality, Pleistocene cave deposits, Lagoa Santa); type, proximal portion of femur, Museum Lundii, Copenhagen, collected 1838 by P. W. Lund. Winge, 1895: 33—a synonym of *Callithrix personata.*

Callicebus personatus brunello Thomas, 1913: 568—BRAZIL: *São Paulo* type locality, Piquete); holotype, male, skin and skull, British Museum (Natural History), no. 1.6.6.3, collected 23 January 1901 by Alphonse Robert.

LECTOTYPE—Adult, mounted skin only, Zoologische Staatssammlung, München, no. 88, collected between July and December 1817 by the Spix and Martius expedition. Spix described a male and female. The individual, sex unknown, number 88, listed by Kraft (1983, p. 432), is here designated lectotype.

TYPE LOCALITY—"*Habitat in provincia Minas Geraes ad flumen das Onças sylvas maritimas inter et Campos agrestes intermedium.*"

At the time of the Spix and Martius expedition (1817–1820), the Capitania de Minas Geraes, according to Arrowsmith (1811), included a piece of modern Rio de Janeiro, all Espírito Santo, and the southeastern panhandle of Bahia. In the likelihood that Spix was uncertain about the state boundaries, the Rio Onças, Municipio Campos,

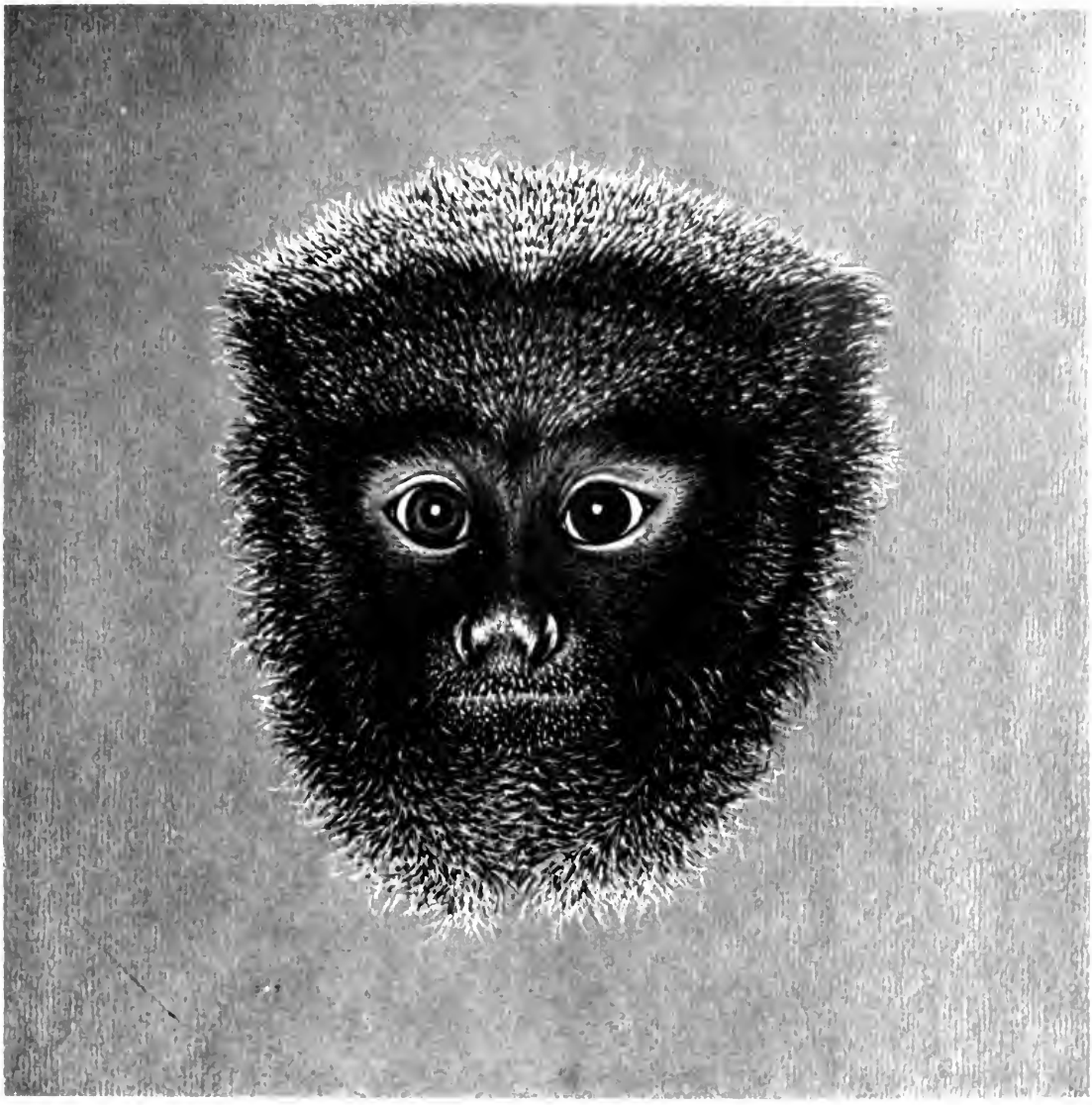

FIG. 40. *Callicebus personatus melanochir* Wied-Neuwied. From color portrait by Zorica Dabich (in Hershkovitz, *Living New World Monkeys (Platyrrhini)*, Volume 2, in preparation).

in Rio de Janeiro (not Minas Gerais), meets all requirements of the stated type locality of *Callicebus nigrifrons*, and is so emended.

DISTRIBUTION (fig. 38)—Southeastern Brazil, in the states of Rio de Janeiro, São Paulo from the Rio Tietê north, and southern Minas Gerais between the Rios Paraná-Paraíba, the headwaters of the Rio São Francisco, and the Rio Jequitinhonha (upper Rio Doce). Contact between *nigrifrons* and *personatus* in Minas Gerais is unknown.

DIAGNOSTIC CHARACTERS—See Key to Subspecies and Fig. 39.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *Callicebus personatus melanochir* and *C. p. barbarabrownae* by blackish forehead, anterior portion of crown blackish with thin mixture of buffy-banded hairs; from *personatus* by blackish front of crown grading into agouti of nape without line of demarcation, throat pale like chest.

SPECIMENS EXAMINED. Total 44. **BRAZIL. Minas Gerais:** Barretos, 3 (USPMZ); Passos, 1 (MNR); Patas, 1 (MNR); Rio Doce, right bank, 3 (USPMZ); São Jaõa Baptista do Gloria, 1 (USNM); Tapera, 1

FIG. 41. *Callicebus personatus nigrifrons* Spix. Photograph courtesy Dr. Russell A. Mittermeier.

(AMNH); Uberlandia, 2 (AMNH); Locality unknown, 3 (MNR, 2; USPMZ); **Rio de Janeiro:** Itatiaia, 7 (MNR, 1; USPMZ, 6); **São Paulo:** Boa Esperanza do Sul, Itaquere, 2 (USPMZ); Franca, 1 (USPMZ); Itatiba, 2 (USPMZ); Lins, Rio Tietê, 2 (FMNH; USPMZ); Maciceira, 1 (AMNH); Matodentro, 1 (NHMW); Monte Alegre, 3 (USPMZ); Piquete, 1 (BM, holotype of *brunello* Thomas); Visconde de Soutelo, 1 (USPMZ); Locality unknown, 5 (AMNH, 2; USPMZ, 3); **State unknown:** 3 (BM).

Callicebus personatus personatus É. Geoffroy (fig. 42)

Simia personata É. Geoffroy, 1812a: 357.
Callithrix personnatus [sic], É. Geoffroy, 1812b: 113—type locality, "Bresil?"

HOLOTYPE—Mounted, sex unknown, originally in the Ajuda Museum, Lisbon, seized by the French in 1808 during the Napoleonic invasion and deposited in the Muséum National d'Histoire Naturelle, Paris; missing since at least 1820.

TYPE LOCALITY—"Bresil?" According to Wied-Neuwied (1826, p. 112), who redescribed the taxon, the habitat is the east coast of Brazil between the Rio São Mateus and Rio Paraiba, or between 18°30′S and 21°30′S. Specific localities where Wied-Neuwied collected or observed individuals are along the Rios Itabapoana, Itapemirim, Iritiba, Reriutaba, and Espírito Santo, north to the Rio Doce. Desmarest (1820, p. 86) presented essentially the same descriptive and geographic data, without citation but obviously from Wied-Neuwied's manuscript. The same information was re-

FIG. 42. *Callicebus personatus personatus* É. Geoffroy. Photograph courtesy Dr. Russell A. Mittermeier.

peated by Desmarest in 1827 (p. 12), this time mistakenly crediting Humboldt for the geographic data. Thomas (1913, p. 569) compounded the confusion by attributing Wied-Neuwied's findings to Auguste St. Hilaire and citing Desmarest, without bibliographic reference, for the geographic data.

Thomas's (1913, p. 569) mention of Espírito Santo as habitat is not a restriction of type locality in the strict sense, and in any case, is vague. The type locality, therefore, is here restricted to the lower Rio Doce, Espírito Santo, Brazil.

DISTRIBUTION (fig. 38)—Southeastern Brazil, in Espírito Santo from southern to northern boundaries and possibly a short distance beyond into northwestern Minas Gerais at least as far as Teófilo Otoni.

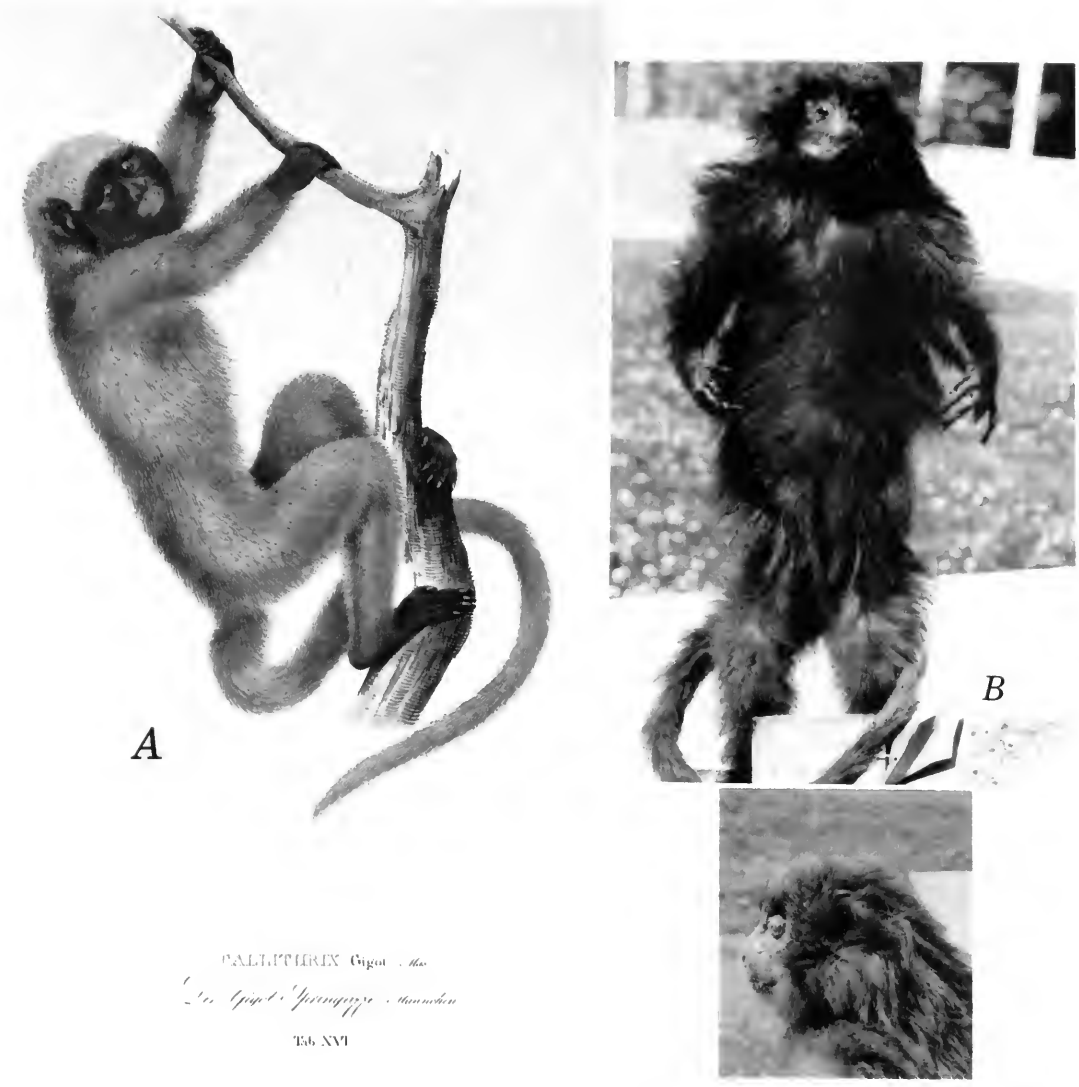

FIG. 43. *Callicebus personatus:* **A,** *Callicebus p. barbarabrownae,* the figure from Spix (1823, color plate 16) mislabeled *Callithrix gigot*; **B,** *Callicebus p. melanochir,* the mounted holotype of *Callithrix gigot* Spix in the Zoologische Staatssammlung, München; **C,** head of holotype.

DIAGNOSTIC CHARACTERS—See Key to Subspecies and Fig. 39.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *Callicebus p. nigrifrons, C. p. melanochir,* and *C. p. barbarabrownae* by blackish forehead, crown to level of ears, cheeks, ear tufts, and throat, the hairs unbanded; back of crown sharply contrasted orange.

SPECIMENS EXAMINED—Total 57. **BRAZIL. Espírito Santo:** Colatina, 9 (USPMZ); Engenheiro Reeve, 4 (BM); Estrada Linhares-São Mateus, 1 (MNR); Fazenda Correga da Barbada, 1 (USNM); Fazenda Dez de Agosto, 1 (MNR); Fazenda São José, 2 (MNR; USNM); Fazenda Tapera, Juiz de Foro, 1 (AMNH); Juparanã, 1 (MNR); Linhares, 2 (MNR); Rio Doce, 7 (NMHW, 3; USPMZ, 4); Rio Suaçui, Rio Doce, 2 (USPMZ); Santa Ana, Lagoa Juparanã, 1 (MNR); Santa Teresa, 2 (MNR); São Domingos, 2 (MNR); São Mateus, 1 (MNR); Sooretama, 11 (USPMZ); Locality unknown, "Paraná River," 1 (USNM); Locality unknown, 4 (AMNH; RNHMS, 3); **Minas Gerais:** Teófilo Otoni, 4 (AMNH; USPMZ, 3).

Callicebus personatus barbarabrownae, new subspecies (figs. 39, 43)

Callithrix gigot Spix, 1823: pl. 16 (animal)—part, color pl. only, not type description in text, p. 22. Wagner, 1833: 994—part, characters of Spix original colored figure.

Callithrix Gigot Wagner, 1833: 994—part, reference to original color plate only. Wagner, 1848: 450—BRAZIL: *Bahia* (a northern variety of *nigrifrons* or *melanochir*).

Callithrix gigot Kraft, 1983: 432—part, not holotype; reference to original color plate of Spix (1823, pl. 16 only).

C[*allithrix*]. *gigot* Reichenbach, 1862: pl. 5, fig. 68 (animal ex Spix). Gray, 1866: 57—part, characters.

Callithrix gigo [sic] Gray, 1870: 57—BRAZIL.

Callicebus gigot Elliot, 1913: 254—part, characters ex original colored figure.

Callicebus gigot gigot Hill, 1960: 140, 143, 146—part, BRAZIL: *Bahia* (Lamarão); specimens in British Museum only; characters; part distribution.

Callicebus personatus Napier, 1976: 53–54—part, BRAZIL: *Bahia* (Lamarão, 300 m; Formosa, 700 m).

Callicebus p[*ersonatus*]. *melanochir* Kinzey, 1982: 462–463 (map)—part, BRAZIL: *Bahia* (Lamarão, Río Itapicuru; Formosa; Bandiera de Mello, Río Paraguassú).

HOLOTYPE—Skin and skull, British Museum (Natural History) no. 3.9.5.7, collected 25 June 1903 by A. Robert.

ETYMOLOGY—The subspecies is named in honor of Associate Barbara E. Brown for her many years of active support of Field Museum of Natural History and valuable contributions to research by the staff of the Division of Mammals.

TYPE LOCALITY—Lamãrao, Bahia, Brazil, altitude about 300 m above sea level.

DISTRIBUTION (fig. 38)—Known only from the coastal highlands of north central Bahia, Brazil, between the Rio Paraguaçu to the south and Rio Itapicuru to the north.

The genus has not been recorded in Bahia north of the Itapicuru basin, west in the Rio São Francisco versant or between the Rio Paraguaçu and Rio Contas. Titis occurring south of the Contas are referrable to *C. personatus melanochir*.

DIAGNOSTIC CHARACTERS—Palest member of the species; general coloration buffy to silvery; forehead, crown, throat dominantly buffy, hairs except fine blackish tips nearly or entirely pheomelanin.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from geographically nearest *Callicebus personatus melanochir* by dominantly buffy (pheomelanic) crown, side of head, throat, trunk, and limbs with the subterminal pheomelanic bands of hairs paler; from *nigrifrons* and *personatus* by forehead not blackish.

EXTERNAL CHARACTERS OF HOLOTYPE—Superciliary vibrissal line blackish, forehead, crown to anterior plane of ears, dominantly buffy, adpressed hairs with tips blackish, remainder of shaft buffy; raised hairs of remainder of crown buffy, the fine tips blackish, bases eumelanin; nape, shoulders dominantly pale bluff, the blackish hair bases showing through surface; hairs of back and sides of body with subterminal pheomelanin band followed by eumelanin band and another pheomelanin band, hair bases eumelanin; thighs, upper arms paler, forearms, legs like back; hands blackish, feet blackish except metatarsal patch buffy like ankles and legs; throat, chest, belly nearly entirely buffy, hair bases dilute eumelanin; tail dominantly orange, upper surface of base paler, or yellowish, hair bases eumelanin, remainder of tail entirely pheomelanin; scattering of fine short pheomelanic facial hairs not concealing blackish skin; ear tufts and skin blackish.

Holotype distinguished by 2 cm midback patch with cover hairs missing, the dark brown underfur fully exposed.

VARIATION—The type series of six specimens from Lamarão are fairly uniform. Two specimens from Formosa appear darker on back, nape, and tail because of the greater exposure of the basal eumelanin of the hairs.

A female (BM 84.3.18.1) without locality data that survived six months in the London Zoo, agrees with holotype but with back and underparts paler, the hairs entirely pheomelanin; skin of face and ears paler.

DIFFERENTIATION (figs. 22, 37)—The discovery of *Callicebus personatus barbarabrownae* reveals an unsuspected dichotomy in the differentiation of the species. It appears that a northern population of the agouti prototype of *C. personatus* evolved into the pheomelanin-dominant *barbarabrownae*, and a southern parapatric population took the eumelanin pathway. Because of habitat destruction and fragmentation of the Atlantic coastal forest, the original boundary between the subspecies is represented by a wide geographic gap.

TAXONOMY—The color plate of *Callithrix gigot* Spix (1823, pl. 16) (fig. 43) indicates an animal distinct from the one named *melanochir* three years earlier by Wied-Neuwied (1820, p. 258). Nonetheless, Wied-Neuwied (1826, p. 114) regarded the two forms as identical but likely had in mind the

description in text. Few authors followed this decision, although Cabrera (1958, p. 139) includes *gigot* in the synonymy of *melanochir*.

Judged by the original color plates only, *Callithrix melanochir* and *C. gigot* are indeed distinct, as noted earlier by Wagner (1833, 1848). *Callicebus personatus melanochir* is figured as a basically grayish-bodied animal with reddish back, forehead grayish, crown in front blackish, tail variegated. The figured *Callithrix gigot* is entirely buffy-bodied, with browline blackish, crown buffy, tail buffy like trunk. Spix's (1823, p. 22) original description of the holotype of *gigot* (fig. 43), however, is of a very different animal. Elliot (1913, p. 255) had already noted that "Spix's figure [of *gigot*] . . . in no way represents the type, which is a darker animal and of quite a different color. Spix's description, however, is fairly accurate." The type specimen of *gigot* I examined in the Munich Museum, and that of a topotype in the Rio Museum (MNR 11201) from Ilhéus, conform fairly well to that of Wied-Neuwied's *melanochir*. On the other hand, the trunk of a specimen (FMNH 20444) from Bandeira do Melo, Rio Paraguaçu, NW of Ilheus, is dominantly buffy as *figured* for *gigot*, its tail deep reddish as *described* for *gigot*. The series of BM specimens from Formosa (2) and Lamarão (6) in the same region NW of Ilhéus, exhibit the same *figured* characters of *gigot*.

If Ilhéus is indeed the type locality of *gigot*, and nothing in Spix's text indicates otherwise, then *gigot* as originally *described* and represented by the *mounted type specimen* in the Munich Museum is indistinguishable from Wied-Neuwied's *C. p. melanochir*. On the other hand, the FMNH skin only from Bandeira de Melo, the BM material from Formosa and Lamarão, together with Spix's *figure* of a titi mistakenly labelled *gigot*, represent the distinct population of the northernmost known geographic limits of the species, here named *C. p. barbarabrownae*.

SPECIMENS EXAMINED—Total 9. **BRAZIL. Bahia:** Bandeira do Melo, Rio Paraguaçu, 1 (FMNH); Formosa, 2 (BM); Lamarão, 6 (BM).

Callicebus torquatus Hoffmannsegg

DISTRIBUTION (fig. 44)—Upper Amazonia; in Brazil, the State of Amazonas from the Rio Negro and Rio Purús west; in Venezuela between the Ríos Caroní and Orinoco; in Colombia between the Río Tomo (northern affluent of the Orinoco), the Río Putumayo (Iça), and the Río Amazonas; in Ecuador, the Río Putumayo and Río Napo basins; in Loreto, Peru, north bank of the Río Marañón-Amazonas between the Ríos Putumayo and Nanay.

DIAGNOSTIC CHARACTERS—Average size larger than that of other species except *C. personatus* (tables 11, 13), ethmoturbinal I larger, projecting farther behind than maxilloturbinal bone (fig. 45), average cerebral index high (table 9), diploid chromosome number = 20 (subspecies unknown), forehead, forearms, sideburns, feet, and tail blackish; crown reddish, reddish brown, mahogany, or blackish; sideburns little projecting; throat collar whitish or buffy, sometimes not well defined or absent; hands blackish, buffy, yellowish, or orange; upper parts from crown to tail base reddish brown, mahogany, or blackish, hairs reddish brown, conspicuously to faintly banded or uniformly colored; chest, belly uniformly reddish, reddish brown, or blackish.

COMPARISONS—Distinguished from *Callicebus personatus* by buffy orange hands (except blackish in *C. torquatus medemi*) sharply contrasted with blackish arms, whitish, buffy to orange throat contrasted with blackish cheeks and reddish brown to blackish chest, tail dominantly to entirely blackish; from *Callicebus brunneus* by contrastingly pale throat or collar, contrastingly pheomelanic hands, distal portion of tail including pencillike proximal; from *C. cupreus* by blackish forehead, crown, arms, and tail; from *C. donacophilus* by blackish tail and contrastingly pale throat or collar and blackish sideburns; from other species by one or more of above characters; from all species (except *C. personatus*) by larger average size and cranial characters given above.

Key to Subspecies of *Callicebus torquatus*

1. Hands, feet, tail, sideburns, and underparts except throat entirely or predominantly blackish ..... *medemi*
1′. Hands whitish, buffy orange to rufous with or without mixture of blackish hairs; tail blackish or with mixture of reddish; underparts except throat blackish, reddish brown, or reddish 2

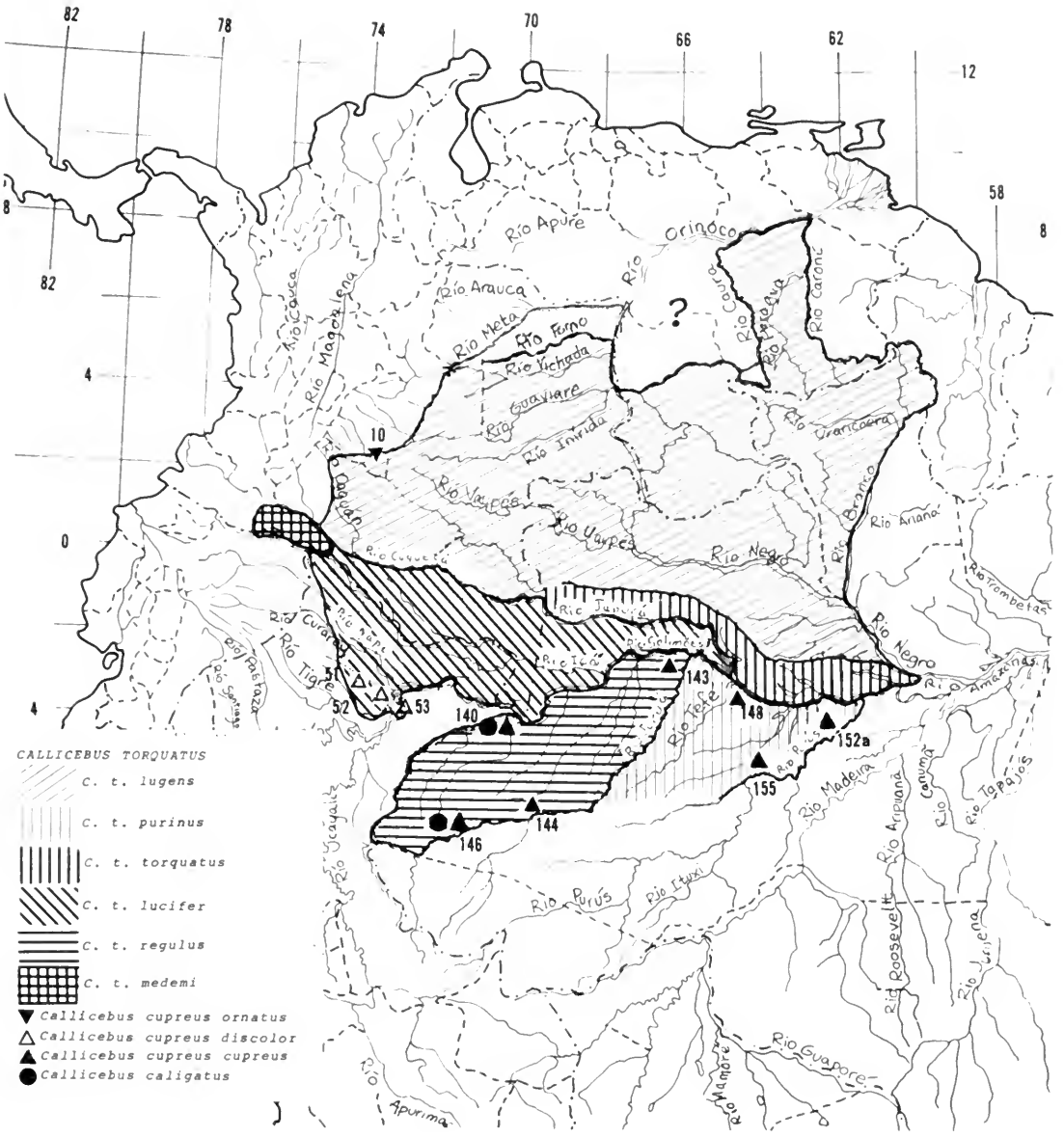

FIG. 44. Geographic distribution of *Callicebus torquatus* and subspecies, in Venezuela, Colombia, Ecuador, Peru, and Brazil. Symbols show where representatives of *Callicebus cupreus ornatus, C. c. discolor, C. c. cupreus,* or *C. caligatus* have been recorded with representatives of *C. torquatus.* See Figure 1 for overlap of geographic ranges and Gazetteer (p. 104) for explanation of numbers.

2. Chest and belly reddish or reddish brown 3
2′. Chest and belly brown or blackish 4
3. Hairs of back and sides strongly to faintly banded; throat collar contrastingly colored buffy, yellowish, or whitish, the collar extending to ear base ..... *purinus*
3′. Hairs of back and sides weakly banded to uniformly reddish brown; throat collar weakly defined, sometimes absent ..... *torquatus*
4. Hairs above and behind ears more or less banded ..... *regulus*
4′. Hairs surrounding ears uniformly blackish 5

5. Hairs of back and sides dark brown or blackish, the hairs uniformly colored or faintly banded ... *lugens*

5′. Hairs of back and sides brownish or reddish brown, the hairs distinctly to weakly banded ... *lucifer*

Callicebus torquatus medemi Hershkovitz

Callicebus torquatus medemi Hershkovitz, 1963a: 16, 52, 66, pls. 5–7 (skull), pl. 11 (dentition).

HOLOTYPE—Female, skin and skull, Field Museum of Natural History, no. 70699; collected 17 March 1952 by Philip Hershkovitz.

TYPE LOCALITY—Río Mecaya, near mouth, right bank Río Caquetá, Putumayo, Colombia; altitude approximately 180 m.

DISTRIBUTION (fig. 44)—Amazonian region of Colombia between the Ríos Caquetá and Putumayo in the Intendencia del Putumayo and southern part of the Intendencia de Caquetá; altitudinal range between 100 and 450 m above sea level.

DIAGNOSTIC CHARACTERS—See Key to Subspecies.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *C. torquatus torquatus* and *C. t. purinus* by darker coloration throughout, including blackish hands, legs, and underparts; from *lucifer, regulus,* and *lugens* by upper surface of hands uniformly or dominantly blackish.

SPECIMENS EXAMINED. Total 17. **COLOMBIA. Caquetá:** Tres Troncos, La Tagua, 1 (FMNH); **Putumayo:** Caño Caucaya, 3 (INDERENA); El Pepinó, 1 (INDERENA); Quebrada El Hacha, 2 (UNICN); Río Mecaya, 9 (FMNH, including holotype of *medemi*); Umbría, 1 (FMNH).

Callicebus torquatus lugens Humboldt (fig. 46)

Simia lugens Humboldt, 1811: 319; 1812: 357.

Saguinus vidua Lesson, 1840: 165—new name for *Simia lugens* Humboldt; *Simia amicta* a variety, *Cebus torquatus* possibly a juvenal. Lesson, 1842: 8—COLOMBIA.

Callicebus lugens duida J. A. Allen, 1914: 647—VENEZUELA: *Amazonas* (type locality, base of Mt. Duida, altitude 700 ft); holotype, male, skin and skull, American Museum of Natural History, no. 36179; collected 25 March 1913 by Leo E. Miller.

TYPE—None in existence, name based on captive animal observed by A. Humboldt during his travels on the upper Río Orinoco.

TYPE LOCALITY—Near San Fernando de Atabapo, at the confluence of the Ríos Orinoco and Guaviare, Amazonas, Venezuela.

DISTRIBUTION (figs. 27, 44)—Eastern Colombia, southern Venezuela, and bordering parts of northwestern Brazil; in Colombia between the Río Tomo in the north, Río Caguán-Caquetá in the south, in the departments of Vichada, Meta east of the Río Ariari, Guainía, Guaviare, Vaupés, and Caquetá east of the Río Caguán; in Venezuela, the states of Amazonas south of the Río Ventuari and Bolívar between the Ríos Caura and Caroni; in Brazil, Amazonas north of the Rio Japurá-Solimões and Roraima west of the Rio Branco and south of the Rio Uraricoera.

DIAGNOSTIC CHARACTERS—See Key to Subspecies.

MEASUREMENTS—See Table 13.

COMPARISONS—Most nearly completely blackish of all subspecies; distinguished from *Callicebus t. torquatus, C. t. purinus,* and *C. t. regulus* by blackish chest and belly; from *C. t. lucifer* by little or no contrast between blackish crown and reddish brown or blackish nape, hairs of dorsum uniformly colored or faintly banded; and from *C. t. medemi* by golden or yellowish orange hands.

SPECIMENS EXAMINED—Total 96. **BRAZIL. Amazonas:** Cachoeira do Quartel, 1 (NHMW); Marabitanas, 1 (NHMW); Monte Curicuriari, 2 (AMNH); Rio Alegría, 1 (BM); Rio Araçá, 2 (BM); Rio Casiquiare, 15 (AMNH); Rio Maturaca, 2 (USNM); Rio Ocama, 5 (AMNH); Rio Tootobi, 1 (MPEG); Rio Uapés, 1 (NHMW); San Carlos, 1 (NHMW); Tahuapunta, 9 (AMNH); Taraqua, Rio Uapés, 2 (MNR); No precise locality, 1 (USNM); **Roraima:** Lago da Cobra, 2 (USPMZ); Rio Mucajai, 4 (MPEG). **COLOMBIA. Guaviare:** Caño Grande, 1 (FMNH); Laguna de Espejo, 1 (FMNH); La María, 2 (FMNH); **Vichada:** Maipures, Río Orinoco, 1 (BM). **VENEZUELA. Amazonas:** Belém, 4 (USNM); Boca Mavaca, 8 (USNM); Capibara, 8 (USNM); Isla Cudamaco, 1 (USNM); Mt. Duida, 12 (including holotype of *duida*); Tamatama, 5 (USNM); **Locality unknown,** 3 (BM, 2; USNM).

Callicebus torquatus torquatus Hoffmannsegg

Callitrix [sic] *torquata* Hoffmannsegg, 1807: 86.

Callithrix amictus É. Geoffroy, 1812b: 114—holotype

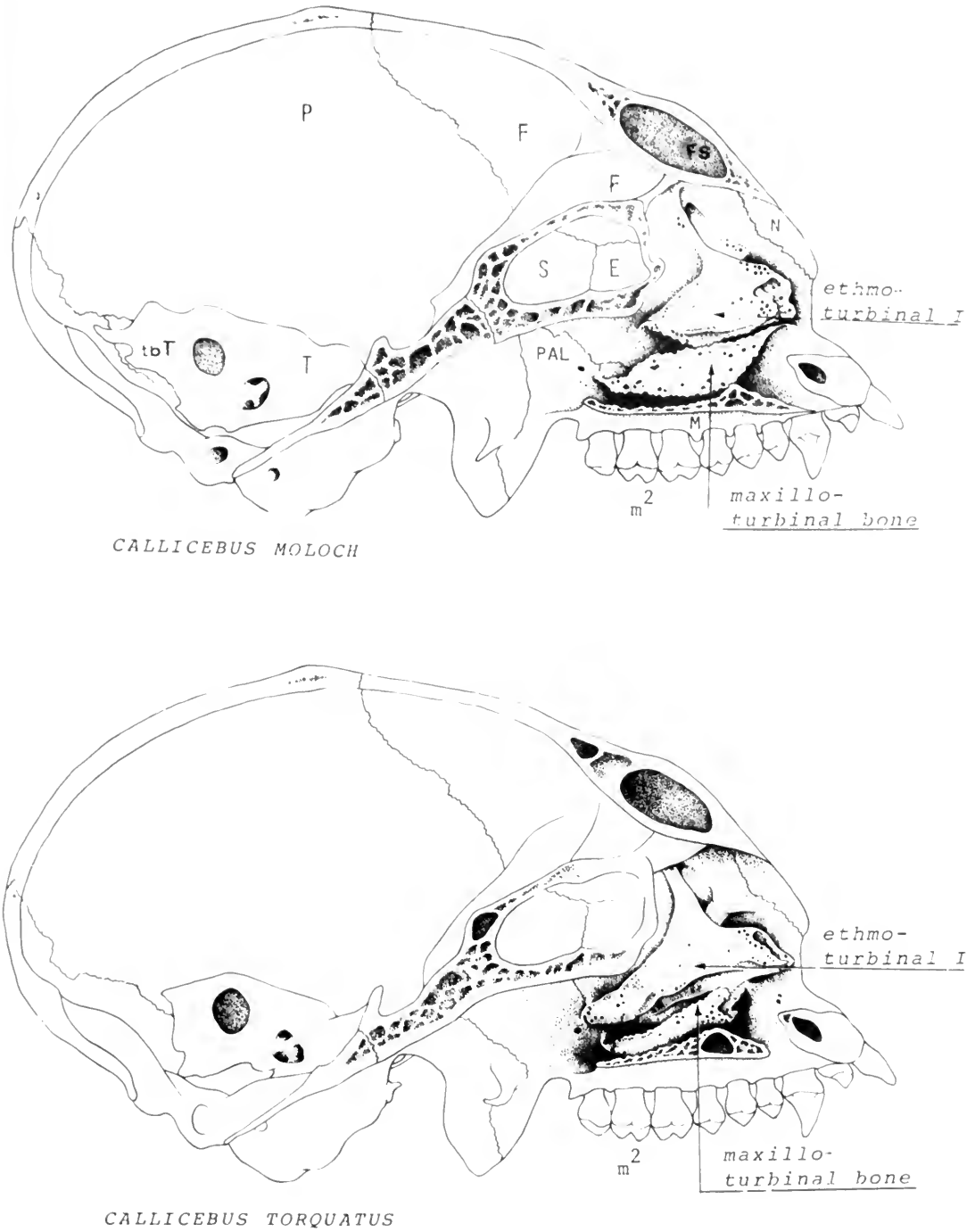

FIG. 45. *Callicebus moloch* and *Callicebus torquatus*, left sagittal section of cranium: **E** = ethmoid bone; **F** = frontal bone; **Fs** = frontal sinuses; **M** = maxillary bone; **N** = nasal bone; **P** = parietal bone; **Pal** = palatine bone; **S** = sphenoid bone; **T** = temporal bone; **tbT** = auditory bulla of temporal bone (adapted from Hershkovitz, 1977, fig. IV 30).

FIG. 46. *Callicebus torquatus lugens* Humboldt. Photograph of dead animal, courtesy the late Dr. Frederick Medem (from Hershkovitz, 1963).

in Paris Museum; type locality, "probablement le Brèsil?"

SYNTYPES—One syntype, perhaps the holotype, possibly still preserved in the Berlin Museum as a mounted specimen; one syntype no. 687 (522) in the Muséum National d'Histoire Naturelle, collected by Friedrich Wilhelm Sieber before 1806 and donated 1808 to the Lisbon museum by Count von Hoffmannsegg, then removed to the Paris museum.

TYPE LOCALITY—Said to be the interior of Pará (sensu lato), Brazil; redetermined by Hershkovitz (1963a, p. 56) as "Codajáz," north bank Rio Solimões above the mouth of the Rio Negro, Amazonas, Brazil.

DISTRIBUTION (figs. 27, 42)—In Amazonas, Brazil; north bank of the Rio Solimões between the lower Rio Negro and lower Rio Japurá, northern limits undetermined but presumably the low divide between the Rios Japurá-Solimões and the Rio Negro-Uapés.

DIAGNOSTIC CHARACTERS—See Key to Subspecies.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *Callicebus torquatus purinus* by blackish crown not sharply demarcated from mahogany nape, hairs of back uniformly colored or faintly banded; from *C. t. regulus* by reddish brown underparts, back of crown not markedly differentiated from forehead or nape; from *C. t. lucifer* and most *C. t. lugens* by reddish brown or mahogany coloration throughout; from *C. t. medemi* by hands yellow, golden, or orange.

SPECIMENS EXAMINED. Total 18. **BRAZIL. Amazonas:** Codajás, 8 (MNR, 1; RNHMS, 7); Lago do Arara, 1 (BM); Manacapurú, 2 (BM; RNHMS); Manaus, 1 (FMNH); "Rio Negro," 2 (BM); Unknown locality, 4 (MNHNP, including syntype of *torquatus* and holotype of *amictus*; FMNH, 2).

Callicebus torquatus lucifer Thomas

Callicebus lucifer Thomas, 1914: 345.

Callicebus torquatus ignitus Thomas, 1927b: 287—BRAZIL: *Amazonas* (type locality, Rio Tonantins, upper Rio Solimões); holotype, immature male, skin and skull, British Museum (Natural History), no. 27.8.11.4, collected 30 September 1926 by W. Ehrhardt.

HOLOTYPE—Male, skin and skull, British Museum (Natural History), no. 14.3.1.2; collected 9 August 1913, by J. J. Mounsey.

TYPE LOCALITY—Yahuas Territory, near Pebas, Loreto, Peru, about 125 m.

DISTRIBUTION (figs. 27, 44)—North bank Rio Solimões-Amazonas in Brazil, Colombia, Ecuador, and Peru; in Brazil between the Rios Solimões and Japurá; in Colombia between the Ríos Caquetá (Japurá) below mouth of Río Caguán, and Ríos Putumayo and Amazonas in the departments of Caquetá, Putumayo, and Amazonas; in Ecuador between the upper Ríos Aguarico and Putumayo, Napo province; in northern Loreto, Peru, between the Ríos Putumayo, Nanay, and Amazonas.

DIAGNOSTIC CHARACTERS—See Key to Subspecies.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *lugens* by brownish agouti upper parts; from *torquatus* and *purinus* by blackish underparts; from *regulus* by hairs surrounding ears uniformly blackish; and from *medemi* by dominantly or entirely orange hands.

SPECIMENS EXAMINED—Total 27. **BRAZIL. Amazonas:** Rio Içá, near Colombian border, 3 (BM; RMNHS, 2); Rio Tonantins, 3 (BM, holotype and 2 paratypes of *ignitus*); Santa Rita, 1 (BM). **COLOMBIA. Amazonas:** Encanto, Río Caraparaná, 2 (FMNH, skulls only). **PERU. Loreto:** Apayacu, 5 (AMNH); Lagarto Cocha, boca, 3 (AMNH); Pebas, 2 (AMNH); Río Curarary, boca, 4 (AMNH); Santa Luisa, Río Nanay, 2 (FMNH); Yahuas Territory, 2 (BM, holotype and paratype of *lucifer*).

Callicebus torquatus regulus Thomas

Callicebus torquatus regulus Thomas, 1927a: 509–510.

HOLOTYPE—Female, skin and skull, British Museum (Natural History), no. 27.3.6.8; collected 5 August 1926, by W. Ehrhardt.

TYPE LOCALITY—Fonte Boa, upper Rio Solimões, Amazonas, Brazil.

DISTRIBUTION (figs. 27, 44)—Amazonas, Brazil, between the Rio Solimões, lower Rio Javarí, and west bank of the Rio Juruá from mouth to about 7°S.

DIAGNOSTIC CHARACTERS—See Key to Subspecies.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *Callicebus torquatus purinus,* the only other south bank representative of the species, by dark brown chest and belly; from *C. t. torquatus* by inner side of arms entirely blackish, throat collar well developed; from *C. t. lucifer* by brownish underparts and sideburns and strongly contrasted reddish crown; from *lugens* by paler back, side, and underparts, reddish crown; from *medemi* by orange hands.

SPECIMENS EXAMINED—Total 9. **BRAZIL. Amazonas:** Fonte Boa, 8 (BM, 5, including holotype of *regulus*; MNR, 3); Rio Juruá, 1 (USPMZ).

Callicebus torquatus purinus Thomas (fig. 47)

Callicebus torquatus purinus Thomas, 1927a: 509.

HOLOTYPE—Male, skin and skull, British Museum (Natural History), no. 26.5.521; collected 11 May 1925, by W. Ehrhardt.

TYPE LOCALITY—Aiapuá (Ayapuyá), lower Rio Purús, Amazonas, Brazil.

DISTRIBUTION (figs. 27, 44)—In the State of Amazonas, Brazil, south of the Rio Solimões between the lower Rio Purús and the Rio Tefé.

DIAGNOSTIC CHARACTERS—See Key to Subspecies.

MEASUREMENTS—See Table 13.

COMPARISONS—Distinguished from *C. t. torquatus* by reddish brown crown sharply contrasted with blackish forehead, marked agouti pattern of back, throat collar well developed and sharply defined from surrounding parts; from *C. t. regulus* and *C. t. lucifer* by reddish brown underparts; from *lugens* by more reddish coloration throughout, crown always sharply defined from nape; from *medemi* by dominantly yellowish or orange hands.

SPECIMENS EXAMINED—Total 11. **BRAZIL. Amazonas:** Aiapuá, 1 (BM, holotype of *purinus*); Ega (see Tefé); Jaburú, 2 (RNHMS); Lago Aíapuá, 4 (FMNH; MNR, 3); Lago Tefé, 1 (AMNH); Lago Tauaríã, Rio Purús, 1 (MNR); Rio Mamoria-Mirim, Rio Purús, 1 (USNM); Tefé, 1 (USNM).

XXII. Acknowledgments

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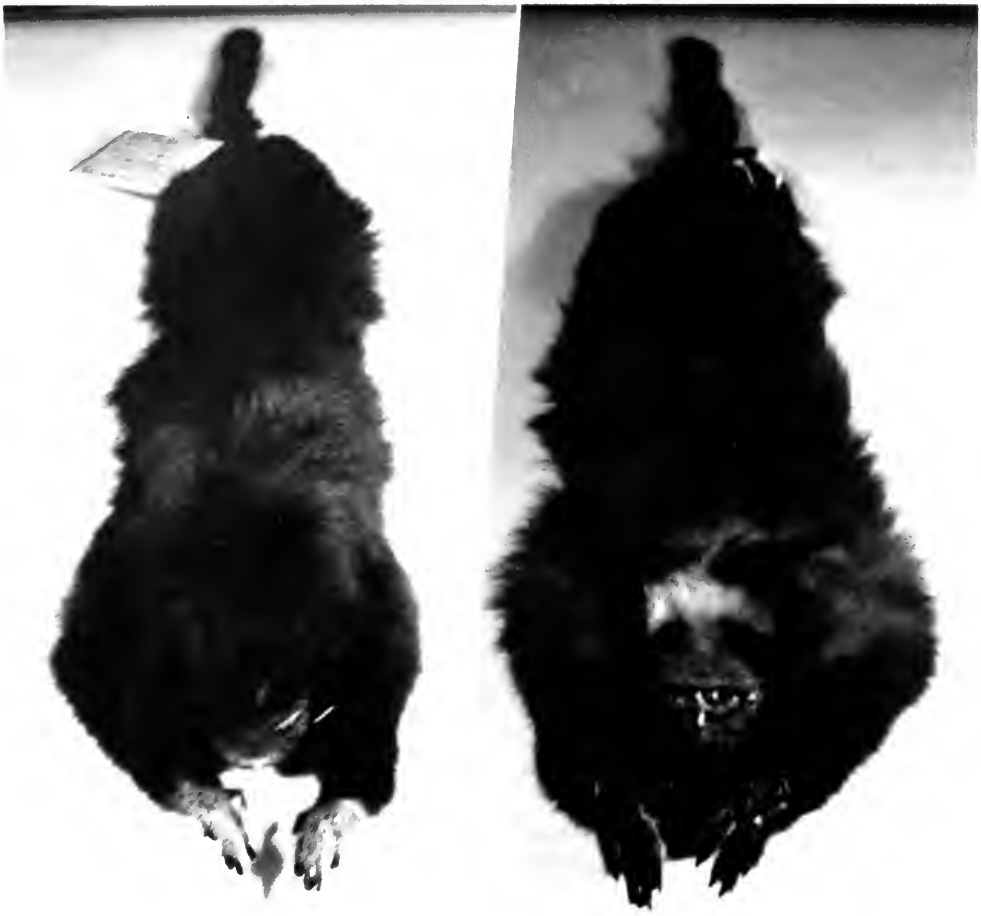

FIG. 47. *Callicebus torquatus purinus* Thomas. Skin of FMNH 38885, from Aiapuá, Rio Purús, Brazil, dorsal and ventral view.

Handley, Jr., and Dr. Richard W. Thorington, Jr., National Museum of Natural History, Washington, D.C.; Dr. Guy G. Musser, American Museum of Natural History, New York; Dr. Philip Myers, Museum of Zoology, University of Michigan, Ann Arbor; and Dr. James L. Patton, Museum of Vertebrate Zoology, University of California, Berkeley.

Color portraits of *Callicebus* reproduced here in black and white were executed by Field Museum staff artist Zorica Dabich. Most of the photographs of titis were contributed by Dr. Russell A. Mittermeier. Prints of other illustrations were made by Ron Testa. Ronald Edwards assisted in preparation of the material, the manuscript, and in the bibliographic and scientific research. Technical Assistant Marcia Daft proofread and Associate Barbara Brown helped in many ways, including typing several drafts of the manuscript. I am extremely grateful to the foregoing persons for their help, contributions, and cooperation.

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TABLE 13. Summaries of measurements of species and subspecies of *Callicebus*.

Callicebus	Head and body	Tail	Hind foot	Ear	Weight
donacophilus					
donacophilus ♂♂	311 (278–330) 6	411 (372–445) 6	91 (89–92) 5	34 (30–37) 6	—
donacophilus ♀♀	340 (305–420) 5	440 (410–460) 4	89 (80–100) 6	36 (32–40) 5	—
pallescens ♂♂	315	420	92	—	800
pallescens ♀♀	360	390	—	32	—
olallae ♂[1,2]	325	425	90	—	—
modestus ♂[1]	315	400	—	—	—
oenanthe ♂♂[1]	300, 303, 306	392, 380, 400	93, 95, 95	30, 27, 28	—
oenanthe ♀♀	315, 385, 313	363, 375, 360	91, 93, 86	30, —, 28	—
brunneus ♂♂	317 (300–345) 7	397 (371–420) 7	90 (82–95) 7	31 (28–35) 7	845
brunneus ♀♀	300, 325	380, 440	85, 85	—, 28	850

Callicebus	Greatest skull length	Condylobasal length	Zygomatic breadth
d. donacophilus ♂♂	60.5 (57.8–63.0) 8	50.2 (45.9–52.5) 10	37.2 (33.3–39.5) 5
d. donacophilus ♀♀	60.0 (58.2–61.7) 7	49.3 (47.6–51.0) 7	36.6 (35.3–39.6) 7
d. pallescens ♂♂	59.9 (58.0–62.2) 5	49.8 (48.1–52.6) 5	37.1 (35.2–38.6) 5
d. pallescens ♀	56.6	45.7	35.0
olallae ♂[1]	60.2	50.8	39.5
modestus ♂[1]	64.7	55.9	38.9
oenanthe ♂♂[1]	64.6, —, —	51.8, —, —	39.6, —, —
oenanthe ♀♀	63.5, —, —	51.6, —, —	40.8, 38.5, —
brunneus ♂♂	64.7 (60.1–68.1) 14	53.1 (49.2–55.6) 14	40.4 (37.8–42.5) 15
brunneus ♀♀	64.8 (60.1–68.1) 15	52.6 (49.2–55.6) 15	40.5 (37.8–42.5)

Callicebus	Biorbital breadth	Postorbital constriction	Braincase length	Braincase width
d. donacophilus ♂♂	32.5 (29.4–34.4) 9	26.7 (21.0–27.5) 9	49.0 (47.8–51.0) 10	31.8 (30.5–33.9) 9
d. donacophilus ♀♀	32.1 (31.2–33.3) 7	27.5 (26.8–28.9) 7	48.2 (46.5–50.1) 7	32.0 (30.8–33.3) 7
d. pallescens ♂♂	31.9 (30.3–34.4) 5	26.8 (25.0–29.2) 4	48.3 (46.8–50.1) 5	30.9 (29.6–32.0) 5
d. pallescens ♀	30.7	21.1	45.1	31.0
olallae ♂[1]	33.8	27.1	46.8	31.4
modestus ♂[1]	33.3	26.4	49.7	30.7
oenanthe ♂♂[1]	33.9, —, —	29.1, —, —	50.2, —, —	34.3, —, —
oenanthe ♀♀	34.2, 32.9, —	29.1, 29.8, —	49.0, 48.7, —	34.2, 32.8, —
brunneus ♂♂	35.6 (34.4–36.7) 14	30.2 (29.1–31.5) 14	51.8 (47.3-54.6) 14	34.8 (32.8–36.5) 14
brunneus ♀♀	33.8, 34.0, 35.9	29.7, 29.4, 33.8	51.7, 48.3, 49.0	34.6, 33.0, 33.8

TABLE 13. Continued.

Callicebus	Nasal length (medial)	Nasal width (greatest)	Interorbital width	I-M³
d. donacophilus ♂♂	8.3 (6.4–10.0) 5	5.1 (4.4–5.9) 5	5.3 (5.0–5.7) 7	21.0 (20.4–21.5) 10
d. donacophilus ♀♀	7.8 (6.5–9.2) 5	4.7 (4.1–5.3) 5	5.0 (4.2–5.8) 6	20.9 (20.1–21.9) 7
d. pallescens ♂♂	8.2 (7.4–8.8) 5	5.6 (4.6–7.4) 5	4.9 (4.3–5.4) 5	21.3 (20.3–22.2) 5
d. pallescens ♀	8.5	4.5	3.2	20.6
olallae ♂[1]	12.0	4.5	5.0	21.4
modestus ♂[1]	9.9	4.1	5.7	21.7
oenanthe ♂♂[1]	10.1, —, —	5.3, —, —	4.8,—,—	22.2, —, —
oenanthe ♀♀	—, 9.9, —	—, 4.7, —	—, 4.9, —	21.2, 21.8, —
brunneus ♂♂	8.5 (7.3–10.0) 10	5.1 (4.6–5.9) 11	6.4 (5.7–7.0) 10	22.0 (20.2–23.7) 14
brunneus ♀♀	8.2, 7.9, 10.8	4.8, 5.1, 5.6	6.3, 5.8, —	21.2, 19.7, 20.8

Callicebus	C-M³	PM²-M³	M¹-M³	I²-I²
d. donacophilus ♂♂	16.8 (15.9–17.6) 10	14.4 (13.6–15.2) 10	9.1 (8.6–10.0) 10	8.2 (7.7–9.4) 9
d. donacophilus ♀♀	16.9 (16.2–17.5) 7	14.3 (13.7–15.1) 7	9.0 (8.5–9.4) 7	8.3 (7.1–9.1) 7
d. pallescens ♂♂	17.1 (16.3–18.0) 5	14.9 (14.2–15.8) 5	9.3 (8.8–9.9) 5	8.1 (7.7–8.6) 5
d. pallescens ♀	16.3	13.8	8.8	8.0
olallae ♂[1]	17.6	14.2	13.3	8.8
modestus ♂[1]	17.8	14.7	9.1	8.2
oenanthe ♂♂[1]	18.0, —, —	14.6, —, —	9.2, —, —	9.6, —, —
oenanthe ♀♀	17.3, 17.2, —	14.5, 14.5, —	9.0, 9.2, —	8.9, 8.5, —
brunneus ♂♂	17.7 (16.3–18.9) 14	15.0 (13.6–16.8) 14	9.1 (8.7–9.8) 14	9.8 (8.9–10.8) 14
brunneus ♀♀	16.8, 15.8, 16.7	14.9, 13.7, 14.7	8.2, 8.8, 8.8	9.2, 8.2, 9.0

Callicebus	C¹-C¹	M¹-M¹	M³-M³	C height (from cingulum)
d. donacophilus ♂♂	12.7 (12.1–13.6) 9	18.4 (17.6–19.7) 8	17.6 (16.3–19.0) 9	3.5 (2.8–4.2) 10
d. donacophilus ♀♀	12.5 (11.7–13.4) 7	18.7 (17.6–20.1) 7	17.9 (17.2–18.8) 7	3.3 (2.7–4.1) 6
d. pallescens ♂♂	12.8 (12.2–13.8) 5	18.5 (17.7–19.4) 5	17.5 (16.4–18.6) 5	3.7 (3.2–4.1) 5
d. pallescens ♀	12.7	18.3	17.7	3.2
olallae ♂♂[1]	13.3	19.0	17.6	2.8
modestus ♂♂[1]	12.9	19.2	17.9	3.6
oenanthe ♂♂[1]	14.8, —, —	20.2, —, —	19.0, —, —	4.0, —, —
oenanthe ♀♀	18.5, 13.8, —	19.9, 19.7, —	18.6, 17.8, —	2.7, 3.0, —
brunneus ♂♂	14.1 (12.9–15.5) 14	20.0 (19.2–21.4) 14	19.0 (17.4–20.6) 14	3.2 (2.5–3.7) 13
brunneus ♀♀	13.6, 13.3, 13.0	19.8, 19.4, 19.5	18.2, 18.0, 19.4	2.5, 3.0, 2.5

TABLE 13. Continued.

Callicebus	Mandible length	Mandible height	Symphyseal angle
d. donacophilus ♂♂	37.3 (32.5–40.5) 9	30.0 (25.0–33.4) 9	44 (37–45) 7
d. donacophilus ♀♀	36.8 (34.8–38.6) 7	28.4 (24.2–31.5) 7	43 (34–51) 6
d. pallescens ♂♂	37.1 (35.6–39.0) 5	30.2 (28.0–32.2) 5	44 (40–50) 5
d. pallescens ♀	34.0	28.4	44
olallae ♂[1]	38.2	33.4	39
modestus ♂[1]	41.9	32.1	44
oenanthe ♂♂[1]	38.0, —, —	29.8, —, —	—
oenanthe ♀♀	38.5, 38.1, —	32.3, 27.7, —	44, 45, —
brunneus ♂♂	38.9 (34.1–41.2) 14	32.0 (30.0–35.7) 14	44 (37–54) 14
brunneus ♀♀	38.4, 37.7, 37.7	29.5, 31.6, 31.2	43, 51, 53

Callicebus	Head and body	Tail	Hind foot	Ear	Weight
hoffmannsi					
hoffmannsi ♂♂	322 (283–360) 14	453 (400–525) 14	94 (87–103) 12	33 (30–35) 4	—
hoffmannsi ♀♀	316 (271–351) 16	465 (420–513) 15	95 (86–104) 15	30, —, —	—
baptista ♂♂	337 (300–414) 5	458 (425–490) 5	96 (90–100) 5	—	—
baptista ♀♀	351 (330–385) 6	446 (415–495) 6	89 (86–96) 6	—	—
moloch ♂♂	333 (285–375) 19	466 (410–510) 18	93 (87–101) 17	34, 37	850, 1,000, 1,200
moloch ♀♀	331 (272–434) 22	448 (350–546) 21	91 (80-101) 22	29 (21–30) 4	877 (700–1,020) 6
dubius ♂	370	470	95	24	—
dubius ♀♀[1]	370, 400, —	390, 440, —	95, —, —	26, 30, —	—
cupreus					
ornatus ♂♂	336 (312–360) 10	428 (405–450) 10	93 (88–97) 9	35 (27–36) 8	1,178
ornatus ♀♀	328 (304–347) 6	414 (383–444) 6	92 (89–94) 4	30 (28–34) 5	1,163
discolor ♂♂	331 (300–351) 18	437 (392–470) 18	92 (84–102) 17	31 (27–45) 13	845, 950, 1,010
discolor ♀♀	319 (285–339) 18	430 (382–510) 19	90 (81–108) 20	30 (27–34) 18	1,075
cupreus ♂♂	321 (290–340) 12	440 (395–480) 22	95 (90–100) 19	30	1,106 (1,000–1,175) 4
cupreus ♀♀	337 (270–410) 9	439 (405–470) 27	92 (85–100) 23	34	—

TABLE 13. Continued.

Callicebus	Greatest skull length	Condylobasal length	Zygomatic breadth	
h. hoffmannsi ♂♂	64.0 (60.5–66.7) 14	52.7 (49.2–58.4) 15	40.7 (38.6–43.0) 13	
h. hoffmannsi ♀♀	63.3 (60.1–66.8) 15	51.7 (46.6–54.8) 15	40.1 (37.3–48.8) 15	
h. baptista ♂♂	63.1 (60.6–67.2) 6	51.4 (49.7–54.7) 6	38.6 (36.6–41.0) 6	
h. baptista ♀♀	62.7 (59.9–66.1) 9	51.6 (48.2–55.8) 9	40.3 (38.0–47.6) 8	
moloch ♂♂	64.1 (61.9–66.4) 24	51.8 (48.3–55.2) 24	40.1 (36.2–42.0) 24	
moloch ♀♀	63.3 (59.7–66.3) 32	51.1 (48.6–54.5) 31	39.3 (36.5–42.4) 31	
dubius ♂	68.8	52.5	41.9	
dubius ♀♀[1]	60.9, 65.1	47.7, 52.1	40.5, 37.4, 39.5	
c. ornatus ♂♂	63.2 (60.9–64.5) 13	51.0 (49.1–52.6) 12	41.2 (39.2–43.3) 11	
c. ornatus ♀♀	62.3 (60.5–63.7) 8	50.0 (47.7–51.9) 8	40.6 (37.9–42.3) 10	
c. discolor ♂♂	64.1 (60.1–68.8) 54	51.9 (46.9–58.5) 53	39.7 (35.4–42.7) 56	
c. discolor ♀♀	63.9 (59.9–67.5) 36	51.3 (48.2–58.3) 34	39.0 (35.4–49.8) 34	
c. cupreus ♂♂	65.5 (62.4–68.9) 36	52.8 (49.3–56.0) 35	40.5 (36.9–43.5) 35	
c. cupreus ♀♀	63.9 (60.0–66.8) 30	51.3 (47.3–55.3) 27	39.0 (36.0–42.0) 31	

Callicebus	Biorbital breadth	Postorbital constriction	Braincase length	Braincase width
h. hoffmannsi ♂♂	37.1 (35.5–39.4) 15	30.5 (28.4–32.0) 15	51.9 (49.2–55.6) 14	34.4 (32.9–35.6) 14
h. hoffmannsi ♀♀	36.7 (30.6–40.0) 15	30.2 (28.5–31.8) 15	51.3 (48.8–52.8) 15	33.6 (30.2–35.9) 15
h. baptista ♂♂	36.7 (33.7–39.0) 6	29.9 (27.6–30.9) 6	51.1 (47.6–54.3) 6	33.4 (30.0–34.7) 6
h. baptista ♀♀	36.7 (35.3–38.0) 9	29.9 (28.0–32.2) 9	50.3 (47.5–52.2) 9	34.0 (32.7–36.0) 9
moloch ♂♂	36.2 (34.7–38.2) 24	30.6 (28.1–34.4) 23	52.4 (50.1–54.8) 24	35.0 (32.9–37.0) 23
moloch ♀♀	35.6 (32.3–38.3) 32	30.1 (28.0–31.9) 32	52.0 (47.3–57.7) 32	34.3 (31.3–36.3) 30
dubius ♂	36.3	30.5	51.5	34.0
dubius ♀♀[1]	36.9, 34.0, 35.6	29.2, 29.0, 30.0	51.4, 50.3, 52.5	34.2, 33.7, 34.1
c. ornatus ♂♂	36.6 (35.3–38.2) 12	30.5 (29.1–31.5) 12	50.6 (47.7–52.3) 12	34.9 (32.8–35.7) 11
c. ornatus ♀♀	35.3 (30.5–37.2) 10	30.4 (28.3–31.6) 10	50.4 (49.1–52.0) 9	35.0 (33.7–36.3) 10
c. discolor ♂♂	35.6 (31.9–38.6) 56	30.1 (27.5–33.7) 55	51.5 (46.5–57.5) 54	34.8 (33.2–38.4) 54
c. discolor ♀♀	35.1 (30.2–39.8)37	29.8 (27.0–33.4) 37	51.0 (43.3–57.8) 36	34.4 (32.1–37.3) 35
c. cupreus ♂♂	36.0 (33.2–40.8) 36	30.7 (28.3–38.7) 36	52.7 (49.7–55.0) 36	34.8 (33.1–36.5) 35
c. cupreus ♀♀	35.4 (32.0–37.6) 31	30.6 (28.5–33.0) 31	51.0 (48.1–54.5) 30	34.6 (33.1–37.0) 30

TABLE 13. Continued.

Callicebus	Nasal length (medial)	Nasal width (greatest)	Interorbital width	I-M³
h. hoffmannsi ♂♂	8.3 (5.0–10.4) 13	6.4 (4.3–6.9) 13	5.7 (4.7–7.0) 13	21.9 (20.8–23.2) 14
h. hoffmannsi ♀♀	8.3 (4.3–11.3) 15	5.6 (5.0–7.3) 15	5.7 (4.5–7.1) 15	21.7 (20.4–23.0) 14
h. baptista ♂♂	7.4 (5.2–11.5) 6	6.5 (4.6–6.7) 6	6.6 (5.6–8.7) 6	21.9 (20.3–23.5) 6
h. baptista ♀♀	7.1 (5.8–9.5) 8	5.6 (4.6–6.4) 8	6.3 (5.3–7.2) 9	22.0 (21.2–23.0) 9
moloch ♂♂	8.4 (5.2–11.5) 18	5.4 (3.7–7.5) 18	6.5 (5.2–7.9) 22	21.5 (20.4–23.0) 24
moloch ♀♀	8.0 (5.5–11.0) 31	5.0 (3.9–6.4) 31	6.2 (5.3–7.3) 31	21.4 (19.8–22.7) 32
dubius ♂	10.3	5.4	6.8	22.0
dubius ♀♀[1]	10.4, —, —	5.2, —, —	6.5, —, —	21.8, 21.1, 21.4
c. ornatus ♂♂	9.8 (8.5–11.6) 9	5.1 (4.2–6.2) 9	6.1 (5.3–6.8) 9	21.5 (20.6–22.9) 13
c. ornatus ♀♀	9.5 (8.0–10.7) 7	4.6 (3.5–5.8) 7	5.8 (5.0–6.6) 9	21.2 (20.0–22.6) 10
c. discolor ♂♂	9.3 (5.5–13.0) 43	5.2 (3.8–6.9) 42	5.8 (3.8–7.2) 42	22.1 (20.2–25.0) 56
c. discolor ♀♀	8.9 (3.9–11.6) 28	4.8 (3.8–6.1) 28	5.5 (4.6–6.5) 27	22.2 (20.1–24.6) 37
c. cupreus ♂♂	9.6 (6.9–12.0) 27	5.0 (2.9–6.1) 30	6.0 (4.4–7.1) 30	22.4 (21.0–24.3) 33
c. cupreus ♀♀	9.6 (5.4–11.4) 22	5.4 (4.0–7.4) 23	5.8 (3.6–7.5) 23	22.0 (19.6–23.7) 31

Callicebus	C-M³	PM²-M³	M¹-M³	I²-I²
h. hoffmannsi ♂♂	17.4 (16.1–19.0) 15	14.7 (13.7–16.1) 15	9.2 (8.4–10.3) 15	9.3 (8.3–10.5) 15
h. hoffmannsi ♀♀	17.2 (15.9–18.5) 11	14.8 (13.9–15.5) 14	9.0 (8.1–9.6) 14	9.7 (8.7–13.4) 14
h. baptista ♂♂	17.4 (16.9–18.1) 6	14.6 (14.2–15.3) 6	9.0 (8.5–9.6) 6	9.4 (8.7–10.0) 6
h. baptista ♀♀	17.3 (16.4–18.0) 9	14.7 (14.0–15.4) 8	9.0 (8.5–9.7) 9	9.4 (8.6–10.2) 9
moloch ♂♂	17.5 (16.5–18.5) 24	15.0 (13.6–16.3) 24	9.2 (8.7–9.6) 24	10.0 (8.7–10.5) 24
moloch ♀♀	17.3 (16.0–18.9) 32	14.7 (13.4–15.9) 32	9.0 (7.3–9.8) 32	9.5 (8.3–11.1) 30
dubius ♂	17.5	14.4	9.0	9.3
dubius ♀♀[1]	16.5, 17.0, 17.2	14.9, 14.8, 14.6	9.5, 8.7, 9.1	10.2, 9.5, 9.5
c. ornatus ♂♂	17.4 (16.7–18.6) 13	14.5 (13.5–15.3) 13	9.0 (8.6–9.8) 13	8.9 (8.2–10.0) 12
c. ornatus ♀♀	17.4 (15.8–18.4) 10	14.6 (13.8–15.3) 10	9.1 (8.7–9.4) 10	9.0 (8.2–10.1) 10
c. discolor ♂♂	17.5 (15.6–19.2) 56	14.9 (13.5–16.8) 56	9.2 (8.4–10.3) 56	8.9 (7.2–9.9) 56
c. discolor ♀♀	17.6 (16.4–19.5) 37	15.2 (13.7–19.4) 37	9.2 (8.3–10.8) 37	9.0 (8.2–10.2) 37
c. cupreus ♂♂	17.9 (17.0–19.4) 35	15.3 (13.7–16.4) 35	9.4 (7.3–10.3) 35	9.4 (8.2–10.5) 35
c. cupreus ♀♀	17.5 (13.9–19.3) 30	15.2 (12.8–17.8) 29	9.3 (8.2–10.0) 33	9.5 (8.5–10.3) 33

TABLE 13. Continued.

Callicebus	C-C	M^1-M^1	M^3-M^3	C. height (from cingulum)
h. hoffmannsi ♂♂	13.8 (9.0–15.3) 15	20.2 (16.9–22.7) 15	19.0 (17.0–21.2) 15	3.1 (2.2–3.9) 13
h. hoffmannsi ♀♀	14.2 (8.5–20.2) 13	19.7 (18.5–21.4) 14	18.5 (17.3–20.3) 14	3.0 (2.4–3.4) 13
h. baptista ♂♂	13.8 (13.1–14.5) 5	20.0 (19.1–20.8) 6	19.4 (18.2–20.4) 6	3.2 (2.6–3.9) 6
h. baptista ♀♀	14.0 (12.8–15.0) 9	20.3 (18.9–21.4) 7	19.1 (18.0–20.3) 9	3.0 (2.6–3.4) 8
moloch ♂♂	14.2 (13.2–15.3) 24	20.3 (18.6–22.1) 24	19.4 (18.2–21.9) 24	3.1 (2.3–3.8) 22
moloch ♀♀	13.8 (12.9–14.6) 31	20.1 (18.7–21.4) 32	18.7 (17.9–20.8) 31	3.1 (2.4–3.7) 29
dubius ♂	14.3	20.3	19.0	3.0
dubius ♀♀[1]	14.1, 14.7, 14.6	21.0, 19.6, 21.1	20.3, 18.2, 20.1	–, 3.1, 3.5
c. ornatus ♂♂	14.1 (13.4–14.8) 11	20.0 (19.4–20.7) 12	19.1 (17.9–20.2) 12	3.5 (2.8–4.1) 11
c. ornatus ♀♀	13.9 (13.1–15.1) 10	19.6 (19.0–20.2) 10	18.8 (17.7–19.5) 10	3.5 (3.1–3.8) 7
c. discolor ♂♂	14.0 (11.6–17.8) 54	19.8 (17.7–21.4) 55	18.5 (13.2–20.3) 56	3.7 (2.3–4.2) 54
c. discolor ♀♀	14.0 (12.2–17.7) 36	19.7 (18.4–21.0) 37	18.4 (13.1–20.5) 37	3.1 (2.0–4.2) 34
c. cupreus ♂♂	14.0 (12.6–15.4) 34	20.1 (19.0–21.4) 35	19.5 (17.2–20.9) 32	3.8 (2.3–4.2) 35
c. cupreus ♀♀	13.7 (12.9–15.0) 31	20.0 (18.2–22.1) 31	19.3 (17.5–21.0) 31	3.2 (2.3–4.4) 29

Callicebus	Mandible length	Mandible height	Symphyseal angle
h. hoffmannsi ♂♂	39.2 (37.2–42.6) 15	32.7 (27.9–36.4) 15	41 (33–52) 13
h. hoffmannsi ♀♀	39.0 (35.0–41.5) 14	31.7 (28.6–35.7) 15	43 (36–47) 15
h. baptista ♂♂	38.3 (36.8–41.2) 6	29.7 (26.7–33.4) 6	45 (40–49) 6
h. baptista ♀♀	38.1 (36.5–41.2) 9	30.0 (28.0–32.3) 9	49 (46–54) 9
moloch ♂♂	38.6 (35.9–41.5) 24	31.1 (26.0–35.0) 24	44 (36–57) 18
moloch ♀♀	37.0 (36.1–40.7) 32	30.6 (26.9–35.0) 32	46 (34–60) 32
dubius ♂	39.3	33.3	41
dubius ♀♀[1]	37.9, 37.6, 38.2	29.7, 26.3, 29.1	49, 60, 52
c. ornatus ♂♂	38.1 (36.5–40.8) 12	31.2 (27.9–34.0) 13	42 (38–45) 13
c. ornatus ♀♀	37.2 (35.9–38.8) 10	29.9 (26.9–31.5) 8	44.9 (40–50) 10
c. discolor ♂♂	38.7 (34.7–42.0) 56	28.2 (25.0–36.7) 56	43 (32–57) 55
c. discolor ♀♀	38.0 (34.9–40.7) 36	30.4 (26.1–35.2) 37	44 (33–60) 36
c. cupreus ♂♂	39.6 (35.6–42.3) 35	32.0 (26.5–41.2) 35	46 (33–57) 31
c. cupreus ♀♀	38.3 (35.1–41.2) 31	30.1 (24.6–35.4) 31	45 (30–58) 29

TABLE 13. Continued.

Callicebus	Head and body	Tail	Hind foot	Ear	Weight
caligatus ♂♂	342 (310–410) 12	422 (380–476) 12	94 (90–100) 10	30 (28–31) 5	—
caligatus ♀♀	326 (300–390) 5	411 (385–460) 5	90 (85–95) 4	30	—
cinerascens ♂♂	330	480	90	34	—
cinerascens ♀♀	342 (320–380) 5	450 (390–480) 5	87 (80–90) 5	31 (30–34) 5	—
torquatus					
medemi ♂	331	478	100	29	1,100
medemi ♀♀	325 (232–360) 9	458 (425–493) 9	100 (94–105) 9	32 (30–33) 8	1,310 (1,151–1,462) 6
lugens ♂♂	336 (312–355) 29	448 (420–485) 30	97 (90–105) 30	30 (26–33) 9	—
lugens ♀♀	337 (300–400) 25	444 (410–490) 25	96 (85–101) 24	30 (28–34) 6	—
torquatus ♂♂	—, 348, 295, 345	430 (405–485) 4	94 (90–95) 4	—	—
torquatus ♀♀	—	456 (420–510) 5	96, 92, 98	—	—
lucifer ♂♂	376 (360–390) 4	474 (465–480) 4	95, 100	30, 32	1,500
lucifer ♀♀	349, 410	456, 450	100	29	—

Callicebus	Greatest skull length	Condylobasal length	Zygomatic breadth
caligatus ♂♂	65.1 (61.8–68.7) 12	52.1 (48.7–55.0) 12	39.7 (38.0–43.3) 12
caligatus ♀♀	63.9 (62.5–66.0) 8	51.2 (49.1–52.5) 8	39.5 (37.3–41.0) 8
cinerascens ♂♂	63.1, 65.7	52.1, 53.7, 53.7	39.9, 40.9, 43.6
cinerascens ♀♀	65.1 (62.1–67.8) 7	52.6 (49.7–54.1) 7	40.6 (38.0–43.1) 6
t. medemi ♂	69.1	56.1	40.7
t. medemi ♀♀	68.5 (65.5–70.5) 8	54.9 (53.6–56.8) 8	41.2 (39.7–42.6) 7
t. lugens ♂♂	68.4 (60.4–72.8) 41	56.5 (49.8–61.8) 39	43.3 (39.3–47.3) 40
t. lugens ♀♀	67.1 (61.8–71.5) 30	54.6 (49.8–57.6) 28	41.5 (36.4–44.4) 28
t. torquatus ♂♂	69.3 (67.1–70.5) 6	56.4 (52.5–58.7) 5	41.7 (38.5–44.0) 6
t. torquatus ♀♀	68.8 (66.0–71.5) 5	56.1 (53.5–60.0) 4	41.6 (39.6–44.9) 5
t. lucifer ♂♂	69.7 (65.8–74.3) 13	54.4 (53.5–60.7) 13	42.9 (39.0–46.8) 12
t. lucifer ♀♀	69.7 (67.8–73.2) 7	55.9 (55.0–57.7) 6	42.0 (39.5–43.3) 6

TABLE 13. Continued.

Callicebus	Biorbital breadth	Postorbital constriction	Braincase length	Braincase width
caligatus ♂♂	35.9 (34.0–38.2) 12	30.8 (27.7–32.9) 12	52.3 (49.9–54.9) 12	35.3 (33.6–37.2) 12
caligatus ♀♀	35.8 (34.7–37.2) 9	30.0 (28.0–32.1) 9	51.2 (49.8–52.7) 8	34.2 (32.1–35.0) 8
cinerascens ♂♂	36.7, 37.8, 37.3	30.6, 33.0, 31.7	—, 52.0, 55.2	34.4, 36.4, 37.7
cinerascens ♀♀	36.8 (34.5–38.4) 7	31.3 (29.7–32.3) 7	52.5 (50.5–54.7) 7	35.0 (33.7–36.6) 7
t. medemi ♂	38.5	32.3	54.6	36.0
t. medemi ♀♀	39.0 (38.2–40.6) 8	32.2 (31.0–34.4) 8	53.5 (51.6–55.3) 8	36.4 (35.0–39.1) 8
t. lugens ♂♂	39.2 (36.2–41.2) 38	32.0 (29.9–33.5) 40	53.3 (50.4–55.7) 41	36.8 (35.5–38.4) 40
t. lugens ♀♀	38.0 (34.5–40.7) 31	31.9 (30.4–32.9) 31	52.7 (48.0–56.7) 31	35.5 (31.5–37.8) 31
t. torquatus ♂♂	39.0 (36.7–40.8) 6	32.1 (30.7–33.5) 6	53.5 (50.2–56.3) 6	36.4 (35.0–37.3) 4
t. torquatus ♀♀	39.1 (37.8–41.5) 5	32.4 (30.8–33.4) 5	52.9 (51.1–55.6) 5	35.4 (33.8–37.2) 5
t. lucifer ♂♂	41.0 (36.5–44.6) 13	32.8 (29.9–35.9) 12	54.2 (51.4–57.6) 13	37.3 (35.1–39.2) 12
t. lucifer ♀♀	40.4 (39.0–41.5) 7	33.4 (30.8–35.0) 6	54.0 (52.4–55.4) 7	36.6 (34.7–39.4) 7

Callicebus	Nasal length (medial)	Nasal width (greatest)	Interorbital width	I-M³
caligatus ♂♂	9.8 (7.4–11.3) 11	4.5 (3.0–5.5) 12	6.2 (5.1–8.1) 12	23.2 (20.6–27.0) 13
caligatus ♀♀	9.8 (8.3–12.8) 7	5.5 (4.2–6.9) 8	5.8 (5.0–6.3) 8	21.6 (19.9–22.8) 9
cinerascens ♂♂	6.4, 6.4, 6.0	6.2, 6.7, 4.8	7.3, 6.8, 5.5	22.2, 22.3, 22.1
cinerascens ♀♀	7.4 (6.4–8.6) 7	4.9 (4.3–6.5) 7	6.6 (6.0–8.0) 7	22.2 (21.3–23.3) 7
t. medemi ♂	12.5	5.7	6.4	23.3
t. medemi ♀♀	12.0 (11.1–13.2) 8	5.6 (4.8–6.6) 7	6.4 (5.5–7.5) 8	23.4 (21.8–24.8) 8
t. lugens ♂♂	10.8 (9.1–12.7) 28	6.5 (4.8–8.9) 28	7.2 (5.8–8.9) 41	23.0 (21.9–24.9) 41
t. lugens ♀♀	10.2 (8.0–12.3) 20	6.1 (4.3–7.9)19	6.9 (4.6–8.4) 30	22.9 (21.2–24.5) 31
t. torquatus ♂♂	10.6 (10.3–11.0) 5	5.2 (4.7–5.7) 5	6.5 (6.1–6.9) 5	23.8 (22.5–25.3) 6
t. torquatus ♀♀	9.1, 10.9, 8.6	6.4, 4.8, 4.7	7.3, 5.8, 5.8	23.2 (22.2–24.4) 5
t. lucifer ♂♂	11.4 (7.2–12.8) 9	5.9 (4.7–7.7) 10	6.8 (5.4–7.6) 10	23.7 (21.9–24.5) 13
t. lucifer ♀♀	11.5 (9.3–14.4) 7	6.1 (5.4–7.0) 7	6.5 (5.4–7.4) 7	23.8 (22.9–24.7) 7

TABLE 13. Continued.

Callicebus	C-M³	PM²-M³	M¹-M³	I²-I²
caligatus ♂♂	18.2 (17.5–20.4) 13	15.4 (13.7–15.9) 13	9.4 (8.6–9.9) 13	9.8 (8.8–10.4) 13
caligatus ♀♀	17.5 (16.8–18.7) 9	14.8 (14.0–15.7) 9	9.2 (8.8–10.0) 9	9.3 (8.5–10.0) 9
cinerascens ♂♂	17.6, 17.6, 18.4	14.7, 15.1, 16.0	9.4, 8.8, 9.8	9.9, 9.5, 9.9
cinerascens ♀♀	17.9 (17.1–18.4) 7	15.4 (14.7–16.0) 7	9.6 (8.4–10.0) 7	10.1 (8.8–11.0) 6
t. medemi ♂	18.6	15.4	9.4	10.2
t. medemi ♀♀	18.8 (17.3–19.9) 8	15.7 (15.0–16.7) 8	9.5 (8.8–10.2) 8	10.6 (10.0–11.1) 7
t. lugens ♂♂	18.2 (17.1–19.6) 41	15.2 (14.1–16.3) 41	9.3 (8.6–10.3) 41	10.1 (9.1–11.1) 41
t. lugens ♀♀	18.3 (17.0–19.7) 31	15.2 (14.3–16.2) 31	9.2 (8.5–9.7) 31	9.8 (9.3–11.1) 31
t. torquatus ♂♂	19.0 (18.0–19.6) 6	15.6 (14.8–16.8) 6	9.5 (9.0–9.9) 6	10.4 (9.4–10.7) 6
t. torquatus ♀♀	18.4 (17.7–19.4) 5	15.5 (15.0–16.1) 5	9.5 (9.1–10.0) 5	10.5 (10.2–10.8) 5
t. lucifer ♂♂	19.3 (18.0–24.1) 13	16.0 (14.9–18.9) 13	9.6 (8.4–10.2) 13	10.5 (9.5–11.2) 13
t. lucifer ♀♀	19.0 (18.4–20.1) 7	15.9 (15.7–16.3) 7	9.5 (9.2–10.1) 7	10.2 (9.5–10.7) 7

Callicebus	C-C	M¹-M¹	M³-M³	C height (from cingulum)
caligatus ♂♂	14.4 (13.2–15.7) 13	20.7 (19.3–22.3) 13	19.3 (17.6–20.0) 13	3.3 (2.8–4.2) 13
caligatus ♀♀	14.3 (13.4–14.9) 8	19.9 (18.4–21.6) 9	19.3 (18.2–20.8) 9	2.9 (2.3–3.5) 9
cinerascens ♂♂	14.2, 14.1, 13.7	20.5, 19.8, 21.0	19.6, 19.5, 20.4	2.8, 4.1, 3.0
cinerascens ♀♀	14.4 (14.2–15.1) 5	20.7 (19.9–21.8) 7	20.2 (19.4–20.9) 7	2.9 (2.5–3.4) 5
t. medemi ♂	14.9	21.7	21.0	4.1
t. medemi ♀♀	15.5 (14.6–16.5) 7	21.9 (21.2–22.7) 8	21.1 (19.0–22.0) 8	3.7 (2.9–4.2) 5
t. lugens ♂♂	15.8 (13.4–17.2) 41	21.7 (20.0–23.2) 41	20.9 (19.0–22.6) 41	3.8 (3.1–4.7) 27
t. lugens ♀♀	15.5 (13.4–16.7) 30	21.5 (20.0–23.7) 31	20.5 (18.9–22.5) 31	3.6 (3.0–4.1) 21
t. torquatus ♂♂	15.8 (15.0–16.3) 6	21.9 (20.8–22.7) 6	21.8 (20.6–22.8) 6	3.7 (3.1–4.3) 6
t. torquatus ♀♀	15.7 (15.2–16.3) 5	22.2 (21.4–23.4) 5	21.4 (20.6–23.0) 5	3.6 (3.0–4.1) 4
t. lucifer ♂♂	16.2 (15.3–17.5) 12	22.5 (19.4–23.5) 13	22.0 (21.3–22.7) 12	3.7 (3.1–4.5) 11
t. lucifer ♀♀	15.7 (14.2–16.5) 7	22.2 (21.6–22.9) 7	21.4 (20.4–22.4) 7	3.6 (2.8–4.2) 4

TABLE 13. Continued.

Callicebus	Mandible length	Mandible height	Symphyseal angle
caligatus ♂♂	38.8 (36.6–41.4) 13	31.9 (28.2–36.2) 13	39 (30–49) 12
caligatus ♀♀	38.2 (35.7–39.3) 9	30.7 (27.2–35.2) 9	43 (37–48) 7
cinerascens ♂♂	39.4, 40.5, 40.3	32.9, 33.7, 32.6	—
cinerascens ♀♀	39.7 (37.0–41.8) 7	31.6 (28.8–35.8) 7	41, 46
t. medemi ♂	41.1	34.2	44
t. medemi ♀♀	42.0 (40.3–43.3) 8	33.2 (31.5–35.2) 8	42 (36–49) 8
t. lugens ♂♂	43.0 (36.7–47.7) 40	35.0 (29.5–40.2) 41	43 (34–52) 38
t. lugens ♀♀	42.3 (36.7–45.9) 29	34.0 (28.6–39.1) 30	42 (30–51) 29
t. torquatus ♂♂	42.6 (39.9–43.9) 6	35.9 (32.5–37.8) 6	34 (29–42) 5
t. torquatus ♀♀	41.7 (39.7–44.0) 5	34.0 (32.0–37.5) 5	38 (35–41) 5
t. lucifer ♂♂	43.8 (39.4–47.2) 13	34.9 (27.7–38.6) 13	41 (27–46) 12
t. lucifer ♀♀	42.6 (41.2–44.4) 7	34.0 (31.7–36.8) 7	43 (38–48) 7

Callicebus	Head and body	Tail	Hind foot	Ear	Weight
torquatus					
regulus ♂♂	440, 380	490, 480	—	—	—
regulus ♀♀	425 (370–450) 4	460 (440–490) 4	—	—	—
purinus ♂♂	430 (400–460) 5	438 (390–470) 5	—	—	—
purinus ♀♀	420, 368, 380	500, 430, 370	—	—	—
personatus					
melanochir ♂	—	—	—	—	—
melanochir ♀♀	330, 360, 370	395, 430, 510	97, 97, 108	30, 30, 34	1,370
nigrifrons ♂♂	300, 331, 395	470, 455, 480	118, 112, 108	—	—
nigrifrons ♀♀	345, 360	490, 500	105, 110	—	—
personatus ♂♂	380 (350–420) 5	508 (470–550) 5	111 (109–112) 4	33 (30–38) 4	1,270 (1,050–1,650) 5
personatus ♀♀	356 (310–400) 7	485 (418–560) 6	104 (95–113) 7	34 (30–39) 4	1,378 (970–1,600) 6
barbarabrownae ♂	—	—	—	—	—
barbarabrownae ♀♀[1]	360, 330, —	430, 395, —	97, 97, —	30, 30, —	—

TABLE 13. Continued.

Callicebus	Greatest skull length	Condylobasal length	Zygomatic breadth
t. regulus ♂♂	72.0, 67.5	56.1, 52.6	43.8, —,
t. regulus ♀♀	65.6, 71.9, 71.3	57.0 (51.6–59.2) 4	42.7 (40.0–44.2) 4
t. purinus ♂♂	70.7, —, 70.0, 73.4	56.7, —, 58.1, 61.6	41.2, —, —, 45.8
t. purinus ♀♀	71.1 (69.0–73.6) 5	57.8 (56.3–59.0) 5	43.2 (41.3–45.0) 4
p. melanochir ♂	66.3	—	—
p. melanochir ♀♀	65.7, 66.4, 71.1	53.7, 53.9, 56.8	38.0, 39.1, 43.7
p. nigrifrons ♂♂	67.8 (65.5–72.4) 7	55.6 (53.9–60.0) 7	42.4 (41.3–44.5) 6
p. nigrifrons ♀♀	69.9 (68.1–72.0) 4	56.9 (53.3–60.0) 5	44.4 (42.2–45.7) 4
p. personatus ♂♂	71.7 (70.3–78.3) 10	58.5 (54.8–63.8) 10	44.3 (40.4–48.8) 11
p. personatus ♀♀	68.9 (64.7–72.7) 10	55.1 (52.1–58.1) 10	42.4 (38.6–46.1) 10
p. barbarabrownae ♂	66.3	—	—
p. barbarabrownae ♀♀[1]	65.7, 64.4, 65.5	53.7, 53.9, 54.1	39.1, 38.0, 39.4

Callicebus	Biorbital breadth	Postorbital constriction	Braincase length	Braincase width
t. regulus ♂♂	42.2	34.7	53.3	38.2
t. regulus ♀♀	40.6 (37.4–41.8) 4	32.3 (31.3–33.8) 4	—, 52.4, 55.5, 55.6	—, 37.1, 38.7, 38.5
t. purinus ♂♂	40.2, —, —, 43.3	30.0, —, —, 31.7	55.5, —, 52.9, 56.8	39.4, —, 37.2, 36.7
t. purinus ♀♀	41.3 (40.6–42.6) 4	32.5 (32.1–33.0) 4	55.6 (52.0–58.3) 5	37.4 (37.0–38.0) 5
p. melanochir ♂	—	—	—	—
p. melanochir ♀♀	38.5 (36.2–41.1) 4	30.1, 31.0, 32.8	53.4 (52.0–55.3) 4	35.9 (33.8–38.5) 4
p. nigrifrons ♂♂	37.8 (36.1–39.7) 7	32.3 (29.6–35.0) 7	55.6 (51.7–59.2) 7	36.6 (35.0–38.4) 6
p. nigrifrons ♀♀	39.4 (36.8–40.3) 4	32.3 (30.1–34.6) 4	58.2 (56.8–60.0) 4	37.8 (36.1–40.0) 4
p. personatus ♂♂	40.5 (38.4–43.3) 11	32.6 (30.9–34.2) 11	57.2 (54.5–60.8) 11	36.4 (34.7–38.1) 11
p. personatus ♀♀	38.6 (36.0–41.2) 10	32.3 (29.0–38.0) 10	55.7 (52.6–58.7) 9	35.9 (30.5–37.7) 10
p. barbarabrownae ♂	—	—	—	—
p. barbarabrownae ♀♀[1]	36.3, 36.2, 37.6	30.1, 31.0, 29.2	52.0, 53.2, 51.0	33.8, 34.5, 33.3

TABLE 13. Continued.

Callicebus	Nasal length (medial)	Nasal width (greatest)	Interorbital width	I-M³
t. regulus ♂♂	—	—	—	25.2
t. regulus ♀♀	—, —, —, 10.2	—, —, —, 6.7	7.4, —, —, 6.8	24.1 (23.0–24.8) 4
t. purinus ♂♂	—, —, —, 10.5	—, —, —, 5.6	6.3, —, —, 6.8	23.7, —, —, 23.6
t. purinus ♀♀	—, 10.4, 10.6, 9.7	—, 7.3, 5.3, —	7.3 (6.2–8.4) 4	24.3 (23.8–25.3) 4
p. melanochir ♂	—	—	—	24.3
p. melanochir ♀♀	8.2	4.8	6.7, —, 6.4	23.2, 24.0, 24.4
p. nigrifrons ♂♂	9.3 (8.3–10.5) 7	7.1 (5.0–7.7) 7	6.7 (5.8–8.1) 7	23.7 (22.5–25.2) 7
p. nigrifrons ♀♀	9.2, 9.7, 10.6	6.0 (4.7–7.6) 4	6.7 (5.6–7.7) 4	23.8 (22.2–24.5) 4
p. personatus ♂♂	10.2 (9.2–12.7) 7	6.9 (5.2–9.8) 7	6.7 (6.0–7.3) 9	24.9 (23.4–27.6) 11
p. personatus ♀♀	11.1 (9.9–13.7) 9	6.3 (4.8–7.3) 9	6.1 (4.7–7.4) 9	23.5 (22.1–24.9) 10
p. barbarabrownae ♂	—	—	—	24.3
p. barbarabrownae ♀♀[1]	—	—	5.7, —, —	24.0, 23.2, 24.7

Callicebus	C-M³	PM²-M³	M¹-M³	I²-I²
t. regulus ♂♂	19.6	16.1	9.7	10.8
t. regulus ♀♀	19.0 (18.4–19.5) 4	15.9 (16.5–16.2) 4	9.5 (9.4–9.7) 4	10.5 (10.4–10.7) 4
t. purinus ♂♂	19.5, —, —, 18.8	16.2, —, —, 15.2	9.5, —, —, 9.4	—, —, —, 10.3
t. purinus ♀♀	19.1 (18.4–19.8) 4	16.3 (15.1–17.3) 4	9.8 (9.4–10.6) 4	10.6 (10.2–11.2) 4
p. melanochir ♂	20.3	16.9	10.5	9.8
p. melanochir ♀♀	19.8 (18.6–20.9) 4	17.0 (16.1–17.8) 4	10.4 (9.5–11.1) 4	10.2 (9.1–12.0) 4
p. nigrifrons ♂♂	19.3 (18.6–20.3) 7	17.0 (16.1–17.9) 7	10.2 (9.5–10.8) 7	10.1 (8.9–10.6) 7
p. nigrifrons ♀♀	19.9 (18.1–20.9) 4	17.7 (16.1–18.5) 4	10.6 (9.4–11.4) 4	10.3 (9.4–11.0) 4
p. personatus ♂♂	20.4 (19.3–21.2) 11	17.7 (16.9–18.6) 11	10.9 (10.3–11.6) 11	10.9 (10.0–11.9) 11
p. personatus ♀♀	19.2 (18.3–20.8) 10	16.8 (15.7–17.9) 9	10.3 (9.8–11.0) 9	10.2 (9.2–11.2) 9
p. barbarabrownae ♂	20.3	16.9	10.5	9.8
p. barbarabrownae ♀♀[1]	19.2, 18.6, 19.7	16.7, 16.1, 16.9	9.9, 9.5, 10.3	9.5, 9.1, 10.6

TABLE 13. Continued.

Callicebus	C-C	M^1-M^1	M^1-M^3	C height (from cingulum)
t. regulus ♂♂	—	21.9	19.6	3.5
t. regulus ♀♀	15.4 (14.1–16.2) 4	22.2 (21.7–22.8) 4	21.3 (20.3–22.1) 4	—, 3.4, 3.8, 3.8
t. purinus ♂♂	—, —, —, 15.9	21.9, —, —, 22.6	20.5, —, —, 22.9	4.6, —, —, 3.4
t. purinus ♀♀	15.6 (14.6–17.0) 4	22.3 (21.8–23.0) 4	22.3 (21.0–25.0) 4	4.6, 2.9, 3.6
p. melanochir ♂	14.1	20.6	20.4	3.4
p. melanochir ♀♀	14.0, 14.1, 15.4	22.2 (20.7–24.4) 4	21.2 (19.9–22.0) 4	3.0 (2.5–3.8) 4
p. nigrifrons ♂♂	14.1 (13.1–14.9) 6	21.8 (20.7–22.4) 7	21.0 (19.6–22.3) 7	2.8 (2.2–3.2) 5
p. nigrifrons ♀♀	14.6 (13.6–15.5) 4	22.1 (21.1–23.6) 4	22.1 (20.9–23.5) 4	2.6, 2.9, 3.5
p. personatus ♂♂	15.7 (14.8–17.9) 11	22.5 (20.7–23.6) 11	21.8 (20.2–23.1) 11	3.3 (2.6–4.0) 10
p. personatus ♀♀	14.8 (13.5–15.7) 9	22.8 (21.8–24.5) 10	21.4 (20.6–22.7) 9	3.3 (2.8–3.9) 7
p. barbarabrownae ♂	14.1	20.6	20.4	3.4
p. barbarabrownae ♀♀[1]	14.1, 14.0, 14.5	21.5, 20.7, 21.5	20.9, 19.9, 20.3	2.9, 2.5, —

Callicebus	Mandible length	Mandible height	Symphyseal angle
t. regulus ♂♂	46.5	38.5	35
t. regulus ♀♀	43.0 (39.2–44.7) 4	34.9 (31.6–36.5) 4	41 (33–50) 4
t. purinus ♂♂	44.3, —, —, 46.7	34.0, —, —, 37.5	44, —, —, 41
t. purinus ♀♀	44.1 (43.2–45.7) 4	35.7 (34.0–36.8) 4	42 (29–50) 4
p. melanochir ♂	41.4	30.5	46
p. melanochir ♀♀	42.2, 41.0 42.9	31.1 (29.0–34.8) 4	48 (44–50) 4
p. nigrifrons ♂♂	41.2 (39.4–42.6) 7	33.0 (30.0–37.0) 7	52 (46–66)7
p. nigrifrons ♀♀	43.0 (40.9–44.4) 4	32.9 (28.5–35.6) 4	50 (35–55) 4
p. personatus ♂♂	44.9 (42.0–49.2) 11	35.8 (33.1–41.3) 11	49 (38–65) 11
p. personatus ♀♀	42.3 (39.9–44.8) 10	32.4 (28.0–37.6) 10	48 (41–57) 10
p. barbarabrownae ♂	41.4	30.5	46
p. barbarabrownae ♀♀[1]	41.0, 42.2, 41.1	30.3, 30.2, 30.3	50, 44, 38

[1] First or only measurements are of type.
[2] External measurements from dry skin.

XXIII. Gazetteer

The alphabetic list includes all collecting localities mentioned in the species and subspecies accounts. The numbers in parentheses correspond to the numbered localities in Figure 2. Closely clustered localities take the same number. This list is followed by a cross index for identification of localities plotted in Figures 23, 27, 29, 36, 38, 44.

Acre (Río), right bank; Pando, Bolivia (74).
Acurizal (Fazenda); Mato Grosso do Sul, Brazil (210a).
Agua Clara (Caño), Río Ocoa; Meta, Colombia (4).
Aguarico (Río); Napo, Equador (48).
Aiapuá, Lago; Amazonas, Brazil (152a).
Aiapuá, Rio Purús, opposite; Amazonas, Brazil (152b).
Alcobaça; Bahia, Brazil (219).
Alegria (Rio); Amazonas, Brazil (129).
Altamira; Pando, Bolivia (75).
Altamira, Río Manu; Madre de Dios, Peru (43).
alto = upper part of a river.
Amacayacu (Rio); Amazonas, Brazil (25d).
Amazonas (Rio), lower; from Rio Negro to mouth, Amazonas—Pará, Brazil.
Amazônia (Parque Nacional da); Pará, Brazil (174).
Amorim (Igarapé); Pará, Brazil (170).
Ampiyacu; Loreto, Peru (56).
Andoas; Loreto, Peru (49).
Andoas; Pastaza, Ecuador (31).
Antabari (Río); Bolívar, Venezuela (100a).
Antavari (Río); Bolívar, Venezuela (100a).
Apaporis (Río); Vaupés, Colombia (24).
Apayacu; Loreto, Peru (56).
Araçá; Amazonas, Brazil (128b).
Aracruz; Espírito Santo, Brazil (247).
Araguaia (Rio); Pará, Brazil (191b).
Aramanai; Pará, Brazil (176).
Aramanay, see Aramanai; Pará, Brazil (176).
Arapium, see Arapiuns; Pará, Brazil (169).
Arapiuns; Pará, Brazil (169).
Arara (Fazenda), Rio Mucurí; Bahia, Brazil (220).
Arara (Lago); Amazonas, Brazil (137).
Arara (Lagoa); Bahia, Brazil (220).
Arara (Morro); Bahia, Brazil (220).
Arara, Rio Tapajós; Pará, Brazil (172).
Araracuara, Río Caquetá; Amazonas, Colombia (25a).
Ariari (Río), Boca; Vaupés, Colombia (9b).
Arinos (Rio); Mato Grosso, Brazil (206).
Aripuanã, Rio Roosevelt; Mato Grosso, Brazil (205).
Arraios (Rio); Mato Grosso, Brazil (209).
arriba = above; up.
Aruã, Rio Arapiuns, Pará, Brazil (171).
Aruma, Rio Purús; Amazonas, Brazil (153).
Arumatéua, Rio Tocantins; Pará, Brazil (190b).
Arumathéua (see Arumatéua); Pará, Brazil (190).
Atalaiha do Norte; Amazonas, Brazil (140).
Aveiro, see Aveiros; Pará, Brazil (177).
Aveiros, Rio Tapajós; Pará, Brazil (177).
Ayapuá (Lago do), Rio Purús; Amazonas, Brazil (152).
Baião, (see Pedral); Pará, Brazil.
baixo = low; lower part of a river.
Balta; Ucayali, Peru (73b).
Bañados de Izozog, Santa Cruz, Bolivia, 19°30′S, 62°30′W (unnumbered).
Bananeira (Cachoeira do), Rio Guaporé; Rondônia, Brazil (199a).
Bandeira do Melo; Bahia, Brazil (213).
Baptista (Lago do); Amazonas, Brazil (163).
Barbada (Fazenda); Espírito Santo, Brazil (241).
Barbascal (Hacienda); Meta, Colombia (6).
Barreirinho; Amazonas, Brazil (130b).
Barreiro; São Paulo, Brazil (265).
Barreiros, see Barreiro; São Paulo, Brazil (265).
Barretos, Rio Grande; São Paulo, Brazil (256).
Barrigón (Puerto); Meta, Colombia (5).
Belén, Río Cunucunumá; Amazonas, Venezuela (107).
Bella Esperanza, Cercado; Santa Cruz, Bolivia (not located).
O. J. Silva, June 1948.
Belmonte (Rio); Bahia, Brazil (217).
Belo Horizonte; Minas Gerais, Brazil (226).
Belterra, Santarém; Pará, Brazil (176).
Blanco; Pando, Bolivia (75).
Boa Vista; Roraima, Brazil (121).
Bobonaza (Río); Pastaza, Ecuador (31).
boca = mouth of river (see name of).
Bogotá; Cundinamarca, Colombia (1).
Bom Jardim; Pará, Brazil (180b).
Borba; Amazonas, Brazil (160).
bosque = forest.
Braço do Sul (Fazenda); Espírito Santo, Brazil (241).
Branco (Rio); Acre, Brazil (194).
Brasília Legal; Pará, Brazil (172).
Bravo (Igarapé), Rio Tapajós; Pará, Brazil (170).
brazo = river arm or inlet.
Buena Vista, see Buenavista; Santa Cruz, Bolivia (89).

Buenavista; Santa Cruz, Bolivia (89).
Buenópolis; Minas Gerais, Brazil (224).
Buenos Aires, Lago del Dorado; Guaviare, Colombia (21b).
Bushimkin, Río Cenepa; Amazonas, Peru (32a).
Cachimbo; Pará, Brazil (188b).
cachoeira = river rapids.
Cachoeira do Quartel, São Miguel, Rio Negro; Amazonas, Brazil (126b).
Cachoeira Nazaré; Rondônia, Brazil (202).
Cacuri; Amazonas, Venezuela (103).
Cacuri (Campo); Amazonas, Venezuela (103).
Caguán (Río); Caquetá, Colombia (17).
Callicebus (Estación Biológica); Loreto, Peru (52).
Camiaco; Beni, Bolivia (82).
camino = road; trail.
Campinha (Field Station); São Paulo, Brazil.
Canabuoca (Lago do); Amazonas, Brazil (150).
Canami (Caño); Amazonas, Venezuela (109).
Canaracuni; Bolívar, Venezuela (102).
Candamo; Puno, Peru (46).
caño = natural canal or river channel.
Caño Grande; Guaviare, Colombia (20).
Cantareira; São Paulo, Brazil (266).
Capibara; Amazonas, Venezuela (115).
Carajas, Serra; Pará, Brazil (191a).
Casa Nova; Pará, Brazil (169).
Cashiboya, Río Ucayali; Loreto, Peru (67).
Casiquiare (Río or Caño); Amazonas, Venezuela (117).
Castanhos (Foz de); Amazonas, Brazil (162b).
Caxiricatuba, Rio Tapajós; Pará, Brazil (176).
Cenepa (Río); Amazonas, Peru (32a).
Centro Branda; Pando, Bolivia (76).
Cercado-Cupesi (Camino); Santa Cruz, Bolivia (not located).
O. J. Silva, April 1938.
Cercado Province ca. 17°30′S, 66°30′W.
cerro = hill or mount.
Cerro Azul; Loreto, Peru (66).
Chaparé (Río); Cochabamba, Bolivia (84).
Chiquitos (see San José de Chiquitos); Santa Cruz, Bolivia (92).
Ciudad Constitución; Pasco, Peru (not located).
Clara; Santa Cruz, Bolivia (90).
Cobra, Lago de, Rio Mucajaí.
Not located; see Mucajaí (Rio) (121).
cocha = lake; pond.
Cocha Cashu (Estación Biológica); Madre de Dios, Peru (42).
Coca (Río); Napo, Ecuador (27).
Codajás; Amazonas, Brazil (136).
Codajáz, see Codajás; Amazonas, Brazil (136).
Colatina; Espírito Santo, Brazil (244).
Conceição da Barra; Espírito Santo, Brazil (238).
Concepción; Concepción, Paraguay (98).
Condamo, see Candamo; Puno, Peru (46).
Contas (Rio); Bahia, Brazil (214).
Copataza (Río); Pastaza, Ecuador (29b).
Correga da Barbada (Fazenda); Espírito Santo, Brazil (241).
Coronel Fabriciano; Minas Gerais, Brazil (231).
Corumbá; Mato Grosso do Sul, Brazil (210b).
Cuçari; Pará, Brazil (184).
Cucuí; Amazonas, Brazil (122).
Cucuhy, (see Cucuí); Amazonas, Brazil (122).
Cudamaco (Isla); Amazonas, Venezuela (112).
Cumaría; Ucayali, Peru (70).
Cumeria, see Cumaría; Ucayali, Peru (70).
Cunucunumá (Río); Amazonas, Venezuela (111).
Curanja, (Río); Ucayali, Peru (73b).
Curaray (Río, boca); Loreto, Peru (50).
Curicuriari (Monte); Amazonas, Brazil (127).
Curuá (Rio); Pará, Brazil (175).
Curua-tinga (Rio); Pará, Brazil (175).
Cururú (Rio), Rio Tapajós; Pará, Brazil (182).
Cussary, see Cuçari; Pará, Brazil (184).
Cuyabeno, Reserva de Producçión Faunistica; Napo, Ecuador (26c).
Defensores del Chaco (Parque Nacional); Chaco, Paraguay (94).
Deslinde; Pando, Bolivia (75).
Dez de Agosto (Fazenda); Espírito Santo, Brazil (241).
Doce (Rio); Espírito Santo, Brazil (246).
Duida (Cerro or Mount); Amazonas, Venezuela (110).
Ega, see Tefé; Amazonas, Brazil (148).
Eirunepé, see João Pessoã; Amazonas, Brazil (144).
El Consuelo, Río Beni; Beni, Bolivia (79).
El Encanto; Amazonas, Colombia (25c).
El Hacha (Quebrada); Putumayo, Colombia (13).
El Merey, Río Casiquiare; Amazonas, Venezuela (111).
El Pepino; Putumayo, Colombia (11b).
El Tapón; Vichada, Colombia.
El Tuparro (Parque Nacional); Vichada, Colombia (22).
El Valle, Arcado; Santa Cruz, Bolivia (90).
Encanto, see San José del Encanto; Amazonas, Brazil (25b).
Engenheiro Reeve, see Rive; Espírito Santo, Brazil (250).
Esmeralda; Amazonas, Venezuela (112).
Espejo (Laguna de); Guaviare, Colombia (21a).
Esperanza (Quebrada); Loreto, Peru (61).
Espírito Santo (Rio); Espírito Santo, Brazil (249).
Estirão do Equador; Amazonas, Brazil (140).

Labrea, Rio Purús; Amazonas, Brazil (157).
La Esmeralda, see Esmeralda; Amazonas, Venezuela (112).
Lagarto, Río Ucayali; Ucayali, Peru (71).
Lagartococha (Río), Río Aguarico; Loreto, Peru (47).
lago = lake.
lagoa = lake; lagoon.
Lagoa Santa; Minas Gerais, Brazil (225).
laguna = lake; lagoon.
La Laguna; Beni, Bolivia (78).
La Laja, Río Orinoco; Amazonas, Venezuela (111).
La Macarena (Finca); Meta, Colombia (7).
La Macarena, Serranía; Meta Colombia (9a).
Lamarão; Bahia, Brazil (212).
La María; Guaviare, Colombia (19).
La Pica; Beni, Bolivia (83).
Leticia; Amazonas, Colombia (25d).
Liguino (or Liguiño) (Río); Pastaza, Ecuador (not located).
Limera; Pando, Bolivia (75).
Linhares; Espírito Santo, Brazil (258).
Lins, Rio Tietê; São Paulo, Brazil (258).
Los Micos, La Macarena; Meta, Colombia (7).
Luzilandia Xinguara; Pará, Brazil (191c).
Macarena (Sierra de la); Meta, Colombia (9a).
Macarena (Finca); Meta, Colombia (7).
Macas; Morona-Santiago, Ecuador (28).
Macieira, Serra do Itatiaia; Minas Gerais Rio de Janeiro, Brazil (235).
Madeira (Rio), see Borba; Amazonas, Brazil (160).
Maica (Caño); Amazonas, Venezuela (104).
Maica, Santarém; Pará, Brazil (186).
Maica (Ilha); Pará, Brazil (186).
Mainas; Loreto, Peru (58).
Maipures; Vichada, Colombia (22).
Mamoriá-Mirim (Rio), see Mamoriázinho, (Rio); Amazonas, Brazil (158).
Mamoriázinho (Rio); Amazonas, Brazil (158).
Manacapurú, Rio Solimões; Amazonas, Brazil (138).
Manaquiri, Rio Solimões; Amazonas, Brazil (149).
Manaus; Amazonas Brazil (139).
Mantiqueira (Serra da); São Paulo, Brazil (262).
Manuel Urbano; Acre, Brazil (192a).
Mapixi (Lago do); Amazonas, Brazil (156).
Marabitanas; Amazonas, Brazil (123).
Maracá-Roraima (Estacão Biológica); Roraima, Brazil (120).
Marañón (Río); Amazonas, Peru (33).
María Espuma (salto); Bolívar, Venezuela (101).
Maripa; Bolívar, Venezuela (100a).
Marucá (Fazenda); Pará, Brazil (175).
Masicamiacu (see Camiaco); Beni, Bolivia (82).
mata = bush; brush; woods; thicket; forest.
Mato Dentro; São Paulo, Brazil (262).
Mattodentro, see Mato Dentro; São Paulo, Brazil (262).
Maturacá (Rio), see Hua, (Salto de); Amazonas, Brazil (124).
Mavaca (Río); Amazonas, Venezuela (116).
Maynas, see Mainas; Loreto, Peru (58).
Mecaya (Río); Caquetá, Colombia (120).
Medina; Cudinamarca, Colombia (2).
Miri-Paraná (Río); Amazonas, Colombia (25b).
Mishana, Río Nanay; Loreto, Peru (52).
Montalvo, Río Bobonaza; Pastaza, Ecuador (30).
monte = bush; brush; woods; thicket; forest (South American Spanish).
Monte Alegre, see Monte Alegre do Sul; São Paulo, Brazil (261).
Monte Alegre do Sul; São Paulo, Brazil (261).
Monte Cristo, Rio Tapajós; Pará, Brazil (179a).
Monte Pascoal (Parque Nacional do); Bahia, Brazil (218).
Moquecerca, Río Amayacu; Amazonas, Colombia.
Morro d'Arara, see Arara (Fazenda); Bahia, Brazil (220).
Mojos; El Beni, Bolivia (80).
Moxos, see Mojos; El Beni, Bolivia (80).
Moyobamba; San Martín, Peru (36).
Mucajaí (Rio); Roraima, Brazil (121).
Mucden; Pando, Bolivia (75).
Mucha Vista; Loreto, Peru (not located).
Mukden, see Mucden; Pando, Bolivia (75).
Mucurí (Rio); Bahia, Brazil (220).
Mucurici; Espírito Santo, Brazil (237).
Nanay (Río), see Mishana; Loreto, Peru (52).
Napo (Río), see Puerto Napo (26a).
Naranjal; Pando, Bolivia (75).
Nareuda (Río); Pando, Bolivia (75).
Neblina (Pico da) (Parque Nacional do); Amazonas, Brazil (126).
Negro (Rio), Mouth at Manaus; Amazonas, Brazil (139).
Nova Brasília; Rondônia, Brazil (201b).
Nova Colina; Rio Jiparaná; Rondônia, Brazil (201a).
Nova Friburgo; Rio de Janeiro, Brazil (253b).
Nova Lombardia (Reserva Biológica); Espírito Santo, Brazil (244).
Nueva Asunción, 19 km by road, WSW km 588; Nueva Asunción, Paraguay (95).
Oberlandia, see Uberlandia; Minas Gerais, Brazil (223).
Ocama (Río); Amazonas, Venezuela (114).
Ocoa (Río); Meta, Colombia (4).

Oito (Mata do), Tefé; Amazonas, Brazil (148).
Olivença, Rio Solimões, see São Paulo de Olivença; Amazonas, Brazil (141).
Onças (Rio); "Minas Geraes" (Rio de Janeiro), Brazil (253a).
Orosa; Loreto, Peru (60).
Otoho (Ribeirão do); Rondônia, Brazil (204).
Otôvo, see Otoho (Ribeirão do); Rondônia, Brazil (204).
Pacaas Novos (Parque Nacional do); Rondônia, Brazil (199b).
Pacaya-Samiria (Reserva Nacional); Loreto, Peru (64).
Pachitea (Río), Río Ucayali; Huánuco, Peru (37).
Pagaat, Río Cenepa; Amazonas, Peru (32a).
Paissandú, see Bom Jardim; Pará, Brazil (180b).
Panguana; Huánuco, Peru (39).
paraná = arm of river separated from mainstream by a large island.
Paraná (Rio) (see Rio Grande); São Paulo, Brazil (255).
Pardo (Rio); Bahia, Brazil (216).
Paricatuba; Amazonas, Brazil (151).
Parintins, Rio Amazonas; Amazonas, Brazil (164).
Parintins (Serra dos); Amazonas, Brazil (166).
parque = park.
Passos; Minas Gerais, Brazil (233).
Pastaza (upper Río), see Copataza (Río); Pastaza, Ecuador (29).
Patinga, Rio Tapajós; Pará, Brazil (170a).
Patos; Minas Gerais, Brazil (222).
Patrimonio (Mata), Tefé; Amazonas, Brazil (148).
Pauini, Rio Purus; Amazonas, Brazil (159).
Pavas, Río Amazonas; Loreto, Peru (not located, "left bank Amazon," *Callicebus cupreus cupreus*).
Payamino; Napo, Ecuador (27).
Payamino (Río); Napo, Ecuador (26).
Pebas, Río Amazonas; Loreto, Peru (56).
Pedral, Rio Tocantins; Pará, Brazil (189b).
Peneya (Río); Caquetá, Colombia (17).
Pepino, see El Pepino, Putumayo, Colombia (11b).
Pindo (Río); Pastaza, Ecuador (29a).
Piquete; São Paulo, Brazil (263).
Piquiatuba, Rio Tapajós; Pará, Brazil (136).
Pontal dos Ilhéus; Bahia, Brazil (214).
porto = port.
Porto do Passagem, Rio Pimenta-Bueno; Rondônia, Brazil (201c).
Porto Velho; Rondônia, Brazil (198).
Prainha, Rio Aripuanã; Amazonas, Brazil (162a).
puerto = port.
Puerto Asis, see El Pepino; Putumayo, Colombia (11b).
Puerto Casado; Alto Paraguay, Paraguay (96).
Puerto Indiana; Loreto, Peru (55).
Puerto Iñirida; Guainía; Colombia (23).
Puerto Leguía; Pasco, Peru (40).
Puerto Leguízamo; Putumayo, Colombia (14).
Puerto Mogue, left bank Rio Amacayacu; Amazonas, Colombia (25d).
Puerto Moquecerca; Amazonas, Colombia (25d).
Puerto Napo; Napo, Ecuador (26a).
Puerto Pinasco; Presidente Hayes, Paraguay (97).
Puerto Rastrojo; Amazonas, Colombia (25b).
Puerto Victoria; Pasco, Peru (40).
Puruname (Río); Amazonas, Venezuela (113).
Putumayo (Río), see Puerto Leguízamo; Putumayo, Colombia (14).
Rastrojo, Puerto, see Puerto Rastrojo; Amazonas, Colombia (25b).
Redempção, see Redenção; Amazonas, Brazil (154).
Redenção, Rio Purús; Amazonas, Brazil (154).
Restrepo; Meta, Colombia (3).
rio = river (Portuguese).
río = river (Spanish).
Rio Acre-Sena Madureira (Estacão Biológica); Acre, Brazil (193).
Rio Branco; Acre, Brazil (194).
Rio Candeias (Fazenda), Porto Velho; Rondônia, Brazil (198).
Rio das Velhas; Minas Gerais, Brazil (225).
Rio de Janeiro; Rio de Janeiro, Brazil (254).
"Rio de Janeiro" (= Río Yavarí); Loreto, Peru. Misrendering of "Río Yavarí" by Rode (1938, p. 35) in recording *Callicebus cupreus*.
Rio Doce (Parque Florestal); Minas Gerais, Brazil (230).
Rio Grande, see Barretos, Rio Grande; São Paulo, Brazil (256).
Rio Onças; Rio de Janeiro, Brazil (253a).
Rio São Matheus; Espirito Santo, Brazil (238).
Rive, see Engenheiro Reeve; Espírito Santo (250).
Rumiyaco (Río): Putumayo, Colombia (11b).
salto = falls; rapids.
San Antonio; Cochabamba, Bolivia (86).
San Antonio (Misión); Cochabamba, Bolivia (85).
San Antonio del Chimoré; Cochabamba, Bolivia (85).
San Antonio, see San Antonio de Lora; Beni, Bolivia (81).
San Antonio de Estrecho, Rio Putumayo; Putumayo, Colombia (11a).
San Antonio de Lora; Beni, Bolivia (81).
San Carlos; Amazonas, Venezuela (118).
San Fernando, Río Yavarí; Loreto, Peru (62).

San Fernando de Atabapo; Amazonas, Venezuela (105).
San Francisco; Napo, Ecuador (26b).
San José del Encanto, see El Encanto; Amazonas, Colombia (25c).
San Juan de Arama; Meta, Colombia (7).
San Martín; Meta, Colombia (6).
San Salvador; Presidente Hayes, Paraguay (97).
Santa Bárbara; Rondônia, Brazil (197b).
Santa Bárbara, Río Orinoco; Amazonas, Venezuela (106).
Santa Cecilia; Loreto, Peru (59).
Santa Cruz, Rio Eirú; Amazonas, Brazil (147).
Santa Cruz, Río Huallaga; Loreto, Peru (63).
Santa Cruz de la Sierra; Santa Cruz, Bolivia (90).
Santa Fé de Bogotá (see Bogotá); Cundinamarca, Colombia (1).
Santa Júlia; Amazonas, Brazil (167b).
Santa Lucía, (Río Nanay), lapsus for Santa Luisa (q.v.); Loreto, Peru (51).
Santa Luisa, Río Nanay; Loreto, Peru (51).
Santa Luzia; Espírito Santo, Brazil (244).
Santarém, Rio Tapajós; Pará, Brazil (175).
Santarém-Cuiabá-Itaituba, BR 163: Pará, Brazil (179a).
Santa Rita, Rio Solimões; Amazonas, Brazil (133).
Santa Rosa; Madre de Dios, Peru (not located).
Santa Rosa; Pará, Brazil (169).
Santa Rosa; Putumayo, Colombia. Not located; see El Pepino (11b).
Santa Rosa, Ilha Urucurituba, Rio Tapajós; Pará, Brazil (169).
Santa Teresa; Espírito Santo, Brazil (248).
Santiago (Río); Amazonas, Peru (32).
Santo Antonio, Rio Eirú; Amazonas, Brazil (144).
Santo Antonio, Rio Tocantins; Pará, Brazil (190a).
São Domingos; Espírito Santo, Brazil (241).
São Gabriel, Rio Negro; Amazonas, Brazil (126b).
São Miguel, Rio Negro, see Cachoeira de Quartel, Amazonas, Brazil (126b).
São João, Aripuanã; Mato Grosso, Brazil (205).
São João, Rio Araguaya; Pará, Brazil (191a).
São João, Rio Jiparaná; Rondônia, Brazil (200).
São João Batista da Glória; Minas Gerais, Brazil (232).
São João da Glória, see São João Batista da Glória; Minas Gerais, Brazil (232).
São José (Fazenda); Espírito Santo, Brazil (241).
São José (Fazenda); Mato Grosso, Brazil (208a).
São Luiz de Mamoria, see Iquirí; Acre, Brazil (195).
São Mateus; Espírito Santo, Brazil (239).
São Mateus (Rio); Espírito Santo, Brazil (238).
São Matheus, see São Mateus; Espírito Santo, Brazil (239).
São Paulo de Olivença; Amazonas, Brazil (141).
Sara (Provincia), see Gutiérrez; Santa Cruz, Bolivia (88).
Sarayacu, Río Ucayali; Ucayali, Peru (68).
Saravita (Finca); Meta, Colombia (7).
Saúde (camp); Pará, Brazil (190a).
Seco (Río); San Martín, Peru (35).
Sena Madureira; Acre, Brazil (192b).
serra = mountain range.
serranía = mountain range.
Shimpunts, Río Cenepa; Amazonas, Peru (32a).
sierra = mountain range.
Socay (Bosque); Meta, Colombia (6).
Socorro; São Paulo, Brazil (261).
Solano, Rio Casiquiare; Amazonas, Venezuela (118).
Sooretama (Reserva Biológica); Espírito Santo, Brazil (240).
Suaçuí (Rio); Minas Gerais, Brazil (229).
Sumaúma (Rio); Pará, Brazil (167a).
Suno (Río), mouth; Napo, Ecuador (27).
Surutú (Río); Santa Cruz, Bolivia (89).
Sussuí (Rio), see Suaçuí, Rio; Minas Gerais, Brazil (229).
Tabatinga, Rio Solimões; Amazonas, Brazil (134).
Tahuamanu (Río); Madre de Dios, Peru (45).
Tahuamanu (Río); Pando, Bolivia (74).
Tahuapunta; Amazonas, Brazil (125).
Tamacury, see Tamaruri; Pará, Brazil (185).
Tamaruri; Pará, Brazil (185).
Tamatama; Amazonas, Venezuela (111).
Tapaiuna (Lago do); Amazonas, Brazil (163).
Tapaiuna, Rio Tapajós; Pará, Brazil (176).
Tapajós (Vila de), see Santarém; Pará, Brazil (175).
Tapera (Fazenda), Juíz de Fora; Minas Gerais, Brazil (234).
Taperinha, Rio Curuá; Pará, Brazil (188a).
Taperinho, Rio Amazonas; Pará, Brazil (186).
Tapiche (Río); Loreto, Peru (65).
Tapirinha, see Taperinho, Rio Amazonas; Pará, Brazil (188a).
Taracua, see Taraquá; Amazonas, Brazil (126a).
Taraquá, Rio Uapes; Amazonas, Brazil (126a).
Tauari, Rio Tapajós; Pará, Brazil (176).
Tauarià Grande (Lago do); Amazonas, Brazil (156).
Tauary, see Tauari; Pará, Brazil (176).
Tavio (Igarapé do), (Rio Tapajós); Pará, Brazil (177).
Tefé (Lago do); Amazonas, Brazil (148).
Tefé, Rio Tefé, Rio Solimões; Amazonas, Brazil (148).
Teffé, see Tefé; Amazonas, Brazil (148).
Teles Pires (Rio); Pará, Brazil (208b).
Teófilo Otoni; Minas Gerais, Brazil (228).

Terra Firma, Santarém, see Belterra; Pará, Brazil (176).
Theófilo Otoni, see Teófilo Otoni; Minas Gerais, Brazil (228).
Tigre (Río); Loreto, Peru (54).
Tigrillo (Río or Quebrada), Río Tigre; Loreto, Peru (54).
Tingo María, Río Huallaga; Huánuco, Peru (38).
Tiquié (Rio), Rio Uapés; Amazonas, Brazil (126a).
Tocantins (Rio); Pará, Brazil (183).
Tocantins (Rio); Pará, Brazil (189a).
Todos Santos, Río Chaparé; Cochabamba, Bolivia (85).
Tonantins (Rio); Amazonas, Brazil (130a).
Tootobi, Rio Demini; Amazonas, Brazil (128a).
Tres Troncos, Río Caquetá; Caquetá, Colombia (15).
Triunfo; Pando, Bolivia (75).
Tseásim; Amazonas, Peru (32a).
Tucuruí; Pará, Brazil (190a).
Tumucuri, see Tamaruri; Pará, Brazil (185).
Uberaba; Minas Gerais, Brazil (221).
Uberlândia; Minas Gerais, Brazil (223).
Umbría (Puerto); Putumayo, Colombia (11b).
Una (Reserva Biológica); Bahia, Brazil (215).
Urubamba (Río); Ucayali, Peru (72).
Urucurituba, Rio Tapajós; Pará, Brazil (172).
Urupá, Rio Jiparaná; Rondônia, Brazil (201a).
Velhas (Rio das); Minas Gerais, Brazil (225).
Ventuari (alto, Río); Amazonas, Venezuela (106).
Victoria, see Puerto Victoria; Pasco, Peru (40).
vila = village (Portuguese).
Vila Bella, Lago Andirá; Amazonas, Brazil (165).
Vila Bella, Imperatriz; Amazonas, Brazil (166).
Vila Braga, Rio Tapajós; Pará, Brazil (172).
Vila de Tapajós, see Santarém; Pará, Brazil (175).
villa = village (Spanish and obsolete Portuguese).
Villa Bella, Lago Andirá; Amazonas, Brazil (165).
Villa Bella Imperatriz; Amazonas, Brazil (166).
Villa Braga, Rio Tapajós; Pará, Brazil (172).
Villa de Tapajós, see Santarém; Pará, Brazil (175).
Villavicencio; Meta, Colombia (3).
Visconde de Soutelo; Minas, Brazil (261).
Voitoco, Río Apaporis; Colombia (not located).
Von Humboldt; Huánuco, Peru (37).
Wheeler, see Fort Wheeler; Presidente Hayes, Paraguay (99).
Xapuri; Acre, Brazil (196).
Yagua (Caño); Amazonas, Venezuela (108).
Yaguas, Río Putumayo; Loreto, Peru (56).
Yahuas; Loreto, Peru (57).
Yali (Río), see Río Yari; Caquetá, Colombia (18).
Yari (Río); Caquetá, Colombia (18).
Yarinacocha; Ucayali, Peru (69).
Yatua (Río), Río Casiquiare; Amazonas, Venezuela (119).
Yurac Yacu, see Yuracyacu; San Martín, Peru (34).
Yuracyacu; San Martín, Peru (34).

Identification of localities plotted by number in Figures 23, 27, 29, 36, 44. The complete gazetteer, with coordinates and names of collectors, is included in *Living New World Monkeys, Volume 2* (in preparation).

10. Guayabero (Río), 02°12′N, 73°55′W, Meta, Colombia. INDERENA
34. Yurac Yacu (= Yuracyacu), Río Mayo, 05°52′S, 77°14′W, San Martín, Peru; type locality of *Callicebus oenanthe* Thomas; R. W. Hendee, June 1926, at about 780 m.
35. Seco, Río, 06°09′S, 77°15′W, San Martín, Peru. H. Watkins, July 1925, at 915 m.
36. Moyobamba, 06°03′S, 76°58′W, San Martín, Peru. L. Rutter, January 1924, at 840 m.
51. Santa Luisa, Río Nanay, 03°35′S, 74°30′W, Loreto, Peru. C. Kalinowski, September, October 1956, at 160 m.
52. Mishana, Río Nanay (Estación Biológica Callicebus), 03°45′S, 73°35′W, Loreto, Peru. W. Kinzey et al. (1977, p. 159); R. Aquino, February 1982.
53. Iquitos, Río Amazonas, 03°46′S, 73°15′W, Loreto, Peru. J. M. Schunke, December 1926; H. Bassler Collection, December 1923; July, August, 1925; October, December 1926; R. W. Hendee, January 1928.
60. Orosa, Río Amazonas, 03°26′S, 72°08′W, Loreto, Peru. Olalla y Hijos, September, October 1926; R. Aquino, February 1982.
73a. Inuya (Río, boca), 10°40′S, 73°37′W, Ucayali, Peru. H. Bassler, September 1927.
73b. Balta, Río Curanja, 10°08′S, 71°15′W, ca 300 m, Ucayali, Peru. J. L. Patton, June 1968; A. L. Gardner, June 1966, July 1968.
78. La Laguna, Río Beni, 14°10′S, 66°56′W, Beni, Bolivia. Ca. 200 m; type locality of *Callicebus olallae* Lönnberg; A. M. Olalla, February 1938.
79. El Consuelo, Río Beni, 14°20′S, 67°15′W, Beni, Bolivia. 196 m; type locality of *Callicebus modestus* Lönnberg; A. M. Olalla, December 1937.
140. Jaquirana, Rio, 04°21′S, 70°02′W, Amazonas, Brazil. Mozart Mello, January 1961.
143. Fonte Boa (Fonteboa), Rio Solimões, 02°32′S,

66°01′W, Amazonas, Brazil. Type locality of *Callicebus torquatus regulus* Thomas; W. Ehrhardt, May, July, August 1926; C. Lako, September 1927.

144. João Pessoã (Eirunepé), Rio Juruá, 06°40′S, 69°52′W, Amazonas, Brazil. A. M. Olalla, July 1936.

146. Juruá (Rio), see João Pessoã, ca. 07°S, 71°W, Amazonas, Brazil. E. Garbe, 1901–1902.

148. Tefé, Rio Tefé, 03°27′S, 64°47′W, Amazonas, Brazil. Type locality of *Callicebus egeria* Thomas; H. W. Bates; W. Hoffmanns, June 1906; Olalla Brothers, July 1925.

149. Manaquiri, Rio Solimões, 03°19′S, 60°21′W, Amazonas, Brazil. J. Natterer, December 1832.

152a. Aiapuá (or Lago do Aiapuá), W bank Rio Purús, 04°27′S, 62°08′W, Amazonas, Brazil. Type locality of *Callicebus torquatus purinus* Thomas; W. Ehrhardt, October 1921, May, October 1925; C. Lako, June 1932, February, August 1932.

152b. Aiapuá (or Lago do Aiapuá), opposite, E bank Rio Purús, 04°27′S, 62°08′W, Amazonas, Brazil. Type locality of *Callicebus dubius* Hershkovitz; C. Lako, June 1931; W. Ehrhardt 1925.

155. Jaburú, Rio Purús, 05°36′S, 64°03′W, Amazonas, Brazil. A. M. Olalla, December 1935.

156. Mapixi (Lago do), Rio Purús, 05°43′S, 63°54′W, Amazonas, Brazil.

161. Humaitá, Rio Madeira, 07°31′S, 63°02′W, Amazonas, Brazil. W. Hoffmanns 1906.

162a. Prainha, Rio Aripuanã 07°16′S, 60°23′W, Amazonas, Brazil. J. L. Silva Filho, October, November, December 1971.

192b. Sena Madureira, Rio Iaco, 09°04′S, 68°40′W, Acre, Brazil. Deane.

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