

# On the origin of allopatric primate species

Marc G.M. van Roosmalen\* & Tomas van Roosmalen

<sup>1</sup>MVRS - Marc van Roosmalen Stichting, Leiden, The Netherlands

\*Corresponding author, e-mail: marc.mvrs@gmail.com

## ABSTRACT

Here we present a theory on the origin of allopatric primate species that follows - at least in Neotropical primates - the irreversible trend to albinotic skin and coat color, called “metachromic bleaching”. It explains why primates constitute such an exceptionally diverse, species-rich, and colorful Order in the Class Mammalia. The theory is in tune with the principle of evolutionary change in tegumentary colors called “metachromism”, a hypothesis propounded by the late Philip Hershkovitz. Metachromism holds the evolutionary change in hair, skin, and eye melanins following an orderly and irreversible sequence that ends in loss of pigment becoming albinotic, cream to silvery or white. In about all extant sociable Neotropical monkeys we identified an irreversible trend according to which metachromic varieties depart from the saturated eumelanin (agouti, black or blackish brown) archetypic form and then speciate into allopatric taxa following the trend to albinotic skin and coat color. Speciation goes either along the eumelanin pathway (from gray to silvery to cream to white), or the pheomelanin pathway (from red to orange to yellow to white), or a combination of the two. The theory represents a new and original evolutionary concept that seems to act indefinitely in a non-adaptive way in the population dynamics of male-hierarchical societies of all sociable primates that defend a common territory. We have successfully tested the theory in all 19 extant Neotropical monkey genera. Our theory suggests the trend to allopatry among metachromic varieties in a social group or population to be the principal behavioral factor that empowers metachromic processes in sociable Neotropical monkeys. It may well represent the principal mechanism behind speciation, radiation, niche separation, and phylogeography in all sociable primates that hold male-defended territories. We urge field biologists who study primate distributions, demography and phylogeography in the Old World to take our theory to the test in the equally colorful Catarrhini.

## KEY WORDS

Neotropical primates; phylogeography; metachromic bleaching; speciation; radiation.

Received 20.12.2015; accepted 09.02.2016; printed 30.03.2016

## INTRODUCTION

We could ask ourselves (Darwin, 1859): “*Why primates constitute by far the most diverse, species-rich and colorful Order in the Class Mammalia? Do primate diversity, metachromism and metachromic processes relate directly to sexual selection? Or, rather to its generally complex, hierarchically*

*organized social structure and male territoriality? If not sexual selection, what could be the principal factor(s) in primate social behavior to be held responsible for metachromic processes, speciation, radiation, niche separation, and phylogeography?*”

Inspired by Alfred Russel Wallace whose concept of the “Origin of Species” was laid down in a paper

he sent for review to Charles Darwin, here we introduce a new and original theory about species evolution taking place in particular in sociable territorial primates. Our theory “*On the tendency of metachromic varieties in sociable primates to depart indefinitely from the agouti archetype and evolve in advanced eumelanin, pheomelanin to albinotic bleached allopatric taxa*” is equally rooted in life-long fieldwork on socio-ecology of all Neotropical monkey genera, both in captivity and in the wild. It closely follows the principle of evolutionary change in tegumentary colors called “metachromism”, a hypothesis propounded by Philip Hershkovitz (1968; 1977). Metachromism holds the evolutionary change in hair, skin, and eye melanins following an orderly and irreversible sequence that ends in loss of pigment through which a taxon of a given genus or phylogenetic clade eventually becomes albinotic, cream to white. Individual hair color or the entire coat changes from agouti (characterized by alternating blackish-brown and reddish bands on the terminal half of the hair) to uniformly blackish-brown, and thereafter to gray, and eventually to white or colorless, called the eumelanin pathway; or, it changes from agouti to uniformly reddish to orange to yellow to cream, and eventually white, called the pheomelanin pathway. The process itself is called saturation, which means the change from the primitive agouti pattern of the hair, or part of the pelage, or the entire coat, to a saturated eumelanin (blackish) or saturated pheomelanin (reddish) coloration. The dilution, or gradual reduction in the amount of pigment deposited in the growing hair, and disappearance of pigmentary colors is called bleaching (Fig. 1). In the color of the skin and iris of the eye, it follows the eumelanin pathway (brown to drab, to gray, or blue), and then it is termed depigmentation. Metachromism applies to all mammalian species. It is thought to also occur in bird feathers.

Our theory suggests that among social groups or populations of advanced intelligent, socially organized, male-territorial mammals, in particular primates, phenotypical varieties (mutants) that show slightly bleached eumelanin or pheomelanin colored skin or coat characteristics do arise indefinitely. Their melanocytes (skin cells that produce the black pigment melanin) are smaller, and for that or any other reason produce less melanin. In general, the tendency of these metachromic varieties is

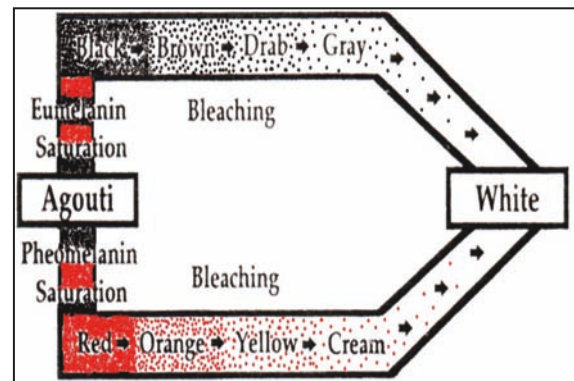


Figure 1. Bleaching from saturated eumelanin and saturated pheomelanin fields to white or colorless. Gradual reduction in the amount of pigment deposited in the growing hair results in apparent change from blackish through brown, drab gray to white or colorless in the eumelanin pathway, and from reddish through orange, yellow, cream to white in the pheomelanin pathway. Switching from the eumelanin to the pheomelanin pathway occurs in saturation but not in bleaching (modified from Hershkovitz, 1977).

neotonic, taking place locally (e.g., naked muzzle, bald head, euchromic blaze/forehead or part of the coat, depilation of skin) or all over the body. Social structure in most primate societies, in particular those of the more advanced monkeys and apes, is hierarchically organized, whereas male over female dominance is the rule, with very few exceptions (e.g., spider monkeys in the Neotropics and pygmy chimpanzees in Central Africa adopted a matriarchal social system, in which males patrol and defend a common territory, and females are allowed to transfer to neighboring social groups). Social selection is the recognition of and preference for the parental (or foster parental) phenotype in societal grouping and mating. Social selection for color or color pattern through assortative mating tends to stabilize within a chromatic range recognized and accepted by free-ranging but chromotypically imprinted members of the social group. Slightly depilated or somewhat eumelanin or pheomelanin bleached individuals deviant from the socially selected skin or hair color pattern, in particular when it is detected in adolescent to subadult males, may be discriminated against by high-ranking (alpha)-males. For that reason alone they can be pushed into the periphery of the group. Depending on the primate taxon or genus, such individual young males may also be expelled from the parental

group, and then become social 'outcasts'. Peripheral or outcast males do suffer on a daily basis from less and shorter access to the group's preferential, comparatively more nutritious food sources. They may join one another for reasons of social comfort and during ranging or foraging they tend to hang out together at the periphery of the group. Eventually, they may decide to leave the pack as all-male parties and roam around in much larger areas than just the home range or territory of the parental group. They then may attract young females from neighboring social groups. Together, they may seek some hitherto overlooked, 'empty' or little-used living space in an attempt to settle down and start their own family or social group. In case the taxon or genus it belongs to shows territorial behavior - which is the case in almost all Neotropical monkeys - these emigrants will be subsequently pushed out from neighboring territories as well. Consequently, they will die from starvation, parasite load and/or diseases forthcoming the dietary constraints they are suffering from. Or, as a matter of luck, in the end they may find some living space that is not (yet) occupied, most likely at considerable distance from the taxon's core distribution. Sometimes, such emigrant parties can be forced to survive in peripheral habitat that has to be considered marginal for that species to occur in. In extremely rare cases, such parties might even manage to circumvent a certain geographical barrier and beyond it find for the species appropriate habitat, where their specific ecological niche is not occupied, as such involving a range extension. In case that habitat is already occupied by a closely related species, a battle for life will take place and the best fitted taxon will drive the other to extinction, the red-handed tamarin *Saguinus midas* that is replacing the bare-face tamarin *S. bicolor*. Only over geological spans of time, for example after a vicariance has taken place, suitable habitat may open up where the taxon's niche is not occupied by another primate. One may imagine that along these paths small reproductively isolated founder-colonies that contain somewhat bleached and/or depilated individuals may establish themselves there. For the sake of survival alone they would unselectively interbreed or hybridize. Inbreeding then may relax stabilizing forces and stimulate or accelerate metachromic and other degenerative (= non-adaptive) processes. The more metachromic advanced each

successively isolated breeding colony is, or the farther it has moved from the center of that taxon's dispersion, the nearer it will come to the end of its metachromic evolution. And, the narrower will be its range of chromic fitness (e.g., prey and predator camouflage). This degenerative process, though, may be counterbalanced if under strong natural selection newly diverged forms, that evolve in a, for the original species marginal or new habitat, niche or landscape, at the same time selectively become better fitted, more cooperative, more inventive, or smarter in the adaptation process. This may happen every time founder-colonies successfully travel across existing geographical barriers, such as rivers, watersheds, mountain ranges, or open areas with arid scrub vegetation. Completion of the processes of metachromic bleaching, depigmentation, or depilation, whether taking place single or combined, eventually will result in extinction of the race or species. Unless the founder-colony or population in time does find and manage to occupy hitherto empty, but suitable habitat. Or: if it adapts to a different ecological niche, where skin and coat color do not have survival value by lack of competition from closely related species. Dead-end, isolated, peripheral, or new habitats may be occupied by metachromic dead-end populations, such as has happened over and over in the Neotropics in advanced albinotic callitrichids, uakaris, sakis, titis, capuchins, howlers, spider, woolly, and woolly spider monkeys.

## RESULTS

In non-territorial, peaceable Dwarf Marmosets *Callibella humilis* neotony and euchromism are clearly demonstrated as infants are overall much lighter colored than adults, showing a tendency to albinotic. Their overall pelage is light brown, their tail alternately light and dark-brown banded, and their face flesh-colored with a circumference of long, bright white hairs. From three months on, they pass through a complete metachromic metamorphosis. Their overall coat turns into saturated eumelanin, the muzzle of their faces into pinkish, and their semicrescent ocular rings or eyebrows into white (Fig. 2). This natural process may be related to slightly smaller melanocytes (skin cells that produce the black pigment melanin) producing overall less melanin.

*Callibella* stands at the base of the phylogenetic tree from which all extant Amazonian marmosets, *Cebuella* and *Mico*, have derived (Van Roosmalen & Van Roosmalen, 2003). It finds itself at the verge of extinction, for it occupies the niche of exudate gouging - that is feeding on resins oozing out of little holes they themselves have gnawed in the bark of certain gum trees and climbers. That niche is filled in by the advanced, larger, highly territorial Amazonian marmoset genus *Mico* (its distributions are shown in figures 5–7). We believe that these aggressive, over twice as big callitrichid monkeys have displaced the non-territorial dwarf marmoset and taken over its specific feeding niche all over its former, much larger range - the entire interfluvium delineated by the Rios Madeira, Amazonas and Tapajós. The genus *Callibella* is thought to have evolved there in the late-Pliocene to early-Pleistocene

landscape that was dominated by lacustrine seasonally inundated clear-water igapó wetlands. Being peaceable monkeys that like their neighbor's company instead of attacking or trying to kill them apparently has not been an evolutionary success among primates (Van Roosmalen, 2013a, b; 2015).

Contrastingly, the pygmy marmoset *Cebuella* that derived from prototypic *Callibella* nowadays occupies the entire western Amazon Basin. We believe it was so successful because *Cebuella*, being allopatric with *Callibella* and *Mico*, could occupy the ecological feeding niche of exudate gouger west of the Rio Madeira. There, it did not have to face competition from other callitrichids over exudate food sources. Indeed, Amazonian tamarins (genus *Saguinus*) that range west of the Rio Madeira (Figs. 7–13) lack the elongated tusked mandibular second incisors needed for tapping sap

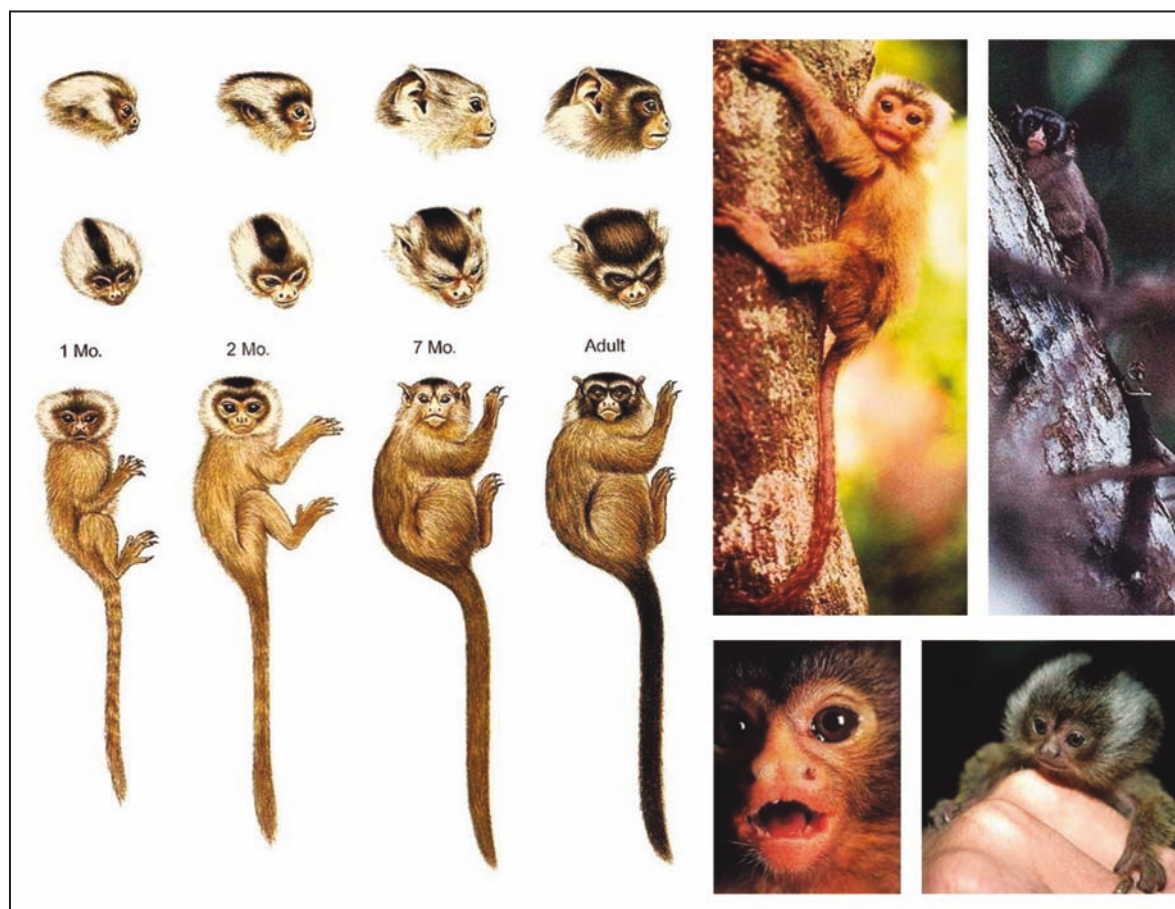


Figure 2. Ontogeny in Black-crowned Dwarf Marmosets *Callibella humilis* Van Roosmalen & Van Roosmalen (2003) based on photos of captive and wild individuals (Van Roosmalen et al., 1998).

from tree barks. As such, tamarins do not directly compete with pygmy marmosets over gum.

Instead, tamarins of different taxa are reported to parasitize on pygmy marmosets by licking the resins from tap holes made by the latter.

*Cebuella pygmaea* being overall agouti colored is clearly the most archetypic among the two extant taxa of pygmy marmoset. Distributed north of the Upper Amazon River (Rio Solimões/Río Marañón) and specialized in exudate gouging, the species (or its precursor) seems to have adapted to seasonally white-water inundated floodplain forest (várzea) habitat. Somewhat pheomelanin bleached colonizers of ancestral *C. pygmaea* (having an orange colored tail and breast, progressively bleached yellow to white belly, yellow-white mustache, naked pink-colored muzzle and circumocular rings) following the trend to allopatry once must have man-

aged to traverse the Amazon River proper, on floating várzea islands and/or passively through riverbend cut-offs (oxbow lakes). By lack of competitors the nearest to albinotic taxon *Cebuella niveiventris* - the form that derived from allopatric archetypic *C. pygmaea* - could then have extended its range from the Rios Javari and Juruá east as far as the Rio Madeira and south of the Amazon River as far as the Bolivian Amazon (Fig. 3). There, it secondarily adapted to never inundating terra firme high forest. Nowadays, it is found there, especially at edges of treefall clearings and in secondary growth. As *C. niveiventris* is fully allopatric with *C. pygmaea* and, moreover, shows completely different habitat preferences, we here propose to attribute both taxa full-species status naming them *C. pygmaea* and *C. niveiventris*. During our systematic surveys of primate distributions and diversity

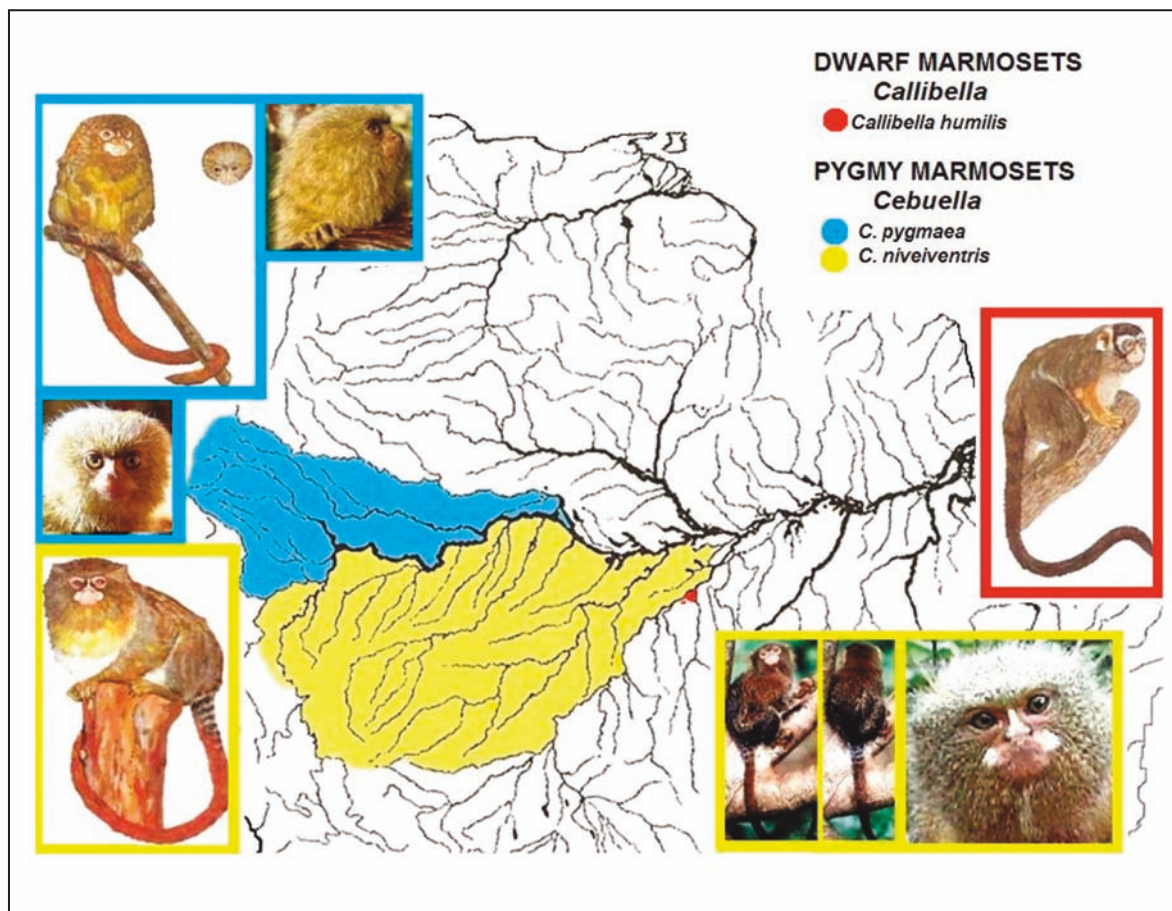


Figure 3. Present-day distributions are here depicted for Black-crowned Dwarf Marmosets genus *Callibella* and Pygmy Marmosets genus *Cebuella*, representing the smallest monkeys in the world. The current distribution of the monotypic genus *Callibella* perhaps has to be considered the smallest of any primate in the Neotropics.

carried out in the matrix terra firme hinterland stretching out behind the floodplain of white-water rivers (i.e., the Rios Javari, Juruá, Purús and Madeira), we were not able to detect any phenotypic difference between individuals sighted at any point along these far-apart rivers. It may indicate that in highly territorial monkeys like pygmy marmosets that occupy large distributions delineated by some of the largest tributaries of the Amazon River, phenotypical characters of skin and pelage coloration and/or local hair growth or depilation seem to have stabilized. In other words, we believe that within a given monkey's distribution something like a gradient of slightly differing phenotypes or color morphs, or geographic races, in reality does not exist. These and other observations from the larger field have led us to attribute full-species status to monkey taxa such as *C. pygmaea* and *C. niveiventris* that we ourselves have confirmed to be phenotypically stable throughout their (sometimes very large) range.

Here, we would like to propose a new species concept: ecospecies. This species concept is further corroborated by the here introduced evolution theory that aims to explain the origin of allopatric primate species. We define ecospecies as follows: “An ecospecies is a genetically isolated population or group of populations of a kind that does not undergo any gene flow from other populations of one or more closely related kinds, and that demonstrates a stabilized, well-defined phenotype over its entire range, in which it occupies and defends a specific ecological feeding niche against any outside competitor”. This definition of a primate species avoids the confusing, rather arbitrary distinction between species and subspecies (or race), for it adds sociobiological factors to geographical, geomorphological and phytosociological ones that act on the evolutionary process of primate speciation and radiation. Following this concept, for instance, an enclave population of *Callibella humilis* that we found living year-round in the seasonally inundated floodplain forest (igapó) along both banks of the Rio Atininga - genetically isolated from the main population occurring in terra firme forest at least one-hundred km to the north - should be given its own species name and treated as such. Or, in case the ranges of two saddle-back tamarins of the *Saguinus fuscicollis* Clade, hitherto taxonomically treated as subspecies, are separated by a con-

tact zone, where territorial behavior effectively impedes gene flow through hybridizing, both populations should be attributed full-species status.

The callitrichids Goeldi's Monkey *Callimico* and Black-crowned Dwarf Marmoset *Callibella* do represent the only monospecific (= monotypic) primate genera in the Neotropics. *Callimico* lives in the upper Amazon Basin region of Bolivia, Brazil, Peru, Colombia, and Ecuador (Fig. 4). Goeldi's monkey coat coloration is saturated eumelanin, blackish or blackish-brown. It forages in dense scrubby undergrowth of low mixed forests with discontinuous canopies and in so-called ‘tabocais’ (low forest dominated by bamboo) at levels of less than five meters. Social groups consisting of monogamous pairs with single offspring count on average six individuals. Groups live in patches of suitable habitat, often separated by miles of unsuitable vegetation. Goeldi's monkeys are vertical clingers and leapers able to leap horizontal distances of up to four meters between branches. As they are peaceable monkeys not showing any form of territoriality, Goeldi's monkeys often associate in mixed species groups with different species of tamarin *Saguinus* (Mittermeier et al., 2013). The fact that this primitive little monkey, just like the dwarf marmoset *Callibella*, remained archetypic in its blackish agouti coat coloration, is peaceable, is not showing any territorial behavior towards its neighbors, is occupying a unique feeding niche (foraging on the ground for fungi and invertebrates, and for fruits at low levels of a discontinuous canopy), and over geological time-span did not diverge into more than one taxon, strongly supports our doctrine that attributes speciation and radiation in male-territorial Neotropical primates primarily to the trend to allopatry as expressed in meta-chromic bleaching.

As shown in the schematic distribution map of all known Amazonian marmosets (Fig. 5), each interfluvium in the area delineated by the most effective riverine barriers - Rio Amazonas in the north, Rio Madeira in the west, Rio Guaporé in the south, and Rios Tapajós-Juruena and Xingú in the east - is inhabited by a different taxon of *Mico*, which species phylogeographically and phylogenetically radiated away from an ancestral, archetypic agouti-colored form much resembling the extant species *M. melanurus* (Van Roosmalen et al., 2000) from the upper Rio Aripuanã basin - the taxon with the

southernmost distribution of all Amazonian marmosets to be placed at the base of *Mico*'s phylogenetic tree.

Four monophyletic cladistic Groups or Clades are distinguished: the Bare-ear *M. argentatus* Clade, the (Tufted-ear or) Tassel-ear *M. humeralifer* Clade, the White-mantle (white-hip) *M. melanurus* Clade, and the Orange-leg *M. marcai* Clade (Figs. 6, 7). Within each Clade, the evolutionary pathway towards advanced metachromic bleached (and ultimately albinotic) taxa can be plausibly retraced. Albinotic forms in dead-end distributions may eventually go extinct (i.e., *M. chrysoleucos* in the *M. humeralifer* Clade; the new *Mico* species that occurs between the Rios Teles-Pires and Ronuro, *M. leucippe*, and *M. argentatus* in the *M. argentatus* Clade; *M. acariensis* and *M. saterei* in the *M. melanurus* Clade; and *M. manicorensis* in the *M. marcai* Clade). In territorial sociable primates the

principle of metachromic bleaching that seems to fuel the trend to allopatry is an irreversible, seemingly non-adaptive evolutionary pattern. The metachromic pathway followed within the *M. argentatus* Clade is a predominantly pheomelanin one, with first the nearest to archetypical, dark orange-colored taxon *M. emiliae* from the Rio Irirí. From *M. emiliae* diverged in southward direction the moderately bleached new species that we identified to occur between the Rios Ronuro and Teles-Pires, and northward the advanced albinotic taxa *M. leucippe* (all white with a pink face) and *M. argentatus* (all white with a black tail). The latter occupy dead-end distributions, as they are pressed at their northern limit against the untraversable Rios Tapajós and Amazonas, respectively. Within the tufted-ear or tassel-ear Clade of *Mico* the metachromic pattern followed the eumelanin pathway, from the darkest agouti-colored taxon *M. mauesi* going straight into

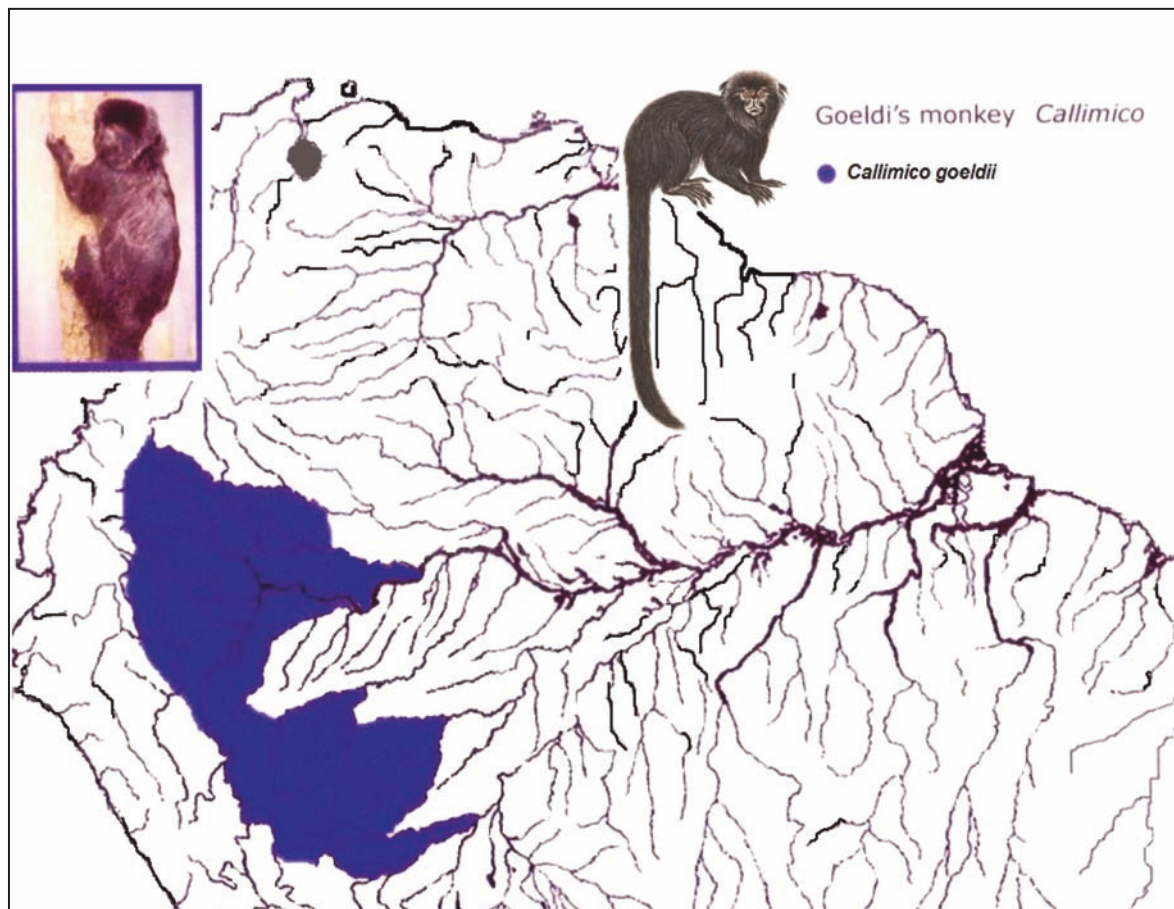


Figure 4. Present-day distribution of monotypic Goeldi's Monkey *Callimico goeldii*.

the overall whitish and gray *M. humeralifer* in the Clade's northernmost dead-end distribution (delineated by the Amazon and Tapajós Rivers). Along the pheomelanin pathway it diverged into the overall orange and white colored golden-white tassel-ear marmoset *chrysoleucos*, the species that occupies the westernmost dead-end distribution delineated by the Rios Madeira and Aripuanã. Within the white-mantle (white-hip) Clade of *Mico* the pathway followed goes from the nearest archetypic agouti-colored taxon *M. melanurus* in northern direction to the advanced pheomelanin bleached half-way albinotic taxa *M. intermedius*, *M. acariensis*, and *M. saterei*. And within the fourth Group of *Mico*, the orange-leg *M. marcai* Clade, the pathway followed in northern direction starts from the metachromic nearest to archetypic taxon *M. marcai* diverging into the advanced euchromic to almost albinotic taxon *M. manicorensis*, and in western direction proto-*marcai* evolved into the slightly but progressively bleached taxa *M. nigriceps* and *M. rondoni*, all three occupying dead-end distributions delineated by the untraversable Rio Madeira (after the Amazon River proper the second strongest river barrier in the entire Amazon Basin).

As all interfluves occupied by a different *Mico* species show dead-end distributions delineated by untraversable rivers at their northern and western limits, each species represents a different stage along the eumelanin or pheomelanin pathway that is frozen in time, but at the end of its metachromic evolution it invariably will turn into albinotic (Figs. 6, 7). Once arrived there, such primate taxa will inevitably go extinct, unless a founder-colony manages in time to cross the geographic (riverine) barrier by means of a river bend cut-off, by hopping on várzea forested floating islands, or by circumventing a geographical barrier. According to the doctrine, the evolutionary rate of metachromism is primarily controlled for by the trend to allopatry, and secondarily by environmental and genetic factors which may accelerate, retard, or terminate metachromic processes, or hold them in dynamic equilibrium, but cannot alter, reverse, or deflect them from their course. Hypothetically, growth and spread of a founder-colony of a certain Amazonian marmoset across a certain interfluve delineated by rivers, entails social selection. Effective selection stabilizes the mean chromotype of the colony at a color tone or grade inbetween that of the founders

and that of the albinotic ones towards which all monkeys tend. Amazonian marmosets (genus *Mico*) represent an advanced stock of callitrichids that evolved as late as the Pleistocene, south of the Amazon River and east of the Rio Madeira, from an ancestral stock of the *Callithrix ouistitis* occurring in Central and SE Brazil (Van Roosmalen & Van Roosmalen, 2003). About 1.5 MYA, a major vicariance took place - the break-through by the proto-Madeira River of the continental watershed running across the Chapada dos Parecis in Rondonia (Grabert, 1991). Thereafter, the entire area south of the Amazon and east of the Madeira drastically reversed its drainage pattern. Former rivers that since the beginning of the Pliocene had been draining the extensive clear-water wetlands in north-south direction, dried up. New rivers (mostly of the black-water type) arose and began to drain the area in opposite direction, from south to north. Most of these rivers emptied out in the Rio Madeira, some directly in the Amazon River. Founder-colonies at different phenotypic stages of metachromic bleaching that derived from archetypic *M. melanurus* - pushed by the trend to allopatry - subsequently invaded and inhabited the newly formed interfluvial terra firme 'islands' that new rivers had been creating. These newly available lands offered them their preferred habitat of terra firme rainforest, in which they filled the niche of exudate gouging, which niche east of the proto-Madeira River was hitherto exclusively occupied by the much smaller and peaceable, non-territorial dwarf marmoset *Callibella humilis* (Van Roosmalen & Van Roosmalen, 2003). Ever since, *Callibella humilis* seems to have lost the battle against the aggressively expanding *Mico* newcomers. Our assumption is that the dwarf marmoset has been locally driven to extinction almost all over its former range since the genus evolved in the late Pliocene. Presently, the black-crowned dwarf marmoset hangs on along the westbank of the lower Rio Aripuanã. As a commensal, it takes refuge on the terras pretas (human-made black-earth farmland) from the deadly attacks of the local Amazonian marmoset *Mico manicorensis* (Van Roosmalen et al., 2000; Van Roosmalen & Van Roosmalen, 2003). This example may well demonstrate that a specific ecological niche such as that of specialized gougers and feeders of gum (exudates) in a certain habitat (e.g., primary rain forest) can only and exclusively be occupied by a

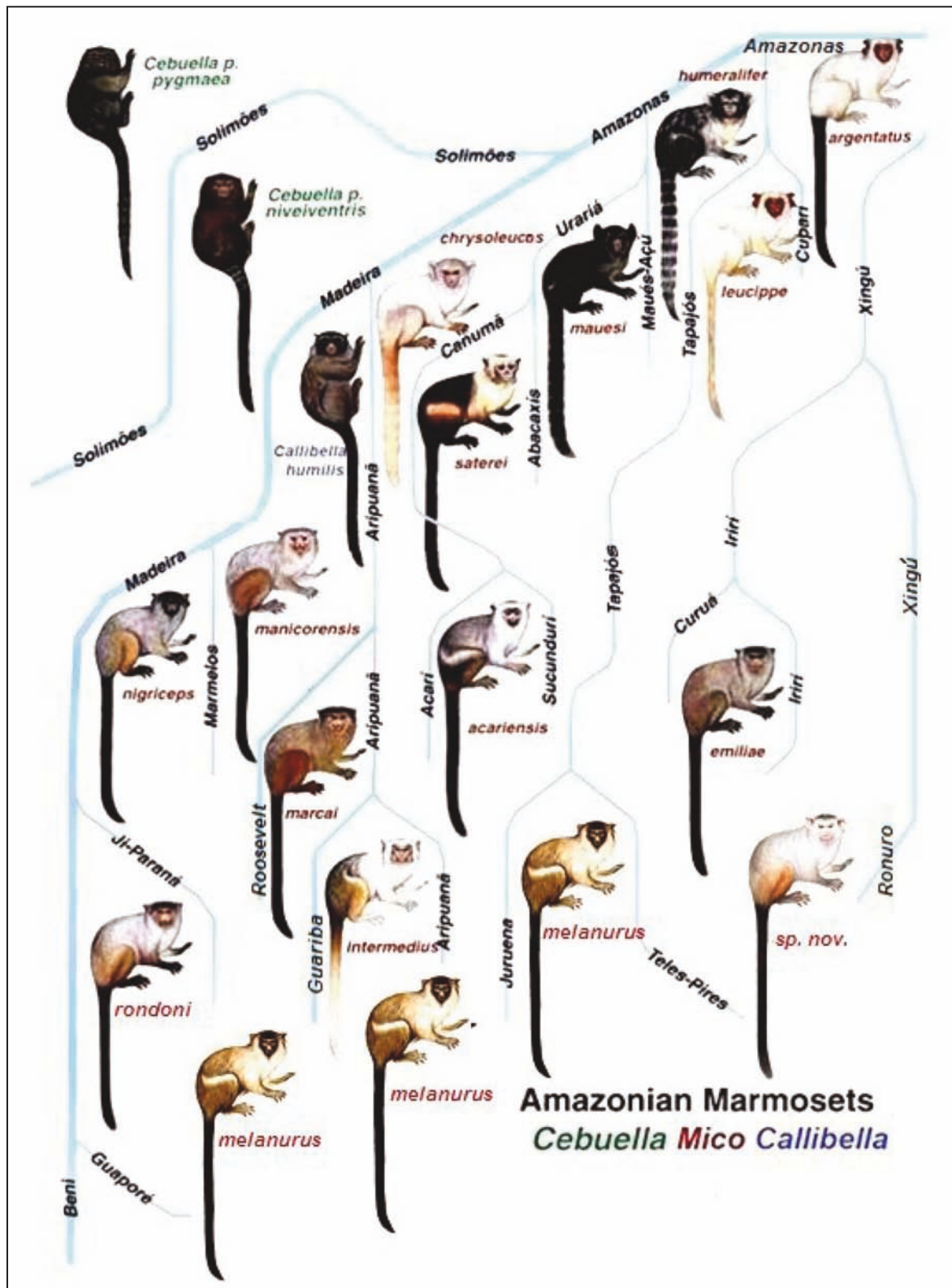


Figure 5. Schematic distributions as delineated by (for Amazonian Marmosets) untraversable rivers drawn for all known Amazonian Marmosets belonging to the genera *Callibella*, *Cebuella*, and *Mico*.

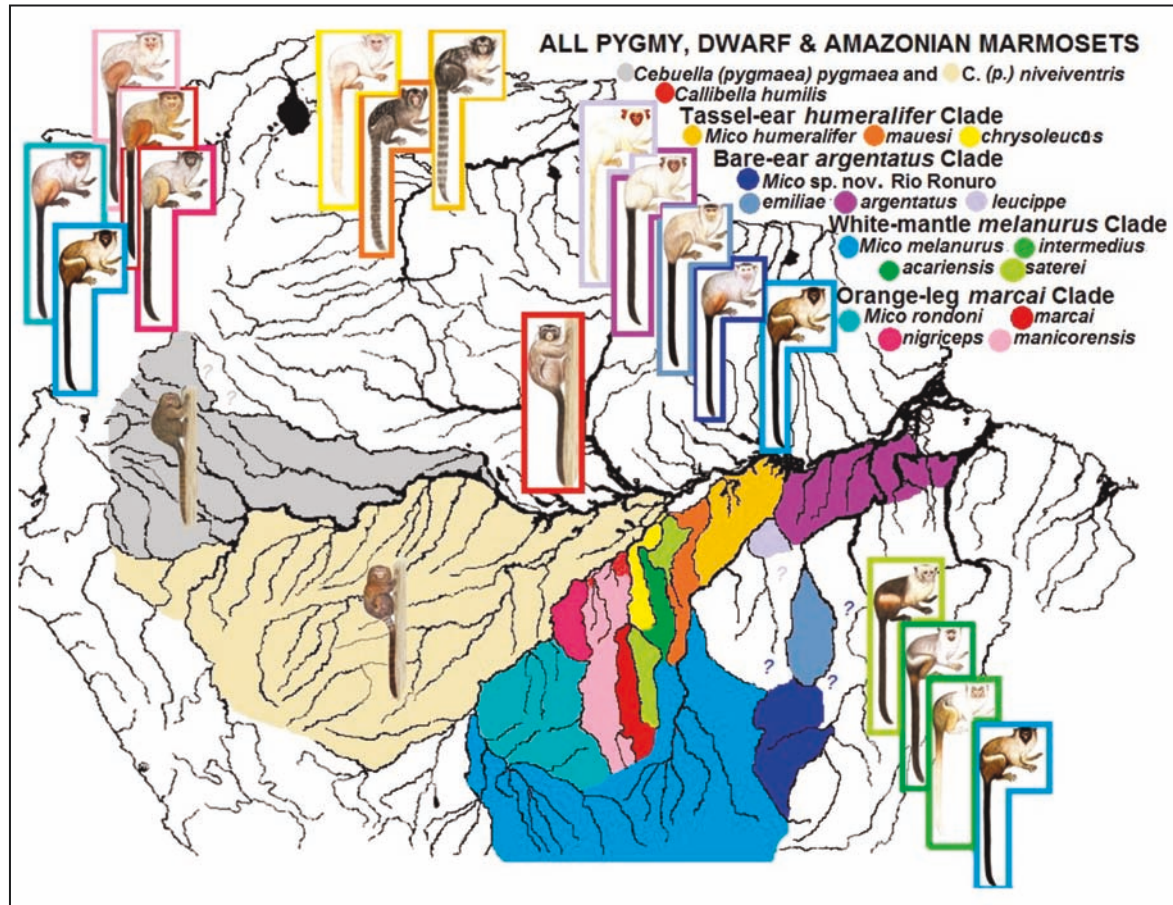


Figure 6. Geographical distributions delineated by rivers drawn in one map for all known Amazonian Marmosets that belong to the marmoset genera *Callibella*, *Cebuella*, and *Mico*.

single taxon that defends it, in this case even beyond generic bounds.

Figures 5–7 demonstrate that about all interfluvies occupied by a single species of *Mico* show dead-end distributions delineated by for rainforest habitat-specialists untraversable rivers at their northern and western limits. At their southern limits, all distributions invariably show a mostly narrow open-end, where a contact zone between two adjacent distributions must exist. Hybridization between Amazonian marmosets, though, has never been seen or reported in the wild. This may well be attributed to strong social and sexual selection. Indeed, all Amazonian marmosets of the genus *Mico* developed hypertrophied external genitalia in each gender that are physically greatly differing among related taxa (Van Roosmalen et al., 2000) (Figs. 8–11).

We ourselves have kept, raised and bred with a number of Amazonian marmosets, both in free-ranging and captive conditions. Expressive and often violent territorial behavior of all members of a social group, aside of species-specific sexual display of external genitalia, pheromones and scent-marking of one another's coat, has always prevented our marmosets from hybridizing (interspecific cross-breeding). For instance, we kept breeding social groups of all three taxa of the tassel-ear *M. humeralifer* Clade (i.e., *M. humeralifer*, *M. mauesi*, and *M. chrysoleucos*). To avoid one group from wiping out the other, we had to keep different species in separate cages, whereas we let only one group of *M. chrysoleucos* free-ranging in the forest that surrounded the compound. Even so, adults were still seen trying to grab and bite one another through the fine-mess wire. From our unique exper-

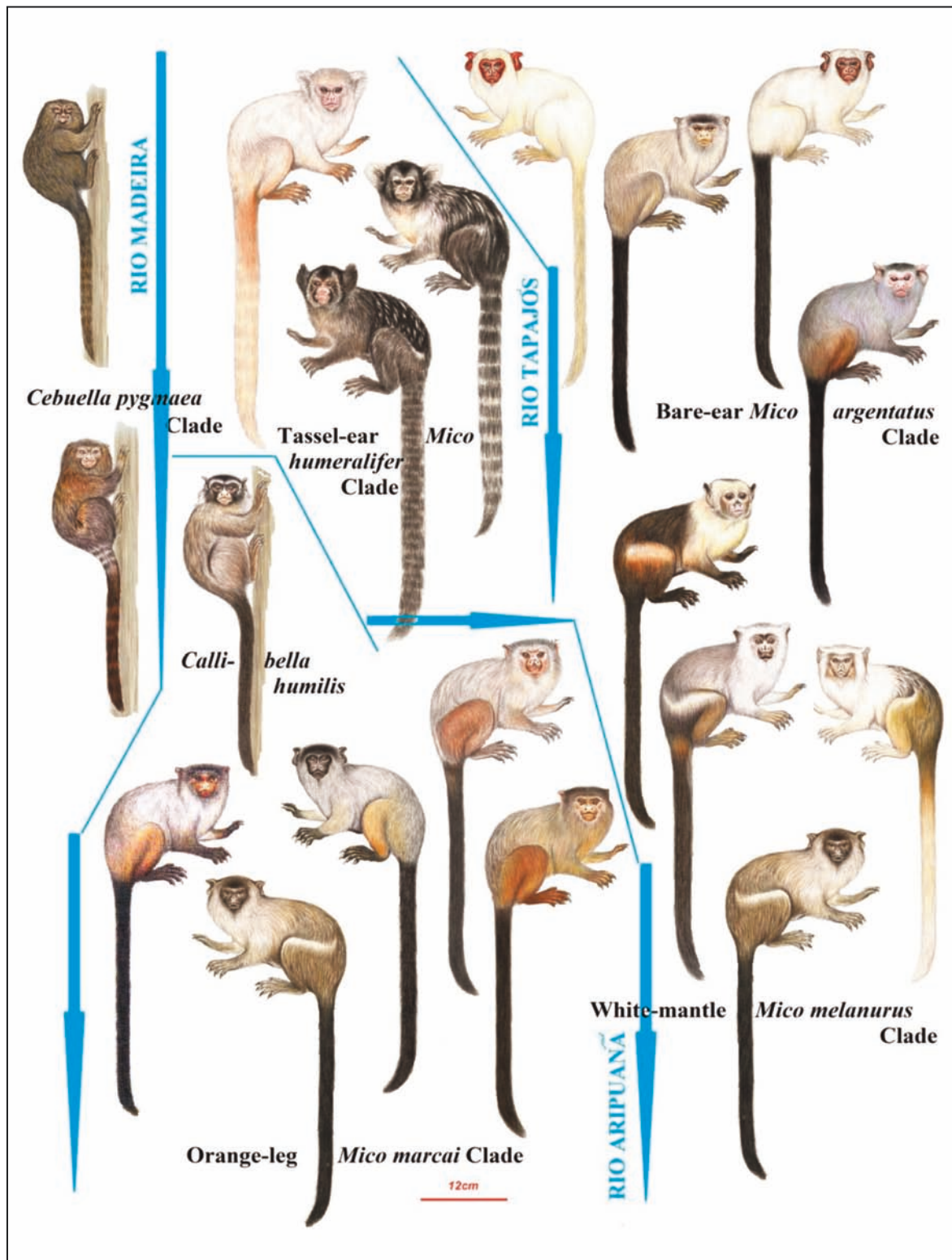


Figure 7. Radiation and metachromic diversification following eumelanin and pheomelanin pathways of metachromic bleaching depicted for all recognized phylogenetic Clades of Amazonian (*Mico*), Dwarf (*Callibella*), and Pygmy Marmosets (*Cebuella*) depicted to scale.



Figures 8–11. In all taxa of *Mico*, both males and females evolved hypertrophied, species-specific, in anatomical respect very differently shaped external genitalia. Fig. 8: male *M. manicorensis* sexually displaying; Fig. 9: exposed pudenda in adult female *M. acariensis*; Fig. 10: pudenda with 2 cm long vaginal lips in *M. saterei*; Fig. 11: pudenda in *M. acariensis*. This feature supports our view that all taxa of *Mico* should be considered different species and not just metachromic color morphs.

ience having kept all kinds of marmosets (until today, not a single zoo in the world has any *Mico* on exhibit) and other callitrichids, both in captivity and free-ranging in a tropical rainforest environment, we believe that where adjacent distributions of two species of *Mico* are not defined by an untraversable river, a sharp-lined contact zone must exist, where cross-breeding never takes place. This assumption concurs with the principle of metachromic bleaching being irreversible. In theory, only through cross-breeding with a darker, overall more saturated eumelanin taxon the metachromic pathway to albinotic could be reversed, something, however, that will never happen in the wild.

As all *Mico* do display strong interspecific territorial behavior - each group defending its living space by means of (often ritualized) territorial

boundary conflicts - within a given contact zone cross-breeding will not take place between neighboring groups of different but related ecospecies, as distance is maintained by regularly performed boundary conflicts. This way, any gene flow between phenotypically different populations is impeded. In phylogeographic terms, the farther radiated away from the origin of a Clade's dispersion - that of the nearest to archetypic species within a monophyletic Clade - the more progressively bleached the species will become. Partly or fully albinotic taxa, therefore, often occur in or near the Clade's dead-end distributions.

In figures 12–15, we have visualized the phylogeographic distributions, radiation, and supposed pathways of metachromic bleaching of all known Tamarin Monkeys genus *Saguinus*. We have di-

vided them up in the following monophyletic Groups or Clades: the Saddle-back Tamarins of the *S. fuscicollis* Clade (Fig. 13); the Black-mantle White-mouth Tamarins of the *S. nigricollis* Clade in one map combined with the Mustached Tamarins of the *S. mystax* Clade, the Red-chested Mustached *S. labiatus* Clade, and the Emperor Mustached *S. imperator* Clade (Fig. 14); and the Bare-face Tamarins of the *S. midas*, *S. bicolor* and *S. geoffroyi* Clades (Fig. 15). To complete the callitrichid picture, we have visualized the distributions of the Lion Tamarins genus *Leontopithecus*, and the True Marmosets or Ouistitis genus *Callithrix*, from SE Brazil (Fig. 16).

In geological history, speciation and radiation within the Saddle-back Tamarins of the *S. fuscicollis* Clade (Figure 13) went along two pheomelanin pathways of metachromic bleaching: one sub-Clade radiated south of the Amazon River from east to

west, from the most saturated eumelanin, nearest to archetypic taxon *S. mura* (green distribution) to the completely albinotic all-white taxon *S. melanoleucus* (blue distribution) via the taxa *S. avilapiresi*, *S. fuscicollis*, and *S. cruzlimai*. The bleaching process took first place in the head parts - muzzle and blaze - and, after having traversed the Rio Juruá back to its right bank, the metachromic bleaching process completed from the overall orange-colored taxon *S. cruzlimai* into the fully albinotic taxon *S. melanoleucus*. Another radiation took place from *S. mura* directly into *S. weddelli*, and, after having traversed the Rio Purús, into the overall light-brown colored taxon *S. primitivus* - both with a fully albinotic blaze and muzzle/mouth. A second sub-Clade of saddle-back tamarins radiated from the Peruvian Amazon in eastern direction, from the saturated eumelanin nearest to archetypic taxon *S. leucogenys* (light blue distribution) into the slightly

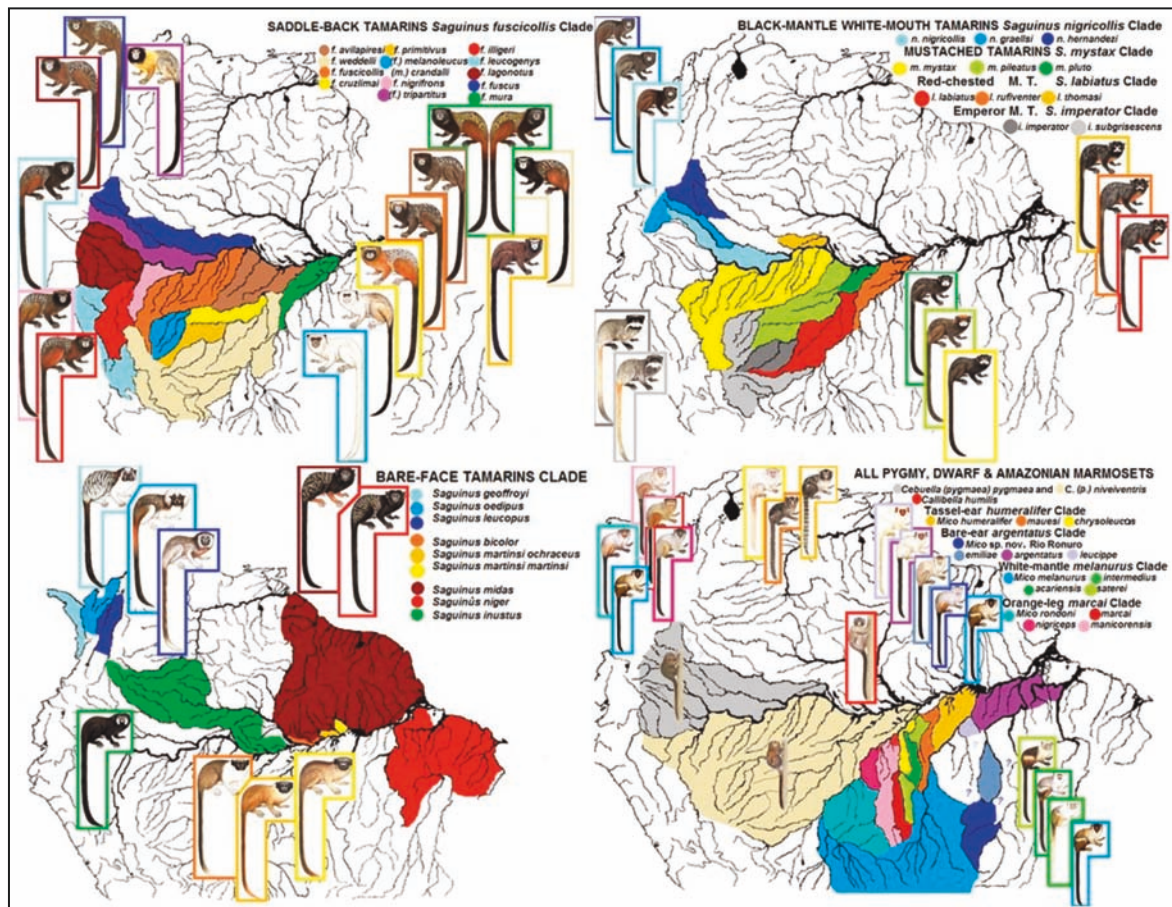


Figure 12. Distributions of all Neotropical Tamarin Monkeys, genus *Saguinus*, compared with those of all Amazonian Marmosets.

bleached taxa *S. illigeri* and *S. nigrifrons*, and after crossing the upper Amazon River (where it is called Río Marañón) northward into the progressively bleached taxa *S. lagonotus*, *S. fuscus*, and *S. tripartitus*, the latter three taxa being distributed north of the Amazon River in the Ecuadorian, Colombian, and Brazilian Amazon.

Within the Black-mantle White-mouth Tamarins of the *S. nigricollis* Clade (Fig. 14) that is distributed only north of the Amazon River in the Brazilian, Ecuadorian and Colombian Amazon, the nearest to archetypic saturated eumelanin taxon is *S. nigricollis*. It radiated northwestward and diverged into the slightly bleached taxa *S. graellsii* and *S. hernandezi*. The *S. nigricollis* Clade is sympatric with the saddle-back tamarins of the taxa *S. lagonotus*, *S. tripartitus* and *S. fuscus* (Fig. 13). However, they occupy different ecological niches and therefore can be seen traveling and foraging in mixed species associations, with the larger-sized black-mantle tamarins in the lead and staying higher up in the canopy of the terra firme rain forest. Within the Emperor Mustached Tamarins of the *S. imperator* Clade both extant taxa are already progressively bleached, the grayish taxon *S. subgriseescens* slightly more so than *S. imperator*. In the upper Rio Purús region there must exist a narrow contact zone between the two taxa along the southernmost open-end distribution of *S. imperator*. Within the Red-chested Mustached Tamarins of the *S. labiatus* Clade, *Saguinus labiatus* occupies the southernmost distribution and represents the nearest to archetypic taxon with a dark red chest and thin-lined white mustache. It radiated north of the Rio IPIXUNA and diverged into the advanced orange-chested taxon *S. rufiventer* that has a more bleached white mustache and head-stripe. The third taxon of the *S. labiatus* Clade is *S. thomasi* the precursor of which once must have traversed the Rio Solimões. It might have been replaced later by *S. inustus* north of the Rio Solimões as far west as the Rio Japurá. *Saguinus thomasi* nowadays only occupies the lower Rios Solimões/Japurá interfluvium. It represents the most progressively pheomelanin bleached taxon of the *S. labiatus* Clade in its light orange-colored chest and the broad-lined triangular white mustache. Within the mustached tamarins of the *S. mystax* Clade, the more saturated eumelanin, nearest to archetypic form is represented by the taxon *S. mystax* that is distributed west of the Rio

Juruá. After traversing the Rio Juruá, the Clade has radiated eastward while further bleaching along the pheomelanin pathway into the orange-crowned taxon *S. pileatus*, and along the eumelanin pathway diverging directly from *S. mystax* into *S. pluto*. The latter taxon is overall more grayish and has a distinctive albinotic spot around the base of the tail. In the lower Rios Juruá/Purús interfluvium we have sighted *S. pluto* ranging always in mixed-species association with the smaller saddle-back tamarin *S. avilapiresi*, with *S. pluto* always in the lead and *S. avilapiresi* rushing behind and below the group of *S. pluto* in the lower strata of high forest, always in a hurry feeding on *S. pluto*'s left-over food items.

A hypothetical pathway of allopatric speciation, radiation and metachromic bleaching followed by the Bare-face Tamarins of the *S. midas*, *S. bicolor* and *S. geoffroyi* sub-Clades may have had its origin in the Guianas (Fig. 15). An all-black, saturated eumelanin archetypic precursor of *S. midas* may once have traversed the lower Rio Amazonas and speciated allopatrically into the black-handed taxon *S. niger*. Or vice-versa (archetypic black-handed *S. niger* may once have traversed the lower Rio Amazonas and speciated allopatrically into the red-handed *S. midas*). The same or another all-black precursor of *S. midas* may have traversed the Rio Negro and allopatrically speciated into the taxon *S. inustus* that is all-black with a white-mottled face. *Saguinus inustus* nowadays occupies the entire interfluvium between the Rio Negro in the north, and the Rios Solimões, Japurá and Caquetá in the south. A founder-colony of a predecessor of *S. inustus* driven by the trend to allopatry may then have ventured from the taxon's westernmost distribution into the NW Colombian Río Magdalena basin. Once having inhabited the Río Magdalena basin, it may have diverged along a pheomelanin pathway into the extant taxon *S. leucopus* that has a white-hairy facial circumference similar to *S. inustus*. *Saguinus leucopus* then may have radiated further into the progressively pheomelanin bleached, almost euchromic taxon *S. oedipus*, and from there into the near-albinotic taxon *S. geoffroyi* that is distributed from extreme NW Colombia into Panama, as such the farthest away from the center of dispersion of the Bare-face Tamarin Clade. With respect to the three derived euchromic taxa of the *S. bicolor* Clade, as we have mentioned elsewhere, these taxa find themselves in the process of being

rigorously displaced from their respective territories by the now sympatric archetypic saturated eumelanin red-handed tamarin *S. midas*. All three taxa (i.e., *S. bicolor*, *S. martinsi*, and *S. ochraceus*) find themselves pushed with the back against the untraversable Rio Negro and/or Rio Amazonas (Fig. 15). At present, the red-handed tamarin *S. midas* is wrapping up the last stage of its range extension towards the south to the cost of all three Bare-face Tamarins of the *S. bicolor* subClade. This battle over a specific ecological (feeding) niche, in which two sympatric, closely related primate taxa are involved, will inevitably lead to the extinction of the most euchromic among the two, that is the Bare-face Tamarins of the *S. bicolor* sub-Clade: the taxa *S. bicolor*, *S. martinsi*, and *S. ochraceus* (Fig. 15).

The eumelanin *S. midas* sub-Clade might have originated in the Guianas north of the watershed with the northeastern Amazon formed by the Tumac-Humac Mountains and the open wet savannas of Roraima and Pará. A predecessor of the *S. midas* sub-Clade, perhaps the extant *S. midas* itself, once may have circumvented the watershed between the Guianas and Brazil by traversing the Parú Savanna, whereafter it may have penetrated far southwards into the northeastern quadrant of the Brazilian Amazon. We assume that before some vicariance took place this vast territory or a large part of it was inhabited by precursors of the closely related Bare-face Tamarins of the *S. bicolor* sub-Clade. Apparently, as the two sub-Clades do occupy the same ecological niche, (proto)-*midas* subsequently has displaced (proto)-*bicolor* over most of its former range. This battle is still being fought over between *S. midas* and each taxon of the *S. bicolor* sub-Clade, but it seems to come close to its end. The process of replacement is accelerated by deforestation and other human disturbance such as road-building that has taken place north of the rapidly expanding megacity of Manaus. This ongoing story clearly demonstrates interspecific intolerance in closely related territorial monkeys that occupy and exploit the same ecological niche. It inevitably leads to displacement, or sooner or later extermination of the more progressively bleached (euchromic) taxon. This kind of replacements may take place after a geographic barrier has been successfully overtaken by the more saturated eumelanin (more adaptive and/or aggressive?) of two related

taxa. Or: after a vicariance has removed a hitherto gene-flow impeding geographic barrier inbetween the distributions of two or more closely related species.

Vicariance (from Latin *vicarius*) means a process by which the geographic range of an individual taxon, or an entire biota, is split into discontinuous parts by the formation of a physical barrier to gene flow or dispersion.

Today, the *S. bicolor* sub-Clade only inhabits a 20–30 km narrow strip of terra firme rain forest alongside the southernmost edge of the Pre-Cambrian Guayanan Shield.

The three *bicolor* taxa are so to speak pushed with the back against rivers that happen to be the widest and most difficult to traverse on the entire South-American continent: the Rios Negro and Amazonas. The three extant taxa of Bare-face Tamarins each occupy what is called a “dead-end distribution”. The distribution of the half-brown, half-white taxon *S. bicolor* measures not more than 20–30 x 200 km, delineated in the west and south by the Rios Cuieiras, Negro, Amazonas, and Urubú. *Bicolor*’s neighbor to the east - the almost fully bleached, ochraceous colored taxon *S. ochraceus* - occupies the interfluvial between the Rios Urubú and Uatumã. To the east of its distribution, the pheomelanin, light orange-colored taxon *S. martinsi* occupies the lower interfluvial between the Rios Uatumã and Nhamundá (Fig. 15). Disputedly, a now extinct precursor of the Bare-face *S. bicolor* sub-Clade that once ranged somewhere to the north of the Amazon River, may have driven the three extant taxa of the *S. bicolor* subClade - each at a different stage of metachromic bleaching - into the small interfluvial dead-end distributions, that they occupy today. The saturated eumelanin (blackish-brown) red-handed tamarin *S. midas* that later expanded its range to the south, is now simultaneously invading the three remaining adjacent interfluvial stronghold territories of the *S. bicolor* sub-Clade.

A sharp-line contact zone drawn between *S. midas* and *S. bicolor* territory has been notified by us in the early 1990s to run at 28–30 km north of and parallel to the Negro and Amazon Rivers. While running a halfway house for orphaned monkeys situated right at the edge of the contact zone, we have repeatedly witnessed different social groups of *S. midas* raiding resident family groups of *S. bicolor*. These incidents invariably ended up

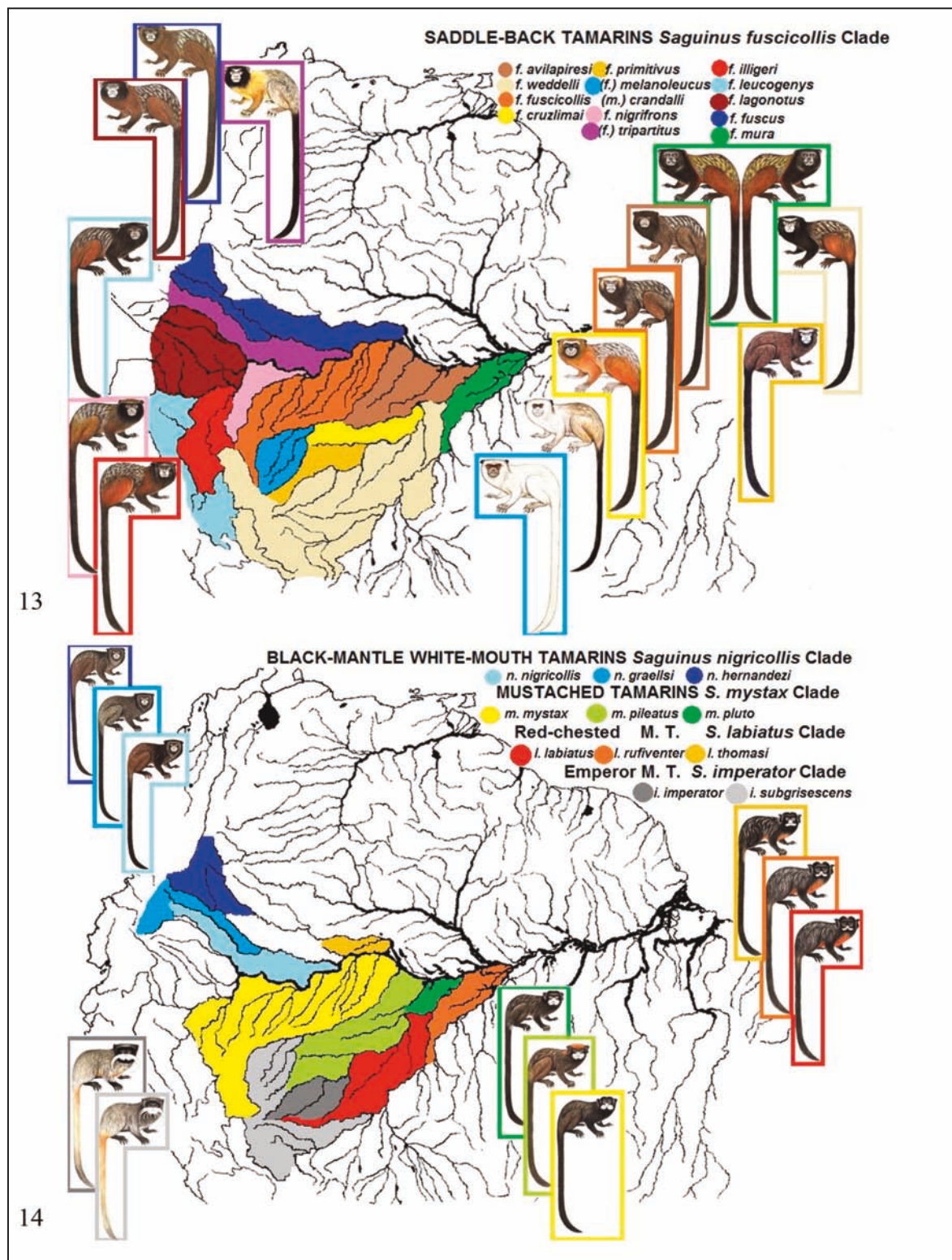


Figure 13. Distributions, allopatric speciation, radiation, and supposed pathways of metachromic bleaching in all known Saddle-back Tamarins of the *Saguinus fuscicollis* Clade. Figure 14. Idem, in the more robust, larger-sized Black-mantle White-mouth Tamarins of the *S. nigricollis* Clade, the Emperor Mustached Tamarins of the *S. imperator* Clade, the Red-chested Mustached Tamarins of the *S. labiatus* Clade, and the Mustached Tamarins of the *S. mystax* Clade.

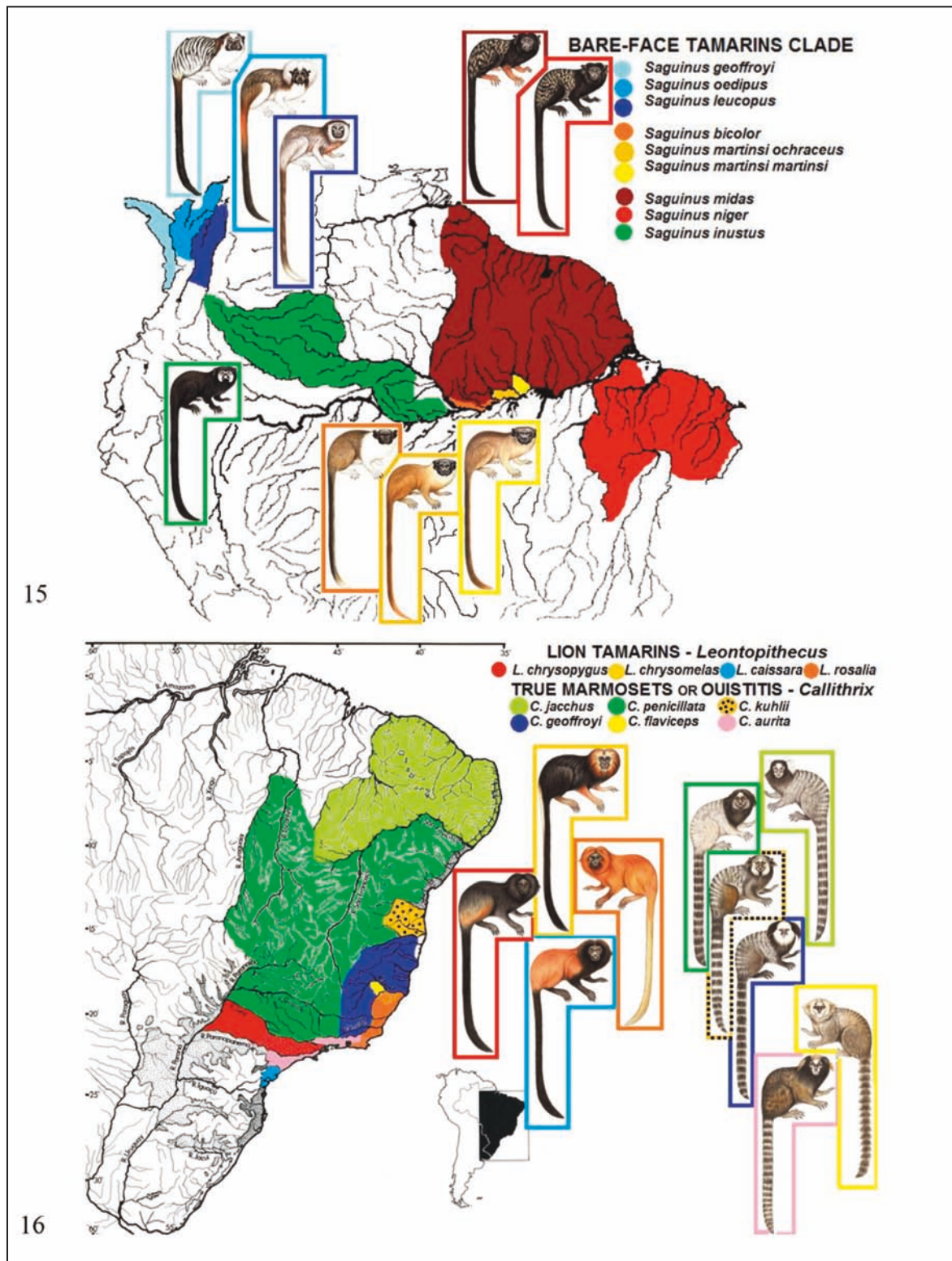


Figure 15. Distributions, allopatric speciation, radiation and supposed pathways of metachromic bleaching in all extant Bare-face Tamarins that belong to the *Saguinus midas*, *S. bicolor*, and *S. geoffroyi* sub-Clades. Figure 16. Distributions, allopatric speciation, radiation and supposed pathways of metachromic bleaching in all known True (or Atlantic Forest) Marmosets (genus *Callithrix*) and Lion Tamarins (genus *Leontopithecus*) from SE Brazil.

in the defensive, less aggressive (more sensitive?) *S. bicolor* bitten to death. Now, about twenty years later, *S. midas* has extended its range at least five km further to the south to the cost of *S. bicolor* occupied territory. As *S. midas* is more opportunistic and flexible in its habitat preferences - venturing also into secondary growth and edge habitats such as roadsides - it rapidly penetrates into *S. bicolor* territory, at some places (e.g., Ducke Reserve) already reaching the outskirts of Manaus. Running a rehabilitation center for orphaned monkeys, we sometimes received whole families of *S. bicolor* that were rescued from isolated pockets of forest in urbanized areas. After some time spent in quarantine, we used to put them in large cages built on poles in the middle of the rain forest about thirty km north of Manaus in an attempt to reintroduce the species where we assumed it had occurred not long before. One day before releasing a wild-caught social group of 8 *S. bicolor*, we found them all bitten to death inside the cage that was fenced with galvanized small-meshed wire. The only animal left alive in the cage was a wild adult *S. midas* that apparently had not found back the little hole in the wire through which he and some other family members had entered the cage that very morning. On the other hand, a hand-tame *S. midas* infant that we raised free around the compound at the time, one day was 'kidnapped' and adopted by the wild *S. midas* group that roamed around in the project area.

Within the True (Atlantic Forest) Marmosets or Ouistitis genus *Callithrix* we distinguish two monophyletic Clades: the *Ca. penicillata* Clade and the *Ca. aurita* Clade (Fig. 16). Within the first monophyletic Clade we consider *Ca. penicillata* the nearest to archetypic, most saturated eumelanin taxon that occupies the largest distribution (dark green area). From there, it radiated in northern direction and diverged into the overall progressively bleached taxon *Ca. jacchus* that has fully albinotic ear-tufts. In eastern direction, from it derived and radiated away the taxa *Ca. kuhlii* and *Ca. geoffroyi* that are progressively bleached euchromic to albinotic in their mantle and head parts (except the black ear-tufts). Their dead-end distributions are pressed against the Atlantic coast. Interestingly, *Ca. kuhlii*'s range fully overlaps with that of *Leontopithecus chrysomelas*. The *Ca. aurita* Clade has *Ca. aurita* representing the nearest to archetypic, overall metachromic agouti taxon that ranges allopatric

with the lion tamarins (*Leontopithecus*) in the Atlantic forest of SE Brazil. From there derived the near albinotic taxon *Ca. flaviceps* that occupies a small area in SE Minas Gerais, allopatric with *Ca. geoffroyi* (Mittermeier et al., 2013).

As for the Lion Tamarin genus *Leontopithecus*, we consider the overall saturated eumelanin, almost all-black taxon *L. chrysopygus* the nearest to archetypic lion tamarin. From it derived in southeastern direction the taxon *L. caissara* that followed a metachromic pathway of pheomelanin bleaching in its bright orange-colored dorsal parts while maintaining the saturated eumelanin black tail, arms, legs, mantle and head of *L. chrysopygus*. Its small range in coastal Paraná State represents the southernmost distribution of any callitrichid. From *L. chrysopygus* derived in northeastern direction along a pathway of pheomelanin bleaching the two other taxa, *L. chrysomelas* and *L. rosalia*. *Leontopithecus chrysomelas* bleached in the orange colored lower arms and legs, and in the light orange to cream-white head and mantle maintaining the rest of its body saturated eumelanin. *Leontopithecus rosalia*, in turn, is evenly light orange-colored over its whole body, with the tail becoming almost albinotic. Both taxa occupy small dead-end distributions in the Atlantic forest along the coast of SE Brazil (Mittermeier et al., 2013).

In a further attempt to falsify the principle of metachromic bleaching and the crucial role we believe it plays in allopatric speciation of (at least) Neotropical monkeys, we now will proceed to examine currently known distributions, allopatric speciation and radiation, and the pathways of metachromic bleaching supposedly followed in all other male-territorial Neotropical monkey genera (i.e., *Callicebus*, *Saimiri*, *Cacajao*, *Chiropotes*, *Pithecia*, *Lagothrix*, *Ateles*, *Brachyteles*, *Alouatta*, *Cebus*, *Sapajus*, and *Aotus*).

Titi Monkeys of the genus *Callicebus* are strongly territorial in behavior, a family marking its territory vocally - a pair calling in duet, or a whole family calling in chorus. In the Amazon, a single taxon of the Collared Titi *Cal. torquatus* Group may occur in sympatry with a single titi of any of the other Non-collared Titi cladistic Groups, once the former titis are only found high up in the canopy of primary terra firme rain forest. Collared titis occupy a different, more frugivorous feeding niche than the titis that lack the white collar. The latter prefer the

lower strata and edges of terra firme rain forest, secondary growth, and savanna forest, being overall more omnivorous in their diet that contains also young leaves and insects, in addition to pulpy fruits (Hershkovitz, 1988; Hershkovitz, 1990; Mittermeier et al., 2013).

In figures 17–20, we show the distributions of all known Titi Monkeys genus *Callicebus*. Within the titi monkeys five phylogenetic cladistic Groups or Clades are recognized: *Cal. personatus* (southeastern Brazilian taxa), *Cal. torquatus* (Amazonian collared taxa), *Cal. moloch*, *Cal. cupreus* and *Cal. donacophilus* (Amazonian non-collared taxa) (Van Roosmalen et al., 2002). Within each titi Clade the irreversible pathway of metachromic bleaching towards partly or fully albinotic, from saturated eumelanin and saturated pheomelanin fields to white or colorless, is clearly demonstrated. The farther radiated away from the prototypic agouti or saturated eumelanin (black or dark brown) taxon - *Cal. melanochir* in the *Cal. personatus* Group, *Cal. medemi* in the *Cal. torquatus* Group, *Cal. cinerascens* in the *Cal. moloch* Group, *Cal. brunneus* in the *Cal. cupreus* Group, and *Cal. modestus* in the *Cal. donacophilus* Group - the more its pelage turns into orange, yellowish or cream to white, first in certain parts of the body, and eventually all over its coat. Near-albinotic forms in dead-end distributions (e.g., *Cal. pallescens*, Rio Xingú titi, Rio Mamurú titi) are doomed to eventually go extinct, as metachromism with the trend to allopatry as the driving behavioral factor is an irreversible, initially seemingly non - adaptive evolutionary pattern in all territorial monkeys. As shown in the maps, in the Amazon all distributions of titis without a white collar are occupied by just a single taxon and are delineated by rivers that function as (for titis that cannot swim) strong geographic barriers. Narrow contact zones between adjacent interfluvial distributions surely do exist, usually near the headwaters, but nowhere interbreeding or hybridization between the two neighboring taxa has been reported to take place.

Our extensive primate surveys carried out throughout the entire Amazon Basin have revealed that, in general, a given monkey taxon looks phenotypically identical throughout its entire range. In contact zones or across opposite banks of rivers that demographically separate two phylogenetically related taxa, we have noticed interspecific boundary conflicts and vocal battles to occur regularly, in

particular performed by social groupings of titis, howling monkeys and spider monkeys. In at least one contact zone between two differently looking titis we have been able to perceive the ‘trend to allopatry’ put in motion in metachromic bleached individuals that were deviant from the commonly seen phenotype. At the far northeastern corner of the distribution of Hoffmann’s Titi Monkey *Cal. hoffmannsi* a small founder-population of an albinotic all-creamwhite form, that we provisionally named the “Rio Mamurú titi”, apparently has been pushed into a dead-end distribution between the right bank of the lower Rio Mamurú, the for titis inhospitable várzeas (seasonally white-water inundated floodplain forest) along the right bank of the Rio Amazonas, and the parapatric distribution of *Cal. hoffmannsi* to the east and south as far as the lower Rio Tapajós (Fig. 17). Only mtDNA sequences may determine what taxonomic status we should allocate to this new, fully euchromic taxon: ‘color morph’ or ‘taxon in the making’. A color morph of *Cal. hoffmannsi*, a subspecies to be named *Cal. hoffmannsi mamuruensis*, or a valid new species to be described as *Cal. mamuruensis*? As mentioned before, here our ecospecies concept could be applied in case the population has been confirmed to be allopatric and genetically isolated (not allowing any gene flow) from the taxon it derived from, or when the enclave population has successfully adapted to a different ecological niche - in this case turning itself into a várzea versus terra firme rainforest habitat specialist. Our ecospecies concept (hereafter named ESC) in combination with the phylogenetic species concept (PSC) is, at least in the field, more practical, less arbitrary, and better defined, in particular when used for the purpose of species and biodiversity conservation. The ESC would put an end to the academic discussion about the arbitrary and controversial subspecies/race concept.

As Groves (2001a; 2001b; 2004; 2005) points out: “*There is no official taxonomy*”. The numerous concepts as to what is and what is not a species are controversial, and every named species is itself nothing more than a hypothesis. Our understanding of the systematics of the primates is constantly growing, not only through the discovery of new species but also with new information brought to bear from diverse fields such as morphology, cytogenetics, molecular genetics, paleontology, biogeo-

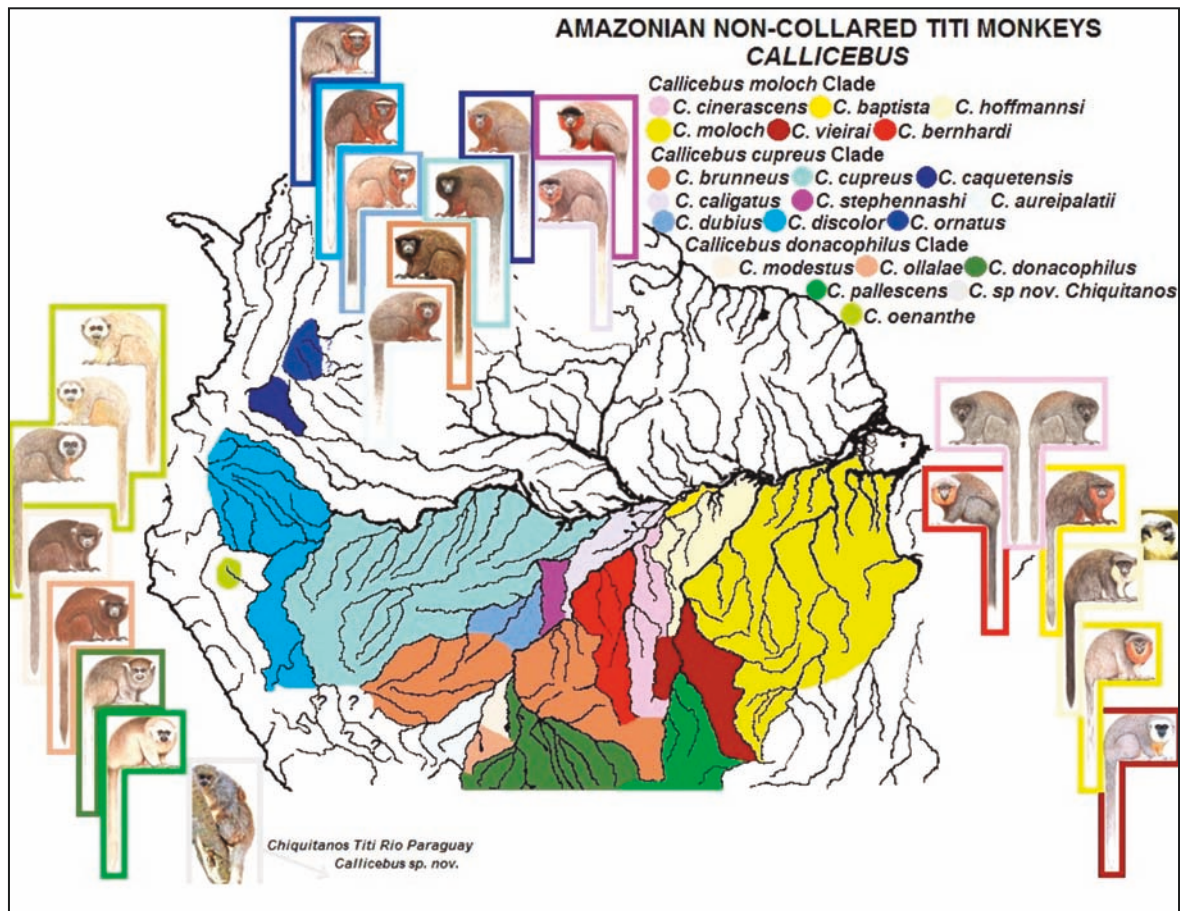


Figure 17. Distributions, allopatric speciation, radiation and supposed pathways of metachromic bleaching in all known Amazonian Non-collared Titi Monkeys genus *Callicebus*.

graphy, physiology and behaviour - contributing to test the hypothesis that a certain organism is a species distinct from another. Distinct in what sense? An individual is distinct, a population is distinct, but when and in what way is it a distinct species?

Among the Titi Monkeys of the *Cal. moloch* cladistic Group (Fig. 17), the all-agouti dark-tailed taxon *Cal. cinerascens*, ranging along the east bank of the Rio Aripuanã and between the right bank of the lower Rio Madeira and the left bank of the Rio Canumã, seems to represent the nearest to archetypic, most original or ancestral titi from which all other taxa of the *Cal. moloch* Group have derived. Phylogeographically, the current central-southern Amazonian distribution of *Cal. cinerascens* is thought to represent the center of dispersion of the *Cal. moloch* Clade. In other words, the upper Aripuanã region in Rondonia may be considered the

cradle of *Cal. moloch* Clade's evolution and dispersion. From there, all taxa of the *Cal. moloch* Clade have diverged, radiating away in all (but southern) directions. A distinct metachromic trend to saturated pheomelanin (orange beard and sideburns) and albinotic (cream to white beard, sideburns, tail and/or whole body) can be seen, which means that the most progressively bleached taxa that demographically radiated the farthest away from the archetype's origin of dispersion tend to euechromic or albinotic (i.e., *Cal. moloch* east of the Rio Tapajós, and *Cal. hoffmannsi* in the northernmost dead-end distribution delineated by the untraversable Amazon and Tapajós Rivers). The supposed metachromic pathway taken is as follows: *Cal. cinerascens* radiated first in northern direction, some founder-colony traversed the Paraná do Urariá, followed the pheomelanin pathway, and diverged

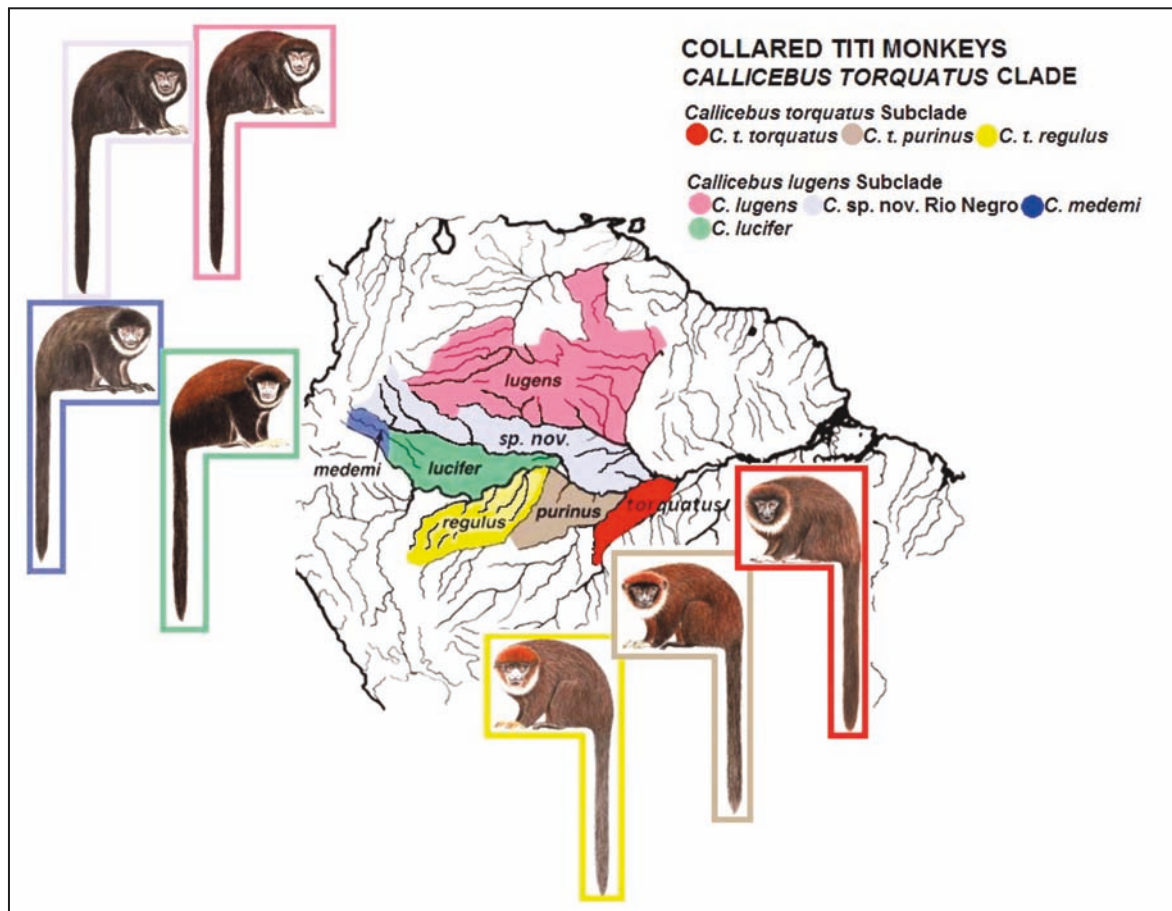


Figure 18. Distributions, allopatric speciation, radiation and supposed pathways of metachromic bleaching in all known Amazonian Collared Titi Monkeys of the *Callicebus torquatus* Clade with two sub-Clades: *Cal. torquatus* and *Cal. lugens*.

into taxon *Cal. baptista* (which has dark orange-colored beard, sideburns, lower extremities, and belly). Radiating eastwards, it diverged into *Cal. hoffmannsi* (its forehead, beard, sideburns, hands, feet, and belly bleached light gray to cream-white). After *Cal. hoffmannsi* happened to traverse the Rio Tapajós, most likely where it is called Rio Juruena, it diverged into the advanced pheomelanin bleached to albinotic taxon *Cal. moloch* that now occupies a large distribution east of the Rio Tapajós and south of the Amazon River. *Callicebus hoffmannsi* also diverged along the upper course of the Rio Tapajós into the recently described taxon *Cal. vieirai* (ranging between the Rios Juruena and Teles Pires), which is near-albinotic.

When a taxon is occupying a given interfluvial distribution delineated by hard to traverse river barriers, it has irreversibly changed its pelage or parts of its coat (e.g., beard, sideburns, ear-tufts,

forehead, tail, hands, feet) following the eumelanin pathway from agouti or saturated eumelanin to albinotic (cream or white), via black, brown, drab, and gray, and/or the pheomelanin pathway via red, orange, and yellow, or a combination of the two pathways in different parts of the body or coat. The trend to albinotic in the *Cal. moloch* Clade is completed near its northernmost dead-end distribution in the all-cream to white new form that we happened to identify along the right bank of the Rio Mamurú (Fig. 21). It must have derived from dark-tailed but cream-bearded and -bellied *Cal. hoffmannsi*. Following the trend to allopatry, this color morph (or ecospecies or 'taxon in the making?') is pushed with the back against the várzeas (white-water floodplain forests) and right bank of the untraversable Rio Amazonas. *Callicebus moloch* Clade's westernmost distribution is represented by the advanced pheomelanin bleached (bright orange

belly, beard and sideburns) to albinotic (white forehead, hands, feet and tail tip) taxon *Cal. bernhardi* which, in turn, is pushed with the back against the also untraversable Madeira River.

Among the Titi Monkeys of the *Cal. cupreus* cladistic Group (Fig. 22), we consider *Cal. brunneus* the nearest to archetypic taxon. Centrally distributed, the overall agouti colored taxon *Cal. brunneus* radiated in northwestern direction via the

progressively pheomelanin bleached taxa *Cal. dubius* and *Cal. discolor* into the most pheomelanin bleached (light orange tail base, beard, sideburns, belly and inner limbs) to albinotic (snowwhite tail, hands, feet and front/blaze) white-fronted taxon *Cal. ornatus* that is distributed north of the Amazon in the Colombian Amazon. From *Cal. brunneus* southwards diverged the advanced pheomelanin bleached taxon *Cal. aureipalatii* in the Clade's

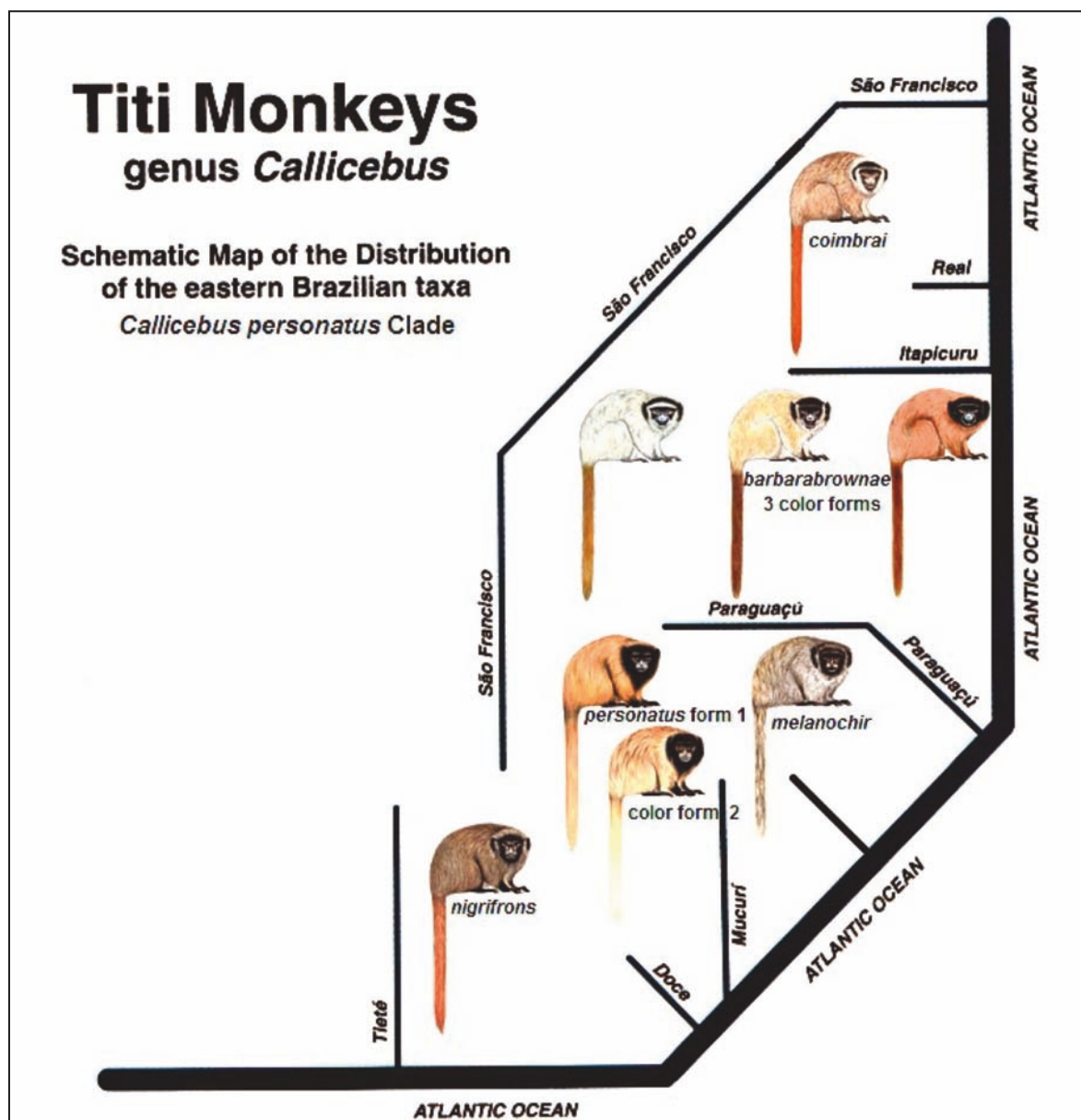


Figure 19. Schematic map of the distributions of the SE Brazilian or Atlantic Forest Titi Monkeys of the *Callicebus personatus* Clade, which are separated by (for these taxa) untraversable rivers.

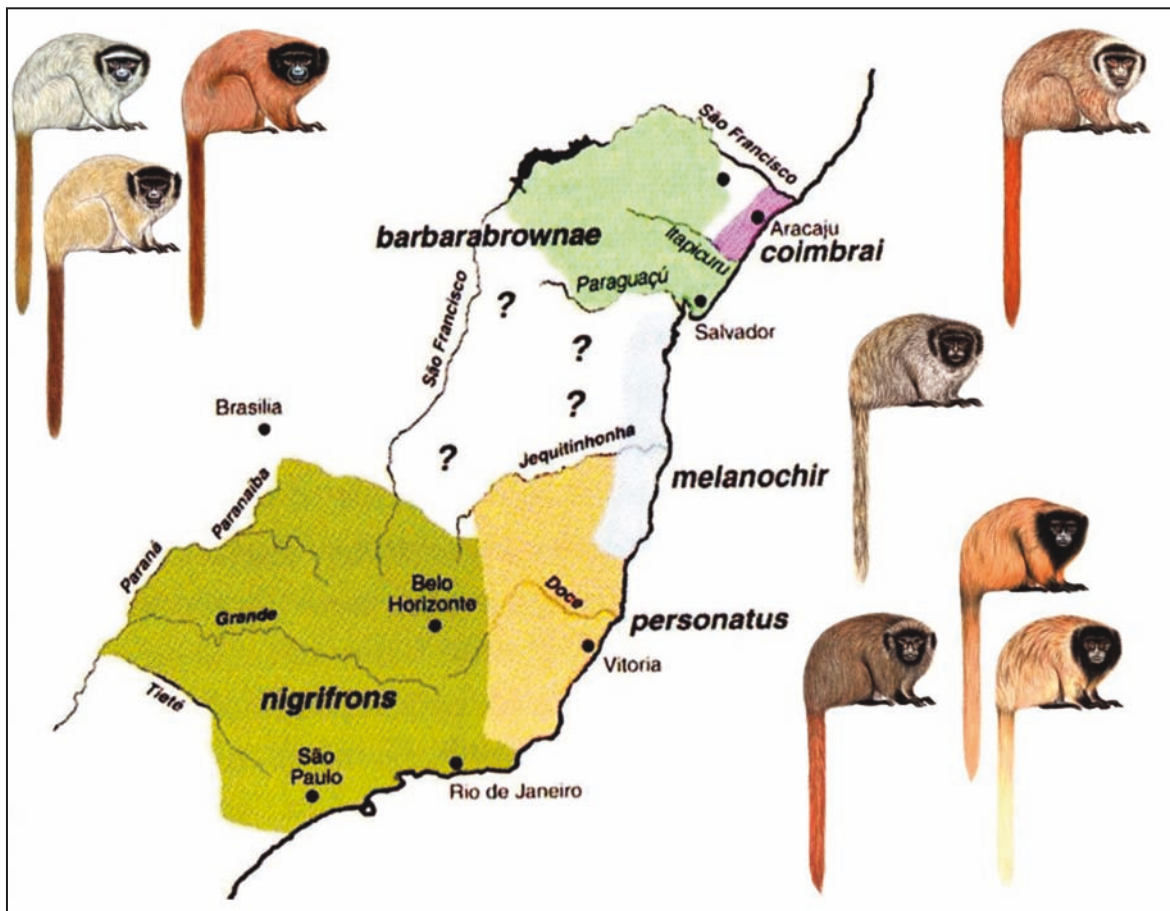


Figure 20. Distributions, allopatric speciation, radiation and supposed pathways of metachromic bleaching in all known SE Brazilian or Atlantic Forest Titi Monkeys of the *Callicebus personatus* Clade.

southernmost distribution (the Bolivian Amazon between the Rios Madre de Dios and Beni). From *Cal. brunneus* radiated away in northern direction first the slightly pheomelanin bleached taxon *Cal. cupreus* that now occupies a large interfluvial area west of the Rio Purús and south of the Rio Solimões. After an ancestral founder-colony of *Cal. cupreus* managed to traverse the Rio Purús to the east, it diverged into the advanced pheomelanin bleached all-orange, but white-tailed taxa *Cal. caligatus* and *Cal. stephennashi* in the northeasternmost dead-end part of *Cal. cupreus* Group's distribution, as the Rio Madeira represents the second strongest riverine barrier on the South-American continent. Last but not least, also from *Cal. cupreus* derived in northwestern direction the recently described, advanced pheomelanin bleached taxon *Cal. caquetensis* that at present occupies

a small, not yet fully identified area north of the Amazon and Caquetá Rivers in the Colombian lowland Amazon, allopatric with and south of the distribution of the white-fronted titi *Cal. ornatus* (Fig. 17).

Among the Titi Monkeys of the *Cal. donacophilus* cladistic Group (Fig. 17), we consider the overall agouti-colored taxon *Cal. modestus* the most original, nearest to archetypic taxon. It occupies the Clade's northernmost distribution delineated by the Rios Beni and Mamoré. It radiated southwards into the slightly pheomelanin bleached orange-brown taxon *ollalae*. Following a eumelanin bleaching pathway, *Cal. modestus* also radiated in southeastern direction, first into the near-albinotic taxon *Cal. donacophilus*, and from there into the fully albinotic taxon *Cal. pallescens*. The latter nowadays occupies the southernmost dead-end

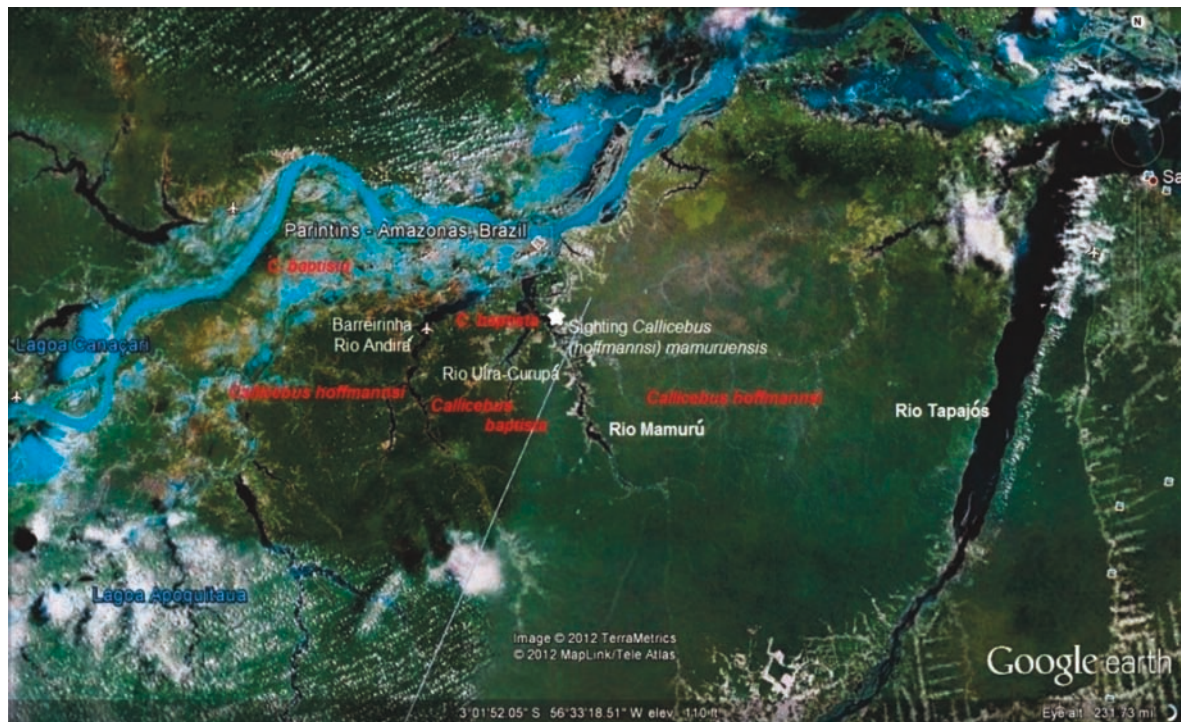


Figure 21. Distributions of *Callicebus baptista*, *Ca. hoffmannsi*, and the “Rio Mamurú titi” - the latter perhaps to be considered a new taxon or one ‘in the making’. This satellite image shows the location of an enclave population of fully albinotic titi monkeys that we have found to exist along the right bank of the Rio Mamurú. This population is on the verge of extinction as it is pushed with the back against for titis inhospitable habitat - the seasonally inundated floodplain forest (várzea) along the Rio Amazonas and the outskirts of the rapidly expanding town of Parintins in the north, and lands occupied by *Ca. hoffmannsi* stretching to the east as far as the Rio Tapajós. The species *Ca. baptista* belonging to the *Ca. moloch* Clade originally ranged only north of Paran  do Canum , P. do Urari  and P. do Ramos, east of the lower Rio Madeira, south of the Rio Amazonas and west of the Paran  do Ramos. South of this narrow distribution evolved the species *Ca. hoffmannsi*, which occupies a large distribution between Rio Canum  in the west, Rio Tapaj s in the east, and Rio Amazonas in the north, east of Paran  do Ramos and Rio Mamur . Baptist’s Titi is much more colorful being dark to bright red on the ventral parts and lower limbs, having a red beard and red sideburns, whereas the rest of its body is grayish to blackish agouti. Hoffmann’s Titi is basically two-colored grayish and yellowish-white to almost white, its sideburns and beard being light cream-white. However, we spotted the *Ca. baptista* titis also along the west bank of the Rio Uira-Curup , hence it once must have traversed the Paran  do Ramos west of the town of Parintins, forming an enclave population there after it displaced Hoffmann’s titis from the interfluvium delineated by the lower Rio Uira-Curup  and Rio Andir . We also spotted advanced metachromic bleached, near-albinotic, pale yellowish to all-white ‘color morphs’ being phenotypically most related to *Ca. hoffmannsi* along the Rio Mamur , the next river to the east, and classic yellowish- white and gray *Ca. hoffmannsi* with black tails along both banks of the middle and upper Rio Andir . These observations may confirm a case of what is called parapatry. The two valid species *Ca. hoffmannsi* and *Ca. baptista* that are allopatric for the greater part of their distributions - phylogeographically separated from one another by untraversable water bodies - exclude one another where *Ca. baptista* happened to traverse a riverine barrier and subsequently replaced the local *Ca. hoffmannsi* population. There, both taxa live parapatric, meaning in adjacent ‘patrias’ not separated by geographic barriers, where gene flow in theory is possible, but in reality does not occur. A plausible explanation would be that the two taxa have already diverged too far from one another. One could only speculate about the future of the fully albinotic form seen along the right bank of the Rio Mamur . It may represent a founder-colony or population of metachromic progressively bleached individuals that have been driven into parapatry by the *Ca. hoffmannsi* populations found to the east and south of Rio Mamur  as far as the Rio Tapaj s. The Rio Mamur  titis eventually might go extinct, unless they manage to adapt to (for titis) inappropriate habitat - the extensive v rzas along the right bank of the Rio Amazonas. If the founder-colony, following the trend to allopatry, would successfully adapt to the ecological niche of v rzea, then a new taxon could derive from *Ca. hoffmannsi*. Through inbreeding, the currently adopted euechromic coat coloration would stabilize phenotypically across the entire population of that new taxon in a relatively short period of time. The hypothetical evolutionary path would then go from a metachromic fully bleached, near-albinotic color morph in a dead-end distribution to a new taxon belonging to the monophyletic *Ca. moloch* Clade. In that case, we would have to name the Rio Mamur  Titi Monkey *Ca. mamuruensis*.

distribution of the *Cal. donacophilus* Clade, penetrating far into the arid Chaco of Paraguay and the pampas of Argentina. A new species of titi, recently collected by the Brazilian ornithologist Marcelo Vasconcellos in the Chiquitanos area along the Rio Paraguay in the Pantanal of Mato Grosso do Sul (for which taxon we identified the holotype in the zoological collection of the AMNH, in 1977 collected by George Schaller and misidentified as *Cal. donacophilus*), represents the easternmost distributed taxon of the *Cal. donacophilus* Clade. Except for its dark gray ears (white in *Cal. donacophilus*), the Chiquitanos titi is overall more pheomelanin bleached towards albinotic than *Cal. donacophilus*, but less so compared to *Cal. pallescens*. Furthermore, from *Cal. modestus* derived in northwestern direction the advanced pheomelanin bleached near-albinotic taxon *Cal. oenanthe* that is nowadays found isolated in a small area in the east-Peruvian Amazon, south of the Río Marañón.

Among the Collared Titis of the *Cal. torquatus* cladistic Group (Fig. 18), we consider the saturated eumelanin black-handed taxon *Cal. medemi* with the westernmost distribution north of the Amazon River the nearest to archetypic form from which derived the all-black but yellow-handed titi from the southbank of the Rio Negro - a newly identified, as yet to be described taxon - and from that taxon derived the all-black, dorsally slightly reddish-tinged taxon *Cal. lugens* with the northernmost distribution of the *Cal. lugens* sub-Clade. From archetypic *Cal. medemi* south of the Rio Caquetá derived, first in eastern direction the dorsally pheomelanin bleached taxon *Cal. lucifer*. Some ancestral founder-colony of the new Rio Negro southbank species then must have managed to traverse the lower Rio Solimões somewhere between the mouth of the Rio Purús and that of the Rio Madeira. From there, collared titis could radiate away back in western direction, though south of the Amazon River, into the further pheomelanin bleached, overall reddish-brown colored white-handed taxa *Cal. torquatus* and *Cal. purinus*, and, after traversing the Rio Juruá, into the advanced pheomelanin bleached red-handed red-fronted taxon *Cal. regulus*.

Within the SE Brazilian Titi Monkeys of the *Cal. personatus* Clade (Figs. 19–20) the nearest to archetypic, most saturated eumelanin taxon is *Cal. melanochir*. It ranges along the Atlantic coast south

of the Rio Paraguaçu in the center of dispersion of the personatus Clade. From *Cal. melanochir* derived in northern direction along the pheomelanin pathway the advanced pheomelanin bleached (all-orange colored) taxon *Cal. barbarabrownae*, and, in a small dead-end distribution delineated by the untraversable lower Rio São Francisco in the north and the Atlantic Ocean in the east derived the almost fully bleached, near-albinotic taxon *Cal. coimbrai*. Radiating in southern direction, ancestral *Cal. melanochir* diverged along the eumelanin pathway into the orange-tailed, but overall dark brown-colored taxon *Cal. nigrifrons*, and along the pheomelanin pathway into the advanced pheomelanin bleached, all-orange colored and near-albinotic taxon *Cal. personatus*.

Within the Squirrel Monkeys genus *Saimiri* (Fig. 22), we phylogeographically distinguish two monophyletic Clades: *Sa. sciureus* - including the Central-American *Sa. oerstedii* sub-Clade - and *Sa. boliviensis* - including the Bare - ear *Sa. ustus* sub-Clade (Hershkovitz, 1984). It is inferred that the genus *Saimiri* evolved relatively recently, with crown lineages diverging as late as the Pleistocene (ca. 1.5 MYA) and other major Clades diverging between 0.9–1.1 MYA. Concurring with Chiou et al. (2011), we include *Sa. oerstedii* in the monophyletic *Sa. sciureus* Clade that originated in the Guianas. North of the Amazon, it radiated in western direction and diverged first into *Sa. cassiquiarensis*, a taxon that is nowadays distributed across the entire Rio Negro basin, its distribution in the south delineated by the Rio Japurá/Caquetá and the lower Rio Solimões. From *Sa. cassiquiarensis* diverged in northern direction the advanced bleached, least colorful taxon *Sa. albigena* that ranges allopatric (north of the Río Guaviare) in the southwesternmost part of the Río Orinoco basin. In concurrence with Chiou et al. (2011), who found evidence for monophyly in the *Sa. sciureus* and *Sa. oerstedii* Groups, we suggest that from *Sa. albigena* or some ancestral precursor of it derived and radiated away in northwestern direction the advanced pheomelanin bleached taxa *Sa. oerstedii* and *Sa. citrinellus*. These now range in *Sa. sciureus* Clade's disjunct northwesternmost dead-end distribution - along the Pacific coast of Panama and Costa Rica. Along a different metachromic pathway derived from *Sa. cassiquiarensis* in southern direction the advanced bleached taxon *Sa. macrodon*. Its distri-

bution is delineated by the Ríos Guaviare and Apaporis in Colombia, and the Rio Japurá in Brazil, and south of the Amazon by the upper Río Marañón in the west, and the Rio Juruá in the east. Within its large distribution, *Sa. macrodon* is excluded from the Ríos Huallaga/Ucayali interfluvium in the Peruvian Amazon that is occupied by *Sa. peruviansis*. In the Guianas, *Sa. sciureus* once managed to traverse the lower Amazon River to the south. As it is a riverbank marsh and mangrove forest specialist, *Sa. sciureus* must have colonized the south bank of the Amazon after reaching it on floating islands covered with várzea or mangrove vegetation. From *Sa. sciureus* south of the Amazon subsequently derived the recently described, advanced bleached near-albinotic taxon *Sa. collinsi* that is confined to Marajó Island - the *Sa. sciureus* Clade's easternmost dead-end distribution delineated by the Atlantic Ocean, and the Amazon and Pará Rivers.

The second monophyletic Clade of Squirrel Monkeys, the *Sa. boliviensis* Clade, has originated in the extensive white-water floodplain forest (várzea) near the confluence of the Japurá and Solimões Rivers. The lower Japurá/Solimões interfluvium does not contain any terra firme. It is seasonally flooded over 6–8 months. Here lives the nearest to archetypic, saturated eumelanin taxon of the *Sa. boliviensis* Clade, *Sa. vanzolinii*. It is overall agouti and black colored, representing the only extant squirrel monkey with an all-black tail. A somewhat bleached *Sa. vanzolinii* founder-colony once must have reached (swimming or on a floating várzea island) the south bank of the Rio Solimões east of its confluence with the Rio Juruá. There evolved from it the somewhat pheomelanin bleached, orange to yellowish taxon *Sa. boliviensis*. It then occupied east of the Rio Juruá the entire area delineated by the lower Purús, upper Madeira and Guaporé

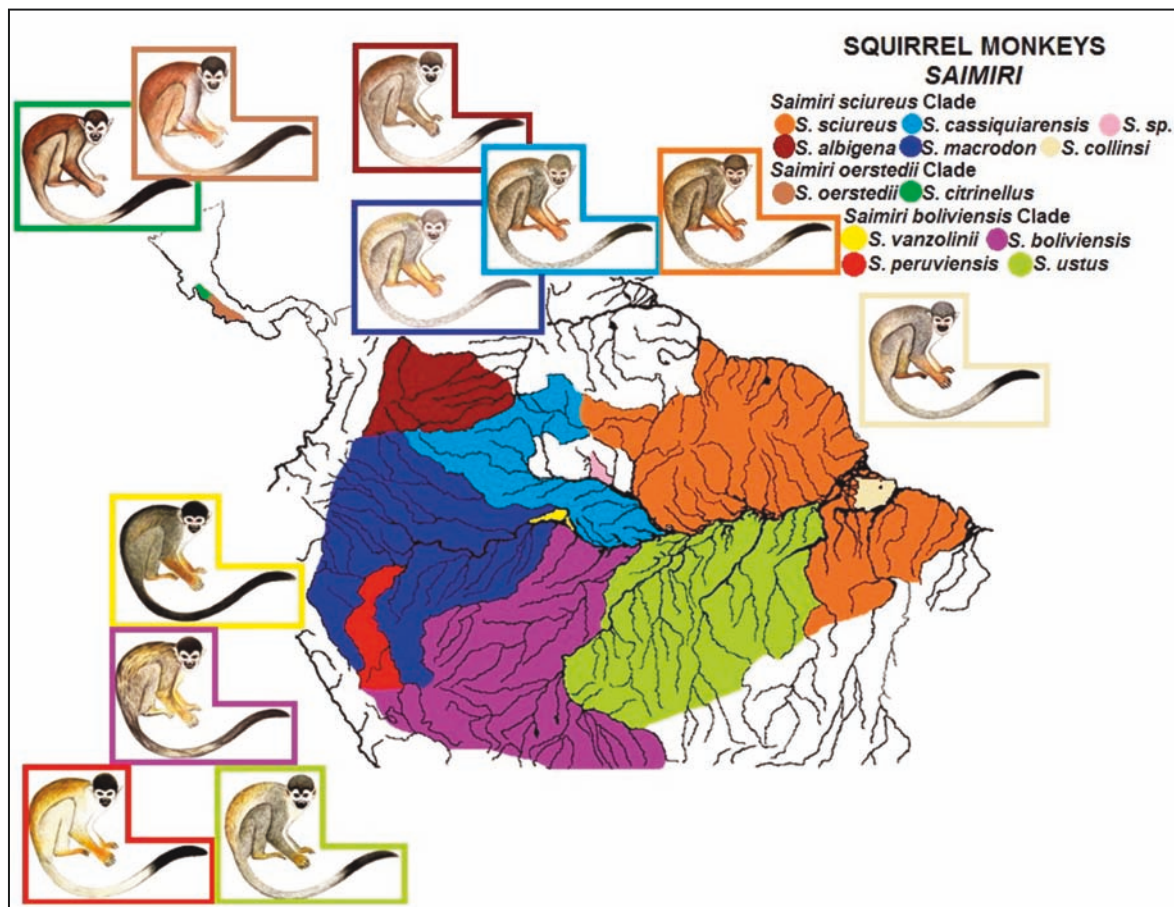


Figure 22. Distributions, allopatric speciation, radiation and supposed pathways of metachromic bleaching in all known Squirrel Monkeys genus *Saimiri* divided up in the *S. sciureus* and *S. boliviensis* Clade.

Rivers, whereas in the south it extended its range far into the Peruvian and Bolivian Amazon. After a founder-colony of somewhat bleached *Sa. boliviensis* happened to traverse the easternmost river barrier, it diverged into *Sa. ustus* - the least colorful, most eumelanin bleached taxon of the *Sa. boliviensis* Clade. Its distribution is confined by the Amazon River in the north, the Rio Xingú in the east (separating the distributions of *Sa. ustus* and *Sa. sciureus*), and the Rio Guaporé in the south. Furthermore, from *boliviensis* in its southwesternmost distribution in the Peruvian Amazon derived the progressively pheomelanin bleached near-albinotic, most colorful taxon *Sa. peruviansis*. It occupies a dead-end distribution - the interfluvium delineated by the Ríos Huallaga and Ucayali - as it is surrounded by *Sa. macrodon* occupied territory.

Historically followed metachromic and phylogeographic pathways, intraspecifically pushed ahead by the trend to allopatry and the principle of metachromic bleaching, within a genus or monophyletic Group of primates may be traced back most expressively, when we examine the distributions, speciation and radiation of all extant Uakari Monkeys genus *Cacajao* (Figs. 23, 24). This exclusively Amazonian genus contains two monophyletic Groups or Clades: the Black-headed Uakaris of the *Cac. melanocephalus* Group, and the Bald-headed Uakaris of the *Cac. calvus* Group (Hershkovitz, 1987a). Among Uakaris, the supposedly nearest to archetypic (prototypic) ancestral form is represented by the extant Black-headed Uakaris, more in particular by the saturated eumelanin, all-black taxon *Cac. ayresi* - the north-easternmost distributed among all Uakaris.

Uakaris are the only monkeys in the Neotropics that lost a functional tail. All other genera evolved either a long pendulous, short-hairy to bushy tail that is in the first place designed to use for balance while moving through the tree tops; or, a long prehensile tail that is used as a fifth limb during vertical climbing and walking on top of or brachiating underneath twigs and thin branches in the periphery of tree tops (where the fruits are hanging). Only after observing Black-headed Uakaris *Cac. hosomi* in the wild along the Rio Cauaburi and in Pico da Neblina National Park, we came to understand why the region drained by the Rio Negro has to be considered the center of dispersion for all uakaris, in other words the cradle of evolution of the genus

*Cacajao*. Simultaneously, we came to understand the very reason why uakaris have lost a functional tail, whereas in all other canopy-dwelling monkeys from the Amazon it seems to be a fifth limb of vital importance.

Across the entire upper Rio Negro basin the type of vegetation that dominates the landscape is a very impoverished sort of thin-stemmed savanna forest. It stands on poorly drained, highly acidic white-sand soils that are deposited on top of an impermeable, several meters thick layer of coarse rounded pebbles. This type of forest is called “caatinga-do-Rio-Negro”, for it resembles much the arid dry seasonally deciduous vegetation in large parts of the Brazilian northeast. It seasonally floods during the long rainy season, but also throughout the year on a daily base during heavy rainstorms. Physiognomically, this forest type resembles two-storey mangrove forest, as most of its trees use pneumatophores (aerial roots) and stilt-roots to cope with frequent flooding conditions. Phytosociologically, the ‘caatinga-do-Rio-Negro’ is dominated by trees belonging to families like Euphorbiaceae and Apocynaceae, known for their often toxic latex and plant parts, most in particular full-grown seeds. Surprisingly, this forest lacks hemi-epiphytic climbing shrubs, vines, and twiners. Over geological times Black-headed uakaris seem to have co-evolved with this natural environment through specializing themselves in the depredation of immature seeds. From early maturation on, the seeds are often loaded with toxic alkaloids and secondary compounds. Uakaris have guts that are specially adapted to neutralize these toxins. Their canines are oversized and wedge-shaped with razorblade sharp edges, as such adapted to open up the toughest-husked fruits and kernels (endocarps) around. Their incisors are procumbent and used to scoop out the seed content (endosperm) from any endocarp or pericarp. Uakaris are full-fashioned seed predators to such length that, if one offers a uakari a juicy pear or apple, the monkey will instantly bite the pulpy pome in half with its powerful canines. Then, it will pick the tiny seeds from the central part, discard the pulp, and delicately split the tiny seeds one by one with their canines. In the end, it has its procumbent incisors scoop out the endosperm from the seed coat. Black-headed uakaris do occupy very large home ranges. They restlessly travel or forage in very large multi-male dominated

social groups that may contain over two-hundred monkeys. Since their preferred habitat 'caatinga-do-Rio-Negro' basically lacks climbing shrubs, the tree tops are not interlinked by vines, twiners and climbing hemi-epiphytes as they are in primary terra firme rain forest elsewhere in the Amazon. By lack of a walkway through the tree tops, Black-headed uakaris co-evolutionarily have adapted to this ancient impoverished, physiognomically discontinuous and frequently inundated forest type by developing the locomotor pattern of so-called 'vertical clinging and leaping'. A traveling or foraging troop of Black-headed uakaris much resembles Madagascar indris, *Indri indri* (Gmelin, 1788) that also make enormous leaps, catapulting themselves for - and upwards by means of their strong muscular upper legs. Like indris in Madagascar, black-headed uakaris lost most of a functional tail while adapting to this type of locomotion. The few cm long tail provided with a tuft is only used for intragroup communication. Black-headed uakaris can curl it upwards and wave it sideways like dogs would do with a largely amputated tail.

Black-headed uakaris of the species *Cac. hosomi* and *Cac. ayresi*, distributed north of the Rio Negro, east of the Cassiquiare and west of the Rio Demeni, and *Cac. melanocephalus* from south of the Río Orinoco, west of the Cassiquiare and north of the lower Rio Solimões and Rio Japurá/Rio Caquetá, have a pitch-black face, a black, forward directed hair-tuft on the forehead, and a short blackish, red or orange-tinged tail. Black-headed uakaris from the Rio Içana basin, being distributed in-between the upper Río Orinoco and the lower Rio Uaupés, show a black upper back and pheomelanin bleached, orange to blond bleached lower back. Perhaps, for that reason they should be taxonomically treated as a valid species (we here suggest *Cac. ouakary*).

The Bald-headed Uakaris of the *Cac. calvus* cladistic Group, which range south of the Amazon/Solimões and Japurá Rivers, have a bald head, bright-red bare face, blue-gray eyes, a shaggy pheomelanin bleached, near-albinotic coat, and a rudimentary tail that is shorter and even less functional than the tail of Black-headed Uakaris (Figs. 23, 24). The *Cac. calvus* Group contains five taxa which according to our phylogenetic ecospecies concept (ESC) should be all given valid species status: 1) *Cac. calvus* living exclusively in the white-water

floodplain forests (várzeas) between the lower Japurá and Solimões Rivers, being cream-white with pheomelanin bleached, orange-brown ventral parts; 2) *Cac. novaesi* occurring in disjunct pockets along both banks of the lower and middle Rio Juruá as far upstream as its confluence with the Rio Tarauacá, its coat being pheomelanin bleached, orange brown-colored, but albinotic from the back of the head to mid-dorsum; 3) *Cac. rubicundus*, the pheomelanin bleached, bright orange-colored (except for the albinotic cream-white back of the head and neck) bald-headed *Cac. uakaris* that occurs in the white-water floodplain forests (várzeas) along the left bank of the upper Rio Solimões in the central-westernmost Brazilian Amazon; 4) *Cac. ucayalii*, its coat overall saturated pheomelanin, dark brown to orangish colored, ranging in the Peruvian Amazon along the right bank of the Ucayali River in the white-water inundated floodplain forest (várzea) as well as adjacent terra firme rain forest; 5) a form newly identified by us in the year 2000, its coat near-albinotic, advanced euchromic bleached to all-white. We provisionally name this new taxon the "Rio Pauini Bald-headed Uakari" *Cacajao* sp., for it is only found in the várzeas along the upper Rio Pauini, a left-bank tributary of the Rio Purús (Figs. 23, 24).

The 'trend to allopatry in metachromic varieties of sociable, but territorial primates' applies to the evolutionary path along which a certain primate race, species, monophyletic clade, or genus has extended its geographic range in the geological past. As a founder - colony or - population at the outer limit of a taxon's current range represents an extremely narrow gene pool, through inbreeding certain phenotypic characters like partial depilation of the skin, or skin/coat coloration will be reinforced in the beginning and therefore advance more rapidly.

Through the process of metachromism (= evolutionary change in tegumentary or hair/skin coloration), with the 'trend to allopatry' in metachromic bleached individuals as the principal behavioral driving force, speciation, radiation, and phylogeography can be plausibly retraced and explained for in all extant Neotropical primates. According to the principle of metachromic bleaching, primate taxa at the base of a phylogenetic tree or clade being the nearest to archetypic, prototypic, primitive, or original, in general are agouti or saturated eumelanin,

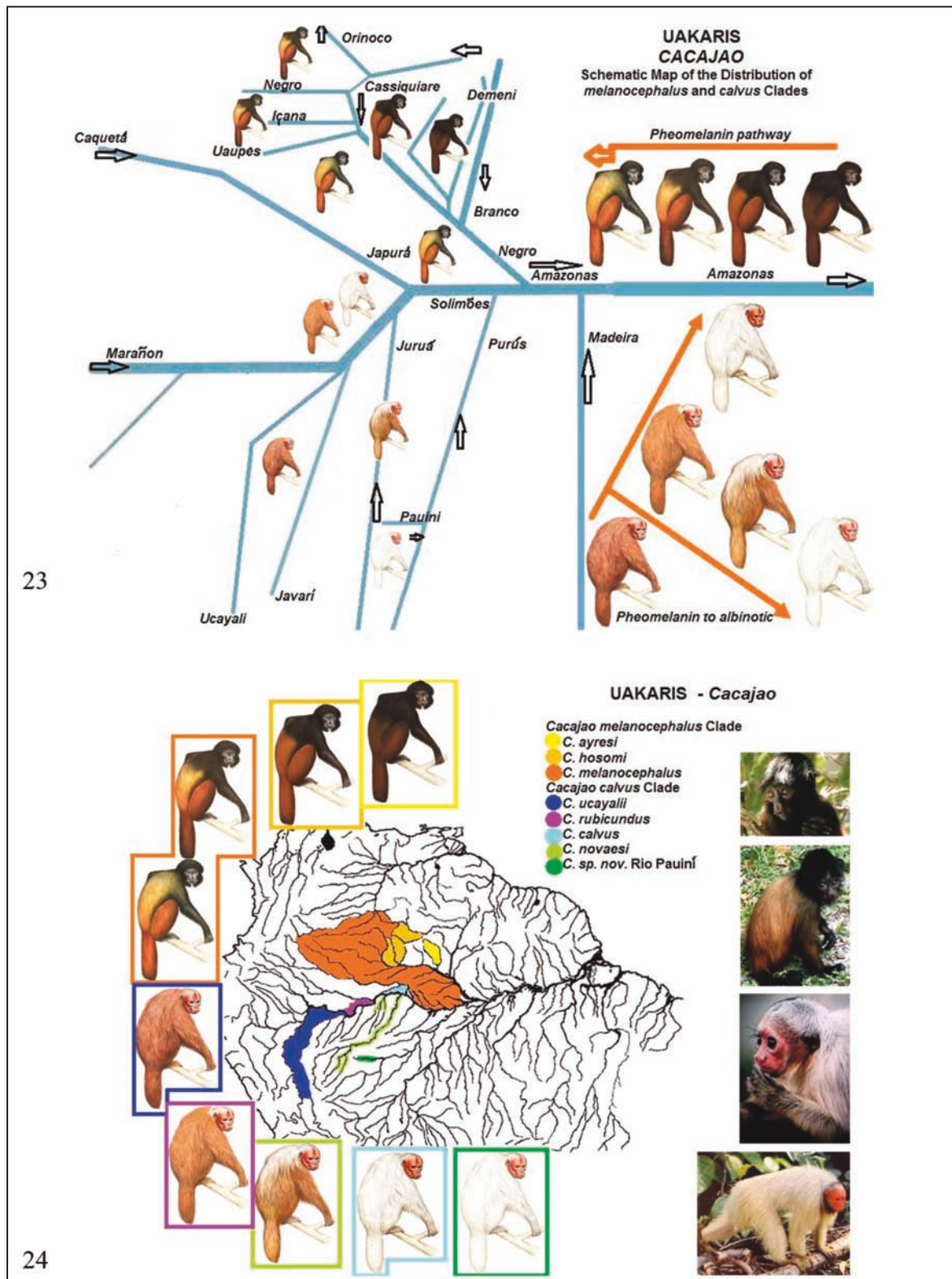


Figure 23. Schematic map of the distributions of Uakari Monkeys of the *Cacajao melanocephalus* and *C. calvus* Clades divided up by (for them) untraversable rivers. Figure 24. Distributions, allopatric speciation, radiation and supposed pathways of metachromic bleaching in all known Uakari Monkeys genus *Cacajao*.

which means the least colorful, agouti, black, or dark brown colored. Among Uakari Monkeys genus *Cacajao*, the origin or center of dispersion is supposed to be located in the northeasternmost part of the Brazilian Amazon, south of the watershed between the Rio Negro and Río Orinoco basins, an area delineated by the Rios Demeni and Aracá (Figs. 23, 24; Fig. 27). Within this interfluvium the landscape is dominated by 'caatinga-do-Rio-Negro', the most impoverished habitat type imaginable, but preferred by uakaris of the *Cac. melanocephalus* Clade. Here lives the saturated eumelanin, least bleached taxon of the Black-headed Uakaris, the recently described *Cac. ayresi* (Boubli et al., 2008). Its coat is all-black and dark-brown colored. It may well represent the proto- or archetypic uakari from which all other *uakaris* have derived. From *Cac. ayresi* in western direction first diverged along the pheomelanin pathway taxon *Cac. hosomi*. It is distributed between the Rio Marauíá, the upper Rio Negro, and the Cassiquiare Channel (we have confirmed its presence in Pico da Neblina National Park and along both banks of the Rio Cauaburi). After an ancestral founder-colony traversed the Rio Cassiquiare - the channel that connects the Rio Negro basin with that of the Río Orinoco in Venezuela - *Cac. hosomi* diverged into an intermediately pheomelanin bleached taxon that differs from classic *Cac. melanocephalus* in the black shoulders, dark-red legs and tail. If this phenotype, which is thought to represent a color morph of *Cac. melanocephalus*, turns out to occur throughout the entire distribution delineated in the north by the Río Orinoco and in the south by the Rio Uaupés, one should consider it a new taxon to be named the "Rio Içana Black-headed Uakari" *Cac. ouakary*. After an ancestral founder-colony of the latter managed to traverse the Rio Uaupés, it has diverged into the progressively pheomelanin bleached blond-backed black-headed uakari taxon *Cac. melanocephalus*. Subsequently, blond-backed *Cac. melanocephalus* have occupied the entire interfluvium south of the Rio Negro, eastwards as far as Archipelago de Anavilhanas located about forty km west of Manaus, and to the west far into the Colombian Amazon, and south as far as the north bank of the Rio Japurá (Río Caquetá in Colombia). We suppose that once upon a time a founder-colony of slightly bald-headed, advanced pheomelanin bleached ancestral *Cac. melanocephalus*, being

pushed out of its westernmost dead-end distribution in the Colombian Amazon, may have managed to traverse the upper reaches of the Río Caquetá. It then could extend its range southwards, eventually reaching the Río Marañón (as the upper Amazon River is called in Peru). A founder - colony of an advanced pheomelanin bleached, bald-headed ancestral form must then have traversed the Río Ucayali. It subsequently occupied terra firme and várzea forests in the interfluvium between the Río Ucayali in the west, the Río Marañón in the north, and the Rio Javari in the east. Nowadays, this interfluvium is inhabited by the bald-headed dark reddish-brown taxon *Cac. ucayalii* that belongs to the bald-headed *Cac. calvus* Clade. Disjunct from *Cac. ucayalii*'s distribution and ranging farther to the east derived taxon *Cac. rubicundus*, a progressively pheomelanin bleached bright- orange colored bald-headed uakari. It is fully adapted to várzea habitat found in abundance along the left bank of the upper Rio Solimões. From *Cac. rubicundus* going farther eastwards, but disjunct from its distribution, along the same (left) bank of the Solimões/Amazon River the almost fully albinotic taxon *Cac. calvus* is found. It fully adapted to white - water inundated floodplain forest (várzea) - the only available habitat in this for the *Cac. calvus* Clade dead-end distribution situated inbetween the banks of the Japurá and Solimões Rivers. Directly from *Cac. rubicundus* to the south of *Cac. calvus*' distribution derived the bald-headed taxon *Cac. novaesi* that ranges along both banks of the Rio Juruá as far south as the confluence with the Rio Tarauacá and Rio Envira. This taxon is near-albinotic from the back of the head to beyond the mid-dorsum, and progressively pheomelanin bleached light orange-brown on the lateral and ventral parts of the body. It ranges in the várzeas of the floodplain, but we have also spotted large troops foraging for immature seeds in the adjacent terra firme rain forest.

In 2000, we identified a fifth taxon of bald-headed uakari, the completely white, fully albinotic taxon that we named "Rio Pauini Bald-headed Uakari" *Cacajao* sp. It lives along the south bank of the Rio Pauini, a left-bank tributary of the upper Rio Purús. It represents the southernmost distributed and the farthest pheomelanin bleached most albinotic taxon of all extant uakaris. It lacks the pheomelanin orange-brown to orange

ventral parts seen in the other near-albinotic taxa *Cac. novaesi* and *Cac. calvus* (Figs. 23, 24).

Analyzing metachromic skin and coat characters as linear and irreversible progressions within Neotropical primate genera and their monophyletic Clades does add substantially to the reconstruction of biogeographic divergence events and phylogenetic relationships over a wide range of Neotropical primate taxa, in particular those that defend their living space or ecological (feeding) niche through male-dominated, hierarchically organized societies. So it does to the Bearded Sakis genus *Chiropotes* (Figs. 25, 26) even if we have confirmed in the field that social groups of (at least) the Guianan taxon *Ch. sagulatus* do freely fuse and fission on a regular base with neighboring social groups. The genus *Chiropotes* clearly shows sexual dimorphism in the larger, more robust males that also grow bigger beards and frontal hair lobes on their heads (Hershkovitz, 1985). During foraging and resting, a large social group of bearded sakis, similar to woolly monkeys, consists of several polygamous dominant males each taking care of his 'harem'. The high-ranking males tend to stick to the center of the foraging troop, whereas lower ranking males with or without harems are pushed closer to the periphery of the foraging troop. This way, adult males do avoid confrontations, for their impressively large wedge-shaped canines designed to crack hard-husked fruits and kernels in order to get to the seed pulp would be lethal if used in fights. But adolescent, subadult, and, we assume, also behaviorally or phenotypically deviant individual males may well be pushed into the periphery of the foraging and ranging troop. More than once, we have encountered a solitary male, or a couple of males traveling at high speed through the canopy in an apparently fixed direction, leaving us no means to determine if these monkeys only temporarily had lost contact with the troop, or if they were expelled from the parental troop, or if they were representing subtly deviant young males that had been forced to leave the pack and search for new living grounds somewhere beyond the limits of the group's home range. Only through long-term field studies one would be able to obtain clear answers to this sort of questions.

Within the Bearded Sakis genus *Chiropotes* we distinguish two monophyletic Groups: the *Ch. satanas* and the monotypic *Ch. albinasus* Group.

The *Ch. satanas* Clade consists of five taxa, among which the nominate species *Ch. satanas* represents the saturated eumelanin, all-black, nearest to archetypic bearded saki. Its distribution in the NE Brazilian state of Maranhão is assumed to represent the cradle of evolution or center of dispersion for the genus. An equally all-black form that we recently identified west of the headwaters of the Rio Xingú (e.g., Rios Ronuro, Batovi and Vonden Steinen) may either represent an enclave population that became disjunct from that of *Ch. satanas* (ranging east of the Rio Pará/lower Rio Tocantins), or a new taxon of the *Ch. satanas* Clade that still has to be collected and described. From *Ch. satanas* diverged in western direction the slightly eumelanin bleached, overall light-brown colored taxon *Ch. utahicki*. It occupies the entire interfluvium delineated by the Rios Amazonas/Anapú/Tocantins-Araguaia/Xingú. An ancestral founder-colony of somewhat pheomelanin bleached, red to orange-brown backed *Ch. utahicki* once must have managed to traverse the lower Rio Amazonas, from which then derived taxon *Ch. sagulatus*. This species occupies the entire area north of the Amazon River and east of the Rio Branco, including most of the Guianas east of the Essequibo River. This taxon is absent from most of Amapá state, French Guiana and also from a wide coastal belt of the Guianas. A founder-colony of ancestral *sagulatus* once must have traversed the Rio Branco and radiated in western direction diverging into the advanced eumelanin bleached taxon *Ch. israelita*. This species is characterized by the albinotic (white instead of pink) genitals and the light-grayish to brownish coat color of the trunk. *Chiropotes israelita* ranges west of the Rio Branco as far north as the Río Orinoco in Venezuela. It seems to be parapatric with Black-headed Uakaris, as *Chiropotes* is a seed-predating terra firme rainforest specialist, and *Cac. ayresi* and *Cac. hosomi* are 'caatinga-do-Rio-Negro'-habitat specialists. The Rios Marauíá and Cauaburi seem to divide their distributions. Our extensive surveys in the Rios Demeni/Aracá interfluvium did not reveal the occurrence of *Ch. israelita*, as the landscape is dominated by 'caatinga-do-Rio-Negro' habitat (Figs. 26, 27).

The second monophyletic Group of Bearded Sakis is that of monotypic *Ch. albinasus*. The Red-nosed Bearded Saki is very different from the *Ch. satanas* Clade, not just in metachromic sense. Its

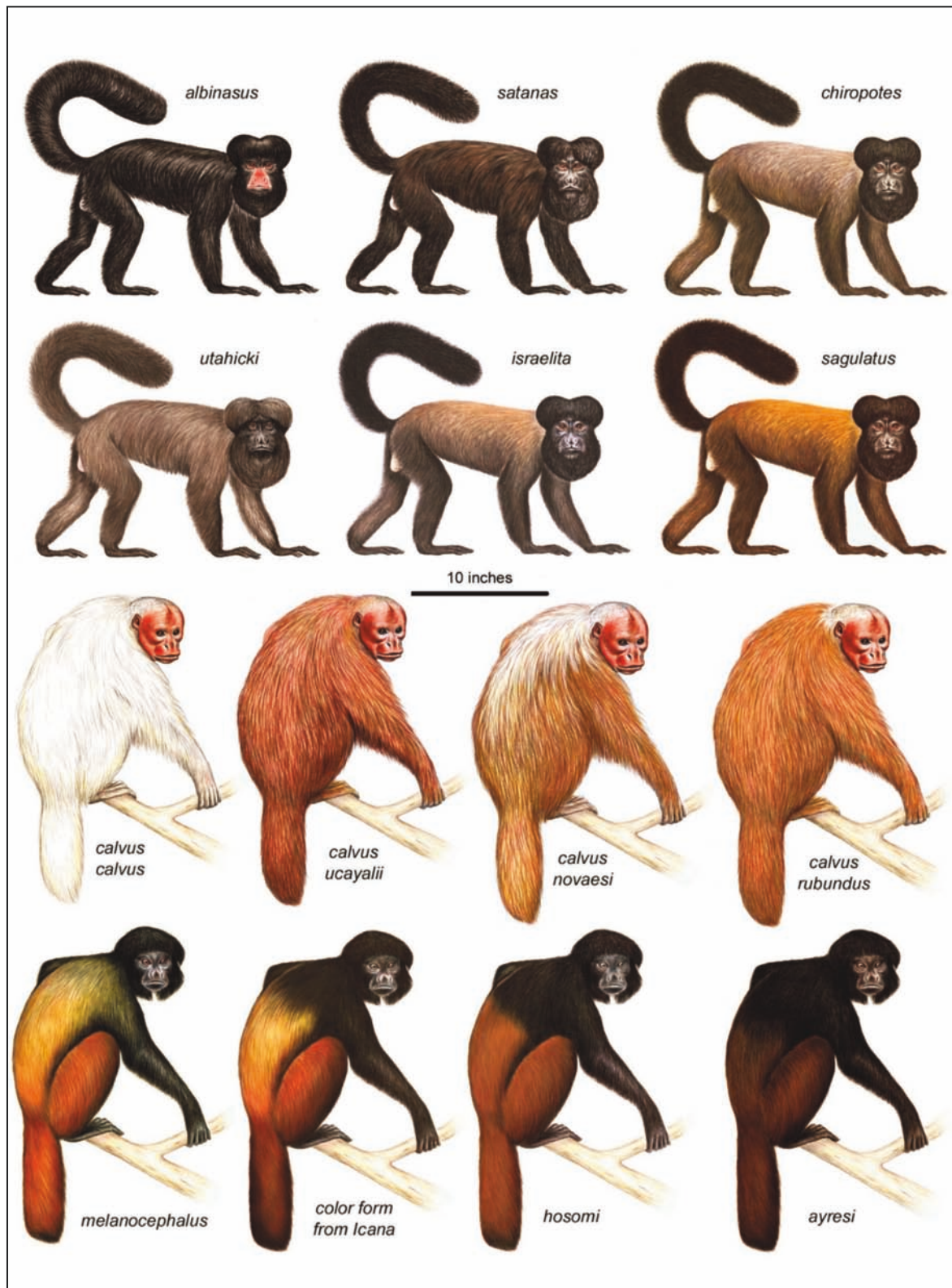


Figure 25. The hitherto recognized taxa of Bearded Sakis genus *Chiropotes* (above) and Uakaris genus *Cacajao* (below), all depicted in one plate (Courtesy of Stephen Nash).

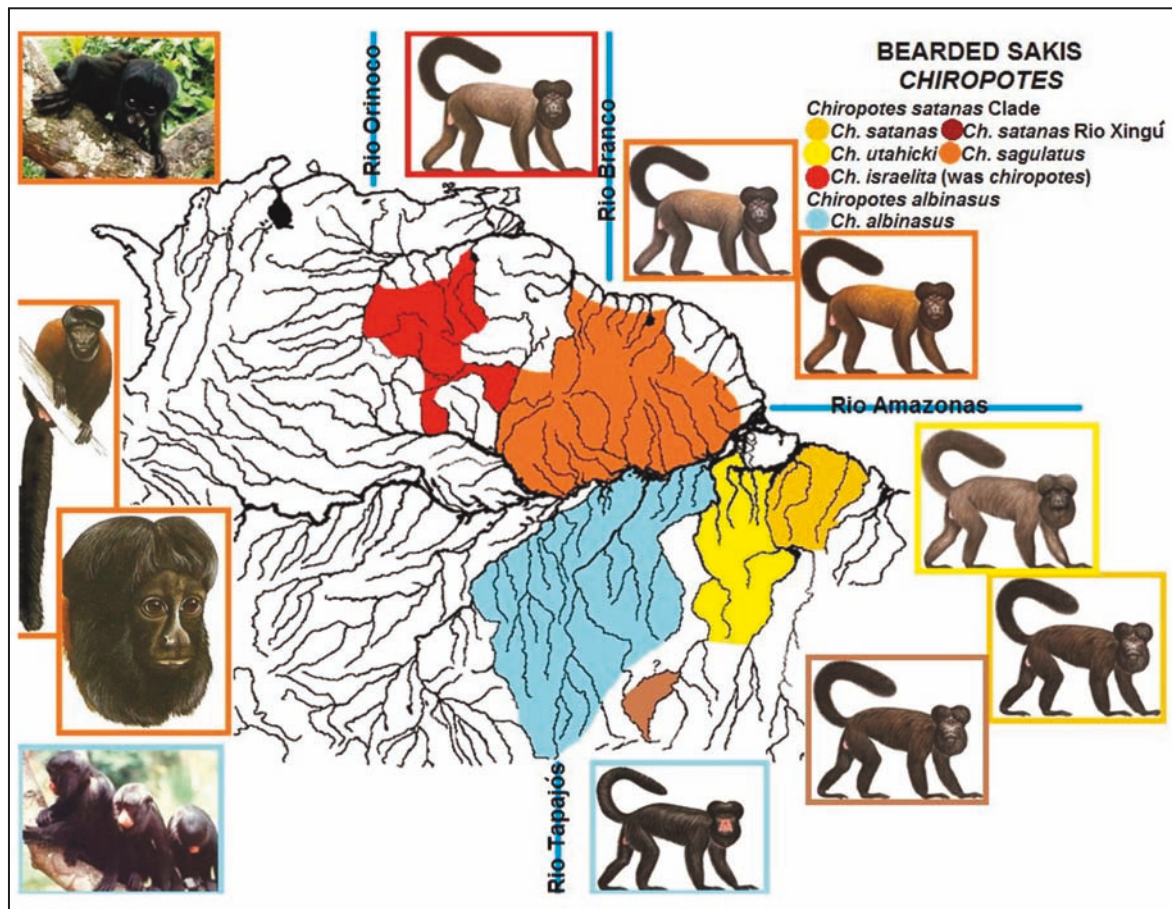


Figure 26. Distributions, allopatric speciation, radiation, and supposedly followed eumelanin pathways of metachromic bleaching in all known Bearded Sakis genus *Chiropotes*.

vocalizations are very different, the beard and tail are shorter-haired, and the genitals of each gender are brightly red-colored as is the muzzle (the scientific name *Ch. albinasus* - Latin for “white nose” - relates to the taxonomist, who may never have seen the monkey he described alive. Furthermore, group size in *Ch. albinasus* is much larger than that of any of the taxa belonging to the *Ch. satanas* Clade, ranging on average from 30–80 individuals. Where *Ch. albinasus* occurs in sympatry with woolly monkeys (i.e., west of the Rio Tapajós-Juruena, east of the Rio Madeira, and north of the Rio Ji-Paraná), they are often seen in mixed species associations. Red-nosed saki groupings mixed with woolly monkeys (*Lagothrix cana*), tufted capuchins (*Sapajus apella*) and/or white-fronted slender capuchins (*Cebus unicolor*) may contain as many as 150 monkeys.

In figure 28, we have depicted the distributions, allopatric speciation, radiation, and supposedly followed pathways of metachromic bleaching in all known Saki Monkeys genus *Pithecia*. Sakis occur exclusively in the rain forests of lowland Amazonia and the Guayanian Shield (Herskovitz, 1987b; Mittermeier et al., 2013). Within the genus *Pithecia* we distinguish three monophyletic cladistic Groups: *P. monachus*, *P. pithecia*, and *P. hirsuta* (Fig. 29).

Within the *P. monachus* Clade allopatric speciation is thought to have followed evolutionary pathways of metachromic bleaching with *P. monachus* representing the nearest to archetypic precursor of all extant sakis. Both sexes have an overall saturated eumelanin, slightly bleached silky coat, except for the cream-white hands and feet. Taxon *P. monachus* ranges along both sides of the Amazon upstream from its confluence with the Rios Juruá and

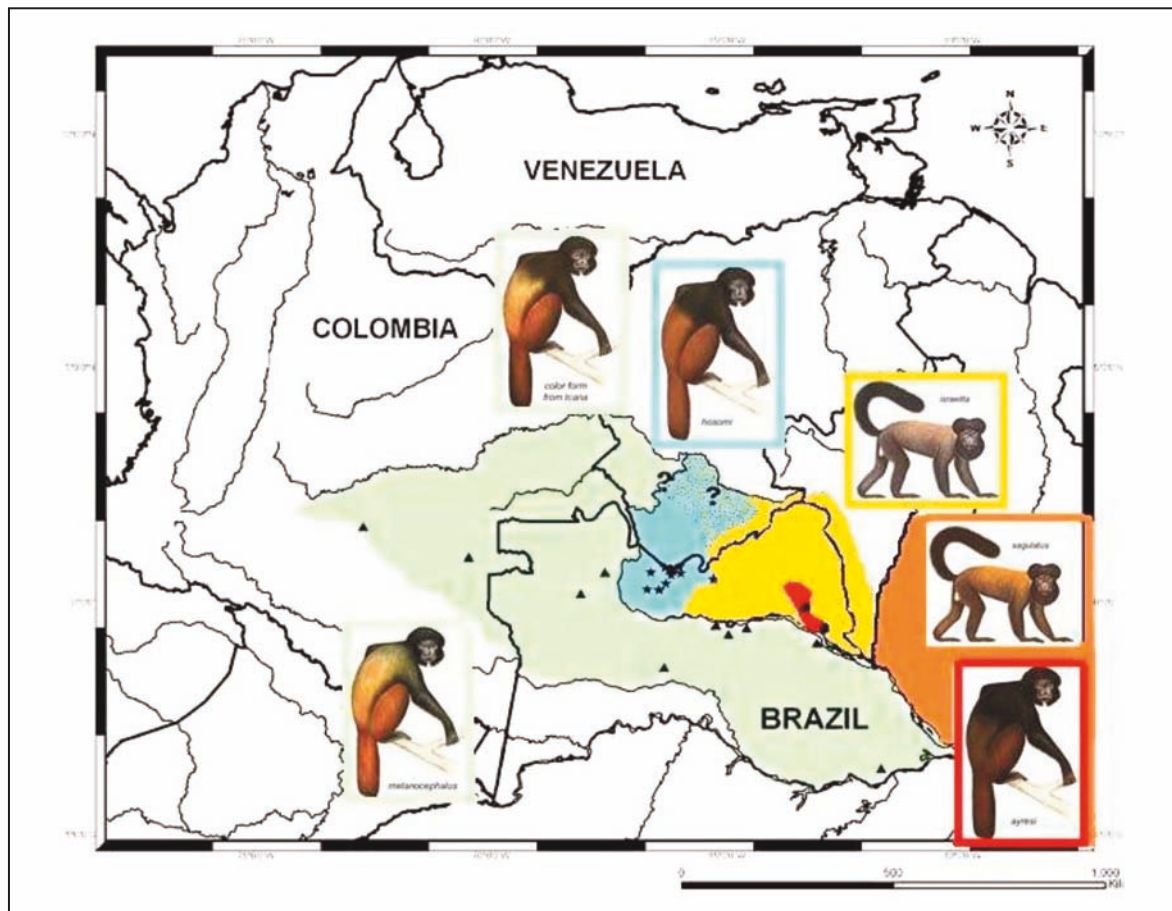


Figure 27. Map showing distributions of the Bearded Saki taxa *Chiropotes sagulatus* and *C. israelita*, and the parapatric Black-headed Uakaris that occur north of the Amazon and Negro Rivers.

Japurá, large rivers delineating its distribution in the east and north. The species is sexually dimorphic, not in size but in metachromic pelage characters of the head. Both sexes have a slightly bleached mask that is light brown in males and cream-white in females. It surrounds a black face with yellow to cream eyebrows and malar stripes. Forehead and cheeks are covered with short, forward directed hairs resembling much that of members of the *P. pithecia* Group. From *P. monachus* diverged in northwestern direction taxon *P. milleri*, supposedly after a metachromic deviant founder-colony of ancestral monachus traversed the Río Caquetá. *Pithecia milleri* nowadays occupies a small part of the Colombian Amazon that is confined by the Ríos Caguán and Putumayo. Both sexes are overall eumelanin bleached, more so in females. The forehead is covered with long, forward directed hairs forming

a kind of hood that is yellowish in males and cream-white in females. The black muzzle is contrasted with the advanced euchromic malar and lip stripes. From *P. milleri* derived the taxon *P. napensis* after a founder-colony of *P. milleri* traversed the Río Putumayo in southern direction. *Pithecia napensis* occupies a small area in the Colombian and Ecuadorian Amazon delineated by the Río Putumayo in the north and the Río Napo in the south. In *P. napensis* both sexes are progressively pheomelanin bleached in the yellowish to orange breast, more so in males that also differ in the silvery grayish lower part of a well-defined mask and in the albinotic hood. After a founder-colony of ancestral *P. napensis* once traversed the Río Napo to the south, the progressively pheomelanin bleached taxon *P. aequatorialis* diverged. It occupies a large area in the Ecuadorian and Peruvian Amazon delin-

eated in the north by the Río Napo and in the south by the Río Tigre. *Pithecia aequatorialis*, in particular in the metachromatic characters of the male's head (fully albinotic mask) and (orange) breast pelage, represents the most advanced pheomelanin bleached taxon in the *P. monachus* Clade. Its dead-end distribution at the end of the phylogeographic radiation of the *P. monachus* Clade is confined at all but western (Andean Mountain range) sides by *P. monachus* occupied territory. We may ponder about what would be the result of any hypothetical hybridization between *P. aequatorialis* females and *P. monachus* males at the contact zone that should exist in the species' westernmost distribution. Even if the offspring would remain fertile, it would never result in parapatric speciation. In concurrence with our theory, deviant young males with metachromatic genes from *P. aequatorialis* would be expelled by

the dominant male(s) of the *P. monachus* parental group, back to *P. aequatorialis* territory.

Within the *P. pithecia* Clade we consider *P. lotichiusi* with the overall darkest agouti (in females) and saturated eumelanin black (in males) pelage the nearest to archetypic taxon. This taxon is only found in the easternmost part of the interfluvial peninsula between the lower Solimões and Negro Rivers, from opposite the city of Manaus as far west as the towns of Manacapurú and Novo Airão. In the past, *P. lotichiusi* may have occupied a much larger distribution, for no untraversable geographic barriers exist when going further west into the Rios Solimões/Negro interfluvium. If so, the *P. pithecia* Clade may have monophyletically derived from the *P. monachus* Clade, when that radiated to the east. A founder-colony of slightly pheomelanin bleached ancestral *P. monachus* may

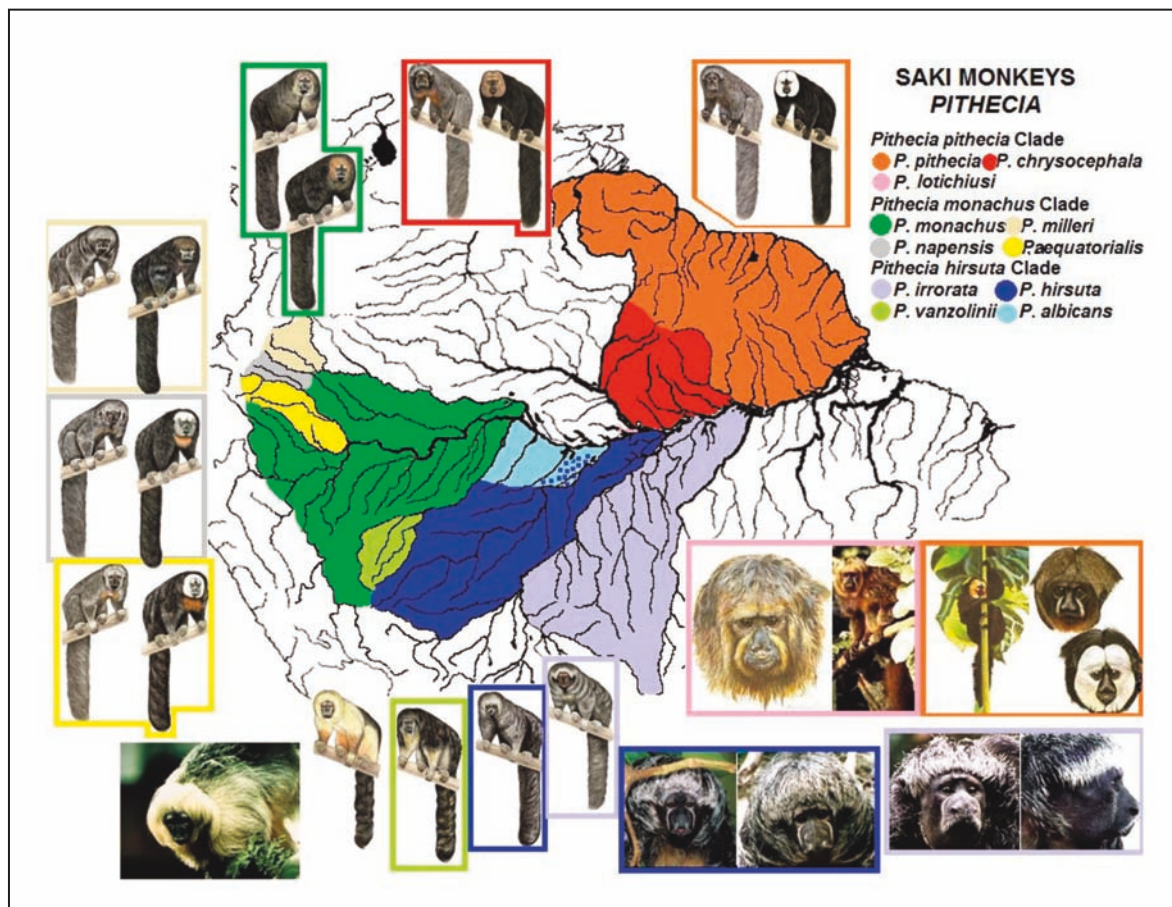


Figure 28. Distributions, allopatric speciation, radiation, and supposedly followed metachromatic pathways of bleaching in all known Saki Monkeys genus *Pithecia*.

have traversed the lower Rio Japurá and thereafter diverged into the allopatric taxon *P. lotichiushi*. The latter then extended its range to the east. During one of the late-Pleistocene glacials, when ocean levels dropped over up to 120 m, a founder-colony of *P. lotichiushi* could well have traversed the lower Rio Negro and then reached the north bank of the Amazon. This way, it may have diverged into the allopatric Golden-faced Saki taxon *P. chrysocephala*. Nowadays, Golden-faced sakis range from the Rio Branco as far east as the Rio Trombetas. After a founder-colony of ancestral *P. chrysocephala* once traversed the Rio Trombetas, taxon *P. pithecia* may have diverged. *Pithecia pithecia* then expanded its range in northwestern direction across the states of Roraima, Pará and Amapá, and

across the Guianas into Venezuela as far west as the lower Río Orinoco. It may have circumvented either side of the watershed formed by the Tumac Humac Mountains. Within the sexual dimorphic *P. pithecia* Clade, females are progressively pheomelanin bleached orange to yellowish brown, whereas males are all-black with a progressively pheomelanin bleached to albinotic mask. In the Brazilian taxa *P. lotichiushi* and *P. chrysocephala* the mask that consists of short, stiff, forward directed hairs is golden to orange-yellow colored. In the Guianan white-faced saki *P. pithecia* the mask is albinotic, white with orange-colored cheeks in males from Guyana and Suriname, and overall white in males from French Guiana.

Sakis of the *P. monachus* and *P. pithecia* Clades

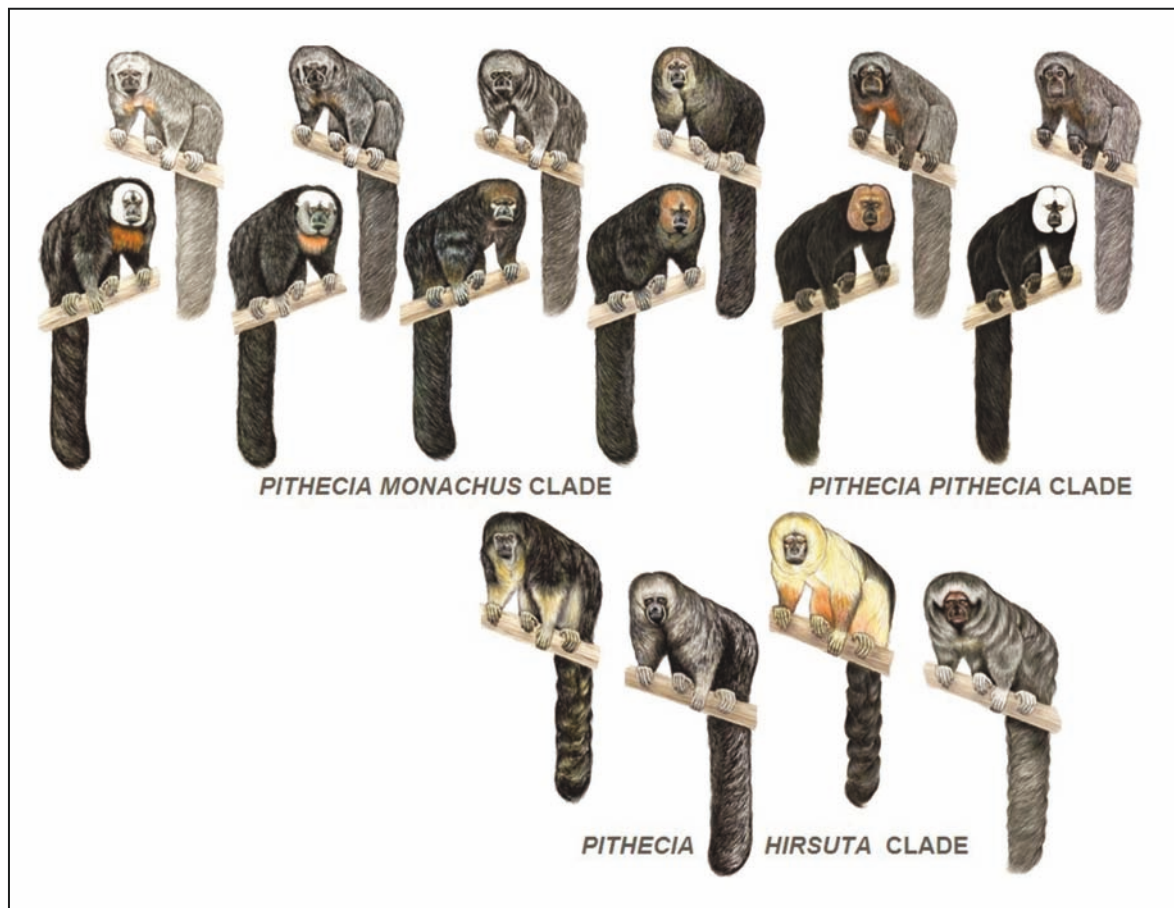


Figure 29. Among the Saki Monkeys genus *Pithecia* three monophyletic cladistic Groups or Clades are distinguished: the *P. monachus* Group containing four taxa (*P. monachus*, *P. milleri*, *P. napensis*, and *P. aequatorialis*), the *P. pithecia* Group containing three taxa (*P. lotichiushi*, *P. chrysocephala*, and *P. pithecia*), and the *P. hirsuta* Group containing four taxa (*P. hirsuta*, *P. irrorata*, *P. vanzolinii*, and *P. albicans*). We only recognize sexual dimorphism as expressed in metachromatic characters in the *monachus* and *pithecia* Clades (Courtesy of Stephen Nash).

distinguish themselves locomotorily from sakis of the third clade - the *P. hirsuta* Clade. A specific locomotor pattern called “vertical leaping and clinging” is performed during foraging and traveling in their preferred habitat, which is the discontinuous lower canopy and understory of terra firme rain forest. As these sakis have to leap from tree trunk to tree trunk, they are commonly known as “flying monkeys”. In contrast, saki taxa of the *P. hirsuta* Clade prefer the middle to upper strata of primary rain and seasonally inundated floodplain forests, which strata are interconnected by thick-stemmed vines and hemi-epiphytic climbing shrubs. For that preferred habitat they have adopted a different locomotor pattern, that of horizontal

leaping, and quadrupedal running or hopping across thick horizontal branches and boughs. A significant difference in limb proportions between taxa belonging to each of the two Clades has been measured, with those of the *P. pithecia* Group being longer relative to trunk length (Hershkovitz, 1987a; 1987b). Another important feature in which the *P. hirsuta* Clade distinguishes itself from the *P. monachus* and *P. pithecia* Clades is mean group size and sexual dimorphism. Social groups of taxa belonging to the *P. hirsuta* Clade are larger and multi-male structured, instead of the extended family group that contains only one or sometimes two adult males in taxa belonging to the other Clades. Moreover, contrary to what recent taxonomies



Figure 30. Satellite image taken from the region, where the várzea floodplain of the Rio Solimões borders on that of the Rio Purús. Behind each floodplain are located black-water backwater lakes (rias), such as Lago Coarí, Lago Uauaçú, and Lago Ayapuá. A red line indicates where parapatric bald-faced saki *Pithecia hirsuta* is encroaching onto buffy saki *P. albicans* territory. (Below) Portraits of different adult males of Gray's saki *P. hirsuta*. (Above, left) White-masked mutant male *P. hirsuta* that was seen roaming around alone far into *P. albicans* territory north of Lago Uauaçú. (Above, right) Adult male buffy saki *P. albicans*; note the black face with the showy albinotic eyebrows and white long-haired hood.

(merely based on museum collections) suggest, we were not able to recognize metachromic sexual dimorphism in any taxon of the *P. hirsuta* Clade. In the field, we failed to distinguish gender among group members of *P. hirsuta*, *P. irrorata*, and *P. albicans*. Nor could we, in captivity, determine their gender without up-close examining the saki monkey's concealed genitals.

Within the Bare-faced Sakis of the *P. hirsuta* Clade we suggest the least eumelanin bleached overall blackish-gray taxon *P. hirsuta* to be the nearest to archetypic taxon. It may well have derived from a founder-colony of proto-*monachus* that once traversed the Rio Juruá in eastern direction. The following pathways of metachromic bleaching and allopatric speciation are recognized. From *P. hirsuta* that occupies the entire interfluvial delineated by the Juruá, Solimões and Madeira Rivers, diverged and radiated away in eastern direction taxon *P. irrorata* after a founder-colony of progressively bleached *P. hirsuta* traversed or circumvented the Rio Madeira (most likely at its upper reaches) during one of the late-Pleistocene glacials. Nowadays, taxon *P. irrorata* occupies the entire interfluvial delineated by the Madeira, Amazonas and Tapajós-Juruena Rivers. Its overall coat is advanced eumelanin bleached in comparison with that of *P. hirsuta*, and albinotic in the distal half of the hood, the hands and feet. Its tail is less bushy, the hairs more curly. *Pithecia irrorata* has an almost bare face, and its forehead is only halfway covered by an albinotic hood that does not conceal the cheeks and temples. As a result, the monkey's profile looks more pronounced. Metachromic skin and fur characters of the head that play such an important role in the taxonomy of monkeys like *Pithecia*, *Sapajus* and *Ateles* are often poorly preserved in museum specimens. Hence, the confusion in most hitherto elaborated taxonomic reviews of these genera. Zoological collections all over the world have lumped misidentified taxa, such as *P. hirsuta* and *P. irrorata*, under the latter. Some leading taxonomists even attribute sexual dimorphism to the Bare-faced Sakis. From *P. hirsuta* to the west diverged taxon *P. vanzolinii*, after a progressively bleached founder-colony of *P. hirsuta* traversed the Rio Envira. *Pithecia vanzolinii* is now confined to the headwaters of the Rio Juruá. It differs in the albinotic lower limbs and ventral parts that contrast much with the blackish-gray dorsal parts and tail.

From *P. hirsuta* to the north derived the overall near-albinotic taxon *P. albicans* that is pheomelanin bleached orangish-yellow only on the lower limbs. Buffy Sakis *P. albicans* occupy the northernmost dead-end distribution of the *P. hirsuta* Clade, which is delineated by the untraversable lower Solimões River in the north, the lower Juruá River in the west, and the lower Purús River in the east. Buffy Sakis are parapatric with the more opportunistic Gray's Sakis *P. hirsuta*, from which they once derived. At its southern limit, its distribution shows an open end running across the Rio Tapauá axis. After it traversed the Rio Tapauá to the north, Gray's Saki *P. hirsuta* was, and still is expanding its range northwards to the cost of the Buffy Saki *P. albicans*. This example may well demonstrate that progressively bleached to albinotic primate taxa that occupy dead-end distributions will eventually go extinct. East of the Rio Coari and north of the Rio Tapauá - a left-bank tributary of the Rio Purús - we have confirmed the sympatric occurrence of the taxa *P. albicans* and *P. hirsuta*, with *P. hirsuta* advancing onto *P. albicans* as far north as Lago Ayapuá (Fig. 30). North of the Ayapuá contact zone in territory exclusively occupied by *P. albicans*, we once spotted and photographed a solitary young male, its head pelage resembling that of male White-faced Saki *P. pithecia* from the Guianas (Fig. 30). We assume that this male was a progressively bleached deviant color morph of taxon *P. hirsuta* that was expelled from or forced to leave its parental group. It may have ventured into adjacent *P. albicans* territory north of Lago Uauacú. As we have often seen *P. hirsuta* groups opportunistically penetrating far into white-water floodplain forest (várzea), this metachromic deviant near-albinotic, sexually dimorphic mutant male of taxon *P. hirsuta* in theory could become the founding father of a new taxon. This could happen after this young male would have attracted one or a few *P. albicans* females to form a small reproductive family group. It then would have to survive making a year-round living in the extensive várzeas found along the south bank of the Rio Solimões. We have never seen any saki, uakari or other seed-predating monkey occupying that ecological feeding niche in the várzeas that fringe the right bank of the middle Rio Solimões. Perhaps, this hypothetical scenario may also explain how metachromic sexual dimorphism in primates could have evolved.

In figure 31, we have visualized the distributions, allopatric speciation, radiation and supposedly followed pathways of metachromic bleaching in all known Woolly Monkeys, genus *Lagothrix*. Woolly monkeys are exclusive matrix terra firme rainforest dwellers that under normal circumstances will never enter white-water floodplain forest (várzea). For that reason alone, the distribution of *Lagothrix* is greatly determined by riverine barriers. Within the genus only one monophyletic Clade is recognized. We consider the saturated eumelanin, metachromic least bleached Poepig's Woolly Monkey taxon *La. poeppigii* with its overall black to dark chestnut-brown coat the nearest to archetypic woolly monkey. In the north, *La. poeppigii*'s distribution is confined by the Amazon River, in the east by the Rio Juruá that is also fringed with extensive várzeas, and in the south and west by the

foothills of the Andean Mountain range. From *La. poeppigii* derived in western direction the Peruvian Yellow-tailed Woolly Monkey *La. flavicauda*, which has (disputedly) been upgraded to its own genus *Oreonax*. It occurs in parapatry with *La. poeppigii*, but genetically isolated from it, as it lives in high-altitude Andean cloud forest. With its albinotic lower half of the circumocular rings, facial muzzle, chin and pheomelanin bleached yellow tail the taxon is following a pheomelanin pathway towards albinotic. From a founder-colony of somewhat eumelanin bleached *La. poeppigii* that traversed or circumvented the upper Rio Juruá and then radiated to the east and north, the darkbrown to black headed taxon *La. tschudii* derived. Its coat is overall dark gray-brown colored, becoming blackish on all five limbs. It occupies the entire interfluvial delineated by the Juruá, Solimões-

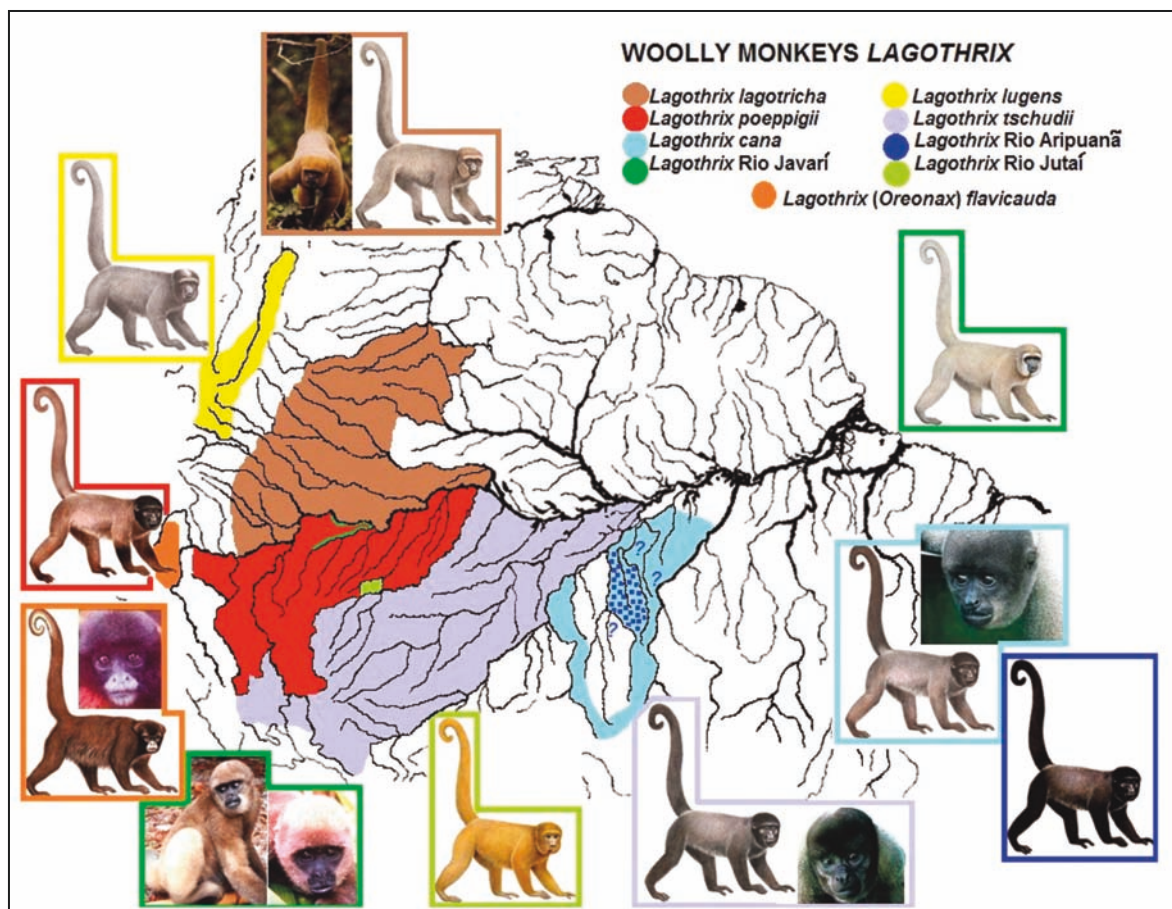


Figure 31. Distributions, allopatric speciation, radiation, and supposed eumelanin pathways of metachromic bleaching in all known Woolly Monkeys genus *Lagothrix*.

Amazonas and Madeira Rivers. From *La. tschudii* in eastern direction diverged the Black-headed or Geoffroy's Gray Woolly Monkey taxon *La. cana*, its entire coat progressively eumelanin bleached, light-gray colored, with a dark-gray to black head. Only as recent as the late- Pleistocene or early Holocene, an advanced eumelanin bleached founder-colony of *La. tschudii* must have traversed or circumvented the upper Madeira River north of the Rio Ji-Paraná (also known as Rio Machado) in eastern direction. It then extended its range by passing the geographic barrier formed by the extensive Tenharim Savanna in Rondonia alongside its southern border. This way, it could enter the interfluvial delineated by the Madeira, Amazonas and Tapajós Rivers. Circumventing the extensive Tenharim Savanna, taxon *La. cana* apparently missed the narrow entrance to the north that exists between the upper Rio Ji-Paraná and the Rio Roosevelt. This could well explain why woolly monkeys are absent from the entire Rios Madeira/Aripuanã interfluvial north of the Rio Marmelos. The relatively recent occupation by *La. cana* of the entire interfluvial delineated by the Madeira, Aripuanã, Amazonas and Tapajós Rivers is near to its completion. Taxon *La. cana*'s current northernmost distribution gets to a halt at the latitude running across the upper reaches of the *Abacaxis* and *Andirá* Rivers, not much south of the untraversable Rio Amazonas. We assume that only when *La. cana* invaded all smaller interfluvials east of the Rio Aripuanã and west of the Rio Tapajós, it began to displace the All-black Woolly Monkey that in the far geological past evolved in the area east of the (proto)-Madeira River. This newly identified woolly monkey still has to be collected and described. We here provisionally allocate the common name "Rio Aripuanã Black Woolly Monkey" to this fully saturated eumelanin, all-black taxon. Apparently, as it occupies the same ecological niche as newcomer *La. cana*, the Rio Aripuanã Black Woolly Monkey finds itself on the verge of extinction. It is smaller, lives in small, socially less complex family groups, and its coat is in metachromatic respect the most primitive or archetypic. It lives in sympatry with *La. cana*, but only hangs on in a small enclave distribution situated between the lower to middle Rio Aripuanã and the Rio Acari. It may well represent the ancient, most original, archetypic taxon of all Woolly Monkeys genus *Lago-*

*thrix* that evolved in the Late-Pliocene east of the proto-Madeira River, fully isolated from the rest of the Amazon.

Woolly monkeys also radiated into the northwestern Amazon, most likely after a founder-colony of taxon *La. poeppigii* circumvented or traversed the upper Amazon River in Peru (where it is called Río Marañón). Two progressively eumelanin bleached forms that derived from *La. poeppigii* once must have occupied the Colombian Amazon: the euchromic light-gray Colombian Woolly Monkey taxon *La. lugens* that occurs at high altitudes in the foothills of the South-Colombian Andes and in the upper Río Magdalena valley, and the Brown or Humboldt's Woolly Monkey taxon *La. lagotricha*. The coat of taxon *La. lugens* is eumelanin bleached charcoal to light-gray colored, but lacks any mixture with brown. On the head, a mid-dorsal stripe and a rim across the eyebrows are advanced bleached to euchromic. Mean body size and weight in *La. lugens* are the largest among all extant woolly monkeys. *Lagotricha*'s coat is progressively eumelanin bleached light-brown colored, except for the blackish hands and feet. Its head is light-brown colored, with a slightly bleached yellowish eyebrow rim and sideburns aside of the blackish-brown face. Taxon *La. lagotricha* ranges across the Colombian, Venezuelan and NW Brazilian Amazon.

Most interestingly, we confirmed the small distribution of a newly identified, advanced pheomelanin bleached, overall orange-colored taxon in the upper reaches of the Rio Jutai. A founder-colony of advanced pheomelanin bleached *La. poeppigii* mutants pushed out of *La. poeppigii* territory must once have successfully adapted to white-water seasonally inundated floodplain forest (*várzea*) located between the east bank of the upper Rio Jutai and the west bank of the Rio Juruá, near the town of Eirunepé. We were not able to determine the exact range of the Rio Jutai Woolly Monkey, for the area is inhabited by uncontacted Amerindians of the Korubo tribe (so-called "caçateiros") that are known to kill any non-indigenous intruder.

We encountered in the zoological collection of the Brazilian Museu Goeldi (MPEG, Belém-PA) an overall orange-colored stuffed juvenile specimen that was deposited without collecting data. This very animal is depicted in Da Cruz Lima's 1945 Mammals of Amazônia. We here provisionally name it the "Rio Jutai Orange Woolly Monkey".

In addition, we found an albinotic overall cream-colored taxon that we provisionally named the “Rio Javari Fair Woolly Monkey” *Lagothrix* sp. It resembles much Humboldt’s Woolly Monkey taxon *La. lagotricha*, but its pelage is longer, softer and silky, besides being overall advanced eumelanic to cream-white colored. It has long-haired white sideburns alongside a pitch-black face, muzzle and chin. A near-albinotic ancestral founder-colony must once have been driven out of *La. poeppigii* territory somewhere near the northernmost border of its distribution. This colony must have been forced to make a living in the white-water floodplain forests (várzeas) that stretch out along the south bank of the Rio Solimões (near the town of Tabatinga) all the way to the left-bank várzeas of the lower Rio Javari. Under normal circumstances this type of habitat should be consid-

ered inappropriate for woolly monkeys to guarantee a durable and sustainable living. This seems to be another case where a progressively bleached, near-albinotic founder-colony of *La. poeppigii* has been driven into a (for woolly monkeys) marginal habitat - seasonally white-water inundated floodplain forest (várzea). According to our theory of allopatric primate speciation, albinotic fair woolly monkeys must have diverged this way from archetypic, saturated eumelanin, dark brown coated *La. poeppigii*. Apparently, it has survived until today in geographic sympatry, but ecological parapatry (inhabiting adjacent but different habitats) with taxon *La. poeppigii*, the species it derived from. In 2002, the second author, while at Colombia University, NY, ran the mtDNA sequences of the Rio Javari Fair Woolly Monkey using earlier preserved DNA-samples. He found 4% divergence from sympatric

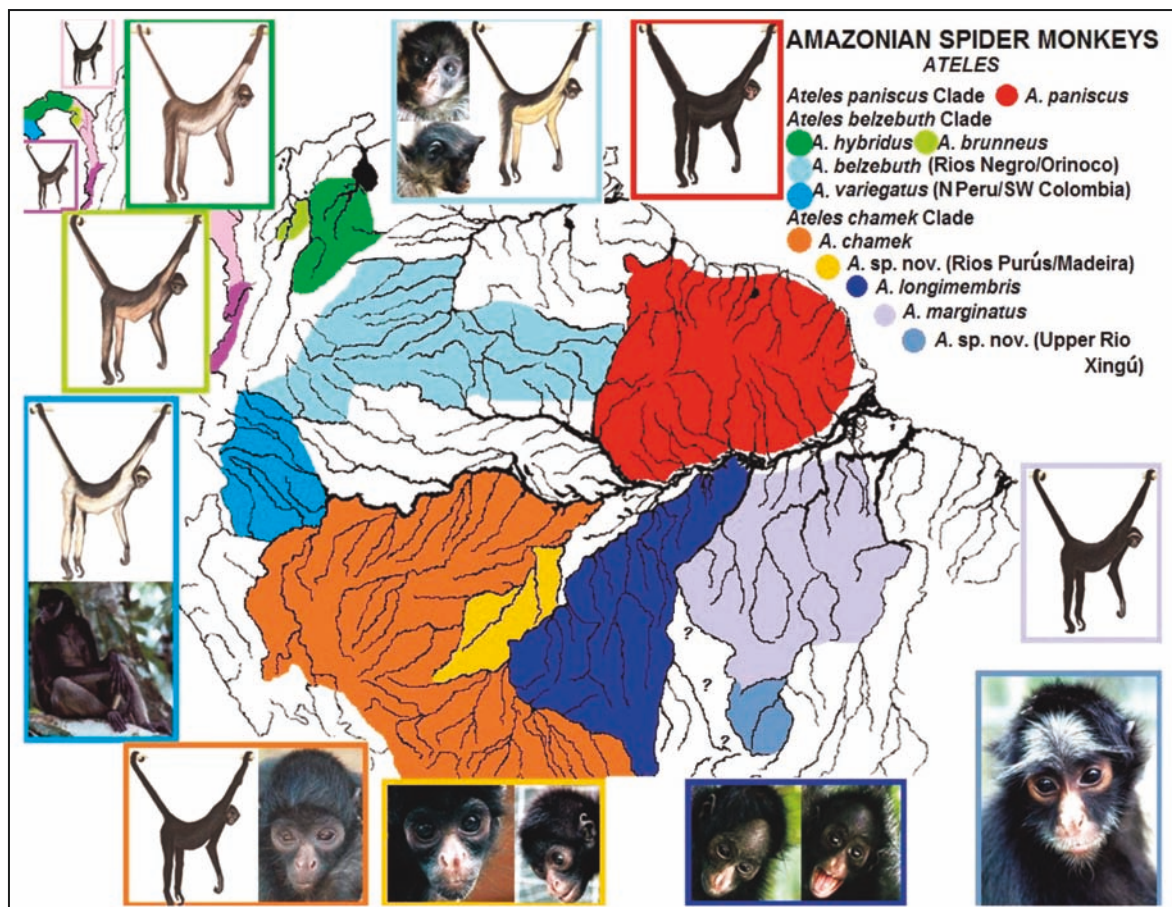


Figure 32. Distributions, allopatric speciation, radiation, and supposed pathways of metachromic bleaching followed in all known Spider Monkeys genus *Ateles* that occur in the Amazon and along the Pacific coast of Ecuador and Colombia.

*La. poeppigii* and over 7% from the allopatric taxon *La. lagotricha*. The AMNH holds three well-preserved skins of the Rio Javari Fair Woolly Monkey *Lagotrix* sp., which were collected by the Olalla Brothers in 1927 along the south bank of the Rio Solimões, somewhat upstream from the town of Tabatinga. All three specimens are misidentified as *La. lagotricha* (Humboldt, 1812).

For Spider Monkeys genus *Ateles*, allopatric speciation, radiation, and phylogeography along different pathways of metachromic bleaching are depicted in figures 32, 33. Four monophyletic cladistic Groups or Clades are recognized: *A. paniscus*, *A. chamek*, *A. belzebuth*, and *A. geoffroyi*. Spider monkeys have evolved during the Pliocene in the Guayanian Shield, most likely from a precursor of the most ancient of the four extant monophyletic cladistic Groups, the *A. paniscus* Clade. The Red-faced Black Spider Monkey *A. paniscus*

from the Guianas represents the nearest to archetypic extant taxon within the genus. This assumption is based on some unique primitive characters that are not seen in other spider monkeys. Here we mention: the presence of a vestigial thumb or, if lacking, at least the metacarpal of the first digit that is maintained in the hand; its incapacity of using the tip of the prehensile tail in picking and manipulating small objects like food items; the overall long-haired coat, in particular around the base of the tail and in the forward directed hairtuft on the forehead that resembles a cap; the overall saturated eumelanin black coat without any sign of early eumelanin bleaching; the advanced pheomelanin bleached bright-red bare face lacking whiskers; the frequent occurrence of albinotic blue-colored eyes; the albinotic cream-white colored, hypertrophied, pendulous clitoris in females and cream-white protruded anus in both sexes, whereas

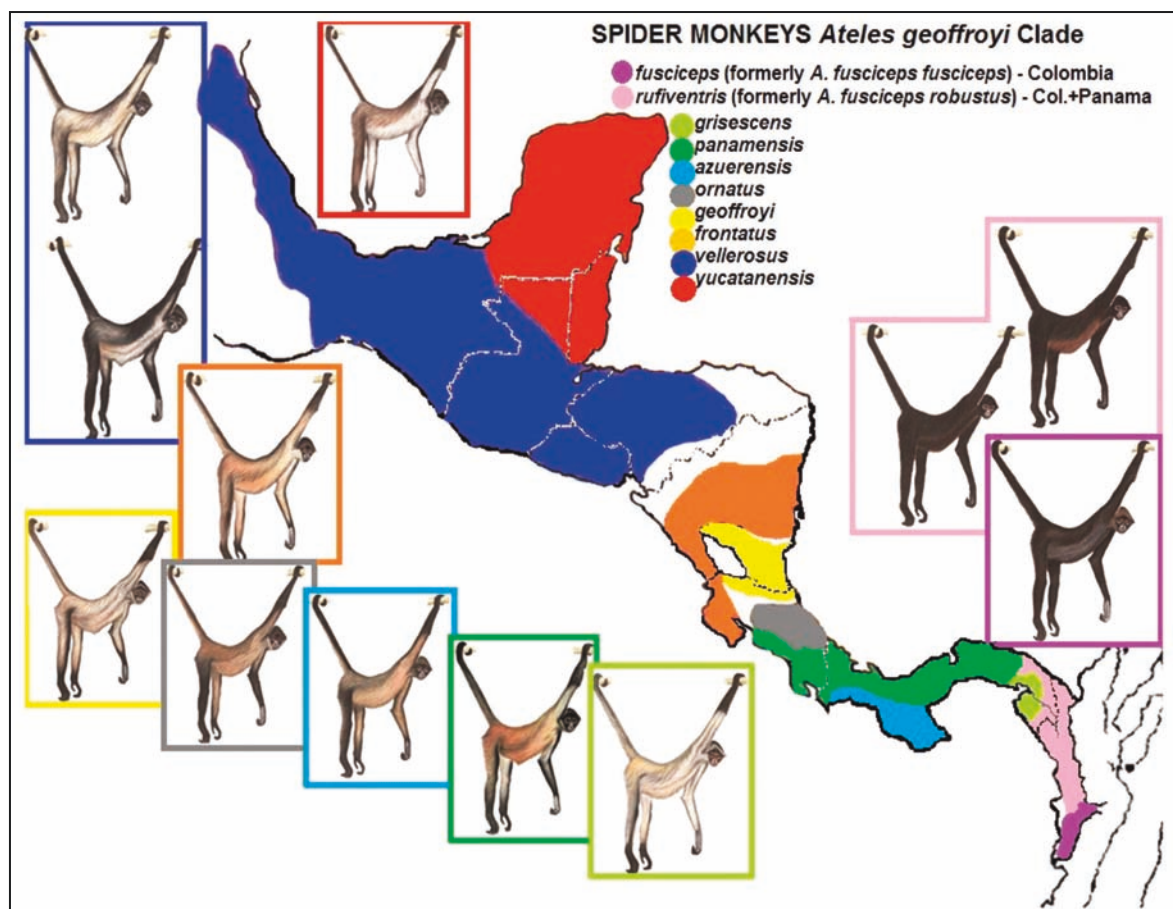


Figure 33. Phylogeographic distribution, allopatric speciation, radiation and metachromic diversification in all known Spider Monkeys (*Ateles*) that occur from the Pacific coast of W Ecuador and NW Colombia far into C America as far N Mexico.

the clitoris is long, flattened and lacking the musculature to erect during foreplay and copulation (Van Roosmalen, 1985a). Moreover, spider-monkey matriarchal social organization is markedly expressed in (leading) female's body size, which in *A. paniscus* may exceed that of males; and in the permanent fusion-fission social structure centered around alpha-females that lead foraging parties on day ranges. As such, complete gatherings of all twenty or so members of a social grouping will never happen (Van Roosmalen, 1985a). This specific type of social organization that is unique among Neotropical primates may well be related to the specific phytosociological composition, phenology and physiognomy of the more ancient, more heterogeneous type of primary terra firme rain forest that evolved uniquely and without major interruptions during the last 60–70 million years on the Guayanian as well as on the Brazilian Shield. Here, available food sources are generally widely dispersed, and rarely clumped at any time of the year. Maturation of nutritious large-seeded fruits - *A. paniscus* is a mature-fruit specialist frugivore - is slower and species-specifically stretched out over longer periods of time (Van Roosmalen, 1985b). Mast-fruiting, as commonly seen in tropical rainforests on other continents, is a phenomenon that does not exist in this ecosystem. Hence, the early evolution of semi-brachiation (brachiation with the help of a prehensile tail) as the principal locomotor pattern, and the fusion-fission type of social structure during traveling and foraging took place in ancestral spider monkeys as the principal adaptation of a large-bodied monkey to a well-defined ecological feeding niche, in a biome that took over 60 million years to develop. It may well explain why the *A. paniscus* Clade did not speciate and radiate any further, as the distribution of extant *A. paniscus* is still confined to the larger part of the Guayanian Shield.

Most plausibly somewhere in the late-Pliocene, from an agouti or saturated eumelanin all-black ancestor of *A. paniscus* derived the phylogenetically distantly related, nearest to archetypic Black Spider Monkey taxon *chamek* of the *A. chamek* Clade. It is distributed south of the Amazon as far south as the Brazilian Shield (in Rondonia and Mato Grosso states). North of the Amazon, the Brown Spider Monkey taxon *A. brunneus* that ranges in N Colombia (in an area confined by the Sierra Nevada

Mountains), may represent the least eumelanin bleached, nearest to archetypic taxon of the *A. belzebuth* Clade. Moreover, in the Pacific coastal forests of Ecuador and Colombia is found the saturated eumelanin Brown-headed Spider Monkey taxon *A. fusciceps* (formerly *A. fusciceps fusciceps*). Along the Pacific coast of N Colombia and S Panama is found the all-black but dark red-bellied Colombian Black Spider Monkey taxon *A. rufiventris* (formerly *A. fusciceps robustus*). All-black Brown-headed Spider Monkey taxon *A. fusciceps* may therefore represent the nearest to archetypic taxon of the *A. geoffroyi* Clade (Fig. 32).

Within the *A. chamek* Clade, nominate *A. chamek* represents the nearest to archetypic taxon. It is saturated eumelanin in its overall black coat color and blackish or slightly bleached pinkish circumocular rings and/or facial muzzle, and in the forward directed black hairtuft on the forehead. It ranges across a large part of the Amazon basin delineated by the Amazon River in the north, the Andes Mountains in the west, the highlands of the Brazilian Shield in the south, and the Purús and Guaporé Rivers in the east. Like the other taxa of the *A. chamek* Clade, the Black-faced Black Spider Monkey *A. chamek* is only found in patches of terra firme rain forest close to major waterbodies, such as lakes, rivers, and creeks. It frequents in particular seasonally inundated marsh forest and black- and clear-water floodplain forest called igapó. We have never spotted spider monkeys belonging to the *A. chamek* Clade in matrix primary rainforest of the hinterland at distances of over ten km from any major waterbody. There, spider monkeys of the *A. chamek* Clade are commonly replaced by woolly monkeys (*Lagothrix*) that occupy the same feeding niche in primary terra firme rain forest. All taxa of the *A. chamek* Clade do laterally migrate to the nearest igapó floodplain forest of clear- and black-water rivers during the 2–3 months lasting fruiting season, which coincides with the peak of the flood. From *A. chamek* diverged and radiated away in eastern direction the Rio Purús Black Spider Monkey that we identified to be new to science. This taxon ranges in the interfluvium between the Purús and Madeira Rivers, south of the Rio Ipixuna and north of the Río Tahuamanu in the Bolivian Amazon, a left-bank tributary of the upper Rio Madeira. The Rio Purús Black Spider Monkey *Atheles* sp. is having a near-albinotic cream to pink

colored muzzle, chin, and ears, and a triangular patch of short, backward directed black hairs on the forehead instead of a cap. After a founder-colony of the Rio Purús Black Spider Monkey traversed the Rio Madeira to the east, the Long-limbed Black Spider Monkey *A. longimembris* diverged. This taxon was already identified as a distinct species by Da Cruz Lima (1945) based on two specimens that were collected by Leo E. Miller along the upper Rio Ji-Paraná in Mato Grosso during the first part of the 1914 Roosevelt-Rondon Expedition. It was first described as *Ateles longimembris* by Allen (1914). Holotype and paratype of *A. longimembris* deposited in the zoological collection of the AMNH under No. 36909 were later misidentified as *A. chamek* and therefore not included in Kellogg & Goldman's (1944) revision of the Spider Monkeys genus *Ateles*. The Latin name that Allen (1914) attributed to this taxon relates to the “*excessively long tail and limbs, the tail length very nearly twice the length of head and body*”. Aside of its elongated and slender limbs, taxon *A. longimembris* is further characterized by the pitch-black face and ears, except for a pale cream-white albinotic triangular patch on the nose, and a wide triangular patch on the forehead that is barely covered with sparse backward directed, stiff, black hairs. Another character of this taxon is the relatively robust incisors and canines that look oversized so that the lips seem unable to conceal them. This feature gives adult Long-limbed Black Spider Monkeys taxon *A. longimembris* a bulldog-like appearance. Moreover, its loud or long-distance calls that are so typical for other spider monkeys do not carry far. They sound like bird whistles blowing in the wind. The distribution of *A. longimembris* is confined by the Rio Madeira in the west, the lower Amazon River in the north, the Rio Tapajós-Juruena in the east and the Rio Ji-Paraná in the south. From a founder-colony of *A. longimembris* that once traversed the Rio Tapajós-Juruena to the east derived the White-whiskered Black Spider Monkey *A. marginatus*. It is all-black and only euchromic in the small triangular forehead patch or blaze formed by backwards directed white hairs. However, we have seen also adult free-ranging *A. marginatus* that had black forehead patches. This taxon occupies the interfluvial delineated by the Rios Tapajós and Teles-Pires in the west, the lower Amazon River in the north, the Rios Tocantins and Araguaia in the east, and the upper Rio Teles-Pires

or Rio Minisuiá-Miçú (both right-bank tributaries of the upper Rio Tapajós) in the south. After a somewhat eumelanin bleached founder-colony of *A. marginatus* once traversed the upper Rio Teles-Pires south of the *A. marginatus* distribution, a new taxon diverged that we name the Upper Rio Xingú White-whiskered Brown Spider Monkey. Its coat is chestnut-brown dorsally, and lighter brown on the ventral parts. The snow-white semi-crescent blaze is much larger than in *A. marginatus*. It widens above the eyes into long sideways directed streaks. This newly identified taxon distinguishes itself also from taxon *A. marginatus* in the long white whiskers that run from below the eyes across the lips and chin. Moreover, facial skin is pink to flesh-colored in the circumocular rings, muzzle, lips and chin. Within the monophyletic *A. chamek* Clade the White-whiskered Brown Spider Monkey from the Upper Rio Xingú represents the furthestmost eumelanin bleached taxon that, in accordance with our theory, metachromically and phylogeographically radiated farthest away from archetypic Black-faced Black Spider Monkey taxon *A. chamek*.

Within the *A. belzebuth* Clade, we recognize the dorsally saturated eumelanin darkbrown Brown Spider Monkey taxon *A. brunneus* as the nearest to archetypic taxon. Belly and inner limbs are eumelanin bleached light-brown colored. The triangular forehead patch formed by backward directed hairs is only slightly bleached brownish-black colored. Taxon *A. brunneus* is found in N Colombia, between the Cauca and Magdalena Rivers. It is taxonomically treated as a subspecies of *A. hybridus*. In the far geological past, the *A. belzebuth* Clade could well have derived from the archetypic, saturated eumelanin, all-black taxon (*A. geoffroyi*) *A. fusciceps* (formerly *A. fusciceps fusciceps*) of the *A. geoffroyi* Clade that occurs west of the Andes Mountains in the Pacific coastal forests of Ecuador and Colombia. An ancestral founder-colony of *A. fusciceps* once may have circumvented the Sierra Nevada north of it and diverged into ancestral *A. brunneus* in the western part of the lower Río Magdalena valley. After a progressively eumelanin bleached founder-colony of *A. brunneus* traversed the Río Magdalena to the east, the light-brown and silvery-white colored Variegated Spider Monkey taxon *A. hybridus* could have derived. It ranges from the northern Colombian Río Magdalena Basin into the southwesternmost corner of Venezuela, in

the foothills of the Sierra Nevada mountain range (near the city of Mérida). Inner parts of limbs, belly and the small triangular forehead patch are silvery white in taxon *A. hybridus*, whereas the rest of the coat is light-brown colored. An advanced eumelanin bleached founder-colony of *A. hybridus* once may have circumvented the Sierra Nevada Mountains to the east and reached the headwaters of some of the Río Orinoco's tributaries in Venezuela's Amazonas state. It then diverged into the furthestmost pheomelanin bleached White-bellied Spider Monkey taxon *A. belzebuth*. It ranges from north of the Río Negro and west of the Río Branco into the Venezuelan State of Amazonas west of the Río Orinoco, and also far into the lowland Amazon of Colombia. Upper parts, head and dorsal coat of White-bellied Spider Monkeys taxon *A. belzebuth* are light-brown, but their pelage on ventral parts and inner sides of limbs are silvery white, often pheomelanin bleached yellow to orange-colored. The skin of muzzle and chin is pale brown to pinkish colored. The triangular forehead patch or blaze is light brown, and the eyebrows, whiskers, and throat are silvery. From a founder-colony of *A. belzebuth* that once traversed the upper Río Caquetá derived in southwestern direction the southernmost distributed taxon of the *A. belzebuth* Clade, *A. variegatus*. This taxon occurs in the N Peruvian, SW Colombian and eastern part of the Ecuadorian Amazon, east of the Andes Mountains and north of the Amazon River (where the river is called Río Marañón). Its coat is dorsally eumelanin blackish to dark gray, and ventrally euchromic to albinotic silvery-white, except for the dark grayish hands and feet. The legs are silvery white, as are the whiskers and the large blaze or triangular patch on the forehead. Advanced pheomelanin bleached color traits (yellow and orange) as seen in *A. belzebuth* are lacking in *A. variegatus*. In accordance with our theory and the principle of metachromic bleaching, within the belzebuth Clade the most euchromic taxon, *A. variegatus*, has phylogeographically radiated the farthest away from the dark-brownish colored, nearest to archetypic taxon *A. brunneus* (Fig. 32).

Within the *A. geoffroyi* Clade (Fig. 33), we recognize the saturated eumelanin Colombian Black Spider Monkey taxon *A. (fusciceps) rufiventris* (formerly *A. fusciceps robustus*) from the Pacific coastal forests of Colombia and South Panama west

of the Andes Mountains as the nearest to archetypic taxon of the *A. geoffroyi* Clade. Its coat is glossy pitch-black, whereas color morphs of this taxon show a saturated pheomelanin dark red colored belly and genital area. Fur on the forehead is slightly brownish tinged. From taxon *A. rufiventris* derived in southern direction the Brown-headed Black Spider Monkey, the nominate taxon *A. (fusciceps) fusciceps* from the Pacific coastal forests of Ecuador and Colombia. It is slightly eumelanin bleached blackish-gray on the belly, brownish black above, with a yellow-brown anterior crown, grading from brown to black on the nape. It often has a white mustache and beard. Taxa *A. fusciceps* and *A. rufiventris* stand at the base of the monophyletic Central-America Spider-Monkey *A. geoffroyi* Clade, which radiated away in northwestern direction across the Isthmus of Panama into Central America as far north as Mexico. From the Colombian Black Spider Monkey *A. rufiventris* derived the advanced euchromic, near-albinotic (except for the saturated eumelanin feet, hands, lower arms and distal part of the tail) taxon *A. (geoffroyi) grisescens*. However, the validity of this taxon is doubtful, for it has never been seen in the wild. It is thought to occupy a dead-end distribution along the Pacific coast from the Río Tuyra valley in SE Panama into the Cordillera de Baudó in NW Colombia. To the east, its distribution is confined by territory occupied by the Colombian Black Spider Monkey *A. rufiventris*. From *A. rufiventris* diverged in western direction the advanced pheomelanin bleached Ornate Spider Monkey taxon *A. (geoffroyi) panamensis*. It is argued that the form *A. panamensis* is a junior synonym of *A. ornatus*. Taxon *A. panamensis/ornatus* has a golden brown, dark red to orange colored back, with saturated eumelanin black pelage on the top of the head, outer sides of legs, hands, feet and distal part of the tail. It is distributed throughout Panama (from Chiriquí Province as far as E of the Canal Zone) and C+E Costa Rica. From *A. ornatus* (or *A. panamensis*) derived in southern direction the advanced pheomelanin bleached Azuero Spider Monkey taxon *A. azueroensis*. Its back is grayish-brown, somewhat darker than the underside. Outer surfaces of the limbs are black, the top of the head and neck are (brownish)-black. Its distribution is delineated by the Panamanian Pacific coast in the south and east. From the Ornate Spider Monkey taxon *A. ornatus* derived in

northern direction into Nicaragua the advanced pheomelanin bleached, near-euchromic Geoffroyi's Spider Monkey taxon *A. geoffroyi*. It is silvery to brownish-gray on the back, upper arms, and thighs. Its coat (except for the black head, elbows, knees, upper arms, lower legs, hands and feet) is overall orangish and cream-white colored. Its face is black, often with flesh-colored 'spectacles' around the eyes. From *A. ornatus* radiated away, first in western direction and from coastal Costa Rica northwards into Nicaragua, the advanced pheomelanin bleached Black-browed Spider Monkey taxon *A. frontatus*. With its orange, black and white coat *A. frontatus* is the most colorful taxon of the entire *A. geoffroyi* Clade. From taxon *A. frontatus* derived the overall most euchromic bleached Mexican Spider Monkey taxon *A. vellerosus*. Its dorsal surfaces range from black to light brown, and contrast strongly with its lighter abdomen and inner limbs. Flesh-colored skin is often present around the eyes. It occupies the entire northwestern part of the Isthmus containing El Salvador, Honduras (along the N coast into the lowlands of La Mosquitia), Guatemala (including the highlands) and E & SE Mexico. From taxon *A. vellerosus* to the north derived the near-albinotic Yucatán Spider Monkey taxon *A. yucatanensis*. It is characterized by the overall advanced eumelanin bleached, light brown and white colored coat. Its fur is brownish-black on the head, neck, and shoulders, grading into lighter brown on the lower back and hips and contrasting with its silvery-white underside, inner limbs, and sideburns. *Ateles (geoffroyi) yucatanensis* occupies a large distribution containing NE Guatemala, all of Belize, and SE Mexico (Yucatán Peninsula). The near-albinotic taxa *A. vellerosus* and *A. yucatanensis* that occupy dead-end distributions confined by untraversable geographic barriers in the northernmost range of the *A. geoffroyi* Clade, phenotypically do resemble taxon *A. grisescens* (from SW Panama) that occupies the southernmost distribution of the *A. geoffroyi* Clade within the Isthmus. These taxa are equally confined to phylogeographic dead-end distributions, therefore fully concurring with our theory that pretends to unveil and retrace allopatric primate speciation and radiation along phylogeographic pathways of meta-chromic bleaching.

Woolly Spider Monkeys or Muriquis genus *Brachyteles* (family Atelidae) from SE Brazil are

disputedly the largest among New World monkeys (adults weighing up to 11–12 kg). It is estimated that alouattines (howling monkeys) and atelines (woolly, spider, and woolly spider monkeys) split about 16 MYA and that the ancestor of Muriquis (*Brachyteles*) and Woolly Monkeys (*Lagothrix*) separated about 10 MYA from the lineage that would eventually lead to the Spider Monkeys (*Ateles*). Amazonian *Lagothrix* and Atlantic Forest *Brachyteles* are therefore considered to be sister groups (Mittermeier et al., 2013). Two species of Muriquis are recognized: the Northern Muriqui *B. hypoxanthus*, and the Southern Muriqui *B. arachnoides* (Fig. 34). Taxon *arachnoides* is distributed in SE Brazil, through the coastal Serra do Mar in the states of Rio de Janeiro, São Paulo, and (the NE of) Paraná. Its northern limits are the Serra da Mantiqueira and the Rios Paraíba and Paraíba do Sul. Taxon *B. hypoxanthus* historically ranged through the Atlantic Forest in the states of Bahia, Espírito Santo, Minas Gerais, and Rio de Janeiro, excluding only lowland forests in the extreme S of Bahia and N Espírito Santo. The northern limit of its distribution was probably the Rio Jequiriçá or the right bank of the Rio Paraguaçu, whereas the southern limit most likely was the Serra da Mantiqueira, in S Minas Gerais state. There, it meets the distribution of the Southern Muriqui taxon *B. arachnoides*. Sexual dimorphism is absent in Muriquis. The Southern Muriqui has a predominantly beige, with light, or dark brown or light gray-brown colored coat. It retains the black pigmentation of the face, palms, and soles of the feet from infancy into adulthood. Adults of both sexes develop only minor depigmentation in small pink or white spots in the pubic region and sometimes on the face. The Northern Muriqui taxon *B. hypoxanthus* has a uniformly beige colored pelage, with light or dark brown or light gray-brown coloration. At birth, the face is black, but at sexual maturity face and genitals lose their pigmentation and become spotty pink or flesh-colored (Fig. 34). Northern Muriquis have a vestigial thumb, which character differentiates them from Southern Muriquis that lack the thumb. The Southern Muriqui seems to be nearer to archetypic woolly spider monkeys than the Northern Muriqui, for the latter is overall progressively pheomelanin bleached near-albinotic in the head characters (white eyebrows, sideburns, and beard), and also in the advanced de-

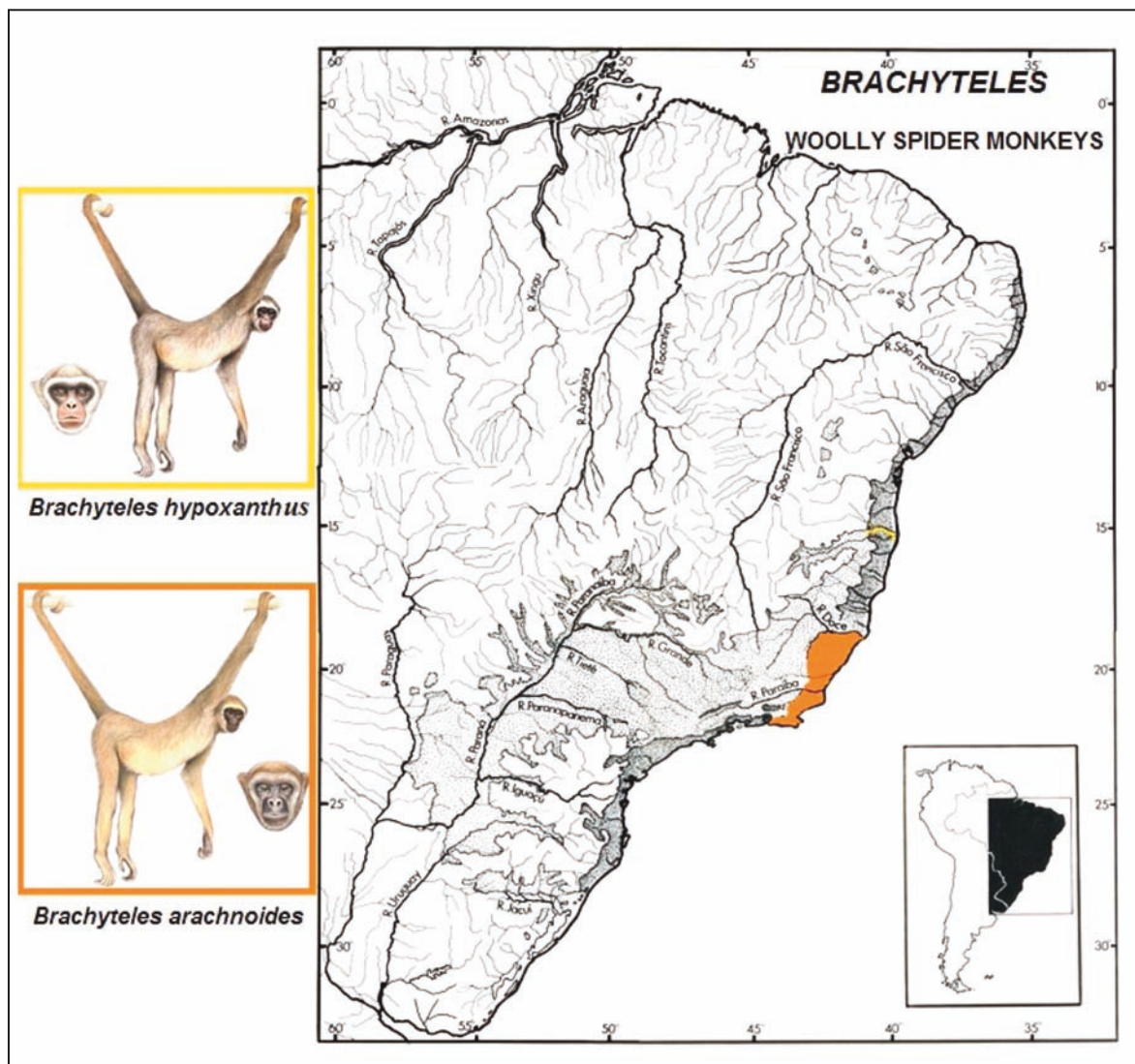


Figure 34. Metachromic bleaching in the Woolly Spider Monkey or Muriqui genus *Brachyteles* from the Atlantic coast of SE Brazil.

pigmentation of the face, in particular the spotty flesh-colored muzzle (Mittermeier et al., 2013).

For Amazonian Howling Monkeys, genus *Alouatta*, allopatric speciation, radiation, and phylogeography along eumelanin and pheomelanin pathways of metachromic bleaching are depicted in figures 35, 36). Two monophyletic cladistic Groups or Clades are recognized: *Al. belzebul* and *Al. seniculus* (Mittermeier et al., 2013). Within the *Al. belzebul* Clade, distributed south of the Amazon, saturated eumelanin all-black howling monkeys of the Amazon Black Howler taxon *Al. nigerrima* range between the Tapajós and Madeira Rivers. A

founder-pair or colony of somewhat bleached *Al. nigerrima* howlers once must have traversed the lower Rio Madeira, most likely lifting on floating logs or on drifting islands covered with chavascal (low type of várzea) forest. Presently, this howler also inhabits almost the entire interfluvial delineated by the Rios Amazonas, Purús and Ipixuna, an area that was formerly occupied by the advanced pheomelanin bleached yellowish-orange colored Purús Red Howler taxon *Al. puruensis* (belonging to the *Al. seniculus* Clade). We have spotted *Al. nigerrima* howlers in the várzea near Carreiro (opposite the city of Manaus) and, also, as far south as the Rios

Igapó-Açú and Tupana - black-water rivers that empty out into the Rio Madeirinha (a white-water left-bank tributary of the Rio Madeira). It seems that the overall orange-colored resident howler *Al. puruensis* and the all-black invasive *Al. nigerrima* howler do co-exist locally. However, the two taxa do not mix nor interbreed. While conducting a canoe survey during the peak of the flood season in the vast igapó floodplain along the Rio Igapó-Açú and Igarapé Cujubim, we have heard and seen the two taxa belonging to different Clades (*Al. belzebul* and *Al. seniculus*, respectively) in the same general area. The more frugivorous *Al. nigerrima* howler was only seen in the middle of seasonally flooded igapó forest during the peak of fruiting, whereas the more folivorous *puruensis* howler stayed back in the adjacent primary terra firme rain forest. We assume that *Al. puruensis* does so by lack of its

elsewhere preferred habitat - seasonally white-water inundated floodplain forest (várzea). It therefore seems that monkey taxa belonging to different monophyletic clades locally can co-exist, but only if they occupy different feeding niches, and within the local landscape parapatric or partly overlapping habitats. As these two howler taxa are considered valid species, they seem to have sufficiently diverged from one another to impede interbreeding in the contact or overlap zone.

Representing the nearest to archetypic taxon of the *Al. belzebul* Clade, the range of the Amazon Black Howler taxon *Al. nigerrima* may well be considered the center of the Clade's dispersion. From here, the other taxa diverged in eastern direction. From *Al. nigerrima* derived east of the Rio Tapajós the pheomelanin bleached Spix's Howler *Al. discolor*. It has an overall dark-brown to mahogany-

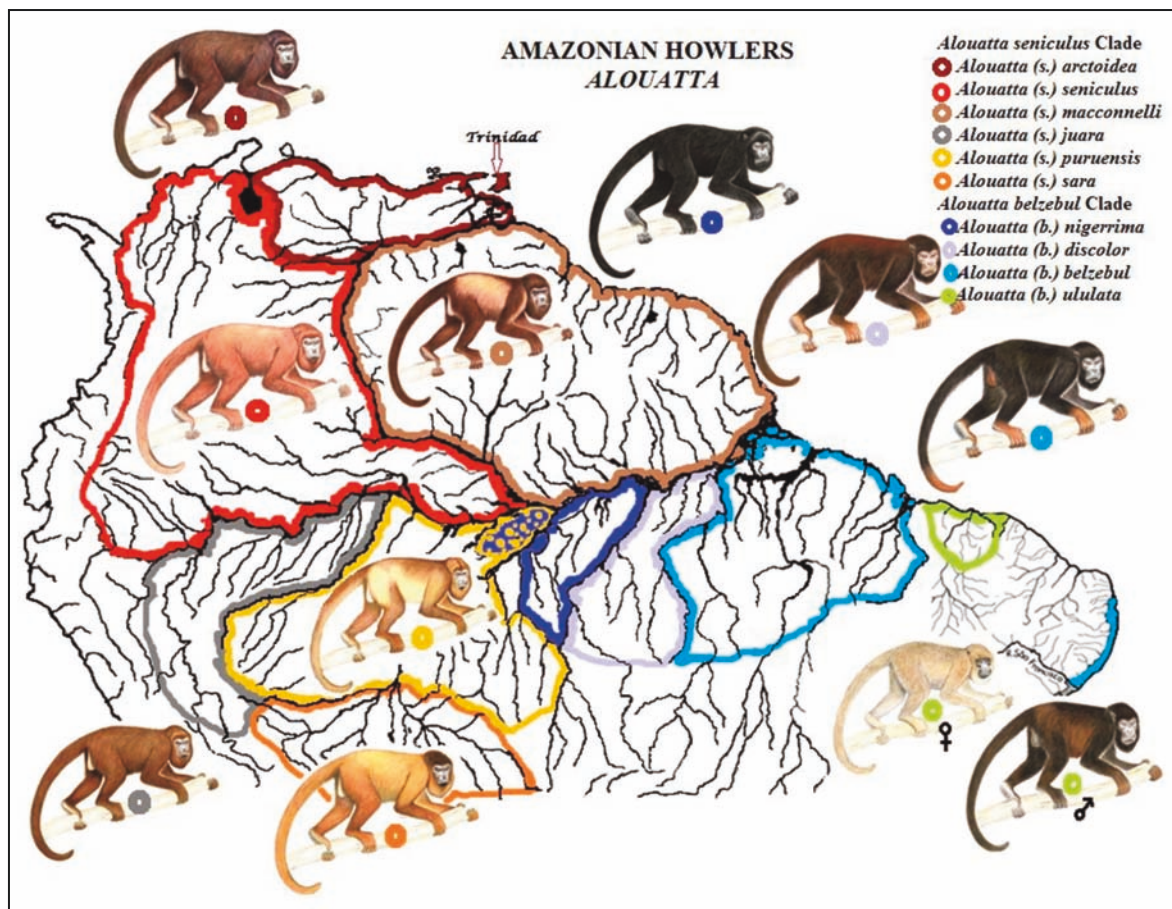


Figure 35. Distributions, allopatric speciation, radiation, and phylogeography along different pathways of metachromic bleaching depicted for all known Amazonian Howlers genus *Alouatta*.

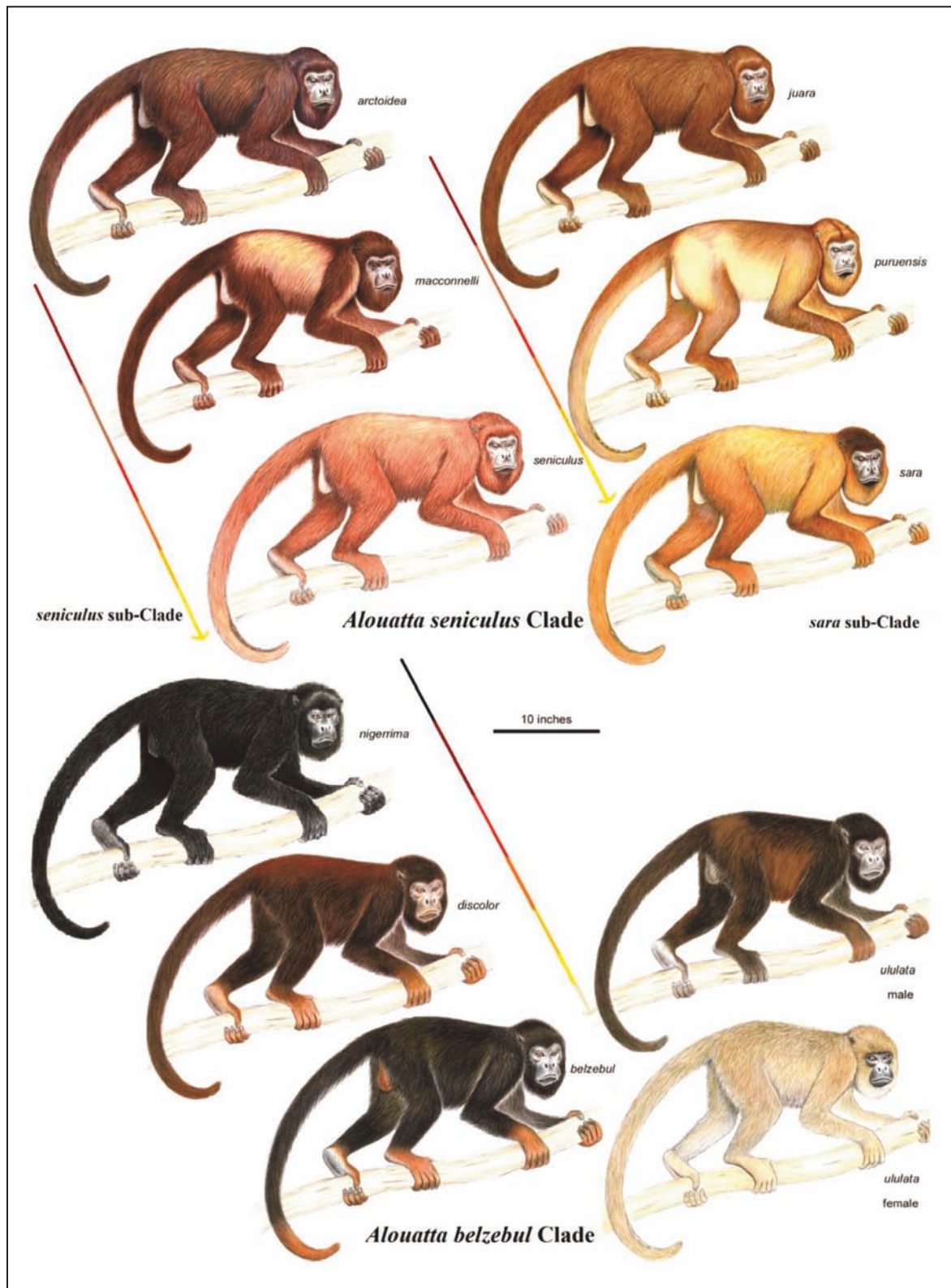


Figure 36. Metachromic variation, radiation, and phylogeography along eumelanin and pheomelanin pathways of metachromic bleaching depicted for all known Amazonian Howlers of the *Alouatta seniculus* and *Al. belzebul* Clades.



Figure 37. Adult male Guianan Red Howler *Alouatta macconnelli*. It was photographed while pulling off a juvenile that tried to seek protection from the human intruder, somewhere along the black-water Rio Jauaperi, a north-bank tributary of the Rio Negro (Courtesy of David Lemmon).

red coat and a rufous-chestnut dorsal band, hands, feet, and tip of the tail. A further pheomelanin bleached founder-colony of *Al. discolor* must once have traversed its eastern distributional limit - the Rio Xingú, Irirí, or Santa Helena (left-bank tributary of the Rio Teles-Pires in Mato Grosso). From Spix's Howler *Al. discolor* derived the dark brown colored Red-handed Howler *Al. belzebul*. This species is progressively pheomelanin bleached in the reddish-brown to yellow hands, feet, tail tip, forehead and back. It is distributed south of the Amazon, east of the Rio Xingú-Irirí, in the states of Pará (including Mexiana, Caviana, and Marajó Islands in the Amazon estuary), Maranhão, Tocantins, and Mato Grosso. West of the Atlantic coast of NE Brazil in the states of Rio Grande do Norte, Paraíba, Pernambuco, and Alagoas, are found enclave populations isolated from what is thought the taxon's former distribution, which must have been continuous through the states of Ceará and Piauí to the Amazonian population. From the Red-handed Howler *Al. belzebul* derived the advanced pheomelanin bleached Maranhão Red-handed Howler *Al. ululata*. This species distributed in NE Brazil occurs in remnant forest patches of dry

forest scrub called caatinga. It enters also the coastal mangrove forests of northern Maranhão, Piauí, and Ceará. The Maranhão Red-handed Howler *Al. ululata* radiated farthest away from the archetypic overall black Central Amazon Black Howler *Al. nigerrima*. It is sexually dichromatic. The male is black with rufous to reddish-brown hands, feet, tip of the tail and flanks. The female is yellowish-brown with sparse grayish hairs, giving it an overall olivaceous appearance (Fig. 36).

Within the *Al. seniculus* Clade we consider the overall dark reddish-brown Ursine Red Howler arctoidea from N Venezuela east of Lake Maracaibo, and from the coast (including the Islands of Trinidad and Tobago) extending S through the llanos to the Río Orinoco, the nearest to archetypic taxon for the monophyletic *Al. seniculus* sub-Clade, which is distributed north of the Amazon. Both sexes have a coat that is dark reddish-brown on the body, contrasting with a darker brown to blackish head, shoulders, limbs, and proximal part of the tail. Male Ursine Red Howlers often have a blackish beard, limbs and tail. From a founder-colony that once traversed the Orinoco River to the east, has derived the advanced pheomelanin bleached Guianan Red Howler *Al. macconnelli*. This taxon ranges east of the Río Orinoco throughout the Guianas, N Brazil (east of the Rio Negro and north of the Rio Amazonas, including Gurupá Island in the Amazon estuary), and S Venezuela (between the Cassiquiare and Orinoco Rivers). The Guianan Red Howler's coat is uniformly dark rufous-brown, the back is pheomelanin bleached yellowish to golden-brown with a dark dorsal stripe, and arms to elbows and legs to thighs are orangish-red. Distal part of the tail is pale-yellow (Figs. 35, 36).

From a founder-colony of further pheomelanin bleached *Al. macconnelli* that once traversed either the upper Rio Negro in the Colombian Amazon, or the Orinoco River at its headwaters, has derived the overall orange-colored Colombian Red Howler *Al. seniculus*. This taxon is now distributed north of the Amazon across E Ecuador and E Peru (east of the Río Huallaga), Colombia, NW Venezuela, and the Brazilian Amazon inbetween the Rio Solimões and Rio Negro. The Colombian Red Howler *Al. seniculus* is overall golden-toned to coppery-red on the body, contrasting with the maroon head, shoulders, limbs, and proximal part of the tail. Male Colombian Red Howlers are much bigger than fe-

males. Within the monophyletic *Al. seniculus* sub-Clade the bright orange-red Colombian Red Howler *Al. seniculus* is phylogeographically the most advanced pheomelanin bleached taxon. It radiated the farthest away from the nearest to archetypic saturated eumelanin, overall dark brown colored Ursine Red Howler *Al. arctoidea*, as such fully concurring with our theory. With respect to the monophyletic *Al. sara* sub-Clade of the *Al. seniculus* cladistic Group that is largely distributed south of the Amazon, we consider the Juruá Red Howler *Al. sara* the nearest to archetypic, least eumelanin bleached (dark brown) taxon. It ranges in the W Brazilian Amazon south of the Rio Solimões, and in the Rio Juruá Basin, extending west into the Peruvian Amazon. It is not sexually dichromatic. Its coat is generally dark reddish-brown, with the middle of the back lighter orange-rufous colored, and limbs and tail base dark rufous to black. The tail is paler, more golden from middle to tip. From a pheomelanin bleached founder-colony that once traversed the Rio Juruá to the east derived the Purús Red Howler taxon *Al. puruensis*. It is distributed across the entire Rios Juruá/Purús interfluvium as far east as the middle Rio Madeira. From there, it extended its range across the upper Rio Aripuanã as far east as the Rio Teles-Pires, and south as far as the Rio Abunã (which forms Bolivia's northern border). The Purús Red Howler *Al. puruensis* is sexually dichromatic. Males are dark rufous or red-brown with a golden upper dorsum and shoulders, whereas females are golden-orange with distal portions of limbs, tail base, and beard dark rufous. From a progressively pheomelanin bleached founder-colony of the Purús Red Howler that once traversed the Rio Abunã, has derived the quite distinct Bolivian Red Howler taxon *Al. sara*. It is distributed across the Bolivian Amazon including the entire Rio Beni Basin, and east as far as the Rios Mamoré/Guaporé interfluvium. The Bolivian Red Howler's coat is brick-red above, with limbs, head, and proximal part of the tail darker, more rufous colored. It represents the most advanced pheomelanin bleached taxon of the *Al. sara* sub-Clade (Fig. 36). It occupies a dead-end distribution in the south bordering the drier savanna and Chaco area (Fig. 35). Going further southwards begins the distribution of the Paraguayan Howler *Al. caraya*.

For extra-Amazonian Howling Monkeys genus *Alouatta*, allopatric speciation, radiation, and phylo-

geography along eumelanin and pheomelanin pathways of metachromic bleaching are depicted in figures 38, 39. Four non-Amazonian monophyletic Clades are recognized: the Brazilian Brown Howler *Al. guariba*, the Paraguayan Howler *Al. caraya*, the Central American Mantled Howler *Al. palliata*, and the Mexican Black Howler *Al. pigra* (Mittermeier et al., 2013). The Brown Howler *Al. guariba* Clade consists of two populations that may represent different valid taxa or species: the Northern Brown Howler *Al. guariba* and the Southern Brown Howler *Al. clamitans*. Taxon *Al. guariba* ranges in the Atlantic Forest from the Rio Paraguaçu, Bahia State, along the coast south as far as Rio Paraíba in Rio de Janeiro State. Inland, it extends into Minas Gerais State. The Southern Brown Howler *Al. clamitans* is distributed in the Atlantic Forest south of Rios Doce and Jequitinhonha, south as far as Rio Grande do Sul State. Taxon *Al. guariba* is not sexually dichromatic and both sexes are red-fawn, with females usually somewhat duller in color. Taxon *Al. clamitans* is generally dark reddish-brown, with males often being lighter colored than females. Males from São Paulo are orange-red to red-brown with a red belly, whereas males from Santa Catarina and Rio Grande do Sul are bright red-orange, having dark brown feet. Females are overall dark brown or blackish. The Northern Brown Howler *Al. guariba* is the lesser metachromic bleached. Taxon *Al. clamitans* derived from it, the males progressively following the pathway of pheomelanin bleaching. The further south it ranges, the more the male's overall coat color tends to red-orange or bright orange (Fig. 39).

The Paraguayan Howler *Al. caraya* forms a monotypic Clade. It is a sister species to the Amazonian red howlers of the *Al. seniculus* Clade. It diverged from a common ancestor about 4 MYA. The Paraguayan Howler *Al. caraya* is distributed across C Brazil, south of the states of Pará, Tocantins, Maranhão, and Piauí, west into the Pantanal, south into Paraguay, E and SE Bolivia, and maybe also into NW Uruguay. Much of its range is in the 'cerrado' of central Brazil and semi-arid 'caatinga' forest scrub in NE Brazil, where it uses gallery and riparian forest and patches of seasonal (semi)-deciduous 'cerradão' (a type of savanna forest). Adults of *Al. caraya* are sexually dichromatic, but both sexes are blond at birth. Mature males are generally uniformly black. Females and young of

either sex are pale grayish-yellow to golden-brown. Male Paraguayan Howlers *Al. caraya* from Bahia and Goiás are black, but those from Mato Grosso and Paraná are black with a brown back and hind parts. Males from São Paulo and Minas Gerais States are brown-black, with yellowish hands, feet, belly, and tail tip. In all male individuals the face is invariably dark, the fur is stiff and lengthy, and the beard is prominent. The scrotum is rust-red colored.

The Pacific Coastal and Central American Mantled Howler *Al. palliata* is, based on geographic distribution, divided in five taxa that could well represent distinct valid species: *Al. palliata* from NE Guatemala, ranging east to E Costa Rica or W Panama; *Al. aequatorialis* from the southern distributional limits of *Al. palliata* ranging through

the Darién into W Colombia, W Ecuador, and south as far as NW Peru; *Al. mexicana* ranging from S to SE Mexico and Guatemala following the southernmost distribution of the Central American Black Howler *Al. pigra*; *Al. coibensis* from Coiba and Jicarón Islands in SW Panama; and *Al. trabeata* from the Azuero Peninsula in SW Panama (Fig. 38). The coat of the Mantled Howler is smooth, very short and upright, being silky black with a mantle of longer, gold or yellowish-brown fur along the flanks. Adult males have a white scrotum.

The Central American Black Howler *Al. pigra* is monotypic. It is distributed across SE Mexico, Belize, and N to C Guatemala. Fur of *Al. pigra* is notably long, soft, and dense. Adults are not sexually dichromatic. They are overall black with traces of brown on the shoulders, cheeks, and back. The



Figure 38. Distributions, allopatric speciation, radiation, and pathways of metachromic bleaching followed in all extra-Amazonian Howling Monkeys genus *Alouatta*. Two Clades occur south of the Amazon: *Al. guariba* from the E Brazilian Atlantic forest, and *Al. caraya* from the 'cerrado' and 'cerradão' of the Central Brazilian Plateau. Along the Pacific coast of Ecuador and Colombia, far into Central America, occur the *Al. palliata* and *Al. pigra* Clades.

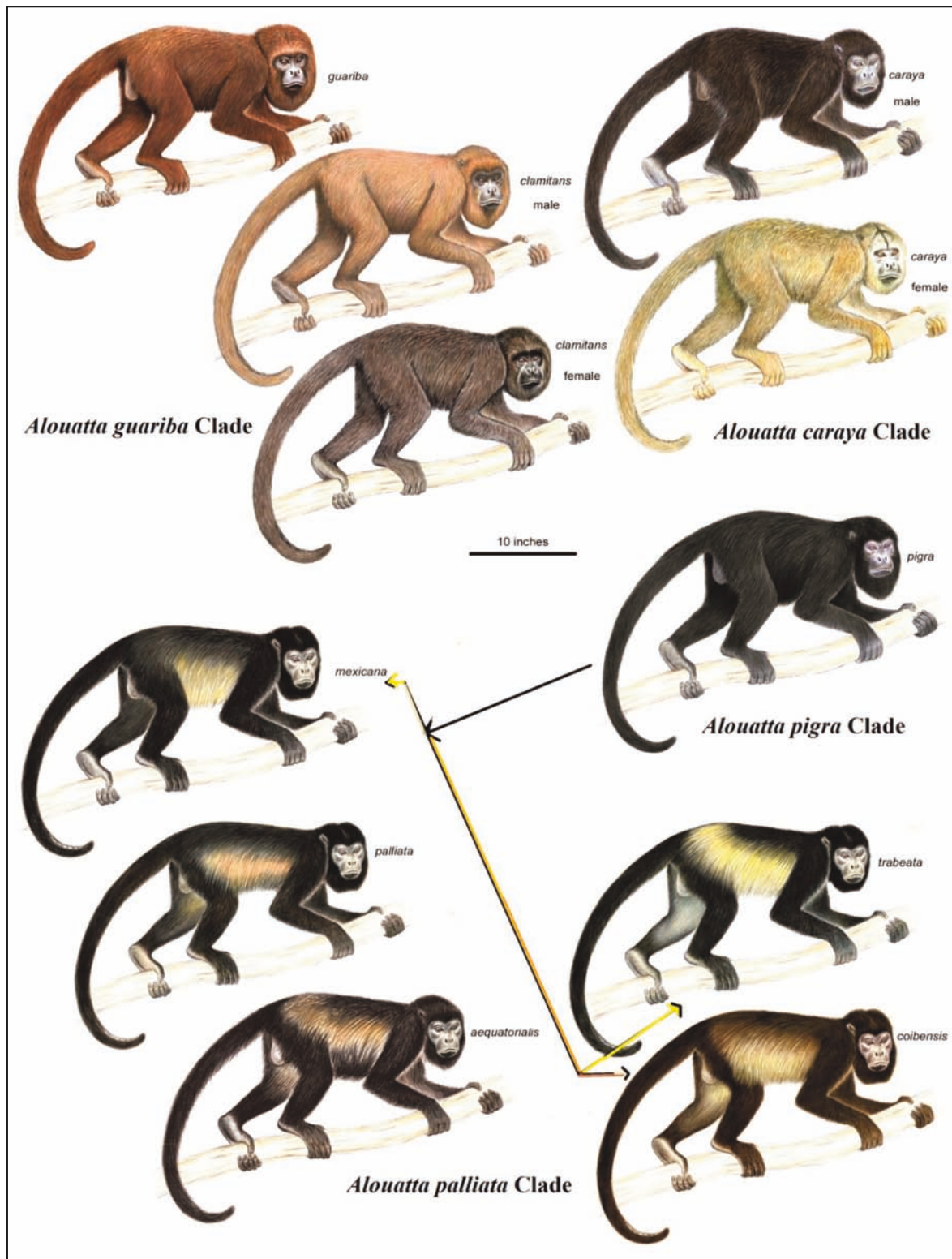


Figure 39. Pelage color variation, radiation and metachromic bleaching along eumelanin and pheomelanin pathways depicted for all extra-Amazonian Howling Monkeys genus *Alouatta* of the Brazilian *Al. guariba* and *Al. caraya* Clades, and the Central-American *Al. pigra* and *Al. palliata* Clades.

Central American Black Howler *Al. pigra* is considered the most saturated eumelanin, least bleached, nearest to archetypic form of the *Al. pigra* and *Al. palliata* Clades. It is also by far the largest howling monkey. The *Al. palliata* Clade is believed to have diverged from ancestral *Al. pigra* about 3 MYA (Mittermeier et al., 2013). Taxon *Al. palliata* is sympatric with taxon *Al. pigra* in Tabasco State, Mexico and in a small part of Guatemala. From the Golden-mantled Howler *Al. palliata* radiating northwards derived the Mexican Howler *Al. mexicana*, and radiating southwards the South Pacific Blackish Howler *Al. aequatorialis*, ranging far south into the Pacific coastal forests of Colombia and Ecuador. There, it is sympatric with the Colombian Red Howler *Al. seniculus*. From *Al. aequatorialis* in SW Panama derived the Azuero Peninsula Howler *Al. trabeata* and the Coiba Island Howler *Al. coibensis* (Fig. 38).

During his long-term fieldwork on the ecology of all eight monkey species that occur in the Guianas, the senior author has repeatedly watched the basic principles of allopatric primate speciation at work. At his study site situated in pristine primary terra firme rain forest in Central Suriname, local populations of the Guianan Red Howler *Al. macconnelli* (Fig. 37), the most territorial among all extant howling monkeys when measured by the size of the hyoid bone, had passed beyond the howler's optimal densities (Van Roosmalen, 2013a; 2015). This was measured by the high frequency of dawn chorus and vocal battles of neighboring groups throughout the day and nighttime in the proximity of territorial boundaries. One day, a subadult male got pushed out of his parental group that ranged close to the campsite area. For several days after being expelled, this young howler male got repeatedly involved in vocal battles with neighboring groups that subsequently chased him out of their respective territories. Weeks later, far away from the campsite, a boundary conflict took place that seemed never ending. The researcher rushed over to the spot. He arrived just in time to witness this very subadult male being attacked by the leader of a resident group in the company of his harem. The whole group chased the young male into an isolated tree close to where he could watch the scene. The subadult male was in the company of a female he presumably had attracted ('stolen') from some resident group that had chased him out earlier. In an

attempt to escape from his attackers, the howler male almost fell out of the canopy. He just could get hold on a thick branch and was hanging underneath it only secured by the grip of his hands and tail. Then, they all began to bite in his hands and tail tip. With a scream, he let loose and came crashing over forty meters down to the forest floor, hitting it at a hair width away from the researcher's head. The monkey looked dead, his motionless body covered with blood. After a few minutes, however, he got back on his feet and slowly climbed up a small tree. Back in the canopy, he sat next to his mate that had been watching the show from a distance. The pair was never seen again within the borders of the 400-ha study area. Some time later, vocal battling recommenced. It came from the same direction, sounding only much farther away. In retrospect, we assume that the couple survived and in the long run found a place to settle down, start a family, and defend a small territory squeezed in between the territories of some resident howler groups far away from their respective parental groups. One may speculate that the howler pair, driven by the trend to allopatry, also may have survived by venturing into some 'empty', marginal, or for howlers unfamiliar habitat. Or, in case the male was expelled from his parental group for his skin or (part of) coat color being somewhat lighter, he could have joined other outcast males that were discriminated upon and pushed out of their parental groups for other mutant metachromic deviances of skin and/or coat characters. For the sake of survival alone, such healthy young individuals may join efforts to stay alive. Together, they may turn into potential founder-colonies venturing into new lands, where they can thrive and reproduce unrestrictedly. At least as long as those lands, in turn, do not reach the taxon's optimal population density. By the time they do so, the generally accepted phenotype of that new parapatric or allopatric taxon or (eco)-species will have been stabilized while showing whatever features of further metachromic bleaching and/or depilation.

Living on an island in the Coppename River at about ten km from his field site, the senior author has repeatedly witnessed the coming and going of small groups of potential howler-founders to and fro Foengoe Island after having been forcefully pushed out from some mainland territory by the ruling group male(s). Pushed against the riverbank, they apparently did overcome their natural fear of water

and then swam toward the island. For some time, such immigrants tried to make a living on the island. Until it became clear to them they were trapped on an island too small to sustain a howler group year-round. Occasionally, such groups were spotted later while ranging along the opposite river-bank. We assume they had traversed the river swimming. Interestingly, a female howler that was raised as a pet and then set free to range across the 30-ha island, was eager to join any howlers coming onto the island. Sadly, when the immigrants eventually swam back to the mainland in search of new lands, the female stayed back on the island. Perhaps, she did so for lack of sufficient bonding or for fear of swimming across the river.

Capuchin Monkeys (genera *Cebus* and *Sapajus*) have diverged from Squirrel Monkeys (*Saimiri*) about 15 MYA. They formed distinct monophyletic

Clades that diverged during the Late Miocene to Early Pliocene, about 6.2 MYA. The Clades diversified during the Plio-Pleistocene era into two groups: Gracile or Untufted Capuchins (genus *Cebus*) in what is today the western Amazon, about 2.1 MYA, and Robust or Tufted Capuchins (genus *Sapajus*) in what are today SE Brazil, E Paraguay, and N Argentina, beginning about 2.7 MYA (Mittermeier et al., 2013). Gracile Capuchins genus *Cebus* are separated into the following five cladistics Groups or Clades: Humboldt's White-fronted Capuchin *Ce. albifrons* with four+ taxa (*Ce. albifrons*, *Ce. yuracus*, *Ce. unicolor*, and *Ce. cuscinus*), Guianan Weeper Capuchin *Ce. olivaceus* with three taxa (*Ce. brunneus*, *Ce. olivaceus*, and *Ce. castaneus*), White-faced Capuchin capucinus with two taxa (Colombian White-faced Capuchin *Ce. capucinus* and Panamanian White-faced Capuchin *Ce.*

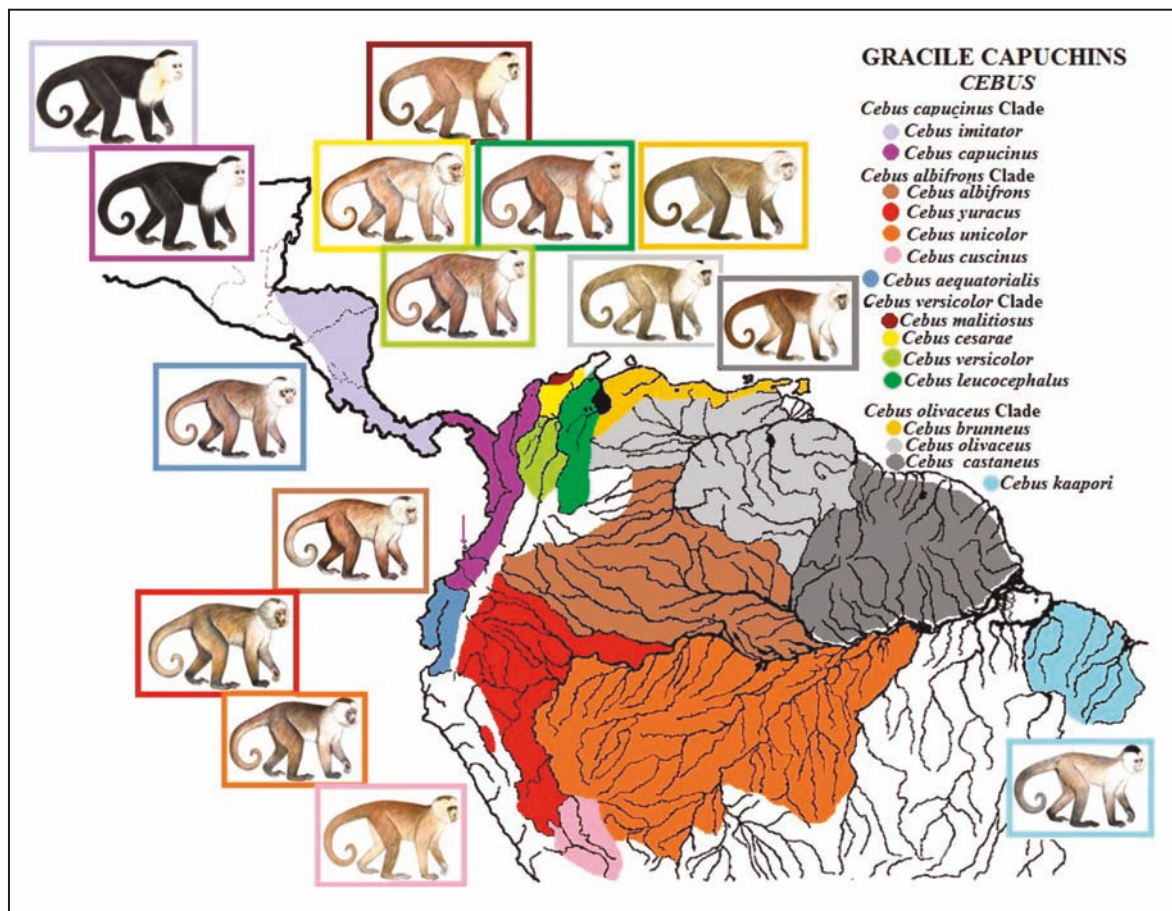


Figure 40. Distributions, allopatric speciation, radiation, and pathways of metachromic bleaching in all hitherto recognized Gracile Capuchins of the five distinguished phylogeographic Clades: *Cebus capucinus*, *C. olivaceus*, *C. versicolor*, and *C. albifrons*. The fifth Clade *C. aequatorialis* is monotypic.

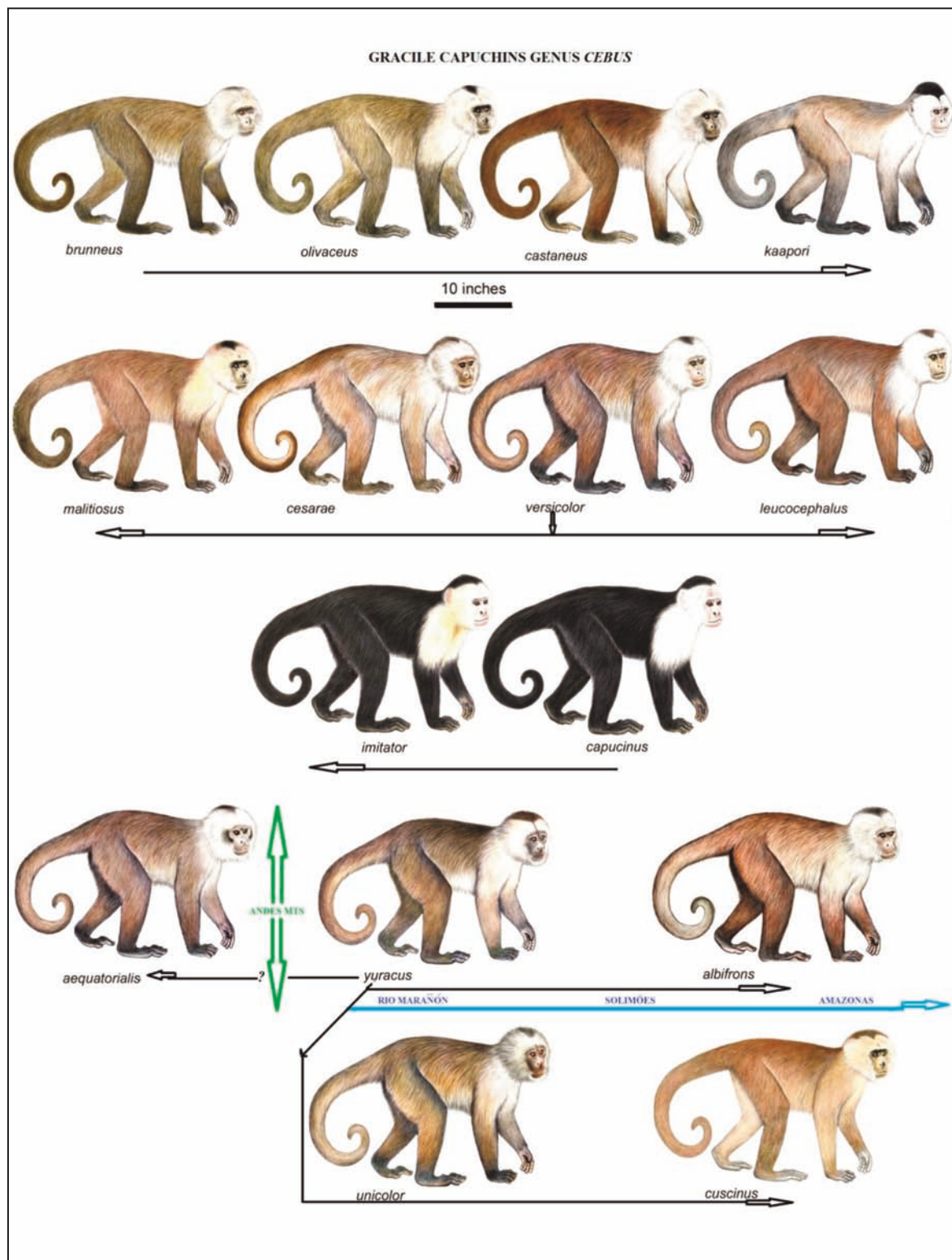


Figure 41. Metachromic diversification along eumelanin and pheomelanin pathways of metachromic bleaching (arrowed lines), speciation and radiation in all hitherto recognized Gracile Capuchins (*Cebus*) of the five distinguished phylogeographic Clades: *Cebus olivaceus*, *C. versicolor*, *Cebus capucinus*, and *C. albifrons*. *Cebus aequatorialis* from W Ecuador and NW Peru is monotypic, but may have derived from ancestral *C. yuracus* that once traversed the Andes Mts.

imitator), and Varied White-fronted Capuchin *Ce. versicolor* with four taxa (*Ce. versicolor*, *Ce. leucocephalus*, *Ce. cesarae*, and *Ce. malitiosus*). The recently discovered Ka'apor Capuchin *Ce. kaapori* ranging S of the lower Rio Amazonas is geographically closest related to the Guianan Weeper Capuchin (i.e., taxon *Ce. castaneus* ranging along the left/north bank of the lower Rio Amazonas) and, therefore, may form a sister Clade to it (Figs. 40, 41).

Within the *Ce. capucinus* Clade we consider the Colombian White-faced taxon *Ce. capucinus* (ranging from E Panama, through W Colombia south as far as NW Ecuador), the nearest to archetypic, least metachromic bleached form. Its body, crown, limbs, and tail are black. The chest is white, extending forward to the face and front of the crown and upward to the shoulders and upper arms. The Gorgona White-faced Capuchin *Ce. curtus curtus* is a small and relatively short-tailed subspecies from Gorgona Island sitting on the Colombian Pacific coast. From taxon *Ce. capucinus* derived *Ce. imitator*, the taxon that ranges from N Honduras, C and W Nicaragua, Costa Rica south into W Panama. It resembles much the typical Colombian White-faced Capuchin *Ce. capucinus*, but females have elongated frontal tufts with a brownish tinge.

Within the *Ce. olivaceus* Clade we consider the Venezuelan Brown Capuchin *Ce. brunneus* from N Venezuela east of the Sierra de Perijá and along the Coastal Range, including the island of Trinidad (where it is possibly introduced), the nearest to archetypic, least metachromic bleached form. Its pelage is thick and long, the upperparts are generally darker along the middle of the back than on the sides, the hairs are dusky basally, with a broad zone of chestnut in the middle, and black at the tips. Face and sides of the head are pale yellowish gray. The crown has a broad V-shaped patch of long hairs, narrowing to a point in front of which a narrow black line runs forward to the nose. Chin and lower parts of cheeks are grayish or fulvous white to whitish. Underparts are blackish brown, with tips of the hairs hazel. The throat is lighter than the chest and belly. Upper arms are maize yellow. Outer forearms are blackish with yellowish tips, inside forearms are much darker. Hands are blackish, hindfeet are nearly black. Tail is colored as back. From ancestral *Ce. brunneus* derived the Guianan

Weeper Capuchin *Ce. olivaceus* that is restricted to the Venezuelan Amazon Basin in forests of the Guayanian Shield, from the upper Río Orinoco east to the left bank of the Río Essequibo in W Guyana. Its pelage is overall dark brown or reddish with black-agouti banding on flanks, limbs, and tail. The face is naked and pink. Cheeks are buffy-white. It differs from *Ce. brunneus* in the advanced bleached albinotic head and upper arms and the wider V-shaped black crown cap.

From ancestral *Ce. olivaceus* derived the Chestnut Weeper Capuchin *Ce. castaneus*. This taxon ranges from the Río Essequibo E through Suriname and French Guiana into N Brazil, where its distribution is delineated by the Rios Negro, Branco, and Catrimani in the W, Río Amazonas in the S, and the Atlantic coast in the E (it also inhabits Caviana and Mexiana Islands in Amazon's estuary). It differs from *Ce. olivaceus* in the narrower black triangle on the crown and the pelage of the head being overall yellowish-white, but reddish-chestnut above the ear and nape, in the advanced pheomelanin bleached reddish-chestnut upperparts of the body and limbs, and pale yellow shoulders and fronts of arms above the elbows. A founder-colony of the Chestnut Weeper Capuchin *Ce. (olivaceus) castaneus* must once have traversed the lower Río Amazonas. From it derived the Ka'apor Capuchin *Ce. kaapori* that ranges in NE Brazil south of the lower Amazon River (NE Pará and NW Maranhão). This taxon is characterized by a longer body in comparison to other *Cebus* species. It is grayish agouti-brown, and lighter on the flanks. Face, shoulders, mantle, and tail tip are silvery-gray, the limbs are agouti, and the hands and feet dark brown or black. The crown has a triangular black cap that extends to a dark stripe down the nose. The pelage of the Ka'apor Capuchin is overall advanced eumelanin bleached to nearly albinotic, as such much contrasting with the saturated eumelanin blackish crown cap, hands and feet. Being phylogeographically farthest radiated away from the center of dispersion (NW Venezuela) of the *Ce. olivaceus* Clade, and occupying a dead-end distribution, where it also has to compete with the Guianan Brown Capuchin *Sapajus apella* (Figs. 42–44), *Ce. kaapori* is clearly the most progressively bleached, near-albinotic taxon within the *Ce. olivaceus* Clade (Fig. 41).

Within the *Ce. versicolor* Clade we consider the Varied White-fronted Capuchin *Ce. versicolor* the

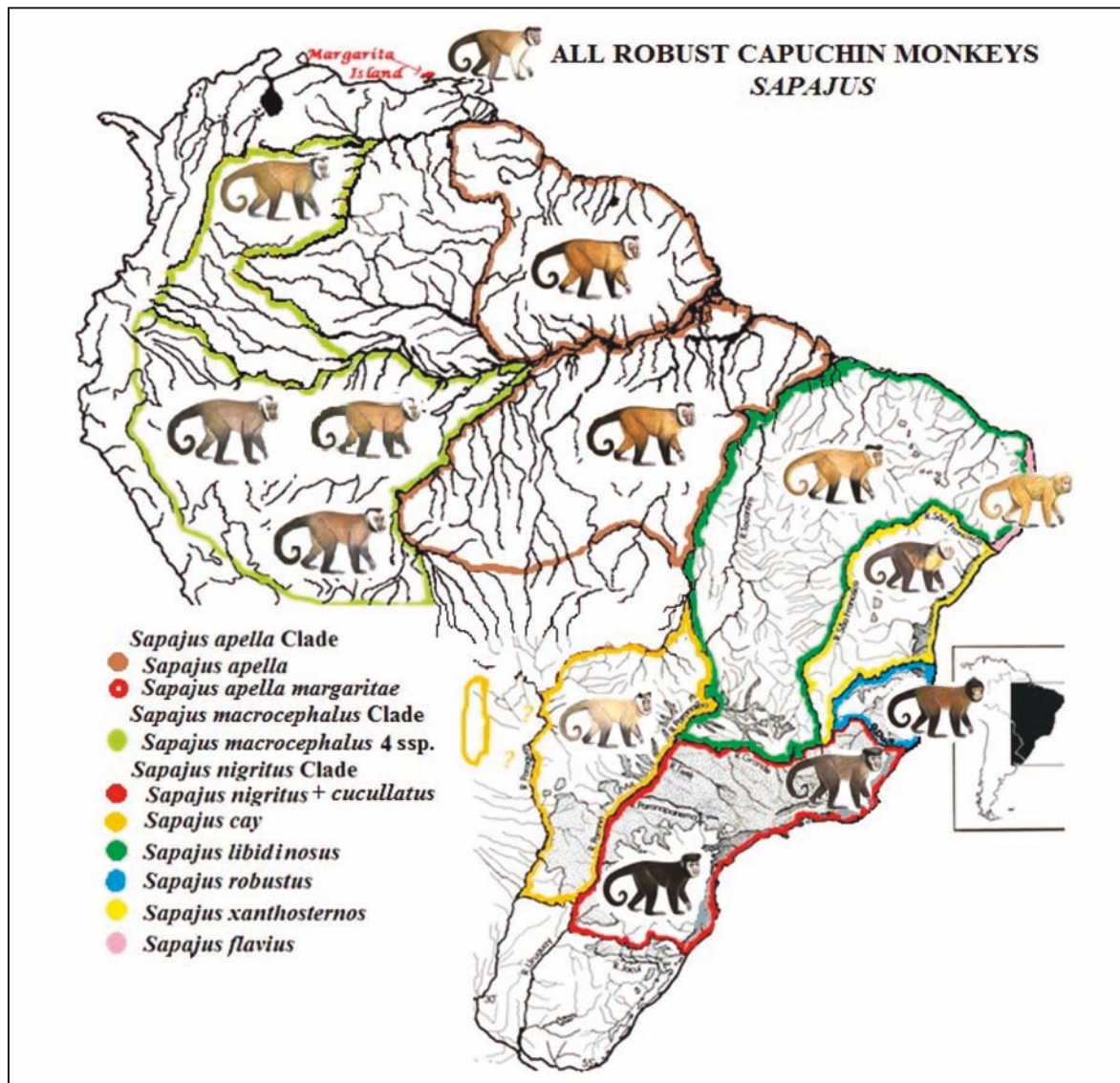


Figure 42. Phylogeography, allopatric speciation, radiation, and pathways of metachromic bleaching followed in all hitherto recognized Robust (Tufted) Capuchins of the three distinguished phylogenetic Clades: *Sapajus nigrinus*, *S. apella*, and *S. macrocephalus*. From an ancestral saturated eumelanin (all-black) form of the *S. nigrinus* Clade, quite recently (an estimated 400,000 YA) radiated away into the Amazon the pheomelanin bleached species *S. apella* (including the insular taxon *S. a. margaritae*), and *S. macrocephalus*, the latter with four different taxa/'species-in-the-making' - from SE to N: *juruanus*, *pallidus*, *maranonis*, and *fatuellus*).

nearest to archetypic, least metachromic bleached taxon. It is distributed in N Colombia in the middle Río Magdalena Basin. It is the darkest among the Clade's four taxa, though a rather pale form with red tones on the mid-dorsal region and foreparts of the limbs, generally contrasting with the rest of the body (Fig. 41). From *Ce. versicolor* derived towards the NE the Sierra de Perijá White-fronted Capuchin *Ce. leucocephalus* that ranges in N Co-

lombia from the W slope of the Cordillera Oriental E to the Ríos Zulia and Catatumbo Basins and NW Venezuela (Zulia State). This taxon is progressively bleached, near-albinotic in the head, chest, and shoulder parts. From *Ce. versicolor* derived towards the N first the Río Cesar White-fronted Capuchin *Ce. cesarae*, ranging in N Colombia, in the Río Cesar Valley, W into the S and E slopes of the Sierra Nevada de Santa Marta. From taxon *Ce. cesarae*,

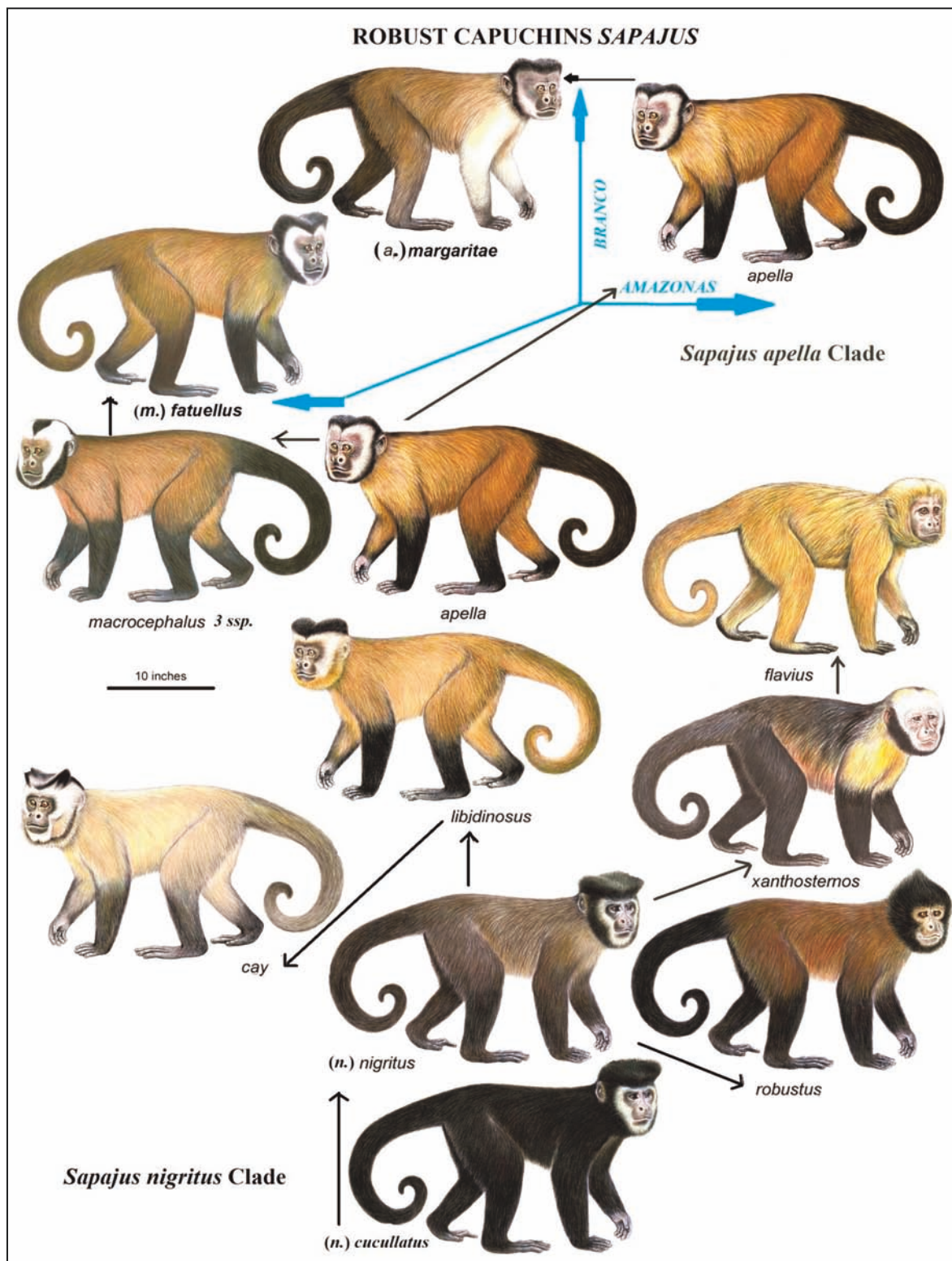


Figure 43. Radiation and metachromic diversification in the *Sapajus nigrinus* and *S. apella* Clades of Robust or Tufted Capuchins. From an ancestral saturated eumelanin form of *S. nigrinus* the species *Sapajus apella* and *S. macrocephalus* radiated away into the Amazon with different taxa 'in-the-making'.

in turn, derived the Santa Marta White-fronted Capuchin *Ce. malitiosus* that is only known from the NW base of Sierra de Santa Marta. It may range also throughout the lower W and N slopes of the Sierra Nevada in N Colombia. The two taxa are the palest among the N Colombian and Venezuelan White-fronted Capuchins. Taxon *Ce. cesarae* is buffy in the head and throat parts and pheomelanin bleached orangish in the cap, middle of the back, forearms, and forelegs, as such contrasting with the sides of back and trunk. Taxon *Ce. malitiosus* is advanced eumelanin bleached in the silvery to cinnamon-brown chest and belly, and a contrasting albinotic area of the front extending well over the upper surfaces of the shoulders and inner sides of upper arms (Fig. 41).

Within the *Ce. albifrons* Clade we consider the Mara  n White-fronted Capuchin *Ce. yuracus* the nearest to archetypic, overall least metachromic bleached taxon (Fig. 41). This taxon is distributed north of the Amazon River in S Colombia, E Ecuador, NE Peru, and presumably W Brazil between the Rios I  a and Solim  es. It is gray-fronted on the forehead, sides of the face, chest, and outer sides of the arms. Its general color is ochreous-brown, contrasting sharply with the grayish to buffy outer sides of forelimbs, and with the pale silvery to orangish underparts. The cap is black, with a median line running down inbetween the eyes. The tail is brown like the back, but paler towards the tip. From ancestral *Ce. yuracus* derived first Humboldt's White-fronted Capuchin, the nominate taxon *Ce. albifrons* that is widely distributed across the upper Amazon Basin of S Venezuela, S and E Colombia (occurring north of the Rio Amazonas and the Rio I  a-Putumayo, N as far as the Rio Meta, and in the lowlands W of the Orinoco, and NW Brazil (N of the Rio Solim  es, and W of the Rios Negro and Branco, as far north as the Rio Uraricoeira). Humboldt's White-fronted Capuchin *Ce. albifrons* is overall pale grayish-brown, darker on the limbs. Hands and feet are yellowish-brown. The tail is ashy above, whitish below, and brownish-black towards the tip. The front is creamy white, and there is a cap of short dark fur on the crown that is rounded in the front and well demarcated from the light-colored forehead. The face is naked and pinkish, flesh-colored. From *Ce. yuracus* derived also Spix's White-fronted Capuchin *Ce. unicolor*, most likely after a founder-colony of ancestral *Ce.*

*yuracus* traversed the upper reaches of the Rio Ucayali in E Peru. It is nowadays widely distributed in the upper Brazilian Amazon Basin, south of the Amazon River and west of the Rio Tapaj  s, throughout the northern parts of Mato Grosso and R  ndonia States, and throughout the Rios Madeira, Pur  s, Juru  , and Javar   Basins as far west as the Rio Ucayali. *Cebus unicolor* is uniformly bright ochreous or grayish-brown with darker grayish-brown flanks and mid-back, with a yellowish or cream-white front and reddish-yellow to reddish limbs and tail. From ancestral *Ce. unicolor* derived later the Shock-headed Capuchin *Ce. cuscinus* that is believed to range from the right bank of the upper reaches of the Rio Pur  s in SE Peru, W into the Cuzco Department including the upper Rio Madre de Dios, and S and E as far as the Rio Tambopata Basin, also extending into NW Bolivia. Taxon *Ce. cuscinus* has a longer, silkier fur than *Ce. unicolor* and is less brightly colored. Its limbs are browner and contrast less with the back. The cap is large, distinct, and dark brown. The forearms are orange-rufous on the outside, darker on the wrists and hands. Underparts are ochreous-orange and silvery, becoming buff on the chest. The fronts of the shoulders and inner sides of the upper arms are whitish. The tail is brown, somewhat paler towards the tip. The male has a broad pale frontal region sharply defining the dark-brown cap. Overall, *Ce. cuscinus* is the most advanced pheomelanin bleached taxon of the *Ce. albifrons* Clade. It is the form that radiated away farthest from the center of this Clade's dispersion (Fig. 40). The Ecuadorian White-fronted Capuchin *Ce. aequatorialis* is monotypic. It may form a sister Clade to the Gracile Capuchins from the upper Amazon Basin. Ancestral Mara  n White-fronted Capuchin *Ce. yuracus* once must have traversed the Andes Mountains somewhere at the upper reaches of the Rio Mara  n and then diverged into *Ce. aequatorialis*. *Cebus aequatorialis* is distributed in Ecuador and NW Peru, in the lowlands west of the Andes (Fig. 34). Its upperparts are pale cinnamon rufous, darker along the midline of the back. Front and sides of the head are yellowish white, with a narrow black transverse line on the forehead forming the cap, from which a narrow median black line descends to the nose. Hands and feet are a little darker, more brownish than the arms and legs. The chest is lighter than the belly (Fig. 41).

During long-term fieldwork in Central Suriname, the first author spotted a few times by chance small parties consisting of phenotypically deviant cream-white, long-haired, fluffy-coated males of the Guianan Weeper Capuchin *Ce. (olivaceus) castaneus*. Such all-male parties seemed to range randomly while travelling at high speed through the vast landscape of pristine matrix lowland rain forest in the middle of which his study area was situated. It is located at more than one-hundred km north of Kaiser Mountains, a hilly country of which the foothills seem to form the Guianan Weeper Capuchin's core distribution. This region that provides this monkey with its preferred habitat - 'mountain savanna forest' - was found to sustain a very large population of this elsewhere in the Guianas extremely rare taxon *Ce. (olivaceus) castaneus*. Mountain savanna forest is typified by an understory that is dominated by the majestic 'bergimaripa' palm *Attalea speciosa* Mart. (Arecales: Arecaceae). Above 400 m altitude, this palm tree is locally so abundant that one gets the impression to walk through a monocultural plantation of the African oil-palm *Elaeis guineensis* Jacq. (Arecales: Arecaceae). The large fruits of *Attalea speciosa* constitute the Guianan Weeper Capuchin's principal daily food throughout most of the year. Mountain savanna forest above 400 m altitude, therefore, may function as a 'keystone habitat' to the Guianan Weeper Capuchin, hence the high population density.

Two decades later, while conducting biodiversity surveys in Pico da Neblina National Park situated in the extreme northwestern corner of the Brazilian Amazon, the authors spotted a population of near-albinotic Weeper Capuchins that were characterized by a very dense, fluffy, overall long-haired, cream-white bleached fur. Their coat features looked very similar to that of the all-male parties that were seen sporadically passing through the Voltzberg study area. The Pico da Neblina population of weeper capuchins was spotted in a low type of cloud forest scrub that grows at high altitudes of 2,000 to 2,500 m. To the astonishment of the researchers, the capuchins were seen spending part of the daytime on the ground in the middle of open tepuí (sandstone table-mountain) 'rock savanna'. They were seen foraging for invertebrates, mostly snails, other organisms endemic to tepuí mountain tops, in addition to vegetable matter (e.g., roots, tubers and pseudobulbs of all sorts of

terrestrial bromeliads and orchids). In retrospect, our sighting may be explained for as follows. In the past, a founder-colony of near-albinotic Guianan Weeper Capuchins, driven by the 'trend to allopatry' out of the center of dispersion of archetypic *Ce. (olivaceus) castaneus*, may have traversed the upper Rio Branco and then reached the Pico da Neblina area. The latter is situated somewhat south of the Río Cassiquiare, the channel that runs through the watershed connecting the basin of the Rio Negro with that of the Río Orinoco. The fully bleached euchromic, long-haired, soft-coated weeper capuchins that were seen foraging in tepuí cloud forest and open rock-savanna at 500–1,000 m below the 3,004 m Pico da Neblina summit much resembled the near-albinotic, fluffy-coated *Ce. (olivaceus) castaneus* from Kaiser Mountains, Central Suriname. If the Pico da Neblina population turns out to represent a new taxon or one in-the-making, the 'Neblina Weeper Capuchin' would occupy a dead-end distribution in the southwestern-most corner of the *Ce. olivaceus* Clade's range, the farthest away from the supposed center of the Clade's dispersion (the Guianas or Venezuelan Coastal Range). The upper Rio Negro forms the division between the distributions of the Guianan Weeper Capuchin *Ce. olivaceus* Clade and the Humboldt's White-fronted Capuchin *Ce. albifrons* Clade (Fig. 39). This example from the field is in line with our theory of allopatric speciation in male-defended territorial primates such as *Cebus*. The 'Neblina Weeper Capuchin' may have radiated away from the *Ce. olivaceus* Clade's center of dispersion in the Guianas following a pathway of metachromic bleaching driven by the trend to allopatry in phenotypically deviant euchromic, long and fluffy-haired males. Interestingly, the mechanism of allopatric speciation and radiation of a monophyletic clade of monkeys like that of Humboldt's Weeper Capuchins at first sight seems non-adaptive, at least in strict Darwinian sense, for it is solely based on discriminatory behavior performed exclusively by high-ranking males. The genes for warm, long and fluffy-haired coats are simply retained in the genes of these capuchin 'founder-colonies'. Such a feature would therefore not a priori be the result of adaptive processes of natural selection. Its warm coat only secondarily happened to have survival value. It only turned adaptive when these gracile capuchins had to adapt in a short

period of time to a new habitat or feeding niche that would not have suited the species they derived from. Following this rationale, one may speculate about a similar metachromic pathway that our hominid ancestors about 6 MYA must have followed when exchanging the canopy of tropical rain forest for a landscape of arid, open savanna scrub. Or a similar pathway of metachromic bleaching towards albinotic (from a black to yellow or white skin color) and/or depilation of the body that different hominids followed between 100,000 and 50,000 years ago, when the trend to allopatry (male discriminatory behavior) forced them to leave the center of hominid dispersion and the cradle of hominid evolution - C and N Africa - to make a harsh living of nomadic big-game hunting/gathering in (for hominids) climate - and habitat - wise new, marginal, unsuitable, or inhospitable landscapes of Central Europe, the Middle-East and SE Asia.

Capuchin Monkeys of the genera *Cebus* and *Sapajus* formed distinct monophyletic Clades that diverged during the Late Miocene to Early Pliocene, about 6.2 MYA. During the Plio-Pleistocene era the Clades diversified into two groups: Gracile or Untufted Capuchins genus *Cebus*, about 2.1 MYA in what is nowadays the western Amazon, and Robust or Tufted Capuchins genus *Sapajus*, beginning about 2.7 MYA in what are today SE Brazil, E Paraguay, and N Argentina. There is strong evidence from molecular genetic studies that Robust Capuchins (genus *Sapajus*) spent most of their evolutionary history in the Atlantic Forest of SE Brazil, NE Argentina, and E Paraguay. And that the current wide-ranging sympatry of Robust and Gracile Capuchins across the larger part of the Amazon Basin is the result of a single, rapid, Late-Pleistocene invasion of Robust Capuchins from the Atlantic Forest, first into the 'Cerrado' and 'Cerradão' of C and NE Brazil, and only recently (about 0.4 MYA) from central South America north into the Amazon Basin and the Guianas (Mittermeier et al., 2013). Though widespread throughout the Amazon Basin and the Guayanian Shield, the genetic differentiation of the Amazonian Robust Capuchins is limited. The fact that the phenotypic diversity of the Amazonian Robust Capuchins is not mirrored by a corresponding genetic diversity strongly supports our theory of allopatric primate speciation. A number of the 16 taxa that are overall recognized in

different taxonomic arrangements (e.g., Groves, 2001a; Silva Jr., 2001; Silva Jr., 2002) may well represent taxa 'in-the-making'. Here, we follow Silva Jr. (2001) in recognizing only two species: the Guianan Brown Capuchin *Sap. apella* with three subspecies distributed in the eastern Amazon and the Guianas, and the Large-headed Capuchin *Sap. macrocephalus* with four subspecies that are distributed across the western Amazon. These taxa form two monophyletic Clades in which little genetic differentiation is shown. In contrast, the non-Amazonian species recognized by Silva Jr. are genetically distinct forming the monophyletic *Sap. nigrinus* Clade (Figs. 39, 40). Among the six species of the extra-Amazonian *Sap. nigrinus* Clade we consider the Black-horned Capuchin *Sap. nigrinus* the nearest to archetypic, less bleached species (Figs. 42, 43). Its southernmost populations representing the darkest, overall most saturated eumelanin form may well be a distinct taxon named *Sap. cucullatus* by Spix in 1823. The Black-horned Capuchin is the most S occurring of all robust capuchins. It is distributed in SE Brazil, S of the Rios Doce and Grande, extending S through the Atlantic Forest, and taxon *Sap. cucullatus* further south E of the Rio Paraná into Rio Grande do Sul State and NE Argentina. The Black-horned Capuchin is a large-sized species with horn-like tufts on either side of the head at the temples. Its fur is overall very dark brown or grayish in *nigrinus*, and black in *Sap. cucullatus*, often with slightly pheomelanin bleached, reddish or yellow-fawn colored underparts. A black to dark-grayish crown (with tufts in adults) contrasts much with the light colored face. The tail is black. From *Sap. nigrinus* derived the monotypic Crested Capuchin *Sap. robustus* after a founder-colony of *Sap. nigrinus* traversed the Rio Doce to the north. It is distributed in SE Brazil from the Rio Jequitinhonha in Bahia State S to the Rios Doce and Suaçuí Grande in Espírito Santo State and E Minas Gerais State, E of the Serra do Espinhaço. This taxon is very dark wood-brown or blackish above and on the limbs, with a faint dorsal stripe. The underparts are pheomelanin bleached red or yellowish, whereas forearms, hands, lower legs, and feet are deep dark brown to black. Its face is dark grayish, with some white hairs on the forehead and temples. The crown tufts are tall and conical in shape. From a founder-colony of the northern Black-horned Capuchin *Sap.*

*nigrinus* that once traversed the Rio Jequitinhonha to the north, derived the Yellow-breasted Capuchin *Sap. xanthosternos*. Yellow-breasted Capuchins tend to be much darker in overall color in the southwestern part (N Minas Gerais State), whereas they are pale in the northern part of this taxon's distribution. The monotypic taxon *Sap. xanthosternos* is further distributed in CE Brazil, S and E of the Rio São Francisco, south to the Rio Jequitinhonha (in S Bahia State). It is generally pheomelanin bleached brindled reddish above with a sharply marked, golden-red underside. Tail and limbs remained saturated eumelanin black. Its crown does not contrast with the body, the cap is black, and the face and temples are fawn. It has small backward pointing tufts. From Yellow-breasted *Sap. xanthosternos* derived the monotypic Blond Capuchin *Sap. flavius*, which was described by Schreber in 1774. Until it was collected in 2005, the Blond Capuchin was only known from an early illustration. Before colonial times, it must have been distributed in Coastal NE Brazil from S Rio Grande do Norte State through Paraíba State into NE Pernambuco. This taxon may extend its range to the left bank of the Rio São Francisco in Alagoas State. The Blond Capuchin is small, distinctive, and untufted. Its body and limbs are uniformly advanced pheomelanin bleached golden-yellow, whereas its lower-body parts are slightly darker golden-yellow. Hands and feet are black, whereas the tail is uniformly golden-blond, but darker on the dorsal side than the rest of the body. It further has a rectangular snow-white cap on the front of the head, to just above the ears, and a furless, pendulous throat flap. Face and forehead are near-albinotic, cream to pinkish colored, the eyes are brown. *Sapajus flavius* occupies degraded Coastal Atlantic Forest and *Montrichardia linifera* (Arruda) Schott (Araceae) swamp in Pernambuco State, and 'caatinga' scrub in W Rio Grande do Norte State. Being advanced pheomelanin bleached to near-albinotic, taxon *flavius* occupies a dead-end distribution. It therefore fully concurs with our theory on the origin of allopatric speciation. The theory suggests that a founder-colony of progressively pheomelanin bleached *Sap. xanthosternos* once was forced to make a living in the (for Robust Capuchins) marginal or unsuitable habitat of swamps and low xerophytic, spiny scrub of profusely branched bushy vegetation up to 8–10 m in height, mixed

with prickly succulent cacti, and spiny, rigid-leaved bromeliads. Blond Capuchins are reported to use even sand dunes and mangroves.

From the northern form of the Black-horned Capuchin derived to the W the Hooded Capuchin *Sap. cay*, and to the N the Bearded Capuchin *Sap. libidinosus* (Fig. 42). The monotypic taxon *cay* is distributed in SE Bolivia, N Argentina, SW Brazil - W of the Rio Paraná through Mato Grosso State into SW Goiás and Mato Grosso do Sul - and Paraguay (E of the Rio Paraguay as far as the Rio Paraná). The Hooded Capuchin *Sap. cay* is a small, short-limbed species without sexual dimorphism, typified mainly by its prominent dark dorsal stripe. *Sapajus cay* is very variable in color, but generally rather pale. Its crown is pale to blackish-brown, with two small hornlike tufts. Dorsal parts of the body (shoulders, front of the upper arms, saddle, rump, and thighs) are grayish-brown. Forearms, hands, wrists, lower legs, and feet are blackish. Eyes, nose, and mouth are surrounded by white hairs. It has a small white beard, and a dark line extends down from the ears to under the chin. From the Black-horned Capuchin derived to the north the monotypic Bearded Capuchin *Sap. libidinosus*. This taxon is distributed in C and NE Brazil, W and N of the Rio São Francisco into Maranhão State, and in the W of Piauí State, and E to C Rio Grande do Norte, NW Paraíba, W Pernambuco, and W Alagoas; to the W it extends to the Rio Araguaia, and its southern limit is the north bank of the Rio Grande in Minas Gerais. To the west, the Bearded Capuchin taxon *Sap. libidinosus* is replaced by *Sap. apella*, to the east by *Sap. flavius*, and to the south of the Rio São Francisco by *Sap. xanthosternos*. *Sapajus nigrinus* occurs just south of the Rio Grande. Some hybridization between *Sap. libidinosus* and *Sap. nigrinus* is reported to occur in the western part of Minas Gerais. The Bearded Capuchin *Sap. libidinosus* is comparatively small and does not show sexual dimorphism. It differs from all other Robust Capuchins by the rusty-red hair on the back of the neck, the dark-brown preauricular stripe running down the side of the face in front of the ears, and the orange-yellow throat and dorsal parts of the body, flanks, outer part of arms, and proximal two-thirds of the tail. Forearms are dark, and the lower back and outer surface of thighs are grayish-brown, mixed with some reddish hairs. The crown is black, with rounded, sometimes bushy, black tufts.

Here, we recognize only two Amazonian Robust or Tufted Capuchins (genus *Sapajus*): the monotypic Guianan Brown Capuchin *Sap. apella* that is distributed in the eastern Amazon and in the Guianas, and the Large-headed Capuchin *Sap. macrocephalus* with a number of forms/morphs/subspecies that are distributed throughout the western Amazon as far north as the Magdalena Valley in N Colombia (Fig. 42). Taxon *Sap. apella* is found in the rain forests of the Amazon Basin of Brazil N of the lower Rios Negro and Amazonas, E of the Rio Branco, extending N to the southeastern part of the Orinoco Delta in Venezuela and the Guianas. Its distributional limits in the S, SE, and E are defined by the extent of the Amazon rain forest, in the S and E of Maranhão State marking the transition zone to xeric deciduous forest and 'caatinga' scrub. In the West, its distribution is limited by the interfluvium of

the Rios Negro and Solimões and the Rio Madeira Basin. The Guianan Brown Capuchin species *Sap. apella* is relatively large and heavily built, with a broad head, flat face, and short limbs. Its coat is long and coarse, with all five extremities darker colored than the rest of the body. It is generally gray-fawn to dark brown above, with a yellowish or red underside. The lower limbs and tail are black, and there is a variably distinct dorsal stripe. The face and temples are light gray-brown. The crown tuft is black and forms short tufts above the ears (the characteristic 'horns'). The crown cap extends down the cheeks forming 'sideburns' that often meet below the chin. There is no sexual dimorphism, but males are slightly heavier and often overall much darker colored. The Margarita Island Capuchin taxon *Sap. apella margaritae* that is endemic to Isla de Margarita off the Caribbean coast of Venezuela

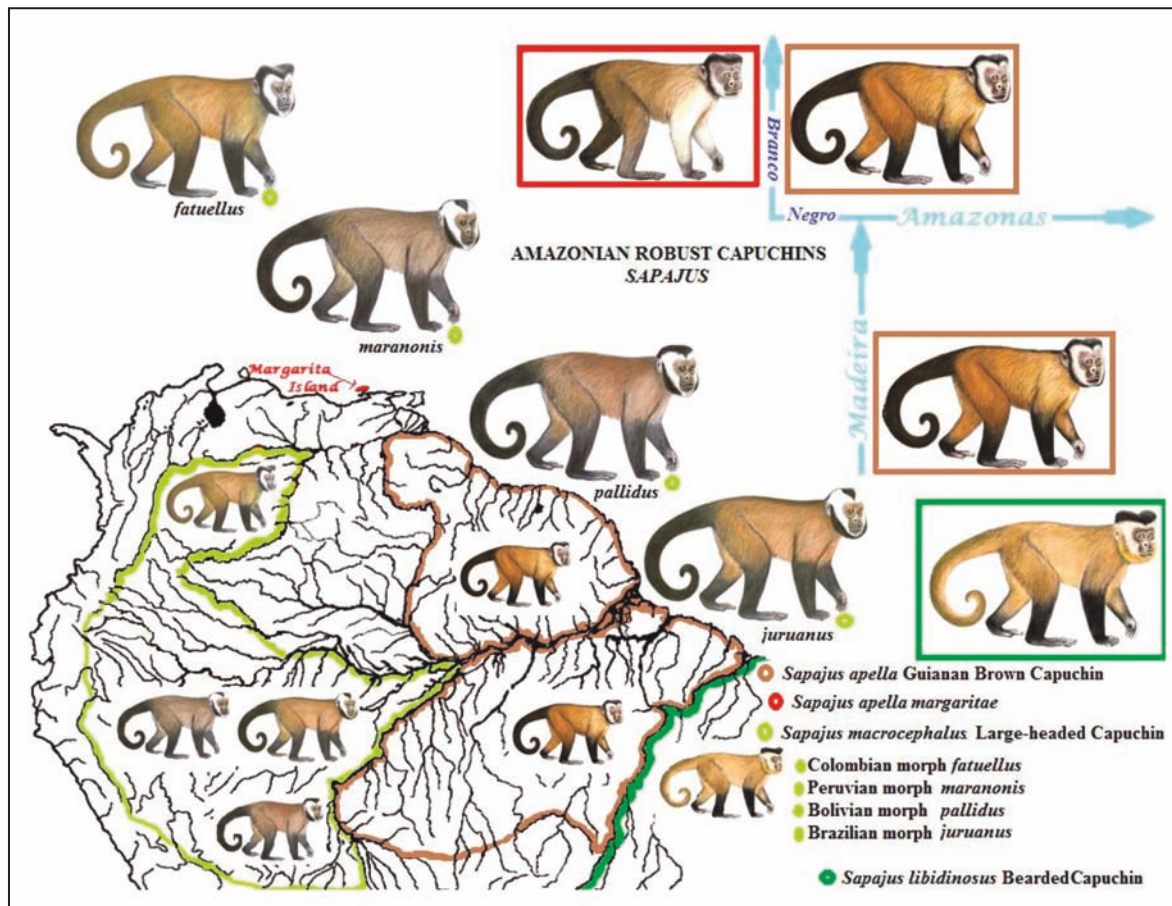


Figure 44. Phylogeography, allopatric speciation, and metachromic bleaching in all Amazonian Robust Capuchins disputedly divided up in *Sapajus apella* and *S. macrocephalus*, the latter with different taxa 'in-the-making'.

distinguishes itself from the nominate Guianan Brown Capuchin by longer dark sideburns in front of the ears, and progressively bleached, pale-yellow or straw colored, near-albinotic upper arms and shoulders. The thighs and rump are pale yellow-brown, and flanks, lower back, and upper chest are pale brown, becoming paler from the upper back to the neck. The face is grayish, tinged pink on the cheeks and chin. The black cap extends in a “V” to between the eyes, with small round tufts above the eyes.

The monotypic Large-headed Capuchin taxon *Sap. macrocephalus* is distributed in the western Amazon Basin, but its taxonomy and distributional limits are poorly defined. According to Silva Jr. (2001) this species includes the forms/morphs/subspecies *Sap. fatuellus* from the upper Magdalena Valley, Colombia, *Sap. maranonis* from Rio Ham-

burgo, Peru, *Sap. pallidus* from the Río Beni, C+N Bolivia, and *Sap. juruanus* from the Rio Juruá, Brazil. Preliminary genetic studies in 2012 failed to indicate that *Sap. apella* and *Sap. macrocephalus* were distinct taxa. Large-headed Capuchins are distributed across the upper Amazon Basin in E Colombia, north as far as the Río Arauca on the border with Venezuela, E Ecuador, E Peru, W Brazil, and C and N Bolivia (S at least as far as the upper Río Beni). Their overall coat color is gray-brown or ochreous to dark brown above, with a dark dorsal stripe, and yellow-fawn or red-gold below. Sides of the neck are lighter, upper arms are pale yellowish, and legs are black with yellow-fawn or red-gold below. Adults have high, pointed crown tufts that resemble horns, which become reduced with age. There is often a gray-white stripe running from eye to ear. Four forms of the Large-headed

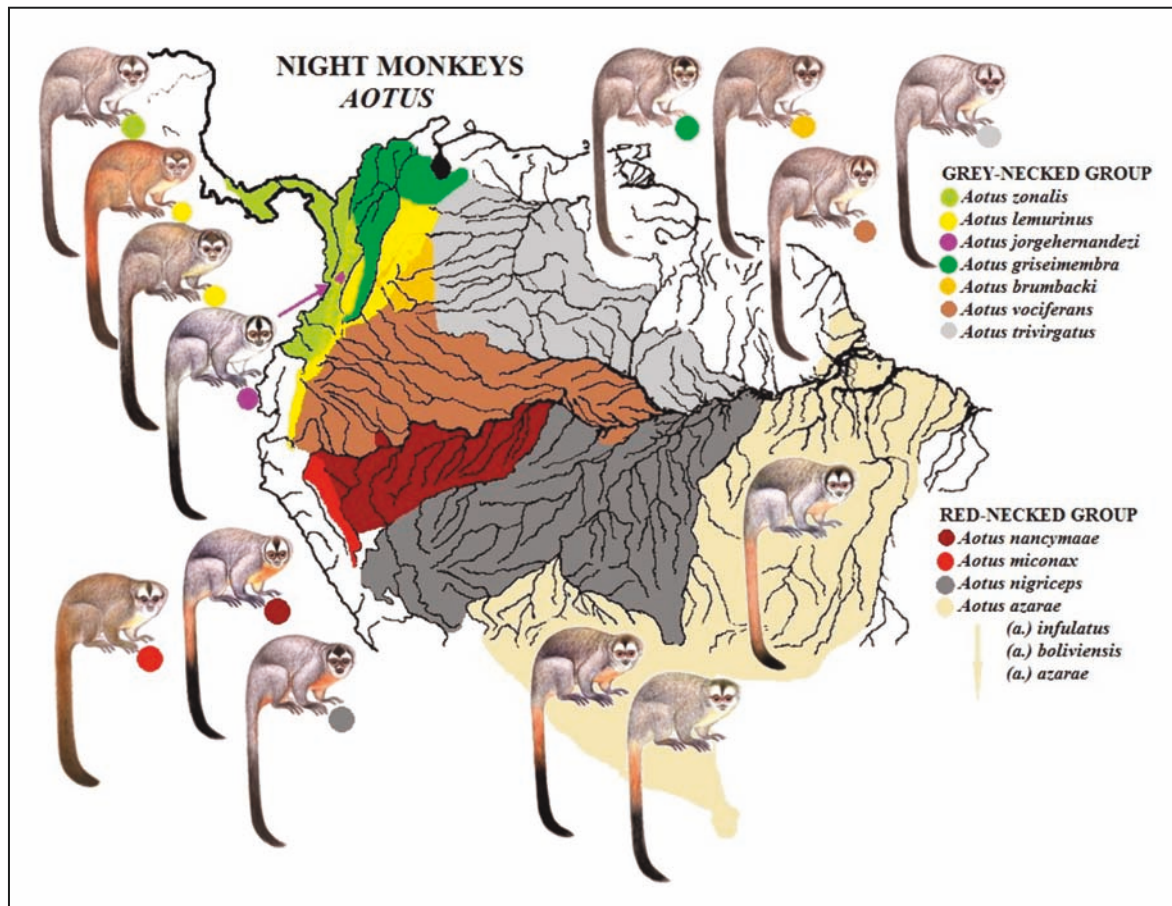


Figure 45. Phylogeography, allopatric speciation, radiation, and metachromic diversification in all hitherto recognized taxa of Night Monkeys, genus *Aotus*.

Capuchin have been distinguished (Fig. 44). The Colombian form *Sap. fatuellus* is bright brown above and red below, having a prominent dorsal stripe. Its face is almost naked and dark-purplish to flesh-colored. The Peruvian form *Sap. maranonis* is uniformly dark chestnut-brown above, becoming more reddish towards the flanks, and deep yellow-brown below. Its legs, tail, and (sometimes) forearms are black. Its cap is distinctly black, whereas temples and sides of the crown are often white. It has a crescent-shaped whitish patch above each eye. There are no crown tufts or they are minimal. The Brazilian form *Sap. juruanus* is reddish-brown above with a very distinct blackish dorsal stripe. The throat and upper chest are blackish or pale reddish-buff, and limbs and tail are dark brown or black. The Bolivian form *Sap. pallidus* from south of the Río Madre de Dios has also been referred to as a subspecies of *Sap. libidinosus*, but such taxonomy would be conflicting with our theory on allopatric speciation, for *Sap. libidinosus* from CE Brazil is overall more advanced pheomelanin bleached in comparison with *Sap. pallidus*. Both the Colombian morph/taxon *Sap. fatuellus* of the Large-headed Capuchin *Sap. macrocephalus* and the insular Margarita Island Brown Capuchin *Sap. apella margaritae* are in their overall advanced pheomelanin bleached coat coloration clearly following the metachromic pathway to albinotic, and therefore fully concur with our theory of allopatric speciation (Fig. 44).

Night Monkeys or Douroucoulis genus *Aotus* represent a very old lineage that is generally placed in a family of its own - Aotidae. The molecular genetic evidence classifies them as a subfamily of the Cebidae. There is also morphological evidence to place *Aotus* in the Pitheciidae. There are generally two Groups distinguished: the “Gray-necked Group” (characterized by grayish to brownish agouti sides of the neck and body), which occurs north of the Amazon River, and the “Red-necked Group” (characterized by partly or entirely orange or yellowish sides of the neck and chest, much contrasting with the grayish to brownish-agouti colored sides of the body), which occurs south of the Amazon River (Mittermeier et al., 2013). Recently, up to eleven species have been recognized, of which at least seven in the Gray-necked Group: the Lemurine Night Monkey *Ao. lemurinus*, the Panamanian Night Monkey *Ao. zonalis*, Brumback’s

Night Monkey *Ao. brumbacki*, the Gray-legged Night monkey *Ao. griseimembra*, Spix’s Night Monkey *Ao. vociferans*, Humboldt’s Night Monkey *Ao. trivirgatus*, and Hernández-Camacho’s Night Monkey *Ao. jorgehernandezi* (Figs. 45, 46). In the Red-necked Group are recognized four species: the Andean Night Monkey *Ao. miconax*, Ma’s Night Monkey *Ao. nancymae*, the Black-headed Night Monkey *Ao. nigriceps*, and Azara’s Night Monkey *A. azarae* (Figs. 45–47). Sexual dimorphism in night monkeys is absent. They are also not sexually dichromatic in coloration and facial markings. The coat is in metachromic sense primitive, archetypic saturated eumelanin, grayish to grayish-tan with a pheomelanin bleached, lighter tan or yellowish underside. In Red-necked species, ventral surfaces of neck, chest, abdomen, and inner sides of arms and legs are orangish or russet colored. The faces have white patches over eyes, topped by black stripes, and a triangular black patch running from the center of the forehead down between the eyes. Black stripes are also extending from the lateral side of each eye to the forehead, varying in width and darkness, and may or may not converge posteriorly with the central stripe. Tails are generally agouti-brown, distally black-tipped. Night Monkeys most likely descended from a diurnal haplorhine. They only are secondarily nocturnal and have retained their color vision.

Within the Gray-necked Clade *Ao. lemurinus* is the nearest to archetypic, saturated eumelanin, less bleached taxon. It is a montane species of the Colombian Andes range, at elevations above 1,000–1,500 m, in the upper Río Cauca Valley and on the slopes of the Cordillera Oriental (but not in the Magdalena Valley that is occupied by the Gray-legged Night Monkey *Ao. griseimembra*), extending its range S into Ecuador through the humid subtropical forests of the Cordillera Oriental. The Lemurine Night Monkey is rather shaggy and long-haired, with the upperparts of the body often eumelanin grayish to buffy-agouti, with a poorly defined brownish medial dorsal band. The underside of the body is pheomelanin bleached yellowish to pale orange. Inner and outer sides of limbs are entirely grayish-agouti, or the inner sides have a yellowish to pale orange tone extending from the chest and belly to the mid-arm or mid-leg. Hands and feet are dark. Temporal stripes may be separated or united behind the head. From ancestral *Ao.*

*lemurinus* derived the Gray-legged Night Monkey taxon *Ao. griseimembra*. It is distributed in N Colombia and NW Venezuela. It occurs in the Río Magdalena Valley and northern lowland forests of Colombia (including the Sierra Nevada de Santa Marta and the Ríos Sinu and San Jorge basins), extending into Venezuela in the vicinity of Lake Maracaibo. It is grayish to brownish-agouti on the side of the neck. Upperparts are grayish to buffy; chest, belly, and inner surfaces of the legs are brownish or yellowish to pale orange. Pelage is relatively short. Hands and feet are light-brown. From taxon *Ao. griseimembra* derived to the NW the monotypic Panamanian Night Monkey *zonalis*. This taxon is distributed in NW Colombia in the Pacific lowlands, S towards the Ecuadorian border, and W into most of Panama; it is absent from SW Panama (Chiriquí). Its overall coat color is brownish in the Canal Zone and Colombia, but it grades into paler and grayer tones along the upper Río Tuira, E Panama. From *Ao. zonalis* derived Hernández-Camacho's Night Monkey *Ao. jorgehernandezi*. This monotypic taxon is believed to occur in the (sub)-montane tropical forests on the western slopes and foothills of the W Colombian Andes (in Quindío and Riseralda). It is advanced bleached to albinotic in the head and ventral parts. Its face has two discrete supraocular white patches separated by a broad black frontal stripe. Moreover, subocular white bands of fur are separated by a thin black malar stripe on each side of the head. Ventral parts of the arms from the wrists running up into the chest and belly are of a thick white fur (Fig. 39). From the Gray-necked Night Monkey Clade's nearest to archetypic taxon *Ao. lemurinus* derived to the SE first Brumback's Night Monkey *Ao. brumbacki*. This monotypic taxon is distributed in NC Colombia in the eastern part of Boyacá Department, E to the highlands of Meta (to at least 1,500 m above sea level). Its coat is dorsally grayish-buffy agouti colored with a dark brown mid-dorsal zone. Ventral parts extending to the elbows, knees, and lower throat are pale orange. Sides of the neck are entirely grayish or brownish agouti, like the flanks and outer sides of the arms. The head shows well-marked, thin, brownish-black temporal stripes. The white above the eyes is yellowish, and the white on the face extends to the chin. From *Ao. brumbacki* derived first to the S Spix's Night Monkey *Ao. vociferans*. This mono-

typic taxon is widespread in the upper Amazon Basin, extending from NW Brazil (W of the Negro, Uaupés, and Amazonas-Solimões Rivers) into SE Colombia (S of the Río Tomo, Orinoco Basin), and S into the Ecuadorian Amazon and NE Peru (as far south as the north bank of the Marañón-Amazonas River). It occurs also S of the Río Solimões in a small area on the lower Río Purús. Spix's Night Monkey's coat is brown-toned above, with an overall white, slightly orange tinged underside, extending to the wrists, ankles, and chin. Hands and feet are black. The proximal one-third to one-half of the ventral side of the tail is reddish or grayish-red, the rest is black. The crown stripes on the head are thick and brownish, with white fur above the eyes confined to two small patches grading into the agouti-colored crown. The temporal stripes are united behind, and the malar stripe can be well defined to absent. The face is white, except for the chin. From *Ao. vociferans* derived to the N and E the monotypic Humboldt's Night Monkey taxon *Ao. trivirgatus*. It is widespread across N Brazil, N of the Ríos Negro and Amazonas and W of the Río Trombetas, N into SC Venezuela and E Colombia. Sides of the neck are grayish-agouti to mainly brownish-agouti colored. Upper parts of the body are grayish to buffy-agouti. The inner sides of the limbs, extending to the wrists and ankles, are similar in color to the orange-buffy of chest and belly. The face has triradiate brown stripes. It is rather grayish in comparison with the usual white of other Night Monkeys. Hands and feet are dark-brown. Taxon *Ao. trivirgatus* can be distinguished from all other Night Monkeys by its parallel temporal stripes on the head and the lack of an interscapular whorl or crest (Figs. 45, 46).

Within the Red-necked Clade of Night Monkeys, the Black-headed Night Monkey *Ao. nigriceps* is the nearest to archetypic, less pheomelanin bleached taxon (Fig. 47). This monotypic species is distributed in the Brazilian Amazon, S of the Río Amazonas-Solimões and W of the Río Tapajós-Juruena, as far south as the right bank of the Río Guaporé and the left bank of the Río Madre de Dios in N Bolivia. It occurs also in SE Peru, west to the Río Huallaga, and north as far as the Río Cushabatay. Its coat is iron-gray above and brownish-agouti on the dorsum. The underside is orange colored with white tones, extending to the neck, throat, chin, and sides of the jaw and also to the

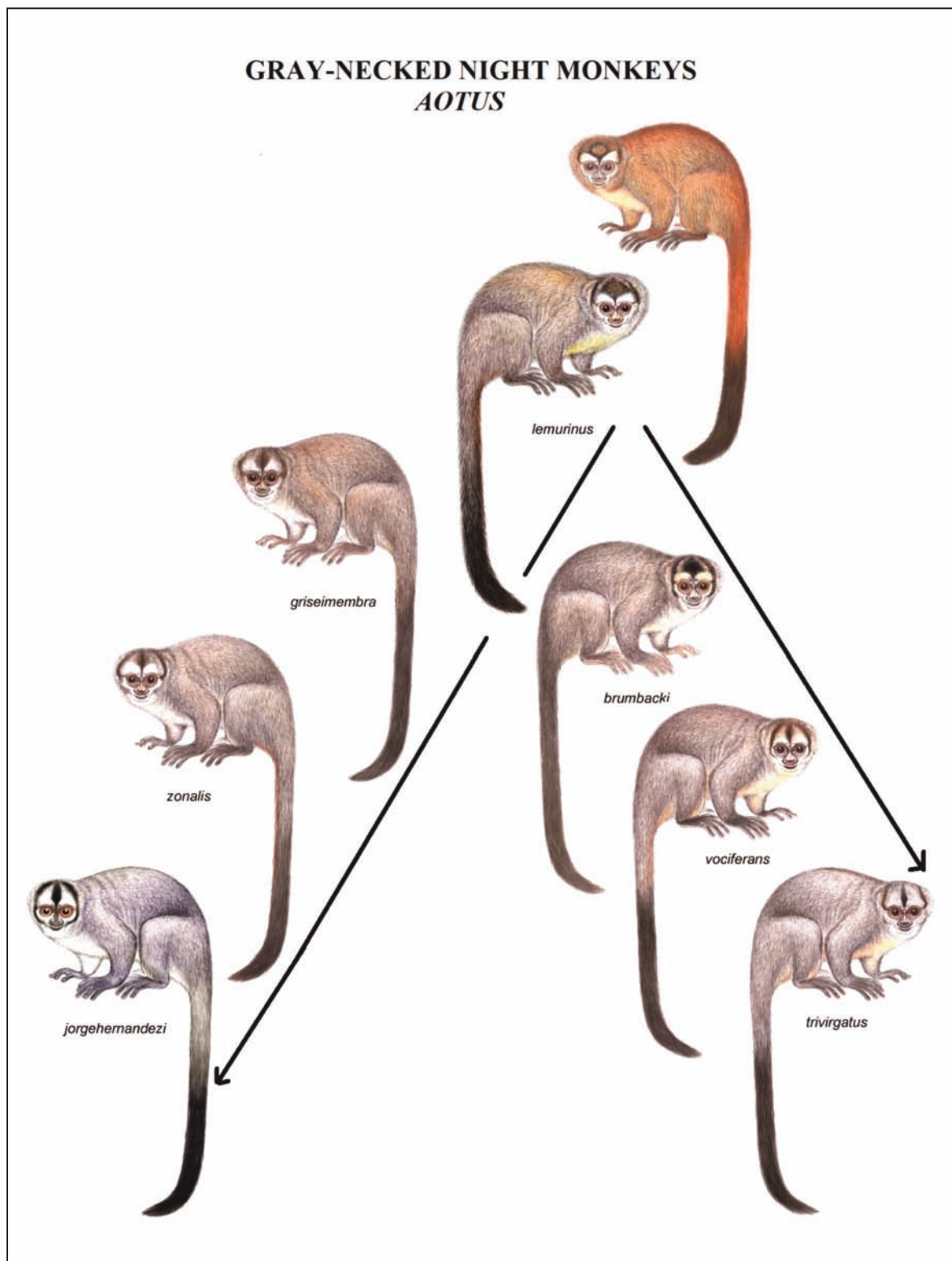


Figure 46. Radiation and metachromic diversification in the Gray-necked Night Monkey Group (*Aotus*), following eumelanin and pheomelanin pathways of metachromic bleaching, in particular in the head, proximal half of the tail, and ventral parts of the body.

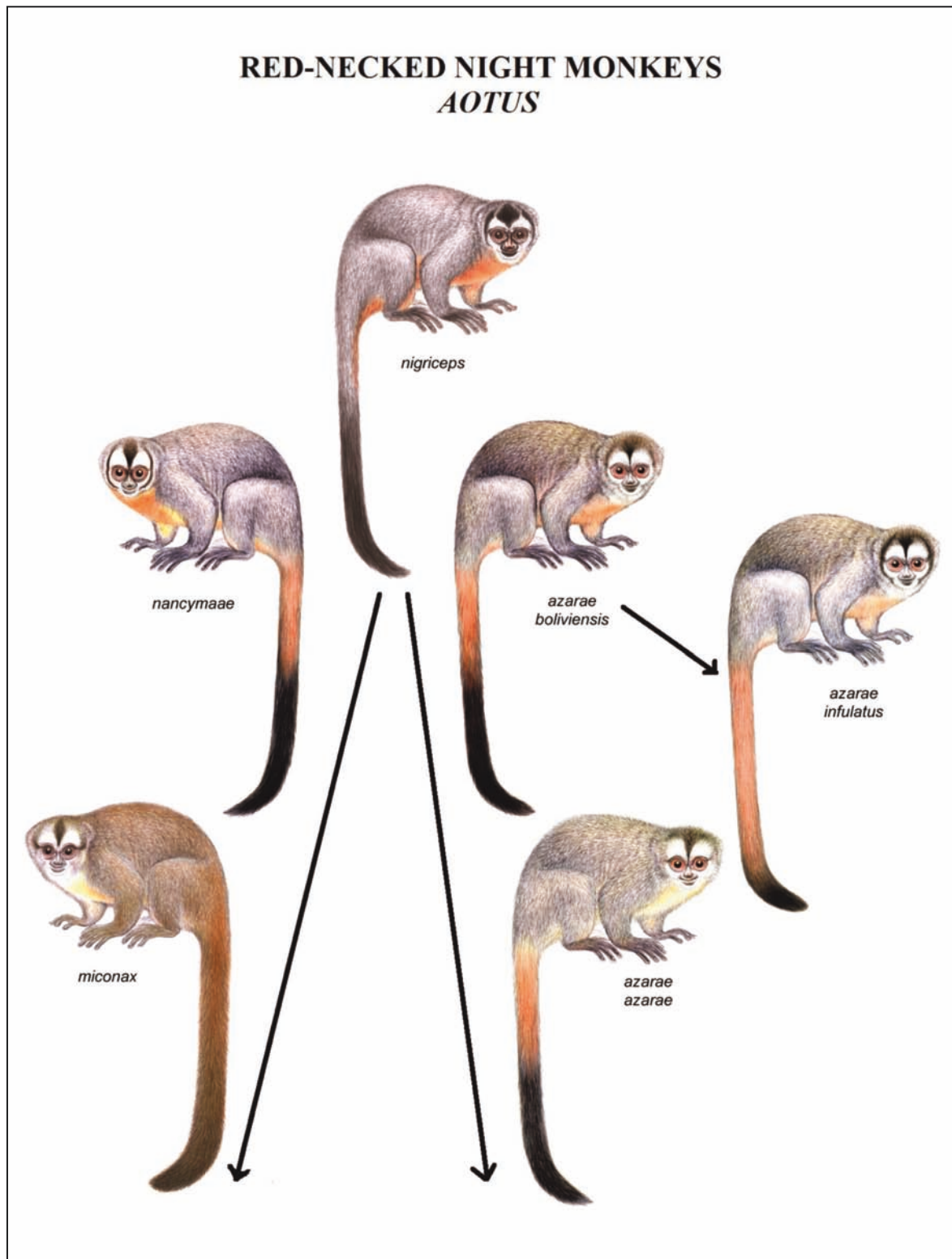


Figure 47. Radiation and metachromic diversification in the Red-necked Night Monkey Group (*Aotus*), following eumelanin and pheomelanin pathways of metachromic bleaching, in particular in the head, tail, and ventral parts of the body.

inner surfaces of the wrists and ankles. The cap is black, the face stripes are broad, and it has distinct areas of white on the face.

From the Black-headed Night Monkey *Ao. nigricaps* derived to the W Ma's Night Monkey *Ao. nancymae*. This monotypic taxon ranges in W Brazil (S of the Rio Solimões from the Rio Javari as far east as the Rio Jandiatuba) and NE Peru (from the Rio Javari W to the Rio Huallaga). This taxon is also found in an enclave between the lower Ríos Tigre and Pastaza. The upper parts of its coat are grayish-agouti, with a dark mid-dorsal zone and a pale orange underside, extending up the sides of the neck and inner limbs. The proximal part of the tail is orange, with a blackish stripe above; the underside is blackish. Its face is grayish-white, the crown stripes are narrow and dark brown colored, and the sides of the throat and jaw are colored like the body (Fig. 41). From *Ao. nancymae* derived to the W the Andean Night Monkey taxon *Ao. miconax*. This monotypic night monkey is endemic to Peru. It is confined to a small area S of the Río Marañón and W of the Río Huallaga. It inhabits the primary and secondary humid, lower-montane cloud forests in the Andes at elevations of 800–2,800 m.

Upper sides of its coat are light gray with a brownish tint, often quite infused with red-brown. Its underside is pale orange, extending forward as far as the chin and on the inner sides of the limbs. Outer surface of the body is overall brownish to buffy-agouti. The tail is bushy, its upper side is blackish, its lower side reddish-orange. Head parts and throat are advanced bleached to near-albinotic. From the nearest to archetypic Red-necked Black-headed Night Monkey *Ao. nigricaps* derived in opposite direction (to the S and E) Azara's Night Monkey species *Ao. azarae*. Three subspecies of *Ao. azarae* are recognized: the nominate taxon *Ao. azarae*, distributed in SC Brazil, S Bolivia, Paraguay, and N Argentina; taxon *Ao. boliviensis*, distributed in SE Peru and Bolivia east of the Andes; taxon *Ao. infulatus*, distributed in Brazil, S of the Rio Amazonas (but with a small enclave in the SE tip of Amapá State), including Marajó and Caviana Islands, extending east into Maranhão State as far as the Rio Parnaíba, S along the west bank of the Rio Tocantins to the Pantanal of Mato Grosso. Taxon *Ao. azarae infulatus*'s western limit is the Rio Tapajós-Juruena. Azara's Night Monkey *Ao. azarae* is highly variable. It generally has an in-

terscapular whorl. Taxon *Ao. azarae* has a long, thick, and shaggy fur that is grayish to pale buffy-agouti above and pale whitish-orange below. Facial stripes are narrow. The basal hairs of the distal  $\frac{1}{4}$  of the tail are orange. Taxon *Ao. boliviensis* has a relatively short fur, with an olive tone above and contrastingly grayer on the limbs. The facial stripes are very narrow except where the middle one expands on the crown; the black temporal stripe in this taxon is poorly defined, the black malar stripe is faint or absent, and there is usually a whitish band between the eyes and temporal stripe. There is a conspicuous whorl between the shoulder blades. The third taxon *Ao. infulatus*, the "Feline Night Monkey", is very similar to subspecies *Ao. boliviensis*, but the white on the face is more prominent. There is no whitish band between the eyes and the temporal stripe as there is in *Ao. boliviensis*. The temporal stripes are black, well defined, and continuous with the malar stripe. The tail is reddish throughout its length except for the black tip. The orange color of the underparts extends to or above the ventral one-half of the sides of the neck. The color of the throat varies from orange, with the anterior one-half grayish-agouti to entirely orange colored (Fig. 47).

Our theory suggests that the trend to allopatry in Neotropical primates resulted from a specific kind of social selection. That the discrimination of somewhat deviant mutant young males by high-ranking males, which push them toward the periphery of the parental group's range, has been the true driver behind metachromic bleaching on the evolutionary path along which a certain race, species, phylogenetic clade, or genus has extended its geographic range in the past. As any founder-colony or population at the limit of a taxon's current range will represent a narrow gene pool, through inbreeding certain phenotypic characters (e.g., local depilation of the skin, change of coloration of the skin, pelage or parts of it) will initially be reinforced and advance more rapidly within the population. Through the process of metachromism (changing hair and skin color) with the trend to allopatry as the behavioral driving force, speciation, radiation, and phylogeography can be retraced and well explained for in all extant Neotropical primates. According to the principle of metachromic bleaching, extant primate taxa at the base of a phylogenetic tree or clade are in general agouti or saturated

eumelanin colored. They are the least colorful, black(ish) or dark brown toned, and therefore considered to be nearest to the ancestral, archetypic, primitive or original form.

Geographic variation and diversification in color patterns of the coat among Neotropical monkeys demonstrates with unusual clarity the unilateral direction and irreversibility of processes that lead to progressively metachromic bleached and ultimately (near)-albinotic allopatric forms, irrespective of environmental factors (Figs. 1–47). The essentially behavioral and genetic driving forces behind metachromic processes, though, have never been studied. They are generally considered enigmatic. The reason may be that they seem to disobey commonly accepted Darwinian rules of evolution. Different from birds, in territorial (Neotropical) monkeys metachromic changes in coat color toward bleaching or albinotic and/or all sorts of local hair growth or loss of hair (depilation) do not seem to play an essential role in sexual display and mate selection. Consequently, they may seem to be non-adaptive. In the wild only rarely one is able to witness how exactly processes of metachromic bleaching do work out. For instance: when somewhat bleached or depilated deviant young males are being pushed from the center into the periphery of a ranging or foraging group. Or: when ‘outcast’ males do join in all-male parties. Or: when such parties set out to look beyond the horizon, for mere survival willing to overtake any habitat delimitation or geographic barrier found on their ‘path to allopatry’. These crucial data will only come available when fieldworkers, like we did, do live for prolonged periods of time among undisturbed primate populations in pristine tropical forest environment. As very few primatologists have done so, at least in the Neotropics, and sample sizes are consequently too small to be published and divulged, it is impossible for us to add more references than our own on the matter. Even though, living over more than a decade in permanent intimate contact with pristine nature, both in the Brazilian Amazon and in the overall even better preserved Guayanian Shield, led us to believe that high-ranking males pushing slightly bleached and/or depilated young males to the periphery of a group’s range, or sometimes beyond its boundaries, could plausibly be the true and principal motor or driver behind allopatric speciation and radiation of taxa in nearly all Neotropical

primate genera - Pygmy Marmosets (*Cebuella*), Tamarins (*Saguinus*), Amazonian Marmosets (*Mico*), True Marmosets (*Callithrix*), Lion Tamarins (*Leontopithecus*), Sakis (*Pithecia*), Bearded Sakis (*Chiropotes*), Uakaris (*Cacajao*), Titi Monkeys (*Callicebus*), Night Monkeys (*Aotus*), Squirrel Monkeys (*Saimiri*), Gracile/Untufted Capuchin Monkeys (*Cebus*), Robust/Tufted Capuchin Monkeys (*Sapajus*), Howling Monkeys (*Alouatta*), Woolly Monkeys (*Lagothrix*), Spider Monkeys (*Ateles*), and Woolly Spider Monkeys (*Brachyteles*). Interestingly, but concurring with our theory (for those monkeys that do not defend a common territory), metachromic bleaching did not take place in peaceably living monkeys like the archetypic agouti and saturated eumelanin colored Black-crowned Dwarf Marmosets *Callibella humilis*, a newly identified monotypic genus of diminutive callitrichid monkeys (Figs. 2, 3). Nor did it take place in saturated eumelanin all-black Goeldi’s Monkeys (*Callimico goeldii*) - the only other monotypic primate genus in the Neotropics that does not behave territorial in any sense and therefore does not defend a common living space against the neighbors of its own kind (Fig. 4). Their external features showing archetypic agouti and saturated eumelanin coat coloration without any sign of metachromic bleaching are in full accordance with their genetics that put them at the base of their respective phylogenetic trees. It further corroborates our theory on the origin of allopatric speciation in primates and the principle of metachromic bleaching, for Dwarf Marmosets and Goeldi’s Monkeys are equally sociable, peaceable little monkeys that do not demonstrate any rate of territorial defense. The primitive agouti and saturated eumelanin (blackish-brown) Black-crowned Dwarf Marmoset stands at the base of the phylogenetic tree of all Amazonian marmosets (Van Roosmalen & Van Roosmalen, 2003). It represents the nearest to ancestral, archetypic marmoset from which all extant, advanced and highly territorial Amazonian marmosets (genus *Mico*) and pygmy marmosets (genus *Cebuella*) have derived in the Late Pleistocene.

Our theory is firmly rooted in over 30-year fieldwork on primates, both in the Guianas and in the entire lowland Amazon Basin. From the very beginning we have given special attention to issues like socio-ecology, ecological feeding niches, territorial behavior, distributions, and phylogeography.

Simultaneously, we have kept, raised, bred, rehabilitated, and reintroduced back into the wild entire families or social groupings of a multitude of monkey taxa representing about all hitherto known Neotropical primate genera. Many unique, extremely rare or sometimes once-in-a-lifetime observations that we gathered in pristine tropical rainforest environment as well as in captivity (the bulk of it never published inherent to 'insignificant' sample sizes) now do add up to the validity of our theory. It basically helps us to better understand the complex distribution patterns, phylogeography, diversification, speciation, and radiation in Neotropical primates. Most likely, the theory applies to all the world's primates (including man), as long as the taxa exhibit social groupings that defend a common living space, home range, or territory. The fact that only two Neotropical primate genera (*Callimico* and *Callibella*) are monotypic strongly supports our theory, as it does not apply to peaceable, non-territorial social primates. By boat, canoe, and on foot we have surveyed entire basins of a number of major tributaries of the mighty Amazon River to study primate diversity and distributions across the entire Amazon Basin, including also large parts of the Brazilian and Guyanan Shields. We have tested and empirically come to fully validate Alfred Russel Wallace's river-barrier hypothesis that he first laid down in his 1852 account *On the Monkeys of the Amazon*, and later in his 1876 paper "The Geographical Distributions of Animals". Herein, Wallace points at the larger rivers that he sailed as the principal evolutionary cause of the Amazon's rich extant primate diversity and complex biogeography, since many rivers effectively block off gene flow between populations along opposite riverbanks (genetic isolation). As the Amazon still represents a largely pristine and vast natural realm that is (not yet) drastically and irreversibly modified by human interference, no better place to study and retrace evolutionary processes that may have acted upon primates and other mammals since the Pliocene era, no matter on which continent. Moreover, most rivers that in the course of millions of years have played a significant role in the demography of Amazonian primates - the majority of which cannot swim or fly- remain acting as such. Therefore, distributions of primate taxa in the Amazon, if correctly studied, documented, and taxonomically treated, do follow a more transparent and rational

overall pattern in comparison with those of the Old World. In SE Asia, instead of rivers, the ocean played an equally important role in the island biogeography of mammals. And in Africa (including Madagascar), the landscape with its complex and diffuse mosaic of vegetation types and habitats seems to have played a more determinant role than rivers in primate distributions. Moreover, massive human disturbance has long irreversibly changed the landscape of the Old World. This may have obscured to some extent the principal factors that influenced and determined distributions and phylogeography in catarrhine primates, most importantly the hominins.

## CONCLUSIONS

Here we discuss the above proposed doctrine on the origin of allopatric primate species and the principle of metachromic bleaching among Neotropical primates as a conclusive socio-ecological answer to the question: why primates are such a highly diversified, species-rich, and colorful order in the Class Mammalia. The Order Primates contains a world total of 73 genera, 414 IUCN-recognized species, and 612+ known taxa of which roughly one third are found in the Neotropics (Mittermeier et al., 2013) (see also Table 1). Globally, only the rodents (Order Rodentia) outnumber the Order Primates. However, compared to primates, rodents are by far not that diversified. They are mostly opportunists, not very sociable, and not particularly colorful. While studying color variation in callitrichid monkeys, Hershkovitz (1968; 1977) proposed the "Theory of Metachromism.". He attributed evolutionary change in mammalian tegumentary colors to social, sexual, and predatory selection, as it seems to be the case in birds. He argued that the highly 'visually' adapted primates may be predisposed to select mates based on coat color and hair adornments. However, primates generally do not sexually display their skin and coat colors, or hair dresses, except for a few genera in the Old World (e.g., *Theropithecus*, *Mandrillus*). Instead, some display their genitals, like both sexes of Amazonian Marmosets (genus *Mico*) do. Or, both sexes of Bearded Sakis (*Chiropotes*), female Spider Monkeys (*Ateles*) or male Woolly Spider Monkeys (*Brachyteles*) do. In that case, their genitals are

mostly hypertrophied (e.g., *Mico*, *Chiropotes*, *Brachyteles*, *Pan*). HersHKovitz's key hypothesis of metachromism, which is tested in tamarins (genus *Saguinus*) and confirmed for many of its predictions by Jacobs et al. (1995), concerns the orderly, irreversible loss of pigment within chromogenetic fields. Its key concept is that genetic drift together with social selection could fix phenotypes departing from primitive agouti or saturated eumelanin (blackish-brown) fields by various degrees of so-called "metachromic bleaching". Thus, an albinotic (nearly white) coat would represent the end point of geographic variation in a series of near-allopatric forms (color morphs) deriving ultimately from an agouti-colored or saturated eumelanin pigmented ancestral form. Using metachromism, we have demonstrated that most Amazonian monkey genera are monophyletic and composed of two or more major phylogenetic Groups or Clades. We found only two genera (i.e., *Callibella* and *Callicimico*) to be monotypic. Contrary to HersHKovitz, who followed the Darwinian fallacy of adaptive evolution by linking evolutionary change in mammalian tegumentary colors ('bleaching') to social, sexual, and predatory selection, we suggest to attribute metachromic diversification in extant social and territorial primates exclusively and uniquely to "male social selection". We propose the "trend to allopatry in somewhat metachromic bleached and/or depilated varieties" to be the principal mechanism and driver behind speciation, radiation, and phylogeography in group-living Neotropical monkeys that defend the group's living space. It arguably applies also to any group-living territorial primate worldwide, including our own species and its ancestors (be it hominids or hominins). For all nineteen genera of Neotropical primates we have presented distribution maps of all known extant taxa and indicated the geographic barriers (rivers, lakes, mountain ranges, seasonally inundated floodplain forests, open scrub areas, etc.) delineating each taxon's distribution. We have also elaborated the phylogeography and radiation within each monophyletic cladistic Group or Clade and related them to the irreversible patterns of metachromic bleaching. Through the process of metachromism (changing hair and skin colors) with the trend to allopatry as the behavioral driving force, speciation, radiation, and phylogeography can be well retraced and explained for in all extant Neotropical primates.

According to the principle of metachromism, primate taxa at the base of a phylogenetic tree or clade are in general agouti or saturated eumelanin (black or blackish-brown) colored - that is the least colorful. Within that Clade they are considered the nearest to ancestral, archetypic, primitive, or original taxon. Based on metachromic skin and fur characters, without a single exception, we were able to retrace phylogeographic pathways of speciation and radiation that were plausibly followed in the evolutionary history of each monophyletic Clade. In all cases we could confirm the trend to allopatry following irreversible eumelanin and pheomelanin pathways of metachromic bleaching. The farther a taxon radiated away from the origin or center of the Clade's dispersion, the more progressively eumelanin or bleached and eventually albinotic its coat/pelage, or part of it, will become.

The great majority of primates are sociable, group-living animals. Group sizes vary from nuclear families (4–7 individuals) to troops of mixed age and sex classes containing 15 to over 200 individuals. The far majority of the world's primate societies are socially structured in a hierarchic way and based on male dominance and ranking. Male defense of the group and its living space within a population benefits from male social selection. Even in matriarchally organized social groups, such as those of spider monkeys (*Ateles*) and pygmy chimpanzees or bonobos (*Pan*), males associate in all-male parties to jointly patrol and defend the group's territory or living space. In social conflicts among males over ranking, inferior males as well as mutant males that show somewhat different, deviant phenotypic characters (such as a slightly bleached pelage here or there or depilated skin in certain body parts) will be pushed into the periphery of the group during ranging and foraging. We have seen this happening, both in the wild and in semi-free ranging conditions, in particular in social groups and societies of monkeys like *Lagothrix*, *Ateles*, *Cebus*, *Sapajus*, *Saimiri*, *Cacajao*, or *Chiropotes*. Depending on the species, such young males also happen to be expelled from the parental group. We have witnessed this in wild and semi-free ranging populations of *Alouatta*, *Callicebus*, *Mico*, *Cebus*, *Sapajus*, and *Pithecia*. Either way, the chances of outcast males to survive and pass on their mutant genes are utterly slim. If this would happen in other mammals - being comparatively

<b><i>Alouatta</i></b> Lacépède, 1799	<b><i>Brachyteles</i></b> Spix, 1823
<i>Alouatta arctoidea</i> Cabrera, 1940	<i>Brachyteles arachnoides</i> (É. Geoffroy Saint-Hilaire, 1806)
<i>Alouatta belzebul</i> (Linnaeus, 1766)	<i>Brachyteles hypoxanthus</i> (Kuhl, 1820)
<i>Alouatta caraya</i> (Humboldt, 1812)	
<i>Alouatta discolor</i> (Spix, 1823)	<b><i>Cacajao</i></b> Lesson, 1840
<i>Alouatta guariba guariba</i> (Humboldt, 1812)	<i>Cacajao (calvus) calvus</i> (I. Geoffroy Saint-Hilaire, 1847)
<i>Alouatta guariba clamitans</i> Cabrera, 1940	<i>Cacajao (calvus) novaesi</i> Hershkovitz, 1987
<i>Alouatta macconnelli</i> Elliot, 1910	<i>Cacajao (calvus) rubicundus</i> (I. Geoffroy Saint-Hilaire et Deville, 1848)
<i>Alouatta nigerrima</i> Lönnberg, 1941	<i>Cacajao (calvus) ucayalii</i> (Thomas, 1928)
<i>Alouatta palliata palliata</i> (Gray, 1848)	<i>Cacajao (melanocephalus) melanocephalus</i> (Humboldt, 1812)
<i>Alouatta palliata aequatorialis</i> Festa, 1903	<i>Cacajao (melanocephalus) ayresi</i> Boubli, Silva, Hrbek, Pontual et Farias, 2008
<i>Alouatta palliata coibensis</i> Thomas, 1902	<i>Cacajao (melanocephalus) hosomi</i> Boubli, Silva, Hrbek, Pontual et Farias, 2008
<i>Alouatta palliata mexicana</i> Merriam, 1902	<i>Cacajao ouakary</i> (Spix, 1823)
<i>Alouatta palliata trabeata</i> Lawrence, 1933	
<i>Alouatta pigra</i> Lawrence, 1933	<b><i>Callibella</i></b> van Roosmalen M.G.M. et van Roosmalen T., 2003
<i>Alouatta sara</i> Elliot, 1910	<i>Callibella humilis</i> (van Roosmalen M.G.M., van Roosmalen T., Mittermeier et de Fonseca, 1998)
<i>Alouatta seniculus seniculus</i> (Linnaeus, 1766)	
<i>Alouatta seniculus juara</i> Elliot, 1910	<b><i>Callicebus</i></b> Thomas, 1903
<i>Alouatta seniculus puruensis</i> Lönnberg, 1941	<i>Callicebus aureipalatii</i> Wallace, Gómez, Felton A. et Felton A.M., 2006
<i>Alouatta ululata</i> Elliot, 1912	<i>Callicebus baptista</i> Lönnberg, 1939
	<i>Callicebus barbarabrownae</i> Hershkovitz, 1990
<b><i>Aotus</i></b> Illiger, 1811	<i>Callicebus bernhardi</i> van Roosmalen M.G.M., van Roosmalen T. et Mittermeier, 2002
<i>Aotus azarae azarae</i> (Humboldt, 1812)	<i>Callicebus brunneus</i> (Wagner, 1842)
<i>Aotus azarae boliviensis</i> Elliot, 1907	<i>Callicebus caligatus</i> (Wagner, 1842)
<i>Aotus azarae infulatus</i> (Kuhl, 1820)	<i>Callicebus caquetensis</i> Defler, Bueno et Garcia, 2010
<i>Aotus brumbacki</i> Hershkovitz, 1983	<i>Callicebus cinerascens</i> (Spix, 1823)
<i>Aotus griseimembra</i> Elliot, 1912	<i>Callicebus coimbrai</i> Kobayashi et Langguth, 1999
<i>Aotus jorgehernandezi</i> Defler et Bueno, 2007	<i>Callicebus cupreus</i> (Spix, 1823)
<i>Aotus lemurinus</i> I. Geoffroy Saint-Hilaire, 1843	<i>Callicebus donacophilus</i> (d'Orbigny, 1836)
<i>Aotus miconax</i> Thomas, 1927	<i>Callicebus dubius</i> Hershkovitz, 1988
<i>Aotus nancymae</i> Hershkovitz, 1983	<i>Callicebus hoffmannsi</i> Thomas (1908)
<i>Aotus nigricaps</i> Dollman, 1909	<i>Callicebus lucifer</i> Thomas, 1914
<i>Aotus trivirgatus</i> (Humboldt, 1811)	<i>Callicebus lugens</i> (Humboldt, 1812)
<i>Aotus vociferans</i> (Spix, 1823)	<i>Callicebus medemi</i> Hershkovitz, 1963
<i>Aotus zonalis</i> Goldman, 1914	<i>Callicebus melanoichir</i> (Wied-Neuwied, 1820)
	<i>Callicebus modestus</i> Lönnberg, 1939
<b><i>Ateles</i></b> É. Geoffroy Saint-Hilaire, 1806	<i>Callicebus moloch</i> (Hoffmannsegg, 1807)
<i>Ateles belzebuth</i> É. Geoffroy Saint-Hilaire, 1806	<i>Callicebus nigrifrons</i> (Spix, 1823)
<i>Ateles chamek</i> (Humboldt, 1812)	<i>Callicebus oenanthe</i> Thomas, 1924
<i>Ateles fusciceps fusciceps</i> Gray, 1865	<i>Callicebus olallae</i> Lönnberg, 1939
<i>Ateles fusciceps rufiventris</i> Sclater, 1872	<i>Callicebus ornatus</i> (Gray, 1866)
<i>Ateles geoffroyi geoffroyi</i> Kuhl, 1820	<i>Callicebus pallescens</i> Thomas, 1907
<i>Ateles geoffroyi azuerensis</i> (Bole, 1937)	<i>Callicebus personatus</i> (É. Geoffroy Saint-Hilaire, 1812)
<i>Ateles geoffroyi frontatus</i> (Gray, 1842)	<i>Callicebus purinus</i> Thomas, 1927
<i>Ateles geoffroyi griseus</i> Gray, 1865	<i>Callicebus regulus</i> Thomas, 1927
<i>Ateles geoffroyi ornatus</i> (Gray, 1870)	
<i>Ateles geoffroyi vellerosus</i> Gray, 1865	
<i>Ateles geoffroyi yucatanensis</i> Kellogg et Goldman, 1944	
<i>Ateles (hybridus) hybridus</i> I. Geoffroy Saint-Hilaire, 1829	
<i>Ateles (hybridus) brunneus</i> Gray, 1870	
<i>Ateles longimembris</i> Allen, 1914	
<i>Ateles marginatus</i> É. Geoffroy Saint-Hilaire, 1809	
<i>Ateles paniscus</i> (Linnaeus, 1758)	

Table 1/1. References of scientific descriptions of all known Neotropical primates (present paper).

<i>Callicebus stephennashi</i> van Roosmalen M.G.M., van Roosmalen T. et Mittermeier, 2002	<i>Lagothrix (lagotricha) lugens</i> Elliot, 1907
<i>Callicebus torquatus</i> (Hoffmannsegg, 1807)	<i>Lagothrix poeppigii</i> Schinz, 1844
<i>Callicebus vieirai</i> Gualda-Barros, Nascimento et Amaral, 2012	
<b>Callimico</b> Miranda Ribeiro, 1912	<b>Leontopithecus</b> Lesson, 1840
<i>Callimico goeldii</i> (Thomas, 1904)	<i>Leontopithecus caissara</i> Lorini et Persson, 1990
<b>Callithrix</b> Erxleben, 1777	<i>Leontopithecus chrysomelas</i> (Kuhl, 1820)
<i>Callithrix aurita</i> (É. Geoffroy Saint-Hilaire, 1812)	<i>Leontopithecus chrysopygus</i> (Mikan, 1823)
<i>Callithrix flaviceps</i> (Thomas, 1903)	<i>Leontopithecus rosalia</i> (Linnaeus, 1766)
<i>Callithrix geoffroyi</i> (Humboldt, 1812)	
<i>Callithrix jacchus</i> (Linnaeus, 1758)	<b>Mico</b> Lesson, 1840
<i>Callithrix kuhlii</i> Coimbra-Filho, 1985	<i>Mico acariensis</i> (van Roosmalen M.G.M., van Roosmalen T., Mittermeier et Rylands, 2000)
<i>Callithrix penicillata</i> (É. Geoffroy Saint-Hilaire, 1812)	<i>Mico argentatus</i> (Linnaeus, 1771)
<b>Cebuella</b> Gray, 1865	<i>Mico chrysoleucos</i> (Wagner, 1842)
<i>Cebuella (pygmaea) pygmaea</i> (Spix, 1823)	<i>Mico emiliae</i> (Thomas, 1920)
<i>Cebuella (pygmaea) niveiventris</i> Lönnberg, 1940	<i>Mico humeralifer</i> (É. Geoffroy Saint-Hilaire, 1812)
<b>Cebus</b> Erxleben, 1777	<i>Mico intermedius</i> (Hershkovitz, 1977)
<i>Cebus aequatorialis</i> Allen, 1914	<i>Mico leucippe</i> Thomas, 1922
<i>Cebus albifrons</i> (Humboldt, 1812)	<i>Mico manicorensis</i> (van Roosmalen M.G.M., van Roosmalen T., Mittermeier et Rylands, 2000)
<i>Cebus brunneus</i> Allen, 1914	<i>Mico marcai</i> (Alperin, 1993)
<i>Cebus capucinus capucinus</i> (Linnaeus, 1758)	<i>Mico mauesi</i> (Mittermeier, Schwarz et Ayres, 1992)
<i>Cebus capucinus curtus</i> Bangs, 1905	<i>Mico melanurus</i> (É. Geoffroy Saint-Hilaire, 1812)
<i>Cebus cesarae</i> Hershkovitz, 1949	<i>Mico nigriceps</i> (Ferrari et Lopes, 1992)
<i>Cebus cuscinus</i> Thomas, 1901	<i>Mico rondoni</i> Ferrari, Sena, Schneider et Silva, 2010
<i>Cebus imitator</i> Thomas, 1903	<i>Mico saterei</i> (Silva et Noronha, 1998)
<i>Cebus kaapori</i> Queiroz, 1992	
<i>Cebus leucocephalus</i> Gray, 1865	<b>Oreonax</b> Thomas, 1927
<i>Cebus malitiosus</i> Elliot, 1909	<i>Oreonax flavicauda</i> (Humboldt, 1812)
<i>Cebus olivaceus olivaceus</i> Schomburgk, 1848	
<i>Cebus olivaceus castaneus</i> I. Geoffroy Saint-Hilaire, 1851	<b>Pithecia</b> Desmarest, 1804
<i>Cebus unicolor</i> Spix, 1823	<i>Pithecia aequatorialis</i> Hershkovitz, 1987
<i>Cebus versicolor</i> Pucheran, 1845	<i>Pithecia albicans</i> Gray, 1860
<i>Cebus yuracus</i> Hershkovitz, 1949	<i>Pithecia (irrorata) hirsuta</i> Spix, 1823
<b>Chiropotes</b> Lesson, 1840	<i>Pithecia (irrorata) irrorata</i> Gray, 1842
<i>Chiropotes albinus</i> (I. Geoffroy Saint-Hilaire et Deville, 1848)	<i>Pithecia (irrorata) vanzolinii</i> Hershkovitz, 1987
<i>Chiropotes chiropotes</i> (Humboldt, 1812)	<i>Pithecia (monachus) milleri</i> Allen, 1914
<i>Chiropotes sagulatus</i> (Traill, 1821)	<i>Pithecia (monachus) monachus</i> (É. Geoffroy Saint-Hilaire, 1812)
<i>Chiropotes satanas</i> (Hoffmannsegg, 1807)	<i>Pithecia (monachus) napensis</i> Lönnberg, 1938
<i>Chiropotes utahickae</i> Hershkovitz, 1985	<i>Pithecia (pithecia) pithecia</i> (Linnaeus, 1766)
<b>Lagothrix</b> É. Geoffroy Saint-Hilaire, 1812	<i>Pithecia (pithecia) chrysocephala</i> I. Geoffroy Saint-Hilaire, 1850
<i>Lagothrix (cana) cana</i> (É. Geoffroy Saint-Hilaire, 1812)	<i>Pithecia (pithecia) lotichiusi</i> Mertens, 1925
<i>Lagothrix (cana) tschudii</i> Pucheran, 1857	
<i>Lagothrix (lagotricha) lagotricha</i> (Humboldt, 1812)	<b>Saguinus</b> Hoffmannsegg, 1807
	<i>Saguinus bicolor</i> (Spix, 1823)
	<i>Saguinus fuscicollis fuscicollis</i> (Spix, 1823)
	<i>Saguinus fuscicollis avilapiresi</i> Hershkovitz, 1966
	<i>Saguinus fuscicollis cruzlimai</i> Hershkovitz, 1966

Table 1/2. References of scientific descriptions of all known Neotropical primates (present paper).

<i>Saguinus fuscicollis mura</i> Röhe, Silva Jr., Sampaio et Rylands, 2009	<i>Saguinus weddelli crandalli</i> Hershkovitz, 1966
<i>Saguinus fuscicollis primitivus</i> Hershkovitz, 1977	<i>Saguinus weddelli melanoleucus</i> (Miranda Ribeiro, 1912)
<i>Saguinus fuscus</i> (Lesson, 1840)	
<i>Saguinus geoffroyi</i> (Pucheran, 1845)	<b><i>Saimiri</i></b> Voigt, 1831
<i>Saguinus illigeri</i> (Pucheran, 1845)	
<i>Saguinus (imperator) imperator</i> (Goeldi, (1907)	<i>Saimiri boliviensis boliviensis</i> (I. Geoffroy Saint-Hilaire et de Blainville, 1834)
<i>Saguinus (imperator) subgriseus</i> (Lönnberg, 1940)	<i>Saimiri boliviensis peruviansis</i> Hershkovitz, 1984
<i>Saguinus inustus</i> (Schwarz, 1951)	<i>Saimiri (cassiquiarensis) cassiquiarensis</i> (Lesson, 1840)
<i>Saguinus labiatus labiatus</i> (É. Geoffroy Saint-Hilaire, 1812)	<i>Saimiri (cassiquiarensis) albigena</i> (von Pusch, 1942)
<i>Saguinus labiatus rufiventer</i> (Gray, 1843)	<i>Saimiri macrodon</i> Elliot, 1907
<i>Saguinus labiatus thomasi</i> (Goeldi, 1907)	<i>Saimiri oerstedii oerstedii</i> (Reinhardt, 1872)
<i>Saguinus lagonotus</i> (Jiménez de la Espada, 1870)	<i>Saimiri oerstedii citrinellus</i> (Thomas, 1904)
<i>Saguinus leucogenys</i> (Gray, 1865)	<i>Saimiri (sciureus) sciureus</i> (Linnaeus, 1758)
<i>Saguinus leucopus</i> (Günther, 1876)	<i>Saimiri (sciureus) collinsi</i> Osgood, 1916
<i>Saguinus martinsi martinsi</i> (Thomas, 1912)	<i>Saimiri ustus</i> (I. Geoffroy Saint-Hilaire, 1843)
<i>Saguinus martinsi ochraceus</i> Hershkovitz, 1966	<i>Saimiri vanzolinii</i> Ayres, 1985
<i>Saguinus midas</i> (Linnaeus, 1758)	
<i>Saguinus mystax mystax</i> (Spix, 1823)	<b><i>Sapajus</i></b> Kerr, 1792
<i>Saguinus mystax pileatus</i> (I. Geoffroy Saint-Hilaire et Deville, 1848)	
<i>Saguinus mystax pluto</i> (Lönnberg, 1926)	<i>Sapajus apella apella</i> (Linnaeus, 1758)
<i>Saguinus niger</i> (É. Geoffroy Saint-Hilaire, 1803)	<i>Sapajus apella margaritae</i> (Hollister, 1914)
<i>Saguinus nigrifrons</i> (I. Geoffroy Saint-Hilaire, 1850)	<i>Sapajus cay</i> (Illiger, 1815)
<i>Saguinus nigricollis nigricollis</i> (Spix, 1823)	<i>Sapajus flavius</i> (Schreber, 1774)
<i>Saguinus nigricollis graellsii</i> (Jiménez de la Espada, 1870)	<i>Sapajus libidinosus</i> (Spix, 1823)
<i>Saguinus nigricollis hernandezi</i> Hershkovitz, 1982	<i>Sapajus macrocephalus</i> (Spix, 1823)
<i>Saguinus oedipus</i> (Linnaeus, 1758)	<i>Sapajus nigrinus</i> (Goldfuss, 1809)
<i>Saguinus tripartitus</i> (Milne-Edwards, 1878)	<i>Sapajus robustus</i> (Kuhl, 1820)
<i>Saguinus weddelli weddelli</i> (Deville, 1849)	<i>Sapajus xanthosternus</i> (Wied-Neuwied, 1826)

Table 1/3. References of scientific descriptions of all known Neotropical primates (present paper).

less intelligent, sensitive, and sociable than primates in general are - being forced to live as outcasts would equal a sure death. But, if it were healthy male individuals deviant from the socially selected skin and/or hair color pattern that are discriminated against merely for being slightly depilated or having its coat somewhat bleached somewhere, such young males pushed out of the group's core area by high-ranking males will ally for the sake of survival alone. Their shared forced-upon marginality could well drive them into looking beyond the horizon and together leaving the pack in search of a living space wherever it could be found. Once that living condition is fulfilled, they can start a new social group incorporating some females that they were able to attract from other resident groups on their way out. This phenomenon is known to commonly take place in hierarchically structured primate societies that are ruled and defended by dominant (alpha)-males (e.g., *Alouatta*). It guarantees a certain primate to reach optimal densities in un-

disturbed populations. Furthermore, it selects for males that are capable to lead and defend a social group. All-male parties of slightly eumelanin and/or pheomelanin bleached, or somewhat depilated males that are pushed out of their parental group's living space and that follow the 'trend to allopatry', will range further and further away from the core of a taxon's distribution. If suitable habitat to settle down is not encountered, the animals eventually will weaken, suffer from diseases, starve to death, or get predated upon. Very rarely, they happen to venture into for that species marginal or unsuitable habitat, being forced to adapt to an alien habitat or a different feeding niche. In extremely rare cases, such founder-groups or -colonies may diverge along this path into a different subspecies (whatever that may be) and eventually into a different species (whatever that may be) or ecospecies. This kind of sympatric speciation may have taken place in such cases as the cream-white, near-albinotic fair woolly monkey living year-round in the várzeas between

the lower Rio Javari and the right bank of the upper Rio Solimões. Or, the pheomelanin bleached, overall orange-colored woolly monkey from the headwaters of the Rio Jutai. Somewhat metachromic bleached founder-colonies of woollies driven by the 'trend to allopatry' once must have diverged from archetypic agouti-colored or saturated eumelanin ancestral *La. poeppigii* while adapting to a different ecological niche that was new to woolly monkeys - in this case that of a frugivorous, canopy-dwelling, brachiating inhabitant of white-water inundated floodplain forest (várzea). During our systematic surveys of primate distribution and diversity carried out in the matrix terra firme rain forest that stretches out behind the floodplain of some white-water rivers (e.g., Javari, Juruá, Purús, Madeira), we were not able to detect any differences in phenotype between individual monkeys of a given taxon that we observed along the entire course (from source to headwaters) of each of these far-apart rivers. Contrary to what is the common presumption among primatologists, this would mean that in territorial monkeys such as pygmy marmosets or saddle-back tamarins that occupy large distributions delineated by some of the largest tributaries of the Amazon, phenotypic characters of skin and pelage coloration, and/or local hair growth or depilation, seem to have stabilized across their entire distributions. In other words, within the distribution of a given Amazonian monkey there does not exist something like a gradient of slightly different phenotypes, color forms, morphs, or races. These observations from the larger field have led us attributing full-species status to primate taxa like *Cebuella pygmaea* and *C. niveiventris* that are phenotypically stable throughout their (sometimes huge) distributions. Consequently, we here introduced the concept of eco-species. This concept is firmly corroborated by the here proposed theory on the origin of allopatric primate species. An ecospecies may be best defined as: "A genetically isolated population or group of populations of a kind that does not undergo gene flow from adjacent populations of one or more closely related kinds; and that shows a stabilized phenotype across the entire range in which it occupies a well-defined ecological niche, which it defends against any outside competitor, even beyond generic level." This eco-species concept (ESC) avoids the often confusing arbitrary distinction between species, subspecies, race,

morph, or form, for it adds sociobiological restrictions to environmental (geographic, geomorphological and phytosociological) ones that use to act on speciation and radiation in sociable territorial primates. Defined as such, the ESC may apply also to similarly socially structured mammals like coatis, peccaries, and some canids. In accordance to this definition, an enclave population of *Callibella humilis* that lives year-round in igapó forest fringing the Rio Atininga - genetically isolated from the main population that lives at least one hundred km to the north in primary terra firme rain forest - should be assigned a different species name in its own right. Or, in case the ranges of two Saddle-back Tamarins of the *S. fuscicollis* Clade, hitherto being treated as subspecies, are only separated by a narrow contact zone - where its aggressive territorial defense effectively impedes any gene flow through cross-breeding or hybridization - each population should be given valid species status. But, wherever a former distributional boundary between two such ecospecies has been disrupted, removed by a vicariance, or overtaken by the more aggressive or opportunistic of two ecospecies, the latter will expand its distribution to the cost of the other. Then, a process of replacement is set in motion along a steadily moving frontline, which inevitably will lead to the extinction of the less aggressive, more vulnerable, or more sensitive of the two ecospecies. According to our doctrine of allopatric primate speciation this will always be the ecospecies that is the more advanced metachromic bleached one. Here we have mentioned at least four cases across the Amazon where such process of replacement (through physical extermination) of one primate by another is ongoing or about to be terminated: 1) the archetypic agouti, gray, and dark red-brown coated Lake Baptista Titi Monkey *Callicebus baptista* extending its range along the southbank of the Rio Amazonas to the cost of the advanced bleached, yellow- and-gray coated Hoffmanns's Titi Monkey *Callicebus hoffmannsi* and the near-albinotic ecospecies from the right bank of the Rio Mamurú; 2) the archetypic saturated eumelanin Midas Tamarin *Saguinus midas* versus the progressively bleached, halfway to fully albinotic Pied Two-colored Tamarin *S. bicolor* (including *S. ochraceus*) and Martins's Bare-face Tamarin *S. martinsi*, the latter three ecospecies being currently at the verge of extinction caused by a rapid southern expansion of midas

(Fig. 10); 3) the saturated eumelanin Weddell's Saddle-back Tamarin *S. (fuscicollis) weddelli* expanding its range to the cost of the near-albinotic Rondon's Marmoset *Mico rondoni*, pushing the frontline eastward into the interfluvium delineated by the Rios Guaporé and Ji-Paraná after having traversed the upper Rio Madeira in the recent past; 4) Gray's Saki *Pithecia hirsuta* (or *P. mittermeieri*) extending its range northwards to the cost of the near-albinotic Buffy Saki taxon *P. albicans*. In cases of replacement it is always the more advanced metachromic bleached to albinotic ecospecies that is loosing the battle and eventually will go extinct. Though only documented by us in semi-captive and free-ranging, but artificially composed multi-species populations, during social conflicts it was invariably the more advanced metachromic bleached individual monkey or group of monkeys that suffered from dominant-male discriminatory behavior, being bullied, repeatedly physically attacked or violently assaulted, and eventually forced out of the core (compound) area, where we provided additional food on feeding platforms constructed up in the canopy. If not moving voluntarily to the periphery, so turning into outcasts, these monkeys could be bitten to death by the invariably less bleached, more aggressive, conspecific leading male(s). In retrospect, we recall that all neotonic, advanced metachromic bleached and near-albinotic individual monkeys kept free-ranging in our respective halfway-houses by comparison were invariably more soft-hearted, more sensitive, cooperative, adaptable, and (not surprisingly?) smarter than the male congeners by whom they were discriminated, pushed into the periphery, or banned from the core area. Applying these observations to the wild, the trend to allopatry boosted by seemingly non-adaptive social selection - leading males that discriminate upon phenotypically deviant mutant young males - in evolutionary sense could well turn out to be truly adaptive. To cite Charles Darwin (1859): "*In the long history of humankind -and animalkind, too- those who learned to collaborate and improvise most effectively have prevailed*". And: "*It is not the strongest of the species that survives, or the most intelligent that survives. It is the one that is the most adaptable to change.*"

Applying the doctrine to the evolution of hominins, in particular *Homo sapiens*, one may ponder and speculate about questions like the following:

"*Why, and driven by what force about six million years ago somewhere in Tropical Africa an ape-like lineage of primates -our hominid ancestors- left the rain-forest canopy and ventured into an arid open-savanna scrub landscape?*"

The common ancestors of the Great Apes and the human line of hominins (*Homo*) were arboreal primates that had adopted brachiation (suspended arm-over-arm-swinging underneath the twig/branch substrate) as a special locomotor pattern. Brachiation allows large-bodied arboreal primates to quickly move through the canopy and get to the fleshy fruits that are, as is the rule in any tropical rain-forest environment, distributed in the far periphery (small-branch/twig micro-habitat) of canopy- and emergent-tree tops. Brachiation is a primarily arboreal type of locomotion that evolved exclusively in some Neotropical Monkeys (i.e., spider, woolly and woolly spider monkeys) as well as in the Old-World Apes (i.e., gibbons, siamangs, bonobos/pygmy chimps, chimpanzees, orang-utans, and gorillas). It may never have evolved in Prosimians, which are the more primitive among all the world's primates. It followed an independent evolutionary path, a convergent or parallel evolution, in a physiognomically similar natural environment - the tropical forests of Southeast Asia, Central Africa, and South America (the larger Amazon Basin). A major intercontinental difference is that some monkeys in the Neotropics developed a prehensile tail as extra support in suspensory locomotion, therefore called "semi-brachiation", whereas apes during the evolutionary process toward brachiation lost a functional tail. Brachiation without use of a fifth limb is called "true brachiation". Most plausibly, our early ape-like hominid ancestors that about 6 MYA descended from the canopy of Central-African rain forest much resembled extant Spider Monkeys in their general locomotor pattern and diet. Brachiation is associated with a dietary preference for ripe, pulpy, nutritious fruits that contain a single to few large seeds. The upright position of the trunk associated with an arboreal life-style involving much brachiation happened to be a crucial pre-adaptation for later bipedal (two-legged) upright walking on the ground. It enabled our early ancestors to leave the trees in the same way as gorillas once did, but different in that the Great Apes adopted 'knuckle-walking' as the principal locomotor pattern to walk on the ground.

Similarities between Spider Monkeys and Chimpanzees are striking as we consider that at least twenty-five million years of evolution on different continents do separate these primates from one another. Cognitive features that both brachiating primates share are the mental capacity to visualize, pre-plan, and map out in time and space complex economic foraging routes to be followed that very day, tomorrow, the day after tomorrow, and perhaps even over several days ahead. Moreover, these primates are able to lay out these foraging routes across a landscape that is covered with dense tropical rain forest containing only few seasonal, widely dispersed food sources at any given time (Van Roosmalen, 1985a; 2013a). Consequently, both spider monkeys and pygmy chimpanzees (bonobos) may well depict a marked period or stage in the evolution of our early ancestors that may have specialized first in feeding upon ripe, juicy, lipid- and protein-rich, large-seeded fruits. Perhaps, that feeding niche may have been the condition that predestined our ancestors, both locomotorily and mentally, to leave the trees and become two-legged ground-dwelling foragers with an advanced use of the hands (e.g., dexterity, precision grips, tool-fashioning). And at the same time growing big babies and three to four times bigger brains (Lynch & Granger, 2008). In physical, anatomical, physiological, and mental respect, therefore, descending from the trees and adapting locomotorily to bipedal walking and running over the ground was not the 'near-impossible' step that it may seem to be. If we put it in Darwinian evolutionary perspective, however, to let it happen, until now an intraspecific social driver was missing that must have acted on the undoubtedly territorially and hierarchically organized communities of these ape-like ancestors with the brain size of contemporary chimpanzees (400 cc). Forthcoming our thirty-five years living in the Amazon and conducting long-term research on captive, feral, as well as wild monkeys - the latter mostly representing pristine populations that were never in any way disturbed by humans - we here suggest the 'trend to allopatry' among slightly depilated and/or metachromic bleached male individuals (mutants) in primate populations being the principal force that has driven founder-colonies of our early ancestors - for the mere sake of survival - out of their preferred habitat -canopy trees- into (to them) new, with respect to natural enemies risky

and hostile landscapes. As sociable and intelligent mammals suffering from intraspecific population pressures and discriminatory social constraints, outcast males must have taken on the challenge to traverse whatever barrier on their way out. So, they ventured into the arid, in many aspects hostile natural environment of savanna scrub and open woodlands. In a similar way as a small population of Gracile Capuchins on the slopes of tepuís like *Pico da Neblina* successfully adapted to a predominantly ground-dwelling life-style; the Mountain *Gorilla* successfully adapted to a fully terrestrial life-style in the cloud forests of the Virunga volcanoes in Central Africa; the Western Chimpanzee of the 'subspecies' *verus* once adapted to a predominantly terrestrial life-style in an arid, for specialist frugivores inappropriate or marginal natural environment - the open savanna scrub of West Africa (Patterson et al., 2006); the near-albinotic Rio Javari Fair Woolly Monkey with an overall cream-white colored coat, and the Rio Jutái Orange Woolly Monkey with an overall orange colored coat, adapted to várzea floodplain forest along the upper Amazon and lower Javari Rivers, and the upper Jutái River, respectively; the Peruvian Yellow-tailed Woolly Monkey in complete isolation adapted to high-altitude cloud forest in the NE Peruvian Andes; the advanced pheomelanin to near-albinotic Bald-headed Uakaris adapted to seasonally inundated white-water floodplain forest (várzea) along the Amazon River and some of its southern tributaries that drain the southeastern flanks of the Andes; among others. Looking at the distribution of Central-American spider monkeys of the *Ateles geoffroyi* Clade, we could speculate about an imaginary evolutionary path that could have been followed by an advanced metachromic bleached, near-albinotic founder-colony of the Central American Yucatán Spider Monkey *Ateles (geoffroyi) yucatanensis* from the tropical forest of Yucatán Peninsula in SE Mexico. By the 'trend to allopatry' forced out of the canopy of a semi-deciduous rain forest somewhere on the Yucatán Peninsula - the taxon's current deadend distribution - some founder-colony may venture into the savanna and desert scrub of SE Mexico and from there further into the Midwest of the US. To survive in such (for spider monkeys) alien landscape it would quickly have to loose a functional tail and adopt bipedal upright walking as its main locomotor pattern. It is tempting

to imagine a similar scenario for progressively metachromic bleached, depilated, red- or white-skinned near-albinotic early hominids 6 MYA radiating away from their archetypic, saturated-eumelanin congeners they had in common with ancestral chimpanzees. Driven by the trend to allopatry, in a similar way founder-colonies may have left the semi-deciduous rain forests of C Africa and ventured first into the savannas, plains and desert scrub of N Africa and, thereafter, into the temperate-clime dominated landscape of S+C Europe, the Middle East and SE Asia. Recent evidence from molecular biology suggests that it took several hundreds of thousands of years for our early ancestors to evolve in two distinct animals: the open savanna explorers leading toward proto-humans, and those remaining arboreal resulting in chimpanzees (Patterson et al., 2006). In accordance with recent phylogenetic research, the modern Chimpanzee *Pan troglodytes* diverged from the proto- or archetypic, saturated eumelanin, overall blackish-brown colored Bonobo (Pygmy Chimpanzee) *Pan paniscus*. The common Chimpanzee is an opportunist having an omnivorous diet, whereas the Bonobo holds a predominantly specialist frugivorous diet. In comparison to common Chimpanzees, Bonobos are egalitarian, peaceable, non-violent creatures that live in loosely organized, matriarchal social groups in which the males may defend their territories, but rather adopt a “Make Love No War” philosophy of life. Bonobos have never been reported to involve in raids on neighboring group males, whereas common chimpanzees have been seen performing a kind of troop-hunting culture in which beta-males led by one alpha-male sometimes do attack neighboring males or small mixed parties, killing and eating some of them. Bonobos live in the dense tropical rain forests of Central Congo. Their distribution is thought to represent the cradle of chimpanzee evolution or the center of chimpanzee (genus *Pan*) dispersion. Applying Hershkovitz’ hypothesis of metachromism, Chimpanzees may well have derived from (proto)-Bonobos. Nowadays, the two species are allopatric. The trend to allopatry may have forced ancestral chimpanzees to swim across or circumvent the Congo River that does act as a geographic barrier in present-day distributions. The farther in any but southern direction from the center of *Pan troglodytes* dispersion, located just north of the Congo River, the more arid the

landscape becomes, the more often chimps do descend from the trees and ‘knuckle-walk’ on the ground, and the more chimps have adapted to what bonobos would consider inappropriate or marginal habitat - unsuitable to highly specialized mature fruit-eaters that bonobos are. At the same time, we see chimpanzees becoming more pheomelanin to euchromic bleached, their skin getting lighter colored (less pigmented), their coat thinner and locally depilated or almost hairless, and elderly individuals becoming gray with age.

Another question to ponder about with the doctrine in mind: “*Why, and driven by what force some of our Homo ancestors between 100,000 and 50,000 years ago left the origin and center of hominid dispersion -Central and North Africa being considered the cradle of human evolution- to venture into the clime- and habitat-wise new, but unsuitable or (at least) marginal landscape of Europe, the Middle East and Asia?*”

After *Homo erectus* having grown much bigger brains on the plains, some millions of years later the trend to allopatry may have been again the principal driving force for some founder-colonies of *Homo sapiens* to move ‘Out of Africa’. The pioneers that ventured into new landscapes to the north could do so only by occupying an ecological feeding niche that was new to former small-game hunter-fisher-gatherers, that of big-game hunter-gatherers. Hereby, the invention to first carrying along fire, soon followed by the skill to kindle it, was essential in the adaptation process to a new feeding niche, as their (our) digestive system is not apt to decompose raw meat. It has to be cooked or barbecued. Apparently, in very low densities - recent estimates place the population of Europe 30,000 years ago at about 5,000 people - these humans following herds of prehistoric megafauna (e.g., mammoth) and driving them to extinction in the Holocene, have spread rapidly across the whole of Europe and Southeast Asia, one route taking them as far as Australia and Tasmania, the other to the far northeastern corner of Siberia. From these places they eventually could reach and inhabit some Pacific Islands, and most amazingly also the continent of South America, first about 30–40,000 years ago by bordering the Antarctic during one of the glacials, and a second time, about 15,000 years ago, via Beringia and North America (Van Roosmalen, 2013c). We could ask ourselves if these all could have been advanced

metachromic bleached, euchromic to albinotic founder-colonies or colonizing parties that were pushed out from dead-end distributions in Africa and Asia following the male-territorial primate-born trend to allopatry?

## ACKNOWLEDGMENTS

We would like to dedicate the theory laid down in this paper to the memory of Alfred Russel Wallace (1823–1913), who inspired us to follow his early footsteps into the Amazonian realm. We are also immensely indebted to the late Philip Hershkovitz of the Chicago Field Museum of Natural History, a true pioneer in the fields of primatology and metachromism. Many thanks are expressed to Russell A. Mittermeier of Conservation International, who supported our fieldwork in the Amazon ever since we started our careers in the pristine ancient forests around the Voltzberg Mt in Suriname, also financially through the Margot Marsh Biodiversity Foundation in the period 1998–2002. We would like to thank Noel Rowe and Doug Brandon-Jones for reviewing an early draft of the paper. Special thanks go to Stephen Nash of Conservation International who kindly provided us with his very fine standardized color illustrations of all known Neotropical monkey taxa. It enabled us to build our theory on the equally colorful speciation, radiation and diversification in New World primates.

## REFERENCES

- Allen J.A., 1914. New South American monkeys. Bulletin of the American Museum of Natural History, Vol. 23, Art. 18: 647–655.
- Boubli J.P., Da Silva M.N. F., Amado M.V., Hrbek T., Pontual F.B. & Farias I.P., 2008. A taxonomic reassessment of *Cacajao melanocephalus*, Humboldt (1811), with the description of two new species. International Journal of Primatology, 29: 723–741.
- Chiou K.L., Pozzi L., Lynch Alfaro J.W. & Di Fiore A., 2011. Pleistocene diversification of living squirrel monkeys (*Saimiri* spp.) inferred from complete mitochondrial genome sequences. Molecular Phylogenetics and Evolution, 59: 736–745.
- Da Cruz Lima E., 1945. Mammals of Amazônia. 1. General introduction and primates. Belém do Pará: Contribuições do Museu Paraense Emílio Goeldi de História Natural e Etnografia.
- Darwin C., 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. J. Murray, London. (Reprint edition: Avenel Books, New York, 1979).
- Grabert H., 1991. Der Amazonas: Geschichte und Probleme eines Stromgebietes zwischen Pazifik und Atlantik. Springer-Verlag, Heidelberg, 235 pp.
- Groves C.P., 2001a. Primate taxonomy. Washington, DC: Smithsonian Institution Press.
- Groves C.P., 2001b. Why taxonomic stability is a bad idea, or why are there so few species of primates (or are there?). Evolutionary Anthropology, 10: 192–198.
- Groves C.P., 2004. The what, why and how of primate taxonomy. International Journal of Primatology, 25: 1105–1126.
- Groves C.P., 2005. Order Primates. In: Mammal species of the world: a taxonomic and geographic reference, (3rd edition) 1, Wilson D.E. & Reeder D.M. (Eds.), Johns Hopkins University Press, MD, 111–184.
- Hershkovitz P., 1968. Metachromism or the principle of evolutionary change in mammalian tegumentary colors. Evolution, 22: 556–575.
- Hershkovitz P., 1977. Living New World Monkeys (Platyrrhini) with an Introduction to Primates. Vol. I. University of Chicago Press, Chicago, 1117 pp.
- Hershkovitz P. 1984. Taxonomy of squirrel monkeys, genus *Saimiri* (Cebidae, Platyrrhini): a preliminary report with description of a hitherto unnamed form. American Journal of Primatology, 7: 155–210.
- Hershkovitz P., 1985. A preliminary taxonomic review of the South American bearded saki monkeys genus *Chiropotes* (Cebidae, Platyrrhini), with the description of a new subspecies. Fieldiana Zoology, 27: 1–46.
- Hershkovitz P., 1987a. Uacaries, New World monkeys of the genus *Cacajao* (Cebidae, Platyrrhini): a preliminary taxonomic review with the description of a new subspecies. American Journal of Primatology, 12: 1–53.
- Hershkovitz P., 1987b. The taxonomy of South American sakis, genus *Pithecia* (Cebidae, Platyrrhini): a preliminary report and critical review with the description of a new species and new subspecies. American Journal of Primatology, 12: 387–468.
- Hershkovitz P., 1988. Origin, speciation, dispersal of South American titi monkeys, genus *Callicebus* (family Cebidae, Platyrrhini). Proceedings of the Academy of Natural Sciences of Philadelphia, 140: 240–272.
- Hershkovitz P., 1990. Titis, New World monkeys of the genus *Callicebus* (Cebidae, Platyrrhini): a preliminary taxonomic review. Fieldiana Zoology, 55: 1–109.
- Jacobs S.C., Larson A. & Cheverud J.M., 1995. Phylogenetic relationships of coat color among tamar-

- ins (genus *Saguinus*). Systematic Biology, 44: 515–532.
- Kellogg R. & Goldman E.A., 1944. Review of the spider monkeys. Proceedings of the United States National Museum, 96: 1–45.
- Lynch G. & Granger R., 2008. Big brain: the origins and future of human intelligence. New York, Palgrave Macmillan, 259 pp.
- Mittermeier R.A., Rylands A.B., & Wilson D.E. (Eds.), 2013. Handbook of the Mammals of the World. Vol. 3. Primates. Lynx Edicions, Barcelona, 951 pp.
- Patterson N., Richter D.J., Gnerre S., Lander E.S. & Reich D., 2006. Genetic evidence for complex speciation of humans and chimpanzees. Nature, 441: 1103–1108.
- Silva Jr. J.S., 2001. Especiação nos macacos-prego e caiararas, gênero *Cebus* Erxleben, 1777 (Primates, Cebidae). Doctoral thesis, Universidade Federal do Rio de Janeiro, Brazil.
- Silva Jr. J.S., 2002. Sistemática dos macacos-prego e caiararas, gênero *Cebus* Erxleben, 1777 (Primates, Cebidae). In: Livro de Resumos, X Congresso Brasileiro de Primatologia: Amazônia - A Última Fronteira, 10–15 November 2002, 35 (abstract). Sociedade Brasileira de Primatologia. Belém, Pará.
- Van Roosmalen M.G.M., 1985a. Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (*Ateles paniscus paniscus* Linnaeus 1758) in Suriname. Acta Amazonica, 15 (Supplement), Sep/Dec 1985.
- Van Roosmalen M.G.M., 1985b. Fruits of the Guianan Flora. Institute of Systematic Botany, Utrecht, the Netherlands, 483 pp.
- Van Roosmalen M.G.M. & Van Roosmalen T., 2003. The description of a new marmoset genus, *Callibella* (Callitrichinae, Primates), including its molecular phylogenetic status. Neotropical Primates, 11: 1–10.
- Van Roosmalen M.G.M., Van Roosmalen T., Mittermeier R.A. & Fonseca G.A.B.Da., 1998. A new and distinctive species of marmoset (Callitrichidae, Primates) from the lower Rio Aripuanã, state of Amazonas, central Brazilian Amazonia. Goeldiana Zoologia, 22: 1–27.
- Van Roosmalen M.G.M., Van Roosmalen T., Mittermeier R.A. & Rylands A.B., 2000. Two new species of marmoset, genus *Callithrix* Erxleben, 1777 (Callitrichidae, Primates), from the Tapajós/Madeira interfluvium, south central Amazonia, Brazil. Neotropical Primates, 8: 1–18.
- Van Roosmalen M.G.M., Van Roosmalen T. & Mittermeier R.A., 2002. A taxonomic review of the titi monkeys, genus *Callicebus* Thomas, 1903, with the description of two new species, *Callicebus bernhardi* and *Callicebus stephennashi*. Neotropical Primates, 10 (Supplement): 1–52.
- Van Roosmalen M.G.M., 2013a. Barefoot through the Amazon - On the Path of Evolution. <http://www.amazon.com> Print version & Kindle e-book version, 500 pp.
- Van Roosmalen M.G.M., 2013b. Distributions and Phylogeography of Neotropical Primates - A Pictorial Guide to All Known New-World Monkeys. <http://www.amazon.com> Print version & Kindle e-book version: 1–71.
- Van Roosmalen M.G.M., 2013c. A Shaman's Apprentice - Bio-History in South America and the Amazon. <http://www.amazon.com> Print version & Kindle e-book version: 1–161.
- Van Roosmalen M.G.M., 2015. Live from the Amazon. <http://www.amazon.com> - Print version & Kindle e-book version, 442 pp.
- Wallace A.R., 1852. On the monkeys of the Amazon. Proceedings of the Zoological Society of London, 20: 107–110.
- Wallace A.R., 1876. The geographic distribution of animals, with a study of the relations of living and extinct faunas as elucidating the past changes of the earth's surface. Boston University. New York: Harper & Brothers Publishers, 668 pp.