CRANIAL VARIABILITY IN AMAZONIAN MARMOSETS

A Dissertation

by

JOHN MARSHALL AGUIAR

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2009

Major Subject: Wildlife and Fisheries Sciences

CRANIAL VARIABILITY IN AMAZONIAN MARMOSETS

A Dissertation

by

JOHN MARSHALL AGUIAR

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Approved by:

Chair of Committee,	Thomas E. Lacher, Jr.
Committee Members,	John Bickham
	Duane A. Schlitter
	James B. Woolley
Head of Department,	Thomas E. Lacher, Jr.

December 2009

Major Subject: Wildife and Fisheries Sciences

ABSTRACT

Cranial Variability in Amazonian Marmosets. (December 2009)

John Marshall Aguiar, B.A.; B.A., University of Richmond;

M.A., Old Dominion University

Chair of Advisory Committee: Dr. Thomas E. Lacher, Jr.

The family Callitrichidae encompasses the marmosets and tamarins, the smallest of the anthropoid primates and one of the most species-rich of platyrrhine families. Seven new species of Amazonian marmosets (*Callithrix*, Callitrichidae) have been discovered in recent years, as well as the exceptional dwarf marmoset *Callibella humilis*. Most of these species were described on the basis of their pelage and presumed separation by major rivers. I performed analyses of craniometric variables by taxa and by river basins, in order to determine if there are significant cranial distinctions between taxa separated by rivers.

I analyzed quantitative cranial and mandibular characters of *Callibella humilis* to determine if it could be distinguished from other callitrichids. I found that *Callibella* is clearly distinct from all other genera of marmosets and tamarins, in particular in the morphology of the lower jaw. I also analyzed representative species of Amazonian *Callithrix* and found support for the theory of separation by river-barriers. In my analyses the Amazonian marmosets were divided into three separate species groups, with the easternmost species (*Callithrix argentata* and *C. leucippe*) strongly distinct and separated from the others by the broad Rio Tapajós. Two additional species, *C. chrysoleuca* and *C. saterei*, formed a discrete group in the central Amazon, and the westernmost species – *C. melanura*, *C. nigriceps* and the Rondônia marmoset – formed a third distinct group. These results from cranial morphology align with recent genetic studies indicating that the Amazonian marmosets are strongly divided by the Rio Tapajós, and offer additional support to the theory of river-barriers.

Although these species are typically considered to be of low conservation priority, many of them are found in areas experiencing accelerated deforestation. An initial analysis of protected-area coverage for the Amazonian marmosets demonstrates that while some species may be found in a number of protected areas, others are virtually uncovered, and the lack of comprehensive information on their distributions may preclude an effective conservation strategy. The dwarf marmoset *Callibella* is known from an exceptionally restricted range, with almost no protected areas, and this unique species should be a conservation priority.

ACKNOWLEDGEMENTS

A great many lives have affected mine during the course of this research, like a river of stars swirling through the galaxy – each with its own unique tug and pull of gravity, all combining their effects to shape the course of my very long and eccentric orbit. As with the galactic disc, some stars have shone more brightly, and others have departed on separate vectors, but each has influenced me in some strong or subtle way.

Brightest among the luminous host is my advisor, Dr. Tom Lacher, who has provided steady guidance, sound advice, and vital perspective, as well as an occasional dose of motivation. He has supported me at all times, in every aspect of this endeavor – and as Stephen Maturin might say, I fear he has burdened me with a debt I can never fully repay. I have also been glad to know his wife Susana, one of my very favorite Brazilians, who (along with her husband) has always encouraged me on my long road towards learning Portuguese.

Another triad of bright stars are my committee members, Dr. John Bickham, Dr. Duane Schlitter and Dr. Jim Woolley, who have been superb in their willingness to help with matters great and small.

The logistics of my travel and research could not have been navigated without support from the staff of the Department of Wildlife and Fisheries Sciences, in particular Vicki Buckbee, Dawn Miles and Diann Radke. I owe special thanks to Janice Crenshaw for helping me through my first semesters, and for her efforts in helping me locate and pursue scholarship opportunities. Tariq Ayyub provided excellent computer support

during my final, intense visits to the department, and Shirley Konecny deserves special mention for her kindness and mother-birding. Thanks are also due to Dr. Jane Packard, whose encouragement of my science writing is much appreciated.

Few can appreciate the intensity, stress and challenge of the graduate experience as deeply as those who have only lately survived it, and so thanks are due to Elizabeth Kennedy, for counsel and support in difficult times, and friendship in the better; and also to Michael Corson, for his patient and unfailing encouragement, and for whom going above and beyond is a signature style. And, thanks to Tom Dolan, fellow wanderer on a parallel course.

I have been fortunate to have an advisor who supported my research travel to the fullest extent, and fortunate that this travel has taken me through many countries, chief among them Brazil. On my first trip to Brazil I was privileged to meet Dr. Adelmar Coimbra-Filho, who has devoted his life to the conservation of the lion tamarins, and what fragments yet remain of their ancient forest home. On that first trip I also met Ilmar Bastos Santos, whose enthusiastic support, both personal and professional, was invaluable for that and subsequent journeys.

Thanks are also due to Dr. Leonardo Sena, for his open and generous assistance during my travels in and around Belém. I owe special gratitude to Vicki Haines (Vitôria), who was a lifesaver during my first visit to the Brazilian Amazon, and to Delfinay Barbosa (Dedão) and his brother Ruy, who kindly took time out of their own lives to guide me in search of a monkey none of us had ever seen.

I am especially grateful to Marc van Roosmalen for making the type skull of *Callibella humilis* available to examine while I was in Brazil, as well as for the dinners and conversation at his home. Thanks are also due to José de Sousa e Silva Júnior and Suely Aguiar of the Museu Paraense Emílio Goeldi in Belém; João Alves de Oliveira of the Museu Nacional in Rio de Janeiro; Mario de Vivo of the Museu de Zoologia da Universidade de São Paulo; and the staff of the Instituto Nacional de Pesquisas Amazônicas in Manaus, for access to their respective collections in Brazil. I also appreciate the opportunity to examine specimens under the care of Linda Gordon and Richard Thorington, Jr. at the United States National Museum of Natural History in Washington, D.C.; Robert Randall at the American Museum of Natural History in New York; Maria Rutzmoser at the Harvard Museum of Comparative Zoology in Cambridge, Massachusetts; and Bruce Patterson at the Field Museum in Chicago. Additional thanks are also due to Olavi Grönwall of the Naturhistoriska Riksmuseet in Oslo, Sweden; Manfred Ade of the Humboldt Museum für Naturkunde in Berlin, Germany; the staff of the Museum National de Histoire Naturelle in Paris, France; and most especially Chris Smeenk of the Rijksmuseum van Natuurlijk Historie in Leiden, the Netherlands.

I am also grateful to Colin Groves and Michael Willig for constructive comments on the details of marmoset morphology and statistical analysis. In addition, thanks are due to Daniel Juhn and Kellee Koenig of Conservation International, who helped me to locate and manipulate the satellite image which became Figure 12. I would like to thank Susan Ford, Lesa Davis, and Leila Porter, organizers of the Marmoset and Callimico Symposium at the 2005 meeting of the American Association of Physical

Anthropology, for inviting myself and Dr. Lacher to participate in the symposium. Additional thanks are due to Susan Ford for her kind advice and support.

Deep thanks are due to Krista Adamek, who spent countless hours working with shapefiles to create the maps, data and supporting materials for Chapters I and V. She did much of this while under course and project deadlines of her own; but whatever the request, she was willing, capable and enthusiastic, and without her the maps most likely could not have been done. Thanks also to Rich Miller, for a vital and timely save.

Finally, several exceptional colleagues at Conservation International deserve a special mention. Kim Meek helped in many ways, and she taught me a great deal about editing and graphic design in a professional environment. Karyn Tabor helped immensely at several key, stressful junctures, and more than once spent hours of her own time solving technical problems for me. And Edward Lohnes, a good pal and stand-up bloke, cheerfully and willingly helped in countless ways.

And a special thanks must go to Stephen Nash, Scientific Illustrator for Conservation International, who has been a kind and generous colleague, and whose artwork is found on so many of the following pages. This dissertation would be far less colorful – and the marmosets themselves only distant, abstract names – were it not for his ready permission to use so many of his illustrations. I feel privileged to be able to include a few of them here, and dream of a day when I can show him a new species to capture with pencil and brush.

And, above and beyond it all, is Mom. And the cats.

TABLE OF CONTENTS

LIST OF FIGURES

FIGURE Page

LIST OF TABLES

CHAPTER I

INTRODUCTION

Primate Diversity

Over four hundred species of primates are now recognized, occupying a broad variety of habitats spread across four global bioregions: Africa, Asia, Madagascar and the Neotropics (Rylands, in litt.). At least eighty of these species have been described since 1990, fifty-one since 2000, and nine of those in 2008 alone (Rylands, in litt.). This great efflorescence of species recognition was born of three interwoven trends, each of which has intensified during the past twenty years: the improved application of molecular techniques to species discrimination; the increasing tendency of primatologists to automatically treat new taxa as full species; and the acceleration of tropical deforestation worldwide.

The continued refinement of molecular taxonomy, combined with aggressive field sampling in regions of primate diversity, has stimulated the description of literally dozens of new primate taxa, most of them prosimians from Madagascar (e.g. Louis *et al.*, 2006; Andriantompohavana *et al.*, 2007; Radespiel *et al.*, 2008). These new taxa are more readily acknowledged as species owing to a broader acceptance, among primatologists, of the phylogenetic species concept (Cracraft, 1983), which has enabled the often automatic, frequently uncritical elevation of terminal taxa to full species status.

This dissertation follows the style of *Neotropical Primates*.

This is typically welcomed by primate conservationists, who accept each new increase in species count as media-ready proof of the great diversity of the primate order – and thus the urgency to act for its preservation.

But this urgency is real: the third factor which contributes to new discoveries is the tsunami of deforestation washing across the tropical world, pushing ever further into what had been, until very recently, remote and untouched havens for primate species, and which now are easily penetrated and laid bare. Primate taxonomists must codify the strands of a tapestry unraveling at both ends: while struggling to assess the decisions and evidence of their predecessors, they must also make sense of a present-day fauna which is facing immense and unprecedented threats – from pervasive deforestation, intense and pandemic hunting, capture for wildlife trafficking and traditional medicine, and the overarching effects of global climate change.

In the most recent evaluation of these and other dangers to the primate order, the 2008 IUCN Red List categorized 48% of all primate taxa as Vulnerable, Endangered or Critically Endangered, with threatened species throughout all four of the primate bioregions (IUCN, 2008). The great apes and the gibbons (Hominidae and Hylobatidae) are the most severely threatened groups: all thirteen species and subspecies of great apes are Endangered or Critically Endangered, while twenty-four of the twenty-five taxa of gibbons are Vulnerable, Endangered or Critically Endangered, and the twenty-fifth may already be extinct (IUCN, 2008; Geissmann, 2008). The summaries for each bioregion suggest where the threats are most intense: 71% of Asian primates are threatened, 43% in Madagascar, 39% in the Neotropics and 37% in Africa (Rylands, in litt.).

Each of the four primate bioregions has its own discrete fauna, with only a handful of crossovers between Africa and Asia. Madagascar and South America, by virtue of their past isolation, each has a primate fauna representing a separate radiation – the prosimian lemurs in Madagascar, and the platyrrhines or New World anthropoids in Central and South America. Of these four regional faunas, the platyrrhines are considered the most speciose, with as many as 141 species now recognized (Rylands, in litt.).

This number has nearly tripled in the past three decades. Philip Hershkovitz, who dedicated much of his professional life to platyrrhine taxonomy, acknowledged approximately 44 species during the 1970s; Mittermeier and Coimbra-Filho (1981) gave a detailed tally of 51 species, encompassing many dozens of subspecies. Mittermeier *et al.* (1988) updated their earlier survey to include 76 species, recognizing many taxa which Hershkovitz had elevated to species in his later work.

A decade later, Mittermeier *et al.* (1999) gave a total of 100 species for the Neotropics, accounting for the description of nine new species in the intervening years, as well as the elevation of over a dozen subspecies, many of which were marmoset forms. Colin Groves, in a millennial review of primate taxonomy (2001), recognized 109 species, more than double the platyrrhine total from twenty years before.

The expansion continued apace; the following year Van Roosmalen *et al.* (2002) elevated all known taxa of *Callicebus*, the titi monkeys, to species status, nearly doubling Groves' tally of 16 to a new total of 28, and by default increasing the platyrrhine total to 122. Similar decisions in the past few years have expanded the total to its current value, which – if the species momentum continues – will undoubtedly rise again.

The majority of these additional species resulted from the elevation of subspecies to full species status – sometimes based on careful consideration of quantitative analyses, sometimes less so. Within the past twenty years, at least fifteen new platyrrhine species have been described on the basis of new discoveries from the field (Rylands, in litt.). Nearly half of those are represented by the seven new marmosets discovered since 1992, doubling the number of marmoset species known from the Amazon.

Of the 141 species now recognized from the platyrrhines, at least 42 are marmosets and tamarins (Rylands and Mittermeier, 2009), considered to be either the Family Callitrichidae (Hershkovitz, 1977; Rylands, 1993; Rylands and Mittermeier, 2009) or the subfamily Callitrichinae within the Cebidae (Groves, 2001; Wilson and Reeder, 2005). Regardless of grade, the callitrichids are now generally accepted to be a monophyletic, diverse and widespread radiation, extending in various forms from the forests of central Panama to the coast of southeastern Brazil (Fig. 1). Ranging in size from small chipmunk (85 g) to large squirrel (700 g), the callitrichids are the smallest of the New World monkeys and the smallest of anthropoid primates now alive. Often very adaptable omnivores, they survive in habitats ranging from dense primary tropical forest to dry scrublands, with certain forms (notably the lion tamarins, the pygmy marmoset and the Goeldi's monkey) showing exceptional if not unique adaptations.

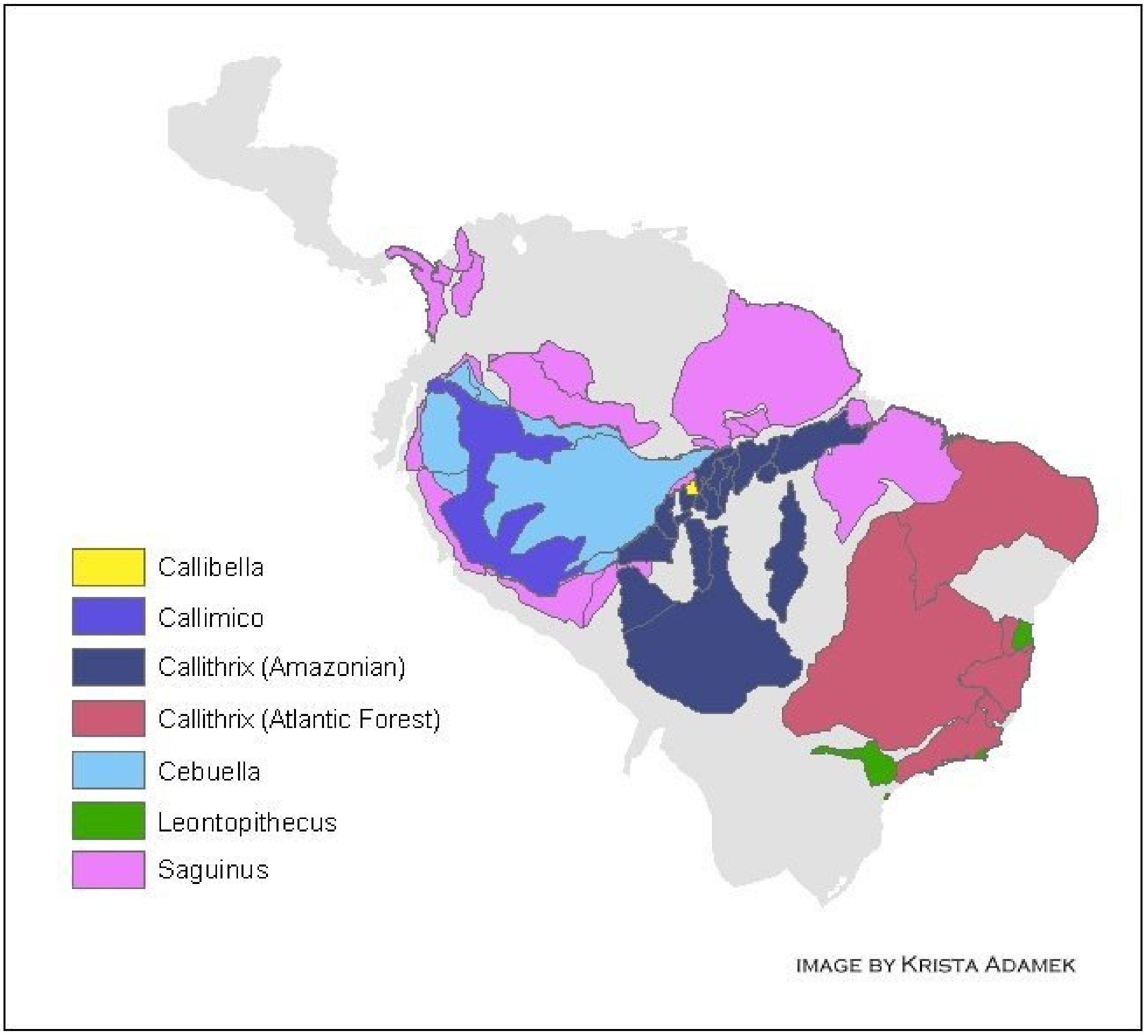

Figure 1. The distribution of the recognized species of the Callitrichidae. Map by Krista Adamek, Department of Wildlife and Fisheries Sciences.

As noted above, the species count for callitrichids has risen manyfold in recent decades, along with the other platyrrhines and the primate order at large. Hershkovitz (1977), never one to name a species when a subspecies would do, allowed for exactly fifteen species in four genera: *Callithrix*, the "ouistitis" or true marmosets, with three species, one in the Atlantic Forest of Brazil and two more in the Amazon; *Cebuella*, the pygmy marmoset of the western Amazon, with a single widespread species; *Saguinus*, the larger tamarins, with ten species north and west of the main Amazon channel; and a single species of *Leontopithecus*, the golden lion tamarin, at 700 g the largest of the callitrichids and restricted to the landscape surrounding Rio de Janeiro.[1] In his arrangement, Hershkovitz first codified what became the two opposing groups of true marmosets: the forms in the Atlantic Forest biome were known as the *jacchus*-group, after *Callithrix jacchus*, his designation for the entire complex; and those in the Amazon became known as the *argentata*-group, after *Callithrix argentata*, one of the two species he recognized for that region.

Soon thereafter, Mittermeier and Coimbra-Filho (1981) recognized seven species of *Callithrix* (by elevating several of Hershkovitz' subspecies, all of them within the *jacchus*-group of the Atlantic Forest) and one additional *Saguinus*, maintaining the monotypic *Cebuella* and *Leontopithecus*. Revisiting this arrangement at the end of the decade, Mittermeier *et al.* (1988) recognized the three subspecies of *Leontopithecus* as full species, elevated one subspecies of *Callithrix* from the *jacchus*-group, recognized de

---

[1] Hershkovitz placed the Goeldi's monkey, *Callimico goeldii*, in its own family, the monotypic Callimiconidae, owing to what he believed was incontrovertible evidence that it was not a true callitrichid. Recent opinion, informed by molecular analyses, now considers *Callimico* to be closely allied with the marmosets (Porter, 2007).

Vivo's (1985) elevation of another from the Amazon, and acknowledged the elevation of *Saguinus tripartitus* by Thorington (1988), for a new total of twenty-five callitrichid species.

De Vivo (1991), in a morphometric review of the genus *Callithrix*, explicitly applied the phylogenetic species concept (Cracraft, 1983) as justification for elevating all taxa to full species – thus recognizing twelve species divided between the Atlantic and Amazonian groups, and edging the callitrichid total to twenty-eight. During the ensuing decade, new discoveries from the Amazon generated an additional seven marmoset species, and a major reassessment of platyrrhine diversity (Rylands *et al.*, 2000) recognized forty-one callitrichid species (including *Callimico*) and separated the fourteen recognized species of Amazonian marmosets into a genus of their own, reviving the older designation *Mico*.

Immediately thereafter, Groves (2001) recognized eighteen species of marmosets – submerging *Cebuella* and *Mico* into *Callithrix* as subgenera – in addition to seventeen species of *Saguinus* and four of *Leontopithecus*, for a total of thirty-nine callitrichid species. In a subsequent revision for the Third Edition of *Mammal Species of the World* (Wilson and Reeder, 2005) Groves recognized forty-three species, while Rylands *et al.* (2008) and Rylands and Mittermeier (2009) maintain forty-two.

The details of these taxonomic arrangements will be discussed in Chapter II, but by this very brief survey one may see how the steady increase in recognized callitrichid species has both kept pace with, and helped to fuel, the taxonomic acceleration throughout the platyrrhines. De Vivo's (1991) invocation of the phylogenetic species concept provided an opportunity for field primatologists to treat new discoveries as de facto new species (e.g. Mittermeier *et al.*, 1992; Van Roosmalen *et al.*, 1998, 2002) without necessarily evaluating those species in a rigorous comparative framework. A thin scattering of tropical mammalogists continue to treat the marmosets as a small handful of variable species (Emmons and Feer, 1997; Thorington, pers. comm.), but the majority operate under the assumption that each new taxon – of which there are yet more in preparation – will be considered a new species by default.

As one example, a problematic population of marmosets had been noted by De Vivo (1985) during an expedition to the Brazilian state of Rondônia, in the central-western Amazon. De Vivo (1985, 1991) referred this population to *Callithrix emiliae*, a completely separate form occupying a narrow range several hundred miles to the east. De Vivo's "*Callithrix* cf. *emiliae*" was quickly recognized as having been misaligned, and although some researchers applied "*Callithrix emiliae*" to the Rondônian population (e.g. Ferrari and Martins [1992]), the general sense was that these marmosets should be described as a new species (Sena, pers. comm.), and for several years Ferrari *et al.* have been in the process of describing the Rondônian marmoset as *Mico rondoni* (Ferrari *et al.*, in press).

Overview of Defining Callitrichid Features

For all their taxonomic diversity and geographic range, the callitrichids are united by a handful of features which distinguish them from other platyrrhines. First among these is their small size: they are the slightest of the anthropoid primates, most of them no larger than a fox squirrel – their resemblance to which has sometimes given rise to easy but misleading comparisons. The largest of the callitrichids, the lion tamarins (*Leontopithecus*), typically mass no more than 700 g in the wild, while the smallest – the inevitably named pygmy marmoset (*Cebuella*) – rarely exceeds 140 g. Once considered to be a signal of their primitive state (Hershkovitz, 1977), the "dwarfed" nature of the callitrichids has been reassessed as a secondary derivation (Ford, 1980; Garber, 1992), enabling a lifestyle which relies on the ability to slip through tight tangles of vegetation, lightfoot across slender vines and cling to the vertical bark of trees.

This latter aspect – a knack for skittering nimbly up and down trees – is made possible by another defining feature of the callitrichids, their sharp-keeled claws or tegulae. Unlike other anthropoids, which have flattened nails on all fingers, the marmosets and tamarins have clawlike tegulae on all digits save the hallux, which retains a flat nail. Again considered by Hershkovitz (1977) to be a primitive holdover, the presence of claws is now also widely believed to be a callitrichid synapomorphy, rather than plesiomorphic from basal platyrrhines.

A third unifying feature of the marmosets is their unique dental arrangement. The typical platyrrhine sequence is 2-1-2-3 (incisors-canines-premolars-molars), common across many anthropoid taxa; for callitrichids this sequence is reversed in the aft series, 2-1-3-2. This holds true for all callitrichids, with the outstanding exception of *Callimico goeldii*, but sports occasionally occur; one specimen of *Leontopithecus rosalia* from the U.S. National Zoo (now NMNH 269705) shows third molars on the lower jaw, and Hershkovitz (1977) noted that “a tiny aborted tooth bud” may appear in the maxillary bone of many specimens.

The fourth commonality shared by virtually every callitrichid – with *Callimico*, again, the peculiar exception – is a strong tendency for twin births. Human pregnancies usually result in twins in slightly over 1% of cases; for callitrichids, twinning occurs in 75-80% of pregnancies (Rylands, 1993), and triplets or quadruplets are not uncommon. The great majority of anthropoids, as well as many lemurs, typically have singleton births, often widely spaced to allow intensive caregiving from the mother. The preponderance of twins among callitrichids places a tremendous burden on the mothers, which has reshaped the social dynamics of these species and given rise to a complex system of cooperative infant care.

The lone exception to this twinning rule, and also to the callitrichid dental pattern, is the Goeldi’s monkey, *Callimico goeldii*. The size of a small tamarin (approximately 350 g; Encarnación and Heymann, 1998) but with subdued brownish-black fur, the Goeldi’s monkey is an anomaly among platyrrhines, with some features clearly placing it within the callitrichid sphere (its small size and clawlike tegulae) and others seeming to align it with the larger platyrrhines (notably the third molar and singleton births). Originally considered to be a primitive tamarin (Thomas, 1928), the Goeldi’s monkey was long placed in a family of its own, the Callimiconidae (Dollman, 1937; Hershkovitz, 1977), but an abundance of recent molecular evidence (reviewed in Porter, 2007) argues for a close affiliation with the marmosets, with whom it is now commonly included (e.g. Rylands *et al.* 2000, 2008, 2009; Rylands and Mittermeier, 2009). A more detailed examination of *Callimico*'s taxonomic history will be presented in Chapter II.

All callitrichids share another feature: the inclination to include exudates in their diet, saps and gums from a great variety of trees, lianas and vines. But there is a major division within the clade as to how they approach and exploit these resources, a division which manifests in their behavior, their skeletal and soft-tissue anatomy, and perhaps even in their cognitive abilities. The larger species, the tamarins and lion tamarins, are sporadic, opportunistic gum feeders. They will lap at exudates when they happen upon a free-flowing source: a natural break in a vine or a tree branch, or damage to the bark by insects – or, most commonly, if they find a tree such as *Parkia pendula*, which coats its seed-pods in a runny gum. But for the most part they are passive consumers, relying on happenstance to come across an occasional source.[2]

By contrast, the various species and genera of marmosets – typically smaller than the tamarins – are able to actively stimulate the flow of exudates from trees and vines, which they evidently know well and often rely on as a substantial component of their diet. The marmosets do this by gnawing at the bark with specially elongated incisors and incisiform canines, a behavior referred to as tree-gouging or simply "gouging." With this behavior, the marmosets are able to control the timing and location of their exudate feeding, to a degree unmatched by the tamarins and lion tamarins. For the latter, exudates are most often a secondary or fallback resource; for the marmosets, they are a major component of the diet and often a dry-season staple. The ability to exploit gums

---

[2] There are occasional reports (e.g. Peres, 1989) of tamarins and lion tamarins biting at vines and feeding on the resulting exudate, but this behavior is sporadic rather than universal.

at will has allowed marmosets to survive in habitats much less amenable to tamarins – in particular the semiarid Cerrado of east-central Brazil – and may have facilitated their expansion and radiation across the Amazon (Lacher *et al*., 1981; de Faria, 1984a,b; Fonseca and Lacher, 1984; Lacher *et al*., 1984; Rylands 1984, 1993).

The division between gouging and non-gouging callitrichids is evident in their cranial and mandibular design; the gouging marmosets have a suite of features to support this ability, including sharp-edged lower incisors, extended masseter and temporalis muscles, and depressed mandibular condyles. The non-gouging tamarins, by contrast, have unmodified incisors and canines and mandibular condyles borne high above the occlusal plane. More detail on the morphology of callitrichid jaws is presented with the genus-level analyses in Chapter III.

Overview of Callitrichid Genera

The following sections present brief overviews of each callitrichid genus, to serve as background for the taxonomic discussion in Chapter II and the genus-level analyses in Chapter III. The distribution maps are derived from GIS data compiled by the IUCN Global Mammal Assessment, and were rendered by Krista Adamek of the Department of Wildlife and Fisheries Sciences, Texas A&M University.

Figure 2. The pygmy marmoset (*Cebuella pygmaea*), the smallest of the marmosets and the smallest living anthropoid monkey. Artwork by Stephen J. Nash and used by permission.

Cebuella

The pygmy marmoset, *Cebuella*, is the smallest of the marmosets; its adult weight ranges from 85-140 g (Nowak, 1999), making it not only a featherweight among platyrrhines, but the smallest of all living anthropoids (Fig. 2). For Hershkovitz (1977) its size was its chief diagnostic: "smallest of known platyrrhines and absolutely smaller than all other callitrichids." He supplemented this with a long list of features which he believed classified it as the most primitive of the callitrichids – themselves the most primitive of platyrrhines, in his estimation, and thus all anthropoids. "The ancestral form of *Cebuella* must have stemmed from near the very base of the ancestral callitrichid stock," he stated; for him, its skull was "the most primitively structured of higher primates," its dentition was "most primitive of all callitrichids" (and of platyrrhines in general), its skeleton was "most primitive of living primates," and the similarity of its juvenile and adult fur coloration "is a primitive characteristic distinctive of *Cebuella* among callitrichids."

This smallest and, for Hershkovitz, unequivocally most primitive of the marmosets is widely distributed throughout the western Amazon, from southernmost Colombia and eastern Ecuador, and throughout the Brazilian Amazon to the northwestern banks of the Rio Madeira (IUCN, 2008; Rylands *et al.*, 2008) (Fig. 3). Pygmy marmosets specialize in riparian growth along the banks of streams and rivers, within a broader matrix of primary forest; this habitat provides an abundance of fruits, insects, small vertebrates and especially exudates from trees and vines (Soini, 1988). *Cebuella* groups usually number from 2-15 individuals (Nowak, 1999), and occupy one

Figure 3. Distribution of the pygmy marmoset in the western Amazon. Map by Krista Adamek, Department of Wildlife and Fisheries Sciences.

of the smallest home ranges of any primate, often less than 0.5 ha (Soini, 1988). In one of the first field studies of pygmy marmosets, Soini (1982) found an average of 52 individuals per square kilometer of upland forest (52 ind./km^2), but a phoenomenal 274 ind./km^2 directly along the riverbanks. Many if not most of these home ranges are centered on a handful of champion gum-producing trees, often just one, which the pygmy marmosets parasitize with hundreds of gouge-holes. “Every family or group seems to own one or more large or thick trees,” wrote Moynihan (1976a), “…which are riddled with small and shallow holes….” When a tree is depleted of its exudates, the pygmy marmosets will abandon it – along with the compact home range they had based around it – and select a new range based on another tree or trees nearby.

Like other callitrichids, pygmy marmosets are eager predators of arthropods, especially orthopterans, as well as small vertebrates such as frogs, lizards and birds. Unlike other marmosets, *Cebuella* often stalks its prey with a deliberate and painstaking approach, which can only be described as “oozing,” much at odds with their more typical, actively springing behavior. Despite their aptitude as opportunistic carnivores, however, pygmy marmosets are fundamentally adapted for life as gum-feeders – the most extreme exudativores among the callitrichids, and perhaps among primates overall. Like other marmosets, but unlike the tamarins, *Cebuella* has elongated lower incisors and incisiform lower canines, which operate together as a self-sharpening chisel to help pry into the bark of trees and lianas. Unlike its larger kindred, *Cebuella* has a uniquely compressed lower jaw, in which the mandibular condyle – the jaw’s point of articulation with the cranium – lies within the occlusal plane of the lower teeth.

These and other features – including *Cebuella*'s more frequent use of vertical clinging postures – have been reinterpreted, not as evidence of basal stock, but as recently evolved and radically specialized for its lifestyle as an extreme exudativore (Ford, 1980; Youlatos, 2009). Owing to their very small size, their reliance on exudates and their preference for lower forest strata, pygmy marmosets occupy a unique ecomorphological space (Youlatos, 2009), and as such they are far more dependent on riparian habitat than any other callitrichid (with the possible exception of *Callibella humilis*) and much more vulnerable to disruptions of same. This extreme specialization does bring risks; it concentrates the pygmy marmosets in a narrow and predictable space, and thus diurnal raptors are major predators. But the benefits of this approach are evident in *Cebuella*'s immense distribution: approximately 1,680,000 km^2, one of the largest of any platyrrhine; among callitrichids it is second only to *Saguinus fuscicollis*, with whose many subspecies it is broadly sympatric (IUCN/Global Mammal Assessment, unpublished data). Moynihan (1976b), based on his observations in the Putomayo of Colombia, commented that pygmy marmosets at particular sites "have certainly become commensals of man."

This may still be true at some locations, but many populations of wild pygmy marmosets are showing the effects of noise pollution and habitat destruction (de la Torre *et al.*, 2000; Yépez *et al.*, 2003). In a prescient essay, Thorington (1978) argued for its protection, since for him this species represented one-quarter of the generic diversity of the callitrichids, as understood at the time. Subsequent assessments, however, have relied on its 1.7 million square kilometers, and assumed that – at least for the time being

Figure 4. *Leontopithecus caissara*, the rarest and most threatened of the four species of lion tamarins. Artwork by Stephen J. Nash and used by permission.

– *Cebuella* is one of the more stable and least threatened of the callitrichids. For many years the IUCN Red List has considered the pygmy marmoset as Least Concern, and the most recent Red List assessments (IUCN, 2008) continue to present it as such.

The easy expectation is that, by virtue of its Lilliputian stature, *Cebuella* is perhaps the least likely to be hunted of any New World monkey, with only a few dozen grams of flesh to reward the hunter. Despite this, *Cebuella* is hunted and eaten by local people in many Amazonian communities, and pygmy marmosets are also killed simply for target practice (de la Torre and Yépez, 2003). In addition, its strong preference for riparian forest makes it especially susceptible to the intense modification or outright obliteration of this habitat – often the first area affected or destroyed by expanding human settlement, as well as illegal mining operations and other human impacts.

Leontopithecus

The lion tamarins are the largest of the callitrichids – adults weigh up to 700 g – and among the most geographically restricted, surviving in a handful of forest remnants in southeastern Brazil (Fig. 4). They are also by far the most threatened of any callitrichid genus: all four species have been classified as at least Endangered, and three of the four were until recently considered Critically Endangered (IUCN, 2008) (Table 1). It is a sign of their immense peril that, when two of those three were reassessed as Endangered, this was considered to be a great stride forward.

The lion tamarins are so fiercely threatened, in large part, because they are primary forest specialists whose natural range happens to lie within the industrialized

Figure 5. Distribution of the four extant species of lion tamarins (*Leontopithecus*) in southeastern Brazil. Map by Krista Adamek, Department of Wildlife and Fisheries Sciences.

Table 1. Threatened species within the Callitrichidae, according to the IUCN Red List (IUCN, 2008). VU = Vulnerable, EN = Endangered and CR = Critically Endangered. Explanations of the more detailed assessment codes are available on the Red List website at <http://www.redlist.org>.

Callibella humilis	VU	D2
Callimico goeldii	VU	A3c
Callithrix aurita	VU	C2a(i)
Callithrix cf. *emiliae* [1]	VU	A2c
Callithrix flaviceps	EN	C2a(i)
Callithrix leucippe [1]	VU	A2c
Leontopithecus caissara	CR	C1
Leontopithecus chrysomelas	EN	A2c
Leontopithecus chrysopygus	EN	B2ab(iii)
Leontopithecus rosalia	EN	B1ab(iii)
Saguinus bicolor	EN	A2c
Saguinus leucopus	EN	A2cd
Saguinus niger	VU	A2c
Saguinus oedipus	CR	A2cd

---

[1] Assessed as part of the genus *Mico*, a position with which Aguiar and Lacher (2002, 2003, 2005, 2009) do not concur.

heartland of modern Brazil (Fig. 5). Of the four species now recognized, only *Leontopithecus chrysomelas* – the northernmost of the genus – still occupies a comparatively large range in the south of the state of Bahia. *Leontopithecus rosalia*, the type species for the genus, survives on the fringes of the metropolis of Rio de Janeiro; *L. chrysopygus* now exists in less than a dozen scattered forest pockets in the state of São Paulo, isolated from each other and encircled by a hostile mosaic of agriculture and urbanization. And *Leontopithecus caissara*, only discovered in 1990, is almost entirely confined to a single coastal island, Ilha Superagüi, where it inhabits some 11,000 hectares of coastal dune forest.

Linnaeus (1758) first described a small, resplendent monkey which he named *Simia rosalia*, included in his overarching genus for the primates. The genus *Leontopithecus* was first established by Lesson (1840), and was submerged and reallocated repeatedly over the next century and a half, until Hershkovitz (1977) reëstablished it as a monotypic entity containing that same species, *rosalia*. He considered the lion tamarin to be more advanced than *Callithrix* or *Cebuella*, and the most specialized of the callitrichids in certain respects, in particular the structure and function of the long-fingered forehands.

Hershkovitz recognized three subspecies – *chrysomelas*, *chrysopygus* and *rosalia* – as “color grades of an otherwise morphologically uniform species.” Mittermeier and Coimbra-Filho (1981) accepted this arrangement without argument, except to suggest recognition of one or more subspecies as full species. Over the next several years, additional research supported this possibility, and Mittermeier *et al.* (1988)

acknowledged these three taxa as full species each. Two years later, Lorini and Persson (1990) described *Leontopithecus caissara* from Ilha Superagüi as a full species, and this arrangement has been upheld by Rylands (1993), Kinzey (1997), Rylands *et al.* (2000), Groves (2001), Wilson and Reeder (2005), and Rylands and Mittermeier (2009), with virtually no dissent.

Unlike other callitrichids, whose clawed forehands are best suited for vertical clinging and walking on narrow supports, lion tamarins have much longer and more nimble fingers, which allow them to be grasping and manipulative in their foraging (Hershkovitz, 1977). This dexterity enables the lion tamarins to probe for unseen prey in holes and crevices, and especially in the recesses at the base of bromeliad leaves, where a wealth of insects, spiders and small vertebrates may hide. Rylands *et al.* (1996) suggested that this specialization, which requires bromeliads in abundance, would in turn oblige the lion tamarins to be generally restricted to primary rainforest, where the greatest concentrations of bromeliads are supported. Kierulff *et al.* (2002), however, note that most field studies on the genus have been in degraded or mosaic forests, where the lion tamarins seem able to survive without pristine primary rainforest; and the overview text on the IUCN Red List website acknowledges that “lion tamarins are an adaptable species well able to live in degraded and secondary forests” (IUCN, 2008).

This evident adaptability gave them some advantage during the early centuries of colonization in Brazil; the German Prince Maximilian zu Wied noted that they were common when he traveled the region in the early 1800s (Mittermeier, 2002). By the middle of the twentieth century, however, wholesale deforestation had taken a

Figure 6. *Saguinus bicolor*, one of the fifteen recognized species of tamarins. This species is restricted to the vicinity of Manaus, where it is threatened by uncontrolled urban expansion. Artwork by Stephen J. Nash and used by permission.

devastating toll, and the survivors of some species could be numbered in the hundreds. One of the first and greatest of Brazilian field primatologists, Dr. Adelmar Coimbra-Filho, carried out a series of extensive surveys during the late 1960s, and estimated 600 survivors of *Leontopithecus rosalia*, 300 of *L. chrysomelas* and 500 of *L. chrysopygus* (Hershkovitz, 1977).

Thirty years of intensive conservation work – spurred almost entirely by Coimbra-Filho's efforts – have helped to stabilize and even augment these populations, even as the remaining scraps of forest continue to be whittled away. A long-term international effort, involving fieldwork, captive breeding and the creation of biological reserves, has developed into a model of integrated conservation, with current estimates of as many as 1000 individuals of *L. chrysopygus* and *L. rosalia*, and some 6000-15,000 of *L. chrysomelas* (IUCN, 2008). *L. caissara* remains Critically Endangered, with some 400 individuals (only half of which are adults) divided between three main populations (Aguiar *et al.*, 2005; IUCN, 2008).

Saguinus

The tamarins, genus *Saguinus*, constitute the most diverse and widespread group of callitrichids, and one of the most diverse genera within the platyrrhines as a whole (Fig. 6, Fig. 7). Rylands and Mittermeier (2009) recognize 33 taxa within *Saguinus*, as compared with 26 in *Cebus* (the capuchin monkeys) and 29 in *Callicebus* (the titi monkeys). Unlike the marmosets, in which the default has been to treat each taxon as a full species, the tamarins remain tessellated among a variety of species and subspecies.

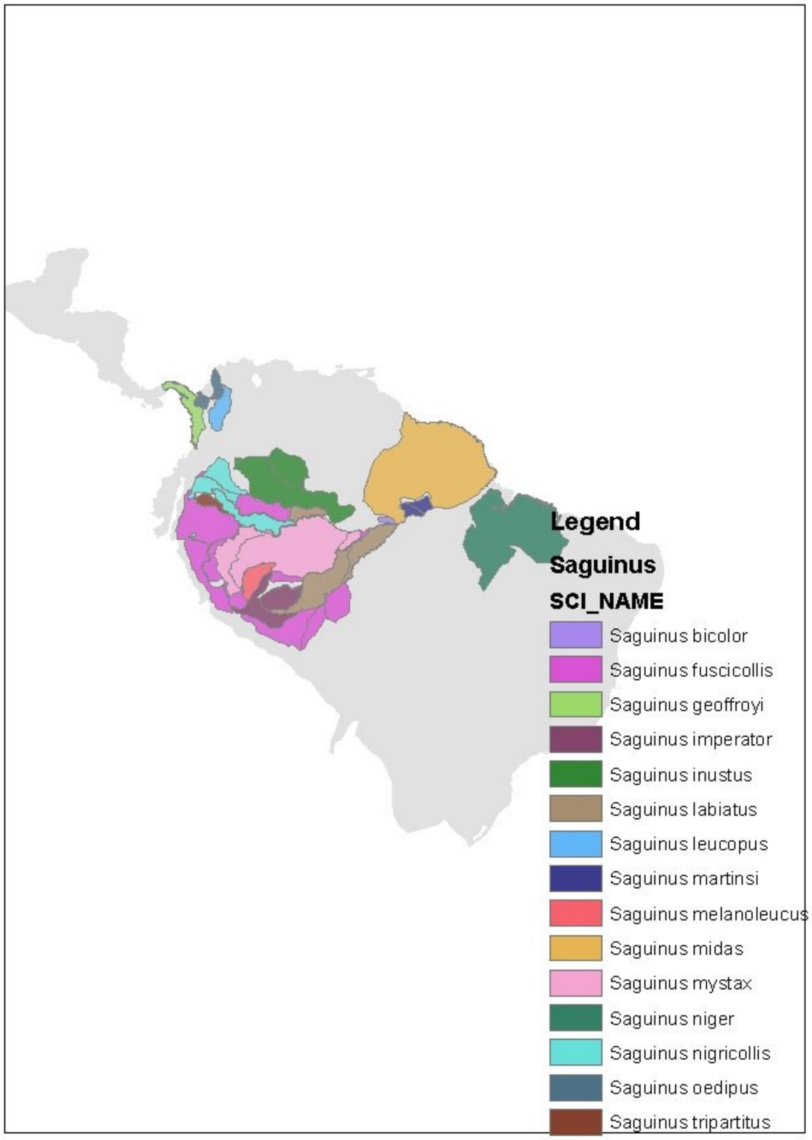

Figure 7. Distribution of the fifteen recognized species of tamarins in the Amazon basin, northwestern South America and southernmost Central America. Map by Krista Adamek, Department of Wildlife and Fisheries Sciences.

Currently 15 full species are recognized – approximately the same number as the Amazonian marmosets – but much of the overall diversity is due to the complex situation of *Saguinus fuscicollis*, the saddleback tamarin, to which Rylands and Mittermeier (2009) allocate ten subspecies distributed widely throughout the western Amazon. In earlier treatments, *S. fuscicollis* encompassed as many as twelve or thirteen subspecies (Rylands *et al.*, 2000; Hershkovitz, 1977, respectively); two of these have now been separated into a discrete species (as *Saguinus melanoleucus melanoleucus* and *S. m. crandalli*) and a third (*S. f. acrensis*) is no longer considered valid (Rylands and Mittermeier, 2009). Its situation is still regarded as a complex problem, and some researchers have indicated they would prefer to follow de Vivo's (1991) example and elevate all taxa of *Saguinus fuscicollis* to full species status (van Roosmalen, pers. comm.).

In many features the tamarins are the most generalized of the callitrichids; they lack the anatomical and behavioral specializations for exudate-feeding which distinguish the marmosets, and while they are accomplished manipulative foragers, they lack the elongated digits of the lion tamarins (*Leontopithecus*), and are not as adapted to primary forest. Tamarins are sometimes called "long-tusked" to differentiate them from the marmosets, but their canines are not necessarily longer than marmosets'; rather their incisors are smaller and slighter, not specialized for chiseling gouge-holes in the bark of trees and vines. Tamarins will eat gums and resins opportunistically, much the same as *Leontopithecus*, but their diet encompasses many other foods: insects and spiders are often prey, especially orthopterans, in addition to small frogs and lizards, and small birds and birds' eggs on occasion. They have also been observed to eat a tremendous range of plant material, including nectar, flowers, leaves, leaf galls, buds, and bark, as well as fungi and snails (Snowdon and Soini, 1988). Like marmosets, tamarins prefer small soft fruit, and likewise prefer areas of secondary or edge forest for fruit, cover and animal prey.

Group sizes in tamarins may range substantially larger than those of other callitrichids, typically 2-12, but sometimes reported at 20 or even 40 individuals, apparently when several family groups commingle (Garber, 1993). Their home ranges are likewise much larger, from 8-10 hectares to as much as 120 hectares (Snowdon and Soini, 1988; Nowak, 1999). These territories are typically defended against conspecifics, but some tamarins will form multispecies groups, often involving the widespread saddleback tamarin (*Saguinus fuscicollis*) and a sympatric species such as *S. mystax* (Garber and Teaford, 1986). These groups will forage together during the day, and Garber and Teaford (1986) have suggested that each group complements the other in its local knowledge of fruiting resources, and that together the two groups are more efficient and successful than they would be if each foraged alone. Alternatively, Ferrari (1993) suggests that *Saguinus fuscicollis* essentially parasitizes the knowledge of other tamarins within its range, offering little to nothing in return. What mixed groups do provide, however, is a greater number of watchful eyes on the lookout for predators both above and below; several researchers have suggested that improved vigilance against raptors and mustelids is a substantial benefit to mixed-species groups (e.g. Porter, 2007).

Unlike tamarins, marmoset species are almost never found in sympatry; the one exception thus far may be *Callibella humilis*, which is apparently sympatric with *Callithrix manicorensis* to the west of the Rio Aripuanã (Van Roosmalen *et al.*, 2000). But there is one region in which *Saguinus* and *Callithrix* are at least sometimes syntopic, in the Brazilian state of Rondônia (Ferrari, 1993). Ferrari and Martins (1992) noted *Saguinus fuscicollis weddelli* in syntopy with the Rondônian marmoset (to be published as *Mico rondoni*; Ferrari *et al.*, in press), and Ferrari (1993) speculated that *S. f. weddelli* – the smallest Amazonian tamarin, at approximately 250 g – was essentially preadapted to live as a commensal with the Rondônian marmoset, taking advantage of the latter's gouging to snap up an effortless meal.

Owing to their broad distribution, the tamarins are much less threatened overall than more restricted genera such as *Callibella* or *Leontopithecus*. The tamarins have a major advantage in that, unlike the lion tamarins, they are better able to survive within the scraps and pockets of secondary growth which remain in the wake of human colonization and settlement. This has been recognized for decades; traveling in the upper Amazon, Moynihan (1976b) commented that, "Parts of it have become almost suburban, rather less neat and clean than Surrey or Bucks County but quite comparable to New Jersey" – hardly a favorable assessment. Regarding tamarins in particular, he noted, "Some kinds of human interference with the environment have been disastrous for monkeys. Others have been favorable, especially to the smaller forms."

Circumstances have not improved in the following thirty years, however, and some of the most threatened tamarins are from the regions that Moynihan explored:

Figure 8. The Maués marmoset, *Callithrix mauesi*, one of the fourteen species of marmosets now recognized from the Amazon basin. Artwork by Stephen J. Nash and used by permission.

Saguinus oedipus, the cotton-top tamarin, is now Critically Endangered in the southwest of Colombia, and the allopatric *S. leucopus* is Endangered, both suffering from intense habitat destruction (IUCN, 2008) (Table 1). The sole endangered tamarin from the central Amazon is *Saguinus bicolor*, whose entire known range is restricted to the city of Manaus and its environs. Efforts have been made to present it as a local flagship species, and it is found in several protected areas and city parks, but a major cause of mortality is individuals being hit by cars as they try to cross city streets. *S. bicolor* may have once ranged through a much larger area, but competition with a more successful tamarin, *Saguinus midas*, appears to have hemmed it into a small remnant of its former range (Egler, 1992).

Callithrix

The true marmosets, *Callithrix sensu lato*, are among the most widespread and diverse of the callitrichids, occupying immense areas in eastern Brazil and the central Amazon (Fig. 8, Fig. 9). At least twenty species are now recognized, divided between two groups according to geography and taxonomic history. The marmosets of eastern Brazil were once considered to be variable races of a single wide-ranging species, *Callithrix jacchus*, and these taxa are still known as the *jacchus*-group or Atlantic Forest marmosets (Hershkovitz, 1975, 1977). *C. jacchus*, the common marmoset, was one of the first primates taken from the New World by early European explorers, and it was included by Linnaeus (1758) in his first arrangement of primates, under the name *Simia jacchus*. The six major forms of the *jacchus*-group are now treated as full species (e.g.

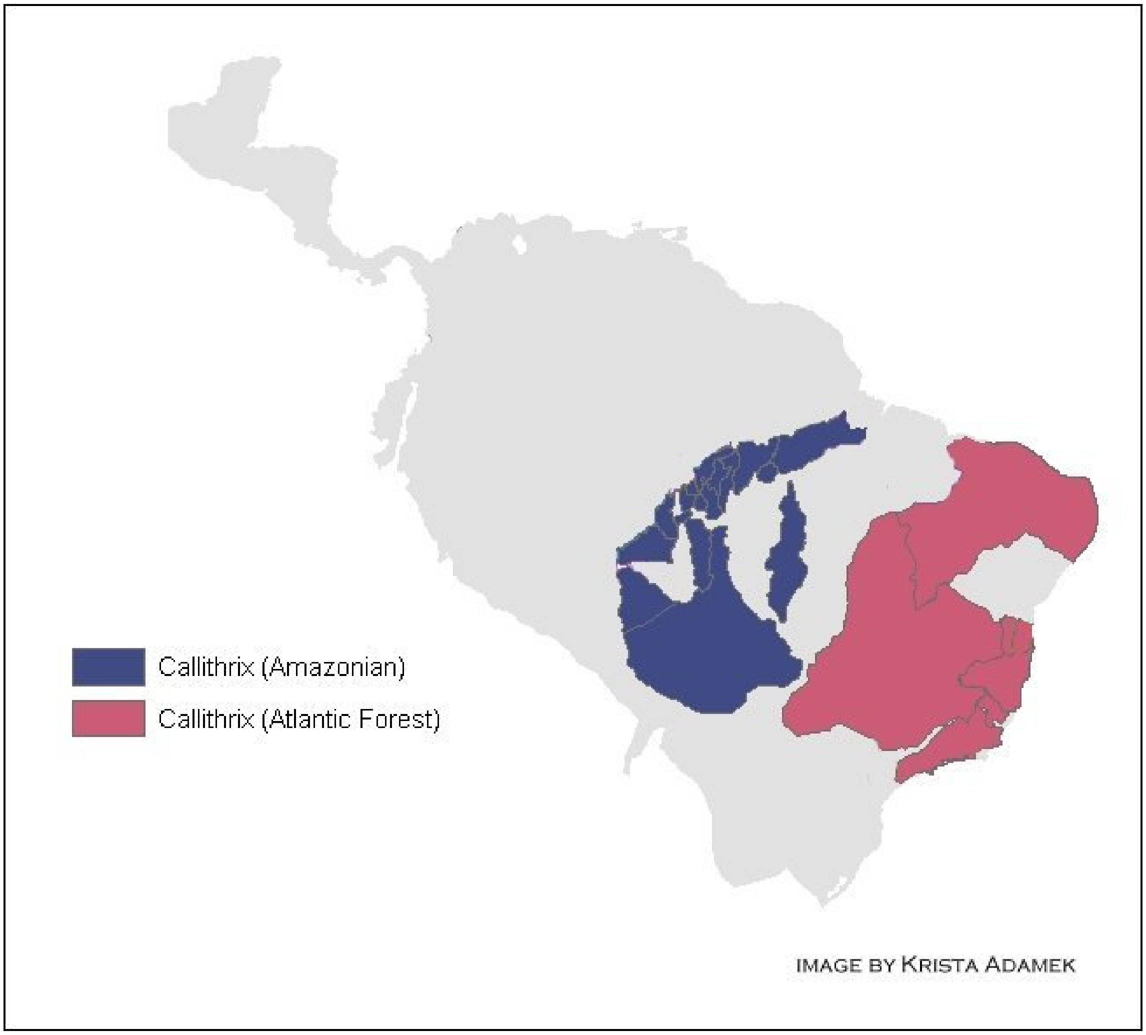

Figure 9. Distribution of the marmosets of the genus *Callithrix*, *sensu lato*. Map by Krista Adamek, Department of Wildlife and Fisheries Sciences.

Rylands and Mittermeier, 2009), although this has been debated for decades; these forms are not always neatly separated by rivers or other biogeographic barriers, and hybrids are common throughout the region.

The marmosets of the central Amazon comprise a larger group of species: fourteen are now recognized (Rylands and Mittermeier, 2009; Rylands *et al.*, 2009), many of which occupy much smaller ranges compared with their Atlantic Forest kin.[3] Unlike the *jacchus*-group species, the Amazonian marmosets are – by implicit definition – almost invariably separated by major rivers, either tributaries of the main-channel Amazon or of the Rio Madeira. The Amazonian marmosets are often referred to as the *argentata*-group, after *Callithrix argentata*, one of the earliest Amazonian species to be recognized. Hershkovitz (1977) considered *C. argentata* to be one of only two full species of marmosets in the Amazon, with several other taxa as subspecies of either *C. argentata* or *C. humeralifer*. But the trend towards recognizing ever-finer subdivisions as full species, based loosely on the phylogenetic species concept, has spurred the elevation of these taxa to species status, and a remarkable series of field discoveries during the 1990s added seven new forms (all described as full species) to the Amazonian clade.

This rise in species numbers dovetailed with a renewed attention to the differences between the Atlantic and Amazonian clades. Basic differences had been noted for some time, both morphological and ecological; the Amazonian species are

---

[3] The average range size of Amazonian species is approximately 107,658 km^2, as opposed to an average of 434,700 km^2 for the Atlantic Forest marmosets (IUCN/GMA, unpublished data). The Amazonian species *Callithrix melanura* occupies an uncharacteristically vast area of the central-western Amazon; excluding this species, the average range size for the thirteen other Amazonian marmosets is only 50,546 km^2.

physically larger than the Atlantic forms, and present a chromosome number of 2n = 44 as opposed to 2n = 46 for the *jacchus*-group (Rylands, 1993). The Atlantic marmosets occupy a greater diversity of habitats, ranging from remnants of the original Atlantic Forest to gallery forest in semi-xeric Cerrado; they cope with more pronounced differences in seasonality and fruit availability, and are more reliant on exudate-gouging as a staple during periods of fruit scarcity (Rylands, 1993).

In a comprehensive survey of platyrrhine taxonomy, Rylands *et al.* (2000) proposed reallocating the Amazonian marmosets to the lapsed genus *Mico*. Their reasoning depended on the status of *Cebuella*, the pygmy marmoset, which several recent molecular studies had suggested was more closely related to the Amazonian marmosets than to the Atlantic species group (e.g. Schneider *et al.*, 1996; Porter *et al.*, 1997; Tagliaro *et al.*, 1997; Canavez *et al.*, 1999). However, Rylands *et al.* (2000) believed that *Cebuella* presented a unique suite of characteristics – in particular its diminutive stature and intensive use of exudates – which deserved recognition as a separate genus. But maintaining *Cebuella* as distinct, they believed, would leave the remainder of *Callithrix sensu lato* as a paraphyletic grouping, and their solution was to divide the two clades into separate genera.

This case for separation is not supported by recent analyses of cranial morphology (Aguiar and Lacher, 2002, 2003, 2005, 2009; Marroig *et al.* 2004; Marroig and Cheverud, 2009). As Marroig *et al.* (2004) point out, it is important to explicitly test the relationships between *Cebuella* and other marmosets, and as yet no true cladistic analysis has been performed to support *Mico* as conceived by Rylands *et al.* (2000).

Groves (2001), in his panoramic survey of primate taxonomy, chose a different approach by subsuming all forms of marmosets into a greatly expanded genus *Callithrix*, within which the Atlantic and Amazonian clades were considered subgenera, together with *Callithrix* (*Cebuella*) *pygmaea*. Groves' views are maintained in Wilson and Reeder (2005), while Rylands *et al.* (2008, 2009) and Rylands and Mittermeier (2009) continue with their arrangement of separate genera for the Atlantic and Amazonian groups.

Meanwhile, blissfully unaware of the taxonomic dissension, the Atlantic and Amazonian marmosets continue to live remarkably similar lives. All species in both regions are specialists in secondary forest patches and regenerating growth, which they find appealing for several reasons. Secondary forest supports the necessary concentrations of small, soft fruits which marmosets prefer, as well as a corresponding density of arthropods – and, to a lesser extent, small vertebrate prey (Rylands, 1993). By its nature, secondary forest is also much denser and more difficult to navigate than primary lowlands rainforest – and this dense vegetation, often overgrown with tangles of vines and lianas, is an asset to squirrel-sized primates at risk from predators both above and below.

Marmosets typically live in groups of 4-12 individuals, although group size varies depending on species and circumstance (Stevenson and Rylands, 1988). The size of their home ranges is likewise extremely variable across species. Fonseca and Lacher (1984) estimated ranges of 2.5 hectares each for two groups of *Callithrix penicillata* in a patch of forest in the Brazilian Cerrado; one group of *Callithrix jacchus* was estimated to use a home range of 0.6 ha (Stevenson and Rylands, 1988). This approaches the exceptionally compact dimensions of the home ranges of *Cebuella*, and for the same reasons: in these cases, the marmosets are focusing their efforts around a concentration of exudate-producing trees (in *Cebuella*, often a single tree). *Callithrix jacchus* and *C. penicillata* are Atlantic Forest species, much more dependent on exudates; Fonseca and Lacher (1984) estimated their groups spent as much of 70% of their foraging time on gouging and exudate-feeding. The Amazonian marmosets, less dependent on gums, have correspondingly larger ranges; Veracini (2009) records a group of *Callithrix argentata* with a home range of 15 hectares, while Rylands (1982) found one group of *Callithrix intermedia* occupying 28 hectares.

Their small size and other characteristics – including their vigorous reproductive output, and their ability to adapt to an artificial and monotonous diet – have endeared them to laboratory primatologists who see them as an ideal study animal, able to survive and reproduce in small indoor cages for many generations. Thus they have become the small primate of choice for biomedical experiments and pharmaceutical research, as reviewed in Stevenson (1977) and still considered valid today. Marmosets in captive situations take readily to monogamous pairing, and early field studies indicated that monogamy was prevalent in wild groups (Stevenson and Rylands, 1988). More recent field research has uncovered a far more complex and variable situation, with polyandry and polygyny reported from different species and groups (e.g. Digby and Ferrari, 1994; Roda and Pontes, 1998; Yamamoto *et al.*, 2009).

The relative conservation status of the Atlantic and Amazonian species groups is strongly influenced by their geography. Of the six species in the *jacchus*-group, two are threatened and one is considered near-threatened, while only two out of the fourteen Amazonian species are considered Vulnerable (IUCN, 2008; see Table 1). Several of the Atlantic Forest species have been at the epicenter of deforestation and development in southeastern Brazil, and the extensive modification of the landscape has created unnatural distributions of species and hybrids (Rylands *et al*., 1996). The marmosets of the central Amazon have thus far been insulated from a similar massive disruption, but industrial logging in the eastern Amazon, as well as small-scale deforestation along tributaries throughout the region, presents an escalating threat.

Callibella

First discovered in 1996, the dwarf marmoset was originally described as *Callithrix humilis*, one of many new marmosets announced during the 1990s (Fig. 10). In the description, Van Roosmalen *et al.* (1998) suggested that it might prove to be a new genus, and soon afterwards they redescribed it as the type species of *Callibella* gen. nov. (Van Roosmalen and Van Roosmalen, 2003). The original description was based on three specimens of an exceptionally small marmoset, scarcely larger than *Cebuella*, taken from the west bank of the Rio Aripuanã in the central Brazilian Amazon. Collected from *caboclos* who had been keeping them as pets, these individuals were kept for a time at the van Roosmalens' backyard primate facility at their home in Manaus; when they died, they were converted to a type series. Several more field expeditions

Figure 10. The dwarf marmoset, *Callibella humilis*, a virtually unknown species from the central Amazon. Artwork by Stephen J. Nash and used by permission.

yielded only a handful of other sightings and captures, suggesting a minuscule range between the Rios Aripuanã and Manicoré (Fig. 11; see also Fig. 12 in Chapter III).

In both the original description and redescription as *Callibella*, the van Roosmalens presented a number of claims regarding its biology which, if substantiated, would have made it a supremely atypical callitrichid. However, the van Roosmalens provided no quantitative support for any of their assertions, and several of their more radical suggestions have been obliquely withdrawn or otherwise not pursued. They did present analyses of mitochondrial DNA, which demonstrated its clear separation from *Callithrix* and *Cebuella* (Van Roosmalen and Van Roosmalen, 2003). Morphological support for its generic status has been provided by Aguiar and Lacher (2003, 2005, 2009) for craniomandibular features, and by Ford and Davis (2005, 2009) from postcranial analyses. Apart from the van Roosmalens' expeditions, only one other brief foray has attempted to locate this species in the field (Aguiar, 2001), and at present there are no data on its ecology and behavior in the wild. From its unique mandibular structure, Aguiar and Lacher (2003) speculated that *Callibella* might fall between *Cebuella* and *Callithrix* in its reliance on exudate-feeding, which agrees with the initial observations reported by the van Roosmalens.

Its exceptionally small range, estimated at less than 6400 km^2 (IUCN/GMA, unpublished data), puts *Callibella* in some danger from the pervasive deforestation which extends along the margins of local rivers. This species may be in particular danger from perturbation of riparian habitat; Van Roosmalen and Van Roosmalen (2003) speculated that it may be ecologically and behaviorally restricted to riparian forest which

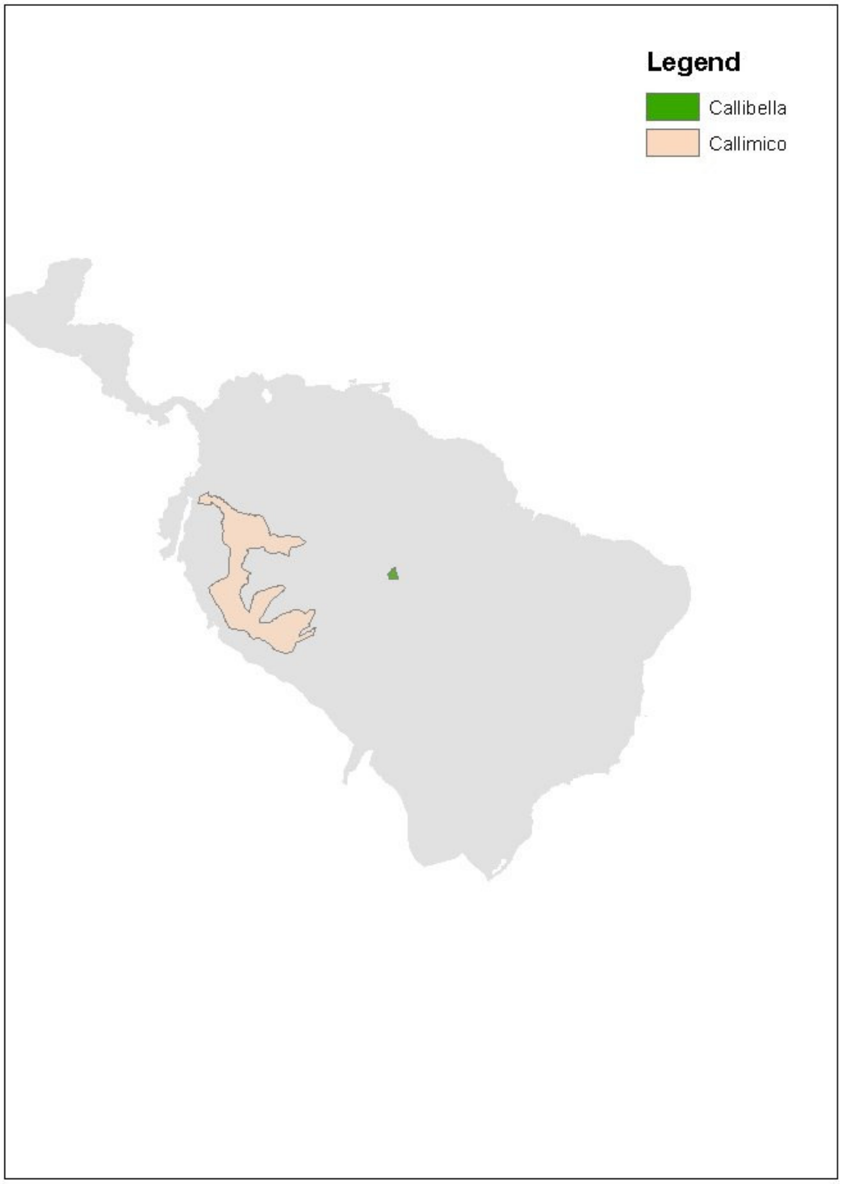

Figure 11. Distribution of the monotypic genus *Callibella*, with a comparison to the widespread *Callimico*. Map by Krista Adamek, Department of Wildlife and Fisheries Sciences.

has been previously modified by human activity, although Aguiar and Lacher (2009) question this logic. The most recent Red List assessment lists it as Vulnerable on account of its restricted range (IUCN, 2008).

The circumstances of its discovery and what little is known of this species are presented in detail in Chapter III, as well as an analysis of its cranial morphology as compared with the other callitrichid genera.

CHAPTER II

TAXONOMY OF THE AMAZONIAN MARMOSETS

Introduction

As Western exploration moved across the New World tropics, naturalists and taxonomists described an ever-increasing number of marmosets: very gradually at first, from the comfort of distant museums, but accelerating in recent years as field primatologists took to describing new species themselves. At this time, with only a few exceptions, researchers have generally accepted a consensus taxonomy for the callitrichids, which invokes the phylogenetic species concept to treat all recognized taxa as full species. This current understanding presents the marmosets as a speciose radiation of widespread but clearly similar forms, occurring throughout much of eastern Brazil and the south-central Amazon.

But this consensus stems from a very recent shift in perspective, prompted both by a change in taxonomic thinking and by a remarkable series of new discoveries in the past two decades. When the marmosets were first considered by the early taxonomists, only a handful of forms were known – often confusing in their similarities – and it sometimes required a great deal of effort for later workers to disentangle the overlapping descriptions.

This situation held true for primates from around the world, but the taxonomy of the New World monkeys – and in particular of the marmosets and tamarins – benefited greatly from the intensive efforts of Philip Hershkovitz (1909-1997), whose monolithic

Living New World Monkeys, Vol. 1 (1977) thoroughly reviewed and restructured callitrichid taxonomy. Although indelibly stamped with his own unique perspectives, and suffused with his often dogmatic opinions, his monograph laid the foundation for the current consensus. A substantial body of new research has appeared in the subsequent thirty years, and new opinions and interpretations abound; but the framework developed by Hershkovitz continues to shape the course of callitrichid taxonomy.

For an overview of the development of the current consensus taxonomy, building on the work of Hershkovitz until the present, please refer to Table 2.

The Genus *Callithrix*

The marmosets were among the first New World monkeys to be noted by European explorers; their striking fur and birdlike calls brought them quick attention, and their tolerance for human settlements made them easy to acquire. Within a few decades of Brazil's discovery, marmosets had become exotic pets for the kings and nobles of Western Europe. By the time formal taxonomies were developed, the marmosets of Brazil's southeastern coast were among the better-known of South American primates – although the understanding of their distributions was often minimal, with type localities frequently listed as "South America" or "possibly Brazil."

Their positions in the first taxonomic arrangements were no more precise, owing both to the infancy of the science and the broad uncertainties of their geographic provenance. In the tenth edition of *Systema Naturae*, Linnaeus (1758) grouped the common marmoset, together with six other New World primates, into his broadly

Table 2. The recognized species of Amazonian marmosets, as interpreted across the past forty years.

Hershkovitz (1968)	Hershkovitz (1977)	Mittermeier & Coimbra-Filho (1981)	Mittermeier *et al.* (1988)	de Vivo (1991)[4,5]	Mittermeier *et al.* (1992)[6]	Rylands *et al.* (1993)[7]	Rylands *et al.* (1995)	Fonseca *et al.* (1996)	van Roosmalen *et al.* (2000)	Rylands *et al.* (2000) [8]	Groves (2001)[9]	Wilson & Reeder (2005)[10]	dos Reis *et al.* (2008)	Rylands & Mittermeier (2009)	Rylands *et al.* (2009)
									acariensis	acariensis		acariensis	acariensis	acariensis	acariensis
C.a.argentata	C.a.argentata	C.a.argentata	C.a.argentata	argentata	argentata	C.a.argentata	argentata	argentata	argentata	argentatus	argentata	argentata	argentatus	argentatus	argentatus
C.h.chrysoleuca	C.h.chrysoleuca	C.h.chrysoleuca	C.h.chrysoleuca	chrysoleuca	chrysoleuca	C.h.chrysoleuca	chrysoleuca	chrysoleuca	chrysoleuca	chrysoleucus	chrysoleuca	chrysoleuca	chrysoleucus	chrysoleucus	chrysoleucus
			emiliae	emiliae	emiliae	emiliae	emiliae	emiliae	emiliae	emiliae	emiliae	emiliae	emiliae	emiliae	emiliae
C.h.humeralifer	C.h.humeralifer	C.h.humeralifer	C.h.humeralifer	humeralifera	humeralifera	C.h.humeralifer	humeralifera	humeralifera	humeralifera	humeralifer	humeralifera	humeralifera	humeralifer	humeralifer	humeralifer
	C.h.intermedius	C.h.intermedius	C.h.intermedius	intermedia	intermedia	C.h.intermedius	intermedia	intermedia	intermedia	intermedius	intermedia	intermedia	intermedius	intermedius	intermedius
C.a.leucippe	C.a.leucippe	C.a.leucippe	C.a.leucippe	leucippe	leucippe	C.a.leucippe	leucippe	leucippe	leucippe	leucippe	leucippe	leucippe	leucippe	leucippe	leucippe
									manicorensis	manicorensis		manicorensis	manicorensis	manicorensis	manicorensis
							marcai	marcai	marcai	marcai	marcai	marcai	marcai	marcai	marcai
					mauesi		mauesi	mauesi	mauesi	mauesi	mauesi	mauesi	mauesi	mauesi	mauesi
C.a.melanura	C.a.melanura	C.a.melanura	C.a.melanura	melanura	melanura	C.a.melanura	melanura	melanura	melanura	melanurus	melanura	melanura	melanurus	melanurus	melanurus
					nigriceps	nigriceps	nigriceps	nigriceps	nigriceps	nigriceps	nigriceps	nigriceps	nigriceps	nigriceps	nigriceps
									aff. emiliae					cf. emiliae	cf. emiliae
							saterei[11]	saterei[12]	saterei[13]	saterei		saterei	saterei	saterei	saterei

---

[4] De Vivo (1991) explicitly invoked the phylogenetic species concept to justify elevating all taxa within this group to full species status. With only minor exceptions, this has become the de facto approach to marmoset taxonomy.

[5] De Vivo also believed that *Callithrix* qualified as a feminine genus and that the specific epithets should be changed to match. This is debatable, but was followed for the remainder of the decade.

[6] In their description of *Callithrix mauesi*, Mittermeier *et al.* (1992) eagerly adopted de Vivo's approach, and also recognized *C. nigriceps*, which had been described as a full species earlier that year.

[7] The galleys for Rylands *et al.* (1993) were evidently too far along to include *C. mauesi*, or to adopt the changes in species designations proposed by de Vivo (1991); all subsequent publications by Rylands have treated all taxa as full species.

[8] Rylands *et al.* (2000) restored the lapsed genus *Mico* to contain the Amazonian marmosets; among other things, this required the epithets be treated as masculine. They also included the former *Callithrix humilis*, which they treated as *Mico humilis*; it has since been elevated to the monotypic genus *Callibella*.

[9] Groves (2001) did not believe the Amazonian marmosets merited a separate genus; he treated them as subgenus *Mico* within the genus *Callithrix*, and thus continues to consider the epithets feminine. His book was apparently too far advanced to include *C. acariensis* or *C. manicorensis*. He noted that *Callithrix saterei* had been announced, but evidently was unable to include the description before his book went to press.

[10] The section on primates in Wilson and Reeder (2005) was written by Colin Groves, who follows his 2001 arrangement, with the addition of *C. acariensis*, *C. manicorensis* and *C. saterei*. Groves includes *Callithrix humilis* in the subgenus *Calibella* (lapsus for *Callibella*).

[11] Rylands *et al.* (1995) included "*Callithrix saterei*, Silva e Sousa Jr. and Noronha 1995," although the species had not yet been described.

[12] Fonseca *et al.* (1996) included "*C. saterei* Silva Júnior & Noronha, 1996," although the species had still not yet been described.

[13] Finally described by Silva Jr. and Noronha (1998).

inclusive genus *Simia*, which harbored a great many other anthropoids as well as our own species. Working soon thereafter, Erxleben (1777) allocated six of these New World species to his new genus *Callithrix*, to which he added the *Simia jacchus* of Linnaeus. Although Erxleben's new genus was at least restricted to species from the Americas, it was nearly as inclusive as Linnaeus' *Simia*, and the original *Callithrix* contained species which have since been allocated into five separate genera.

Erxleben's failure to indicate a type species only added to the developing confusion. Illiger (1811) created the genus *Hapale* to contain three species – *rosalia*, *midas* and *jacchus* – which Erxleben had included together in *Callithrix*, and which today are positioned in three distinct genera. As a further complication, Illiger used the newly emptied *Callithrix* to hold two other platyrrhine species, *capucina* and *sciurea*, which had never been included in Erxleben's original conception of the genus, and which today occupy two other genera of their own.

Immediately thereafter, Alexander Humboldt (1812) published the first volume of his long sojourn in South America, in which he described several new marmoset species based on an advance reading of a manuscript by Etienne Geoffroy Saint-Hilaire. For several years Saint-Hilaire had been working in Paris on specimens which had been plundered from Lisbon in 1808, when Napoleon's army had driven the Portuguese royal family into exile in Brazil. Saint-Hilaire's work was published later in 1812, but Humboldt's authorship of the names has received a dubious priority ever since. Humboldt (1812) named five new marmosets, including them with two species of Linnaean vintage in the new genus *Jacchus*. Humboldt employed *Callithrix* to contain one of Illiger's choices for that genus (the squirrel monkey *sciurea*, now in *Saimiri*) and expanded it to encompass another group of small-bodied monkeys, the titi monkeys, which today also occupy a genus of their own.

Several authors writing between Erxleben and Humboldt had borrowed or copied Erxleben's approximate arrangement, and with few exceptions they tightened the sense of the genus from the broadly inclusive *Callithrix* (*sensu* Erxleben, 1777) to the narrowly defined *Hapale* (Illiger, 1811). Humboldt's genus *Jacchus*, although an unnecessary duplication at the generic level, was reasonably exacting in its constituent species, and Humboldt included seven closely related forms which have remained the core species of the marmoset clade ever since.

Writing across the subsequent century, a variety of other authors created a variety of other approaches, most of whose new genera reshuffled species which had already been described. Lesson (1840) created the subgenus *Mico* for the silvery marmoset, which Erxleben (1777) had designated *Callithrix argentata*. But despite Humboldt's prescient use of *Jacchus*, throughout the 1800s it was Illiger's *Hapale* which was maintained by other authors as the genus containing the marmosets, while *Callithrix* – for which Erxleben had designated no type – continued to refer to squirrel and titi monkeys, neither of which had been part of Erxleben's original intention.

This situation remained in effect for the remainder of the century, until Oldfield Thomas (1903), decrying the "common laxity about nomenclature," correctly noted that no titi monkeys had been included in Erxleben's description of *Callithrix*, which therefore could not be applied to them. Thomas could find no appropriate synonyms –

Callithrix having been misapplied for so long – and so he created *Callicebus*, a portmanteau name which reflected the apparent overlap, embodied in the titi monkeys, between the small-bodied marmosets and the larger cebids. Thomas noted that three alternative generic names existed prior to Illiger's *Hapale*, and of them, Erxleben's *Callithrix* was the unarguable senior synonym. This, in turn, made Humboldt's (really Saint-Hilaire's) *Jacchus* a junior synonym, and simultaneously opened Saint-Hilaire's genus *Midas* to the tamarins. In just two pages of typeset text, then, Oldfield Thomas reversed a century of taxonomic negligence, established two genera which have persisted until today, and – in a final aside – designated the family name of the marmosets as the Callitrichidae.

These alterations declared by Thomas were not immediately accepted – owing in part to his own curious retraction a decade later, in which Thomas (1914) argued for the retention of *Hapale*. His specific argument was denied in a 1925 decision by the International Commission of Zoological Nomenclature, but *Hapale* remained in wide use for decades thereafter, perhaps owing to the very taxonomic inertia which Thomas (1903) had complained against. In a later reorganization of the Callitrichidae, Thomas (1922) divided the marmosets according to their ear-tufts, elevating *Mico* to a full genus containing the bare-eared marmosets, and retaining *Hapale* for those with tufts. By the 1950s the use of *Hapale* had faded, but the name was not entirely abandoned until several major systematic works in the 1960s and 1970s – most notably that of Hershkovitz (1977), whose exhaustive taxonomic survey confirmed the use of *Callithrix* and reinforced its modern sense, rejecting *Hapale* as invalid and *Mico* as unnecessary.

Already accepted by the new cadre of Neotropical primatologists, who had begun their pioneering field studies in the 1960s and 1970s[14], the use of *Callithrix* for the marmosets as a whole remained unchallenged for a quarter-century, until accumulating cytogenetic evidence (e.g. Nagamachi *et al.*, 1999) prompted Rylands *et al.* (2000) to propose restricting *Callithrix* to the marmosets of the Atlantic Forest alone, and to revive the abandoned genus *Mico* for the Amazonian clade.

Rylands *et al.* (2000) cautioned that their review was not intended to be a decisive taxonomic survey, but rather "a working basis for the action of the IUCN/SSC Primate Specialist Group," which had convened a workshop on primate taxonomy in early 2000. Despite this caveat, the workshop results have been influential throughout contemporary primatology for their comprehensive approach and their attempt to reach a consensus among participants – consensus not having been a predominant feature of primate taxonomy in the past.

Although earlier studies had noted divisions between the Atlantic and Amazonian marmosets – in particular their differing chromosome numbers – the revival of *Mico* was based less on compelling evidence from the species themselves than on a necessary trick of taxonomic logic. At issue was the placement of the pygmy marmoset, smallest of the living anthropoids and first described by Spix (1823) as congeneric with other marmosets. Gray (1866, 1870) elevated the pygmy marmoset first to a subgenus and then a genus of its own, *Cebuella*, which persisted for over a century thereafter and which Hershkovitz (1977) maintained. But several morphologists (Rosenberger, 1981;

---

[14] Including such researchers as Adelmar Coimbra-Filho, Gustavo Fonseca, Warren Kinzey, Thomas Lacher Jr., Russell Mittermeier, Anthony Rylands, Richard Thorington and M.G.M. van Roosmalen.

Rosenberger and Coimbra-Filho, 1984; Natori, 1994) suggested that *Cebuella* would be more appropriately subsumed within the genus *Callithrix*, although this was not immediately adopted (e.g. Mittermeier *et al.*, 1988). In the 1990s, however, a series of molecular studies argued that *Cebuella* was more closely related to the Amazonian marmosets than the Atlantic Forest clade, and thus the correct name of the pygmy marmoset should be *Callithrix pygmaea*. Rylands *et al.* (2000) disagreed, considering *Cebuella* distinctive enough to warrant its independent status. But they noted that if the Amazonian marmosets were indeed more closely related to *Cebuella* than to the Atlantic Forest clade, then the genus *Callithrix* would be effectively paraphyletic.

In 1840 Lesson had separated *Simia argentata* (Linnaeus, 1771) into the subgenus *Mico* within the genus *Hapale*, which Thomas (1922) had later elevated to a full genus to contain the bare-eared marmosets. Rylands *et al.* (2000) judged this to be the oldest available synonym which applied exclusively to the Amazonian marmosets, and addressed *Mico* to what had become a considerable number of Amazonian species. Groves (2001) accepted the distinctiveness of all three clades, but preferred to retain (*Callithrix*), (*Cebuella*) and (*Mico*) as subgenera of the existing genus *Callithrix*. Groves (2001) maintained the marmosets as distinct species, although listing only eleven from the Amazon – apparently not having seen the long-delayed description of *Callithrix saterei* (Sousa e Silva Jr. and Noronha, 1998) or the most recently described species, *C. acariensis* and *C. manicorensis* (Van Roosmalen *et al.*, 2000).

One of the species listed in Rylands *et al.* (2000), the newly designated *Mico humilis*, had been first described as an exceptional *Callithrix* in Van Roosmalen *et al.*

(1998). Atypically small – approaching the size of *Cebuella* – and apparently anomalous in its behavior, ecology and distribution, *Callithrix humilis* had not been easy to classify, and soon thereafter Van Roosmalen and Van Roosmalen (2003) redescribed it as the monotypic genus *Callibella*. In an analysis of cranial morphology, Aguiar and Lacher (2003, 2005, 2009) found *Callibella* to be distinct in its cranial and mandibular morphology from *Callithrix* and all other callitrichids, but did not find compelling evidence for the generic separation of *Callithrix* and *Mico* using the same data. Ford and Davis (2005, 2009), by contrast, analyzed the postcranial skeleton of *Callibella* and found it to be radically different from any other callitrichid, which in their view supported the genus-level distinction between *Callibella*, *Callithrix*, *Cebuella* and *Mico*.

In the most recent overview of mammal taxonomy, Wilson and Reeder (2005) do not agree with the separation of these four clades into full genera. Written by Colin Groves and following Groves (2001), their section on the primates instead recognizes *Callibella* as one of four subgenera in the genus *Callithrix*. In accordance with the trend established by de Vivo (1991) and upheld by Mittermeier *et al.* (1992), all known terminal taxa are treated as full species, yielding a total of six species from the Atlantic Forest (their subgenus *Callithrix*), thirteen from the Amazon (their subgenus *Mico*) and the two monotypic subgenera *Callibella* and *Cebuella*.[15] This yields a current total of twenty-one species of marmoset, fifteen from the Amazon basin; but descriptions are pending for at least two more Amazonian taxa (Rylands, pers. comm.), which will

---

[15] In an apparent lapsus, Wilson and Reeder (2005) spell the genus as "Calibella," a variant which has never appeared in any prior publication. It is no single error; they repeat the misspelling twice on p. 129 and again on p. 131. At no place in the text does the correct spelling *Callibella* occur.

almost certainly be presented as full species in the genus *Mico*. The most recent reviews of callitrichid taxonomy (Rylands and Mittermeier, 2009; Rylands *et al.*, 2009) continue to recognize the Amazonian marmosets as the separate genus *Mico*, but they depart from Groves (2001) and Wilson and Reeder (2005) in also maintaining *Cebuella* and *Callibella* as full and distinct genera.

Callithrix argentata

In 1743 the French explorer La Condamine received a live silvery marmoset as a gift from the governor of Pará, Brazil. Although it died on the return voyage to France, it was preserved in spirits and later mounted at the Museum National in Paris. From this single specimen, Linnaeus (1771) described *Simia argentata* – one species among many others in his strikingly catholic genus of primates. Subsequent authors transferred it among a variety of taxonomic schema, all the while relying on Linnaeus' judgement that it represented a valid species. The description of the similar but darker-furred *Simia melanurus* (Humboldt, 1812) stirred question that this new race was the authentic species, of which the type of *argentatus* had been only an albino form. (Kuhl (1820) retained the silvery marmoset as a valid species, *Hapale argentata*, and mentioned a white-tailed form in another collection which may have been *Callithrix leucippe*.)

Isidore Geoffroy Saint-Hilaire (1827), the son of Etienne, proposed *argentata* as an albino subspecies of *melanurus*; Wagner (1840) agreed in principle, but retained *argentata* as a full species. In 1851 Geoffroy took the next step and synonymized *argentata* with *melanura*, presenting *Hapale melanura* as the senior synonym despite its having been described three-quarters of a century after the first silvery marmoset was collected. Reichenbach (1862) agreed with the fact of the synonymy but not its order, and presented *argentata* as the senior synonym.

No new perspectives appeared until Schlegel (1876), supplied with the best geographic information to date, argued that *argentata* was geographically separated from *melanura*, and thus the two taxa deserved recognition as discrete and coequal. Although accurate and prescient, Schlegel's arguments were not universally accepted, and subsequent commentators were divided as to whether these two forms were, in fact, the same. Elliot (1913) retained them as synonyms, but followed Reichenbach in naming *argentata* as senior of the pair.

Allen (1916) approved of both *argentata* and *melanura* as valid taxa, but considered them closely enough related to present *melanura* as a subspecies of *argentata*. Thomas (1920) disagreed without comment, describing *Hapale emiliae* as a member of a tribe which also included *H. argentatus* and *H. melanurus*. In 1922, Thomas described the new species *leucippe*, part of the same tribe, which he elevated to the genus *Mico*.

Cruz Lima (1945) followed this arrangement, but the majority of authors followed Allen (1916) in treating *melanura* as a subspecies of *argentata*. Hershkovitz (1977) endorsed this arrangement as part of his concept of clinal bleaching, which he termed metachromatic evolution, and which was the iron standard for nearly fifteen years – until de Vivo (1991) considered the two taxa distinct, noting in particular the great distance between their separate distributions.

Although Mittermeier *et al.* (1992) readily accepted de Vivo's universal elevation – including that of *melanura* to full species status – Rylands *et al.* (1993) followed the path first laid by Allen and later paved by Hershkovitz, treating *melanura* and *leucippe* as subspecies of *argentata* – although they held *emiliae*, the fourth of Thomas' (1922) old *Mico* tribe, to be the separate species *Callithrix emiliae*. Rylands *et al.* (1993) offered no specific rationale for their decision, citing Hershkovitz (1977) and focusing on field sightings rather than details of taxonomy. Soon thereafter, however, in their first comprehensive assessment of the conservation status of New World primates, Rylands *et al.* (1995) adopted de Vivo's approach and considered all marmoset taxa as full species, which at the time numbered six from the Atlantic Forest and a total of eleven from the Amazon.

By the time of their second major assessment, Rylands *et al.* (2000) listed a total of fourteen Amazonian species, now in the genus *Mico*; and so the designation *Mico argentatus*, which Lesson (1840) and Thomas (1922) had each proposed, once again came into play. Groves (2001) maintained the marmosets as distinct species, but considered the Amazonian clade as a subgenus of *Callithrix*; thus the silvery marmoset would be *Callithrix (Mico) argentata*. This view is upheld in the most recent overview of mammal taxonomy (Wilson and Reeder, 2005), while Rylands and Mittermeier (2009) and Rylands *et al*. (2009) continue to maintain it as *Mico argentatus*.

Callithrix chrysoleuca

As with several other species of marmosets, *Callithrix chrysoleuca* was described more than once during the long discovery of South America's primate fauna, and much of its taxonomic history revolves around the slow unraveling of the original error – and the perpetuation of new ones. In 1842, J. A. Wagner, working with specimens collected by Johann Natterer, described the distinctively golden-tailed *Hapale chrysoleucos*. A quarter-century later, J. E. Gray (1868) described the distinctively golden-tailed *Mico sericeus* on the basis of "an interesting American monkey" living in the London Zoo, which had arrived with no information on its exact origins. Gray placed the new species in *Mico*, together with *Mico argentatus* and *M. melanurus* – two black-tailed, bare-eared species which might not seem close kindred of a golden-tailed marmoset with prominent ear-tufts. A few pages later, in the same issue of the London Zoological Society's *Proceedings*, P. L. Sclater treated the same zoo specimen as *Hapale argentata*. Apparently neither Gray nor Sclater had read Wagner (1842) before their publications, but by a year later Sclater (1869) had recognized the mistake and corrected the record, naming *M. sericeus* as a junior synonym of *H. chrysoleucos*. Unfortunately, in the process he conflated the range of *chrysoleucos* with that of *H. argentata*.

Shortly following, Gray (1870) allowed that his *sericeus* did not belong in *Mico* together with the bare-eared species, and he created the genus *Micoella* to contain both *sericeus* and *chrysoleucos*, which at least had the advantage of a strong similarity. Sclater (1871), Schlegel (1876) and Pelzeln (1883) corrected the taxonomic situation – upholding *Hapale chrysoleucos* and relegating *Mico sericeus* to synonymy – but

Sclater's (1869) error of geography, in which the range of *chrysoleucos* was confused with that of *argentatus*, was repeated by several other authors until Trouessart (1904) corrected the error.

But there were more to come: Allen (1916) noted a specimen of what he named *Hapale chrysoleucos* from the site of Pimental on the Rio Tapajós – the type locality designated by Oldfield Thomas (1922) in his description of *Mico leucippe*. Allen (1916) apparently believed *Hapale chrysoleucos* to be "merely a local form of *Callithrix argentata*," ignoring the difference between tufted and untufted ears much as Gray had done half a century before. In his description of *leucippe*, Thomas (1922) noted its sharp distinction from *chrysoleuca*, explicitly commenting that the ears of *leucippe* were untufted and the hindquarters "golden yellow, not so strong as *chrysoleuca*." He went on to note, "This beautiful white marmoset had been supposed to be *Hapale chrysoleuca*, but is readily distinguished by its wholly untufted and almost naked ears."

Despite these persuasive distinctions, Cruz Lima (1945) synonymized *leucippe* into *chrysoleuca*, claiming that the specimens used by Thomas had been damaged and the ear-tufts might have broken off. Hill (1957) perpetuated this synonymy, while Carvalho (1959) considered the bare-eared taxon *leucippe* to be valid – but only as a subspecies of the tufted-eared *chrysoleuca*.

Hershkovitz (1966a) associated *chrysoleuca* as a bleached subspecies of *Callithrix humeralifer*, apparently on the strength of parallels he found with the dark/light pair of *melanura* and *argentata*. Soon thereafter, Ávila-Pires (1969) treated *chrysoleuca* and *humeralifer* as distinct species, but strangely considered *Mico sericeus*

– Gray's long-defunct synonym for *chrysoleuca* – as a synonym instead of *leucippe*, confusing the distribution of *chrysoleuca* with that of *leucippe*.

By a decade later, Hershkovitz (1977) recognized only two species of Amazonian marmoset, *Callithrix argentata* and *C. humeralifer*, the latter containing *chrysoleuca*, *humeralifer* and *intermedius* as subspecies. Deeply impressed if not completely cowed by Hershkovitz's monograph, most authors in the following years accepted his taxonomic configuration without serious question (e.g. Mittermeier and Coimbra-Filho, 1981; Mittermeier *et al.*, 1988). But in 1991, Mario de Vivo reassessed the known taxa in the genus *Callithrix*, and – finding almost no evidence of interbreeding among any of the forms – elevated them all to full species status, *Callithrix chrysoleuca* among them. Mittermeier *et al.* (1992) immediately adopted this approach, which has been followed by nearly all authors since (e. g. Sousa e Silva Jr. and Noronha, 1998; Van Roosmalen *et al.*, 2000). In their millennial survey of primate taxonomy, Rylands *et al.* (2000) restored the defunct genus *Mico* to distinguish the Amazonian marmosets; the species is listed in the current taxonomy of the Primate Specialist Group (Rylands, in litt.) as *Mico chrysoleucus*, and retained as such by their most recent treatments (Rylands and Mittermeier, 2009; Rylands *et al.*, 2009). In accordance with his view of *Mico* as a subgenus of *Callithrix*, Groves (2001) lists the species as *Callithrix (Mico) chrysoleuca*, and the new primate taxonomy of Wilson and Reeder (2005) – which was written by Groves – does the same.

Callithrix emiliae

In 1920 Oldfield Thomas described a new species of marmoset in honor of Emilia Snethlage, the tireless field collector who had sent him a tremendous number of mammal specimens from eastern Amazonia over the past decade. Thomas (1920) considered *Hapale emiliae* to be a member of the "*H. argentatus*" species group, together with *H. melanurus*, *H. chrysoleucos* and *H. melanoleucos* (now known as *Saguinus fuscicollis*). Based on its "white muzzle and the absence of a light hip-stripe," Thomas considered *H. emiliae* "evidently a very distinct new species." In his reorganization of callitrichid genera two years later, Thomas (1922) included *emiliae* in the reconstituted genus *Mico*, together with *M. argentatus*, *M. leucippe* and *M. melanurus*. (He referred *H. melanoleucos* to the genus *Mystax*, later synonymized with *Saguinus* by Hershkovitz (1977).)

Cruz Lima (1945) included *emiliae* in the genus *Callithrix*, but disagreed as to its status, presenting it as a subspecies of *C. argentata*; this was plausible not only for its similarity in coloration, but also its geographic proximity. Hill (1957) and Cabrera (1958) maintained *emiliae* as a subspecies of *argentata*, but Ávila-Pires (1969) and Hershkovitz (1977) both denied its validity as a separate taxon, believing the specimens to be darker individuals of *C. a. argentata*. In a major survey of platyrrhine taxonomy, written soon after the appearance of Hershkovitz's monograph, Mittermeier and Coimbra-Filho (1981) accepted this judgement without question, and the name *emiliae* does not appear in their taxonomy, not even to note its demise. Ávila-Pires (1986), however, later restored *emiliae* as a subspecies of *argentata*.

In 1985, Mario de Vivo examined a series of marmosets from Nova Brasília in Rondônia – many hundreds of miles and several large rivers to the west of the type locality of *emiliae* in Pará – and inexplicably referred the Rondônian marmosets to *emiliae*, despite their different coloration and their physical division by the range of *Callithrix melanura*. Unable to find evidence of intergradation between *emiliae* and other Amazonian taxa, de Vivo (1985) proposed its elevation to full species status as *Callithrix emiliae*, incorporating populations from both Rondônia and Pará.

In their second comprehensive survey of platyrrhine taxonomy, Mittermeier *et al.* (1988) accepted de Vivo's elevation of *C. emiliae*, and included it as coequal with *C. argentata* and *C. humeralifera* in the *argentata* group. De Vivo (1991) maintained *C. emiliae* as a distinct species, while elevating all other taxa of *Callithrix* to full species status. Subsequent field studies of the Rondônian marmoset (e.g. Ferrari, 1993) referred to this form as *Callithrix emiliae*.

Rylands *et al.* (1993), however, noted the interposition of the range of *Callithrix melanura* between the two putative sections of *C. emiliae*, and suggested that the Rondônian form should be renamed, while the true *C. emiliae* remained in Pará, from where it had originally been collected by Emilia Snethlage. Mittermeier *et al.* (1992), in their description of *Callithrix mauesi*, maintained *C. emiliae* as a separate species, and this arrangement was followed by Sousa e Silva Jr. and Noronha (1998), Van Roosmalen *et al.* (1998), and Van Roosmalen *et al.* (2000) in their respective descriptions of *Callithrix saterei*, *C. humilis*, and *C. acariensis* and *C. manicorensis*. In the latter two papers, the Rondônian marmosets were set apart as "cf. *emiliae*" or "aff. *emiliae*."

In a phylogenetic survey of *Callithrix* based on the COII gene, Sena (1998) found that the Rondônian marmoset appeared to be a basal species in the *argentata* group, and noted that this form and true *C. emiliae* from Pará were widely believed to be two distinct species. Ferrari *et al.* (1999) also found the Rondônian form to be distinct from true *emiliae*, but did not formally rename it. In their survey of platyrrhine taxonomy, Rylands *et al.* (2000) noted the dilemma but listed a single species within the genus *Mico*, once again drawn into service to distinguish the Amazonian marmosets from those of the Atlantic Forest. Wilson and Reeder (2005) list *Callithrix (Mico) emiliae* in reference to Thomas' original species, and note the Rondônian form as a separate, undescribed form "which is likely to be distinct." In the current taxonomy maintained by the IUCN/SSC Primate Specialist Group (Rylands, in litt.), the original marmoset from Pará is maintained as *Mico emiliae*, while the Rondônian form is tentatively designated *Mico* cf. *emiliae*, pending its formal description as *Mico rondoni* (Ferrari *et al*., in press).

Callithrix humeralifer

The type specimen of what would become *Callithrix humeralifer*, along with many other specimens, was taken from the Royal Museum in Lisbon by Napoleon's army in 1808 and delivered as plunder of war to Paris, where Etienne Geoffroy Saint-Hilaire examined the stolen material as part of his work on primates. Alexander Humboldt (1812), publishing the results of his long expedition, based several of his new primate species – including *Simia humeralifera* – in large part on an advance reading of

Saint-Hillaire's manuscript. Saint-Hilaire (1812) published his final work only months after Humboldt, and his description of *Jacchus humeralifer* has been credited by many subsequent authors as having priority, although de Vivo (1991) argues for Humboldt's priority on the basis of differences in the two men's diagnoses of the same material.

In the decades following its description, most authors followed the combined judgement of Humboldt and Geoffroy without comment, although Desmarest (1827) believed *humeralifer* to be indistinct from *Jacchus*, and both Wagner (1840) and Schlegel (1876) synonymized the two. Most taxonomists of the 19th century, however, treated the two as separate species.

In 1893, Matschie described *Hapale santaremensis*, based on two specimens supposedly captured on opposite sides of the miles-wide mouth of the Rio Tapajós. Although visibly identical to *humeralifer*, this error survived for decades; Oldfield Thomas (1912) noted a specimen of "*Callithrix santaremensis*" from Boim on the Tapajós – and in his restructuring of marmoset taxonomy a decade later, Thomas (1922) listed *humeralifer* and *santaremensis* as coequal species in the genus *Hapale*. Opinion remained divided for decades thereafter as to whether *santaremensis* was truly distinct from *humeralifer* and whether *humeralifer* itself was only a junior synonym of *Jacchus*.

Hershkovitz (1966a) settled both questions by establishing the validity of *Callithrix humeralifer* and dispensing with *santaremensis* as a synonym. Soon afterwards Hershkovitz (1968) placed *humeralifer* as a subspecies of *Callithrix chrysoleuca*, without any explanation; but by the publication of his 1977 monograph, he had reversed this approach and treated *chrysoleuca* as a subspecies of *Callithrix* *humeralifer*, together with the new subspecies *C. h. intermedius*. Ávila-Pires (1969), meanwhile, considered both *chrysoleuca* and *humeralifera* to be discrete species, but owing to a mistake of geography he also believed they were sympatric. This became a minority perspective; for over a decade after Hershkovitz (1977) stamped his mark on callitrichid taxonomy, most authors followed his approach without question. Mittermeier and Coimbra-Filho (1981) adopted the three subspecies of *humeralifer* – *chrysoleuca*, *humeralifer* and *intermedius* – without argument, and retained the three subspecies in *C. humeralifer* in Mittermeier *et al.* (1988). Only Ávila-Pires (1986) disagreed, holding *intermedius* to be a subspecies of *C. argentata* instead.

In the first major revision of *Callithrix* since Hershkovitz (1977), de Vivo (1991) recognized eleven taxa in the genus *Callithrix*, all of which he elevated to species level. Mittermeier *et al.* (1992) accepted this willingly and have maintained the species-grade status of all terminal taxa in *Callithrix* ever since. Based on comparative analysis of protein sequences, Miereles *et al*. (1992) suggested that *Callithrix humeralifer* was a subspecies of *C. argentata* – an exceptional perspective in the context of contemporary research, and one which has been neither seconded nor widely adopted. The recent treatments of Rylands *et al.* (2000), Rylands and Mittermeier (2009) and Rylands *et al*. (2009) all maintain the species as *Mico humeralifer*.

Callithrix intermedia

Hershkovitz (1977) described *Callithrix humeralifer intermedius* from three specimens from the southern Rio Aripuanã; he fitted the new form between *C. h.*

humeralifer and *C. h. chrysoleuca* in his scheme of metachromatic evolution, in which marmoset species evolved from dark to progressively lighter forms, a process culminating in their inevitable extinction. For Hershkovitz, the tassel-eared subspecies *humeralifer*, *intermedius* and *chrysoleuca* were both a geographic and evolutionary cline, in exact parallel to the bare-eared Amazonian marmosets, *C. melanura*, *C. argentata* and *C. leucippe*.

De Vivo (1991) re-examined the type specimens of *intermedius* and noted a discrepancy: while Hershkovitz had depicted *intermedius* with a ringed tail, similar to *humeralifer* and *chrysoleuca*, the actual specimens had a smooth and ringless tail more closely allied to the bare-eared species. For de Vivo, the name *intermedius* took on a broader significance; the species was not intermediate between *humeralifer* and *chrysoleuca*, but rather between the two main morphoclades of the Amazonian marmosets: the ring-tailed, tufted-ear species such as *humeralifer*, and the black-tailed, bare-eared *argentata* tribe. In accordance with this halfway position, de Vivo described the ear-tufts of *intermedius* as “relatively poorly developed” and structurally different from those of its erstwhile conspecifics. Finding no more evidence of intergradation in *intermedius* than he did in any other Amazonian taxon, de Vivo elevated it to full species status as *Callithrix intermedia*.

In their description of *Callithrix mauesi* the following year, Mittermeier *et al.* (1992) concurred with de Vivo’s taxonomic decisions, including his interpretation of *intermedia* as broadly transitional between the ring-tailed and smooth-tailed marmoset tribes. Continuing his logic, they suggested that two subgroups should be recognized in the Amazonian marmosets: the *humeralifera* subgroup, containing *humeralifera*, *chrysoleuca* and *mauesi*, and the *argentata* subgroup, including *argentata*, *emiliae*, *leucippe*, *melanura* and *nigriceps*, with the status of *intermedius* uncertain pending additional taxonomic research. Mittermeier *et al.* (1992) upheld the elevation of all marmoset taxa to species level, which has characterized the taxonomic approach to the marmosets for the subsequent decade and beyond.

In presenting the results of the Orlando workshop on primate taxonomy, Rylands *et al.* (2000) separated the Amazonian marmosets into the restored genus *Mico*, including *intermedius* together with thirteen other species, seven of which had been described in the previous decade. Rylands *et al.* noted that based on its fur patterns and geographic distribution, *Mico intermedius* would be more closely allied to *Mico argentatus*.

Callithrix leucippe

In his *Anatomie*, Kuhl (1820) commented on a strange, white-tailed specimen of *Hapale argentatus* which he had seen in what may have been a private collection, one whose identity – not to mention its contents – failed to survive the ensuing decades. De Vivo (1991) suggests this may have been the first reference to *Callithrix leucippe*. Nearly a century after Kuhl's cryptic observation, Allen (1916) mentioned a marmoset specimen from Pimental which he identified as *Hapale chrysoleucos*.

Several years later, the British Museum of Natural History – already hosting the world's oldest and largest mammal collection – found it necessary to reorganize its many series of callitrichid specimens, which prompted Oldfield Thomas (1922) to reconsider their competing genera. To create a unified scheme, Thomas combined elements of Pocock (1917) with aspects of Elliot (1912), and restored two genera which had fallen from use – *Cebuella*, for the pygmy marmoset, and *Mico*, which he employed for *argentatus* and its close allies. On the following page, based on two specimens from Pimental, Thomas described a new species to join *argentatus* and its kin: *Mico leucippe*, a "beautiful white marmoset" which Thomas described in careful opposition to *chrysoleuca*, noting the new form's untufted ears and grouping it with the other bare-eared marmosets.

Despite these attempts to distinguish *leucippe* from *chrysoleuca*, Cruz Lima (1945) synonymized the bare-eared former with the tufted latter, believing their differences to be only a matter of individual variation. Cruz Lima also presented an unnamed, all-white marmoset, which he suggested might be an albino of *Callithrix argentata*. This opinion was followed for another fifteen years, until Carvalho (1959) restored *leucippe* halfway, as a subspecies of *chrysoleuca*. Hershkovitz (1966a) noted its bare, untufted ears and reallocated the form to *Callithrix argentata*, retaining it as a subspecies – following the spirit if not the letter of Thomas (1922).

De Vivo (1991) accepted *leucippe*'s distinctiveness and raised it to species level with the other marmoset taxa, although Rylands *et al.* (1993) continued to treat it as a subspecies of *Callithrix argentata*. Mittermeier *et al.* (1992) presented it as a full species, however, following de Vivo's approach. Rylands *et al.* (1995) concurred with this decision, and five years later Rylands *et al.* (2000) separated all Amazonian marmosets into the genus *Mico* – ensuring that Oldfield Thomas' "beautiful little monkey" would return to the name with which it was first described.

Recent Discoveries

In the last decade of the 20th century, seven new marmosets were described from the Brazilian Amazon, more new species than had been described for the group in the previous century. Much of the taxonomic effort between Linnaeus and Hershkovitz had been spent wrangling over the exact status of a relatively small number of species, whose distributions were poorly understood if not completely unknown. This situation was complicated by the fact that the majority of those taxonomists and commentators (with the exception, in recent times, of Hershkovitz) had never explored the Neotropics for themselves and had only rarely seen any of their subjects alive.

As field studies became more common in the 1960s and 1970s, a new cadre of scientists emerged – young field researchers whose travels and experience in tropical wilderness, coupled with formal training in ecology and behavior, gave them a unique perspective on the primates of the Amazon. Collectors, field observers and taxonomic authorities were no longer separate lives and careers, but rather – hearkening back to Humboldt – were combined in the same individuals. Drawing on their personal experience with the living creatures, primatologists were able to incorporate new aspects of their subjects' lives, such as diet, behavior, and vocalizations, to inform their taxonomic opinions.

They were also, by virtue of their explorations, in a far better position to encounter new species than any museum-based taxonomist had ever been. And unlike most earlier taxonomists, who made leisurely comments on abstract issues with more passion for their opinions than the organisms themselves, the new generation of primatologists were keenly aware that the landscapes of South America were suffering across the continent – and that species assumed to be common might soon no longer exist.

So the modern explorers best suited to discover and assess new forms were also those who, by virtue of their experience, were most aware of the need for their conservation – and often with a personal stake in promoting species diversity, and thus predisposed to follow de Vivo's example and treat each new discovery as a separate (and newsworthy) species. This pattern showed clearly enough in the 1990s, when new marmosets began to be described on an almost predictable basis.

In 1992, two new species were announced in quick succession. Ferrari and Lopes (1992) described *Callithrix nigriceps*, which seemed closely allied to *C. argentata*, and Mittermeier *et al.* (1992) presented *C. mauesi*, which both physically and geographically appeared most closely related to *C. humeralifera*. The latter authors also took the opportunity to adopt de Vivo's (1991) approach to treating all marmoset taxa as full species, which has become the default assumption when presenting new forms.

The following year, Alperin (1993) described *Callithrix argentata marcai* on the basis of three badly damaged skins of dubious locality, collected on the Roosevelt expedition (Allen, 1916) across what became Rondônia, in the southwestern Brazilian

Amazon. Not accepting the approach of de Vivo (1991) and Mittermeier *et al.* (1992), Alperin treated *Callithrix emiliae* and *Callithrix leucippe* as subspecies of *C. argentata*, and described the new form *marcai* in that context. His publication appeared too late to be included in Rylands' (1993) survey of the callitrichids, which treated *nigriceps* as a full species but made no mention of *mauesi*. (This is no criticism of Rylands, since *mauesi* was described in an occasional publication of the Goeldi Museum, and the galleys of Rylands' book may have been too far advanced to include either *marcai* or *mauesi*.) By the time of their first conservation assessment of the platyrrhines, Rylands *et al.* (1995) had included both *marcai* and *mauesi* together with the other marmosets, all of which they elevated to full species status.

Rylands *et al.* (1995) also included another new species, listed as "*C. saterei* Silva e Sousa Jr. & Noronha, 1995," another new form which had been recently discovered. But it became the subject of a bitter dispute among several primatologists, and its publication was delayed until 1998. In the meantime, yet another marmoset had since been discovered – a unique and perplexing form first seen by Marc van Roosmalen in 1996, and published by Van Roosmalen *et al.* (1998) as *Callithrix humilis*, although they later reconsidered it as the new genus *Callibella*. Van Roosmalen, who had traveled extensively on the rivers of the central Amazon, also encountered two additional forms, which were jointly published as full species, *C. acariensis* and *C. manicorensis*, in Van Roosmalen *et al.* (2000).

In their second assessment of primate taxonomy and conservation status, Rylands *et al.* (2000) accepted all of these new taxa as full species within the reconstituted genus

Mico, which then included a total of fourteen species – its most extensive population to date. Groves (2001) included only eleven species, having apparently been unable to find the 1998 description of *Callithrix saterei*, although he notes its listing in Rylands *et al.* (1995). Groves was also apparently unable to find the joint description of *C. acariensis* and *C. manicorensis* (Van Roosmalen *et al.*, 2000), which may have been delayed in publication beyond the time when Groves (2001) went to press.

The most recent assessment of callitrichid diversity is the review of mammalian taxonomy by Wilson and Reeder (2005), which follows Groves (2001) in considering *Mico*, *Cebuella* and *Callithrix* as subgenera of *Callithrix*, in which they also include *Callibella*. Two new forms of marmosets have recently been discovered and are awaiting description (Rylands, pers. comm.; Sena, pers. comm.), and will most likely be described as full species within the genus *Mico*.

Callimico

The clear dichotomy between the marmosets and the remainder of the platyrrhines – which had been established early in the 1800s, and maintained for nearly a century – began to dissolve with the discovery of the Goeldi's monkey, first noted by E. Goeldi at the zoological gardens of the Pará Museum in Belém. Writing in a catalog of the museum's holdings, Goeldi and Hagmann (1904) commented on a tamarin-like monkey with an unusual, white-patched coat of fur, which they believed was a *Midas weddelli* showing the effects of a long life in captivity. In a footnote to the catalog, they mentioned that Oldfield Thomas thought it might be a new species entirely, for which he had proposed the name *Hapale goeldii*.

Although Thomas wrote to Goeldi soon afterward, agreeing it was probably not a new species after all, he reversed his opinion once he received the animal's skin upon its death. Based on a detailed study of the skin alone, Thomas (1904) described it as *Midas goeldii*, commenting that its coloration was "quite unique" despite the anomalous white patches. He noted, however, that "I cannot be entirely certain that this marmoset is not a *Callithrix*," as the skull had not been preserved.

By 1911, the Pará Museum had acquired another live specimen for its zoological annex, and this individual caught the notice of the Brazilian zoologist Alipio de Miranda Ribeiro. Apparently unaware of Thomas' earlier description, Miranda Ribeiro (1912) described the species as *Callimico snethlageri* – simultaneously honoring the prolific collector and creating a new genus which, by its name, was meant to stand midway between *Callicebus* and *Mico*. Once that individual died, it was also forwarded to the British Museum of Natural History – this time with its skull intact – and Thomas immediately recognized it as the species he had already described. Working with a skull as well as a skin, he agreed with Miranda Ribeiro's creation of the new genus, and Thomas (1913) established its name as *Callimico goeldii*.

Its name was the only thing about the animal which was easily settled. *Callimico* presented a fusion of features which, until its discovery, had been neatly divided among the two presumed clades of Neotropical monkeys, the marmosets and all the rest. Critical to this division was the number of upper molars: *Callimico*, like all cebids, had three molars, as opposed to the callitrichids with only two. But like the callitrichids, *Callimico* had claws on all digits save the hallux, a specialization which allowed it to cling vertically to trees and lianas; and like the callitrichids, *Callimico* was no larger than a squirrel. Unlike the callitrichids, which typically gave birth to twins, *Callimico* almost always produced a single infant, just as the cebids did. And yet although the overall molar pattern was cebid, the fine structure of those molars most closely resembled the marmosets'.

This haphazard mosaic of traits, which until then had been sorted out cleanly between the two great clades, made the classification of *Callimico* problematic at best, and it has been so ever since. Rosenberger (1981) argues that it was the need to account for *Callimico* in a coherent way, more than anything else, which led the taxonomists of the New World primates away from the purely descriptive taxonomy of the 19th century and into the phylogenetic approach of the 20th. But the principles of character-weighting, especially at the beginning of the century, often blended invisibly with simple intuition.

Thomas (1913) had included *Callimico* with the larger cebids, giving more weight to their shared dental formula. Elliot (1913) first treated the species as *Callithrix goeldii*, but soon followed Thomas in considering *Callimico* as a unique subfamily of the Cebidae. Pocock (1920) examined three specimens and, impressed by the similarity of their hands and feet to those of the marmosets, reassigned *Callimico* to the callitrichids, supposing that they had reduced their size secondarily, from a larger cebid ancestor.

Thomas (1928) agreed that *Callimico* was most likely a primitive callitrichid, reversing his earlier position.

Dollman (1937) took the new approach of separating *Callimico* from both the cebids *and* callitrichids, creating the new family Callimiconidae. Miranda Ribeiro (1940), based on the assumed primitive nature of *Callimico*, declared that all platyrrhines comprised a single family, in which the Callimiconinae was a monotypic subfamily. More conservatively, Cruz Lima (1945) included *Callimico* as a subfamily of the cebids, noting that it was a "transition stage" between cebids and callitrichids. For Cruz Lima, the skull of *Callimico* embodied features of both great clades: "…the shape of the brain case," he wrote, was one of the features "unquestionably justifying its allocation to the [Cebidae]," along with its dental formula. And yet, "the shape of the pterygoids is identical to that found in the Callitrichidae," as well as other features of the skull and the fine details of the molars themselves.

Osman Hill (1957) at first retained *Callimico* in its own family; but soon afterward, in a monograph on its anatomy, Hill (1959) presented it as a basal callitrichid, an offshoot of the first group of ur-marmosets to have diverged from the proto-cebids – "a stage in the evolution of the Hapalidae prior to the final loss of the last molars," and thus a primitive link between cebids and callitrichids. Hill considered the remaining callitrichids to be derived rather than primitive, following the early ideas of Pocock (1920) and Gregory (1916), and Hill believed that *Callimico* supported this view "in so far as it fills a gap" in the phylogenetic history which Gregory (1916) had proposed.

The first chromosomal studies, published soon after Hill's monograph, offered no simple resolution. Bender and Mettler (1960) reported 2n = 48 for the *Callimico* karyotype, different from the 2n = 44 of Amazonian marmosets or 2n = 46 for the Atlantic Forest clade. As Hill had done before them, Bender and Mettler (1960) considered *Callimico* to be primitive and the callitrichids more specialized. Egozcue (1969) considered *Callimico* to be in a direct line between the cebids and callitrichids, while De Boer (1974) believed *Callimico* had evolved independently following an early separation from the proto-callitrichids.

Hershkovitz (1977) surveyed all these perspectives and disparaged nearly every one – reserving his harshest criticism for Hill (1959), whose meticulous survey of anatomical features "lacks phylogenetic content." Hershkovitz dismissed any value from karyology, noting the broad range of primate diploid values, and excoriated the body of opinion – developed by Pocock, Gregory, Hill and Miranda Ribeiro – that the signature anatomy of the callitrichids had been secondarily derived from a proto-cebid ancestor.

In concert with this opinion, he rejected any notion that *Callimico* could be evolutionarily allied with one group or the other. "No primate having three molars like *Callimico* could evolve from a callitrichid," he stated flatly, "and no primate with a quadritubercular molar could evolve into a callitrichid." For Hershkovitz, *Callimico* was uniquely divergent and bore no relation to either cebids or callitrichids; its features were a hodgepodge of primitive retentions. "*Callimico* is the lone and comparatively little differentiated survivor of a line of primitive platyrrhines," which in his view had arisen independently some time during the Tertiary. In accordance with this ironclad perspective, Hershkovitz placed *Callimico* in a family of its own, reviving Dollman's (1937) third platyrrhine family of the Callimiconidae.

Such was the impact of Hershkovitz's monograph that a silence fell in its wake. Coimbra-Filho and Mittermeier (1981) avoided committing *Callimico* to one clade or another, although its position in their chapter – placed between *Leontopithecus* and *Aotus* – clearly indicates they followed the conventional opinion of *Callimico* as a transitional form. Writing in the same volume, however, Rosenberger (1981) divided the platyrrhines in an unprecedented manner, grouping *Callimico* together with the callitrichids, as well as *Cebus* and *Saimiri*, to create a radically new version of the Cebidae – while allocating the remainder of the platyrrhines, the atelids and the pitheciids, to the new family Atelidae.

Rosenberger (1984) continued to group *Callimico* together with the marmosets, rejecting its placement in a separate family as "of limited heuristic value," which would potentially obscure a more complex phylogenetic pattern. (Osman Hill, had he been inclined to ironic vengeance, might have added that it lacked phylogenetic content.) Rosenberger went on to claim that much of the controversy about *Callimico*'s position had been "steeped in philosophical and methodological confusion," with most of the prior taxonomies – up to and including Hershkovitz – having been based on essentially pre-evolutionary concepts of taxonomy, rather than "an evaluation of the phylogenetic affinities of the genus." This, in his view, inevitably made *Callimico* a close affiliate of the marmosets.

Rylands *et al.* (1993), while carefully reviewing Rosenberger's theories, did not endorse them, omitting *Callimico* entirely from their consideration of callitrichid biogeography. In the same volume, however, Snowdon (1993) included *Callimico* as another genus within the Callitrichidae, presenting the Goeldi's monkey as basal to callitrichids, although similar in its vocalizations to the tamarins.

In the past decade, a series of molecular studies have presented a new concept of *Callimico*'s position completely at odds with the morphological consensus. In contrast to the standing view of *Callimico* as a basal callitrichid, the molecular results suggest that *Callimico* may in fact be most closely related to *Callithrix* and *Cebuella*, long supported by morphological and behavioral evidence as the most derived members of the family. Results from a variety of molecular studies (e.g. Neusser *et al.*, 2001) indicate that *Callimico* is a sister group to the *Callithrix-Cebuella* clade.

Following the first molecular studies – though not explicitly influenced by them – Rylands *et al.* (1995) included *Callimico* as another genus in the Callitrichidae, while being careful to emphasize that their arrangement was not intended to endorse any particular taxonomic cause. Rylands *et al.* (2000) again included it as a genus of the callitrichids – this time in the context of a workshop devoted to primate taxonomy, intended to "serve as a working basis for the action of the IUCN/SSC Primate Specialist Group," which for a time maintained *Callimico* in the subfamily Callimiconinae, as a sister group to the remaining callitrichids in the Callitrichinae (Rylands, in litt.). Groves (2001) also maintains *Callimico* as a callitrichid genus, though without the subfamilial distinction, an approach which Wilson and Reeder (2005) have upheld, presenting it as coequal to their expanded genus *Callithrix*.

Rylands and Mittermeier (2009) briefly comment on recent molecular studies which find *Callimico* is most closely allied with *Callithrix* – and which, they believe, invalidates their former use of the subfamily Callimiconidae. Instead they now include *Callimico* as a monotypic genus within the Callitrichidae, although interestingly enough they maintain its implicitly transitional status – no longer between the older conceptions of Callitrichidae and Cebidae, but now balanced between the marmosets (*Cebuella*, *Callibella*, *Mico* and *Callithrix*) on the one hand, and the tamarins (*Saguinus* and *Leontopithecus*) on the other.

CHAPTER III

CRANIAL MORPHOLOGY OF THE DWARF MARMOSET *CALLIBELLA* IN THE CONTEXT OF CALLITRICHID VARIABILITY[*]

Introduction

The dwarf marmoset (*Callibella humilis*) first appeared as one of seven new marmoset species discovered like a string of firecrackers in the final decade of the twentieth century. Of all these species, the dwarf marmoset was the most surprising: an atypical callitrichid which showed aspects of *Mico* (Amazonian marmosets) in a body scarcely larger than *Cebuella* (the pygmy marmoset), blending traits of each into an enigmatic whole. First heralded as a "missing link" between the two genera, or a deep-rooted ancestral form – some unknown ur-marmoset – the unexpected monkey was originally described as *Callithrix humilis* Van Roosmalen *et al.*, 1998. At the time, the Amazonian marmosets were still considered part of the genus *Callithrix*; having already discovered several other marmosets, the authors made the decision to present the new species as one more Amazonian form, during a period when new finds were almost routine.

According to the description, Marc van Roosmalen and his son Tomas first saw an infant dwarf marmoset on April 16, 1996 in the Amazonian town of Novo Aripuanã, on the eastern bank of the Rio Aripuanã where it flows into the Rio Madeira (Fig. 12,

---

[*] Reprinted with permission from *The Smallest Anthropoids: The Marmoset/Callimico Radiation*, by Susan Ford, Leila Porter and Lesa Davis (eds.), 2009, Springer, New York.

Figure 12. The Madeira-Aripuanã interfluvium, which covers the known range of the dwarf marmoset (*Callibella humilis*) and the Manicoré marmoset (*Callithrix manicorensis*). The Rio Madeira, flowing across the image from left to right, is a major tributary of the Amazon, and serves as the boundary for the genera *Callithrix* and *Callibella*, occurring to the river's southeast. By contrast, the third genus of Amazonian marmosets, *Cebuella*, only occurs north and west of the Madeira. The Rio Aripuanã flows from south to north at the far right of the image; most of the sightings of *Callibella humilis* have been made along its western bank. Smaller tributaries of the Madeira dissect the landscape, much of which remains thinly inhabited; lighter patterns along the margins of the Madeira indicate the settlements of *caboclos* and their fields, extending partway down the tributaries. Lakes and river-bays appear as sharp black patches; the broader grey features are *pantanal*, or swampy terrain. Those sightings of *Callibella humilis* which were reported with coordinates have been marked with cross-points; others are labeled in the approximate region. *Rivers and lakes*: A – Rio Madeira; B – Rio dos Marmelos; C – Rio Manicoré; D – Rio Atininga; E – Rio Mataurá; F – Rio Jatuarana; G – Rio Uruá; H – Rio Mariepauá; I – Rio Arauá; J – Rio Aripuanã; K – Lago Capanã; L – Lagoa Matupiri; M – Lagoa do Acará; N – Lagoa de Jenipapo; O – Lagoa Xadá; P – Lagoa Preta. *Towns and localities*: 1 – Auxiliadora; 2 – Manicoré; 3 – Seringal São Luis (type locality for *Callithrix manicorensis*); 4 – mid-reaches of the Atininga; 5 – Santa Cruz; 6 – Novo Aripuanã; 7 – Guariúba; 8 – Nova Olinda (type locality for *Callibella humilis*); 9 – Monte Alegre; 10 – Novo Oriente; 11 – Terra Preta.

Loc. 6). This infant, the van Roosmalens were told, had been taken from its mother's back some distance upriver on the Aripuanã, from the community of Nova Olinda on the river's western bank (Fig. 12, Loc. 8). Bringing it to their home in Manaus, where for many years their family operated a facility for orphaned primates, the van Roosmalens showed it to Russell Mittermeier and Gustavo Fonseca of Conservation International, both of whom were experienced primatologists themselves. The consensus was that the infant monkey represented a new species – although of what, no one could be sure.

In July of that year the van Roosmalens returned to the Aripuanã to search for another specimen, without success; but on a third trip in November, Marc van Roosmalen found a group of dwarf marmosets at a settlement close to the community of Nova Olinda. Immediately thereafter, Mittermeier and Fonseca arrived at the site with David Quammen, a noted science writer who dramatized their journey in an article for *Sports Illustrated*, making for one of the most unusual citations in the callitrichid literature (Quammen, 1997).

Appearing in print several months before the formal description, Quammen's article presented a more detailed account of the prelude to the first field sighting of dwarf marmosets. According to Quammen's timeline, van Roosmalen first saw a dwarf marmoset at the door of his own home in Manaus, where a *caboclo* – a resident of the interior Amazon – had brought it for adoption. At the time, van Roosmalen's facility for Amazonian primates was widely known, as well as his interest in discovering new species. The *caboclo* with the infant monkey may have been hoping for some compensation for his trouble, since (according to Quammen) the monkey had been captured somewhere on the Rio Madeira and then brought downriver on the ferry from Manicoré (Fig. 12, Loc. 2), a river town some 125 km to the southwest of Novo Aripuanã. Although reluctant at first, van Roosmalen accepted the orphan once he saw how unusual it was, and he showed it to Mittermeier soon afterwards.

Quammen does not mention the April 1996 trip to Novo Aripuanã reported in the formal description, nor give a date for the *caboclo*'s arrival in Manaus with the infant dwarf marmoset in hand. But he does detail the subsequent forays that year, culminating in Marc van Roosmalen's discovery of a semi-habituated group feeding on a morototó tree (*Didymopanax morototoni*) near the home of Antônio da Silva Pereira, close to the community of Nova Olinda. On many of these trips – including the one to Senhor Antônio's home – van Roosmalen traveled with an experienced boatman named Valquemar Souza de Araújo, also known as Gordo, whose intuition Quammen credits with clinching the discovery.

Quammen's article closes with that success; but according to the formal description, the van Roosmalens returned twice more to Nova Olinda and brought back a second specimen, an adult male that had been kept as a pet. Despite their care, it died soon afterwards in Manaus, and Marc van Roosmalen donated its skin and skull to the Museu Paraense Emílio Goeldi in Belém, Pará. Registered as MPEG 24769, the specimen serves as the holotype for the species initially described as *Callithrix humilis* (Van Roosmalen *et al.*, 1998; see also Ford and Davis, 2009) (Fig. 13).

The van Roosmalens settled on that name after first experimenting with several others, believing for some time that their new monkey was simply another species of

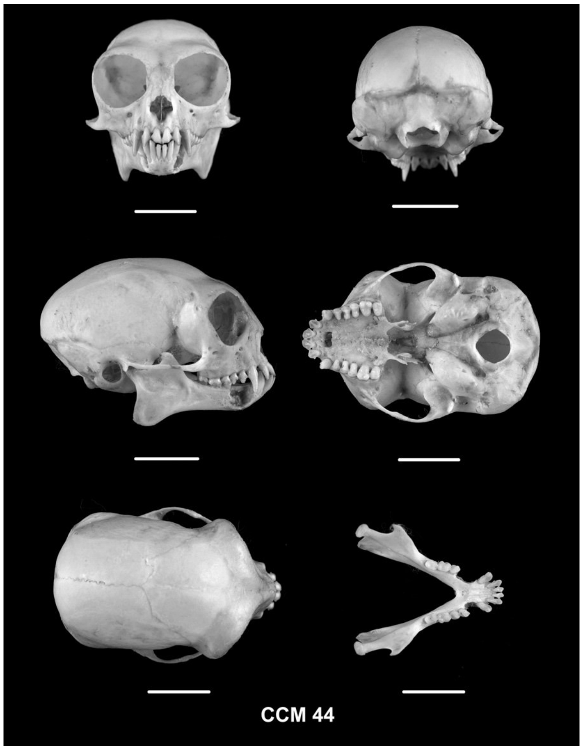

Figure 13. Skull of the adult male holotype of the dwarf marmoset, *Callibella humilis* (MPEG 24769). Photographs by Stephen D. Nash and used with permission. Scale bar = 1.0 cm.

Cebuella gone astray. *Cebuella pygmaea*, the pygmy marmoset, is the world's smallest living anthropoid, and its substantial geographic range extends north from the Rio Madeira (Rylands *et al.*, 1993; Rylands *et al.*, 2009). A new species of *Cebuella* living south of the Madeira would be exceptional enough; but by the time the van Roosmalens published their description with Mittermeier and Fonseca, they had witnessed the first infant grow to maturity, and observed the second adult as well – and they had seen enough to convince them that it was no ordinary *Cebuella*. In their 1998 description, van Roosmalen *et al.* listed five possibilities for its identity and origin: it was either a *Cebuella* that had somehow crossed the Madeira, or an intermediate between *Cebuella* and the Amazonian marmosets, or maybe some primitive form of *Callithrix* – all theories which they felt were improbable – or, more likely, it was either a strange, locally modified form of *Callithrix* (now *Mico*), or else an entirely new genus representing a distinct callitrichid radiation.

For the purposes of their initial description, the authors chose what they considered the conservative approach of naming the new monkey as another species of *Callithrix*, one which "just happens to be considerably smaller than any of its relatives" (Van Roosmalen *et al.*, 1998: 12). Other than this conservatism, they offered no quantitative criteria for selecting *Callithrix* as its genus, although they presented a list of behavioral attributes in which the new species overlapped more broadly with *Callithrix* than with *Cebuella*. The authors also emphasized "striking physical similarities" binding *C. humilis* to the genus *Callithrix* – chiefly aspects of its fur coloration which seemed to parallel those of *Callithrix jacchus*, the common marmoset from northeastern Brazil.

Of the list of behavioral attributes, presented in their Table 3 (Van Roosmalen *et al.,* 1998: 20), *C. humilis* shared nine with *Callithrix* and only one with *Cebuella*. (Their text on p. 12, however, states that "the new species shares only five out of 13 behavioral features with other Amazonian *Callithrix*….") The authors claimed that several of these attributes, including its lack of territoriality, marking behavior or pungent urine, were unique to *C. humilis*. These claims were presented without supporting data, suggesting that at the time of publication the research had yet to be completed.

In the following years the van Roosmalens were able to acquire several more dwarf marmosets, at least two of whom gave birth in captivity. From close observation of these individuals, the van Roosmalens became convinced that they were in fact members of a new genus, which was first announced as *Callibella* at the 19th Congress of the International Primatological Society in Beijing (Van Roosmalen, 2002) and formally described the following year (Van Roosmalen and Van Roosmalen, 2003).

The redescription of the dwarf marmoset as *Callibella humilis* relied primarily on a genetic analysis of mitochondrial DNA, supplemented by a long list of features which the authors considered "remarkable," and which together justified its presentation as a novel genus. A number of these characteristics, however, are not unique to the dwarf marmoset, and serve more to strengthen its similarity to *Cebuella* than to distinguish the two species – in particular its "diminutive" size, its "parking" of the young, and its strong reliance on exudate-gouging. In addition, they claimed there is no pheromonal inhibition of female reproduction, and that more than one female may be reproductively active in a group. But they offered no observations to support this, gave no details on the number of groups and females observed in the wild, and did not address the fact that multi-female groups have been reported from other callitrichid species (see Yamamoto *et al.*, 2009) – all of which weakens the value of these traits as distinguishing features.

As in the 1998 description, other aspects of *Callibella*'s behavior – such as the lack of territoriality and the prevalence of singleton births – are presented without any observational context. Two of the most intriguing and potentially distinctive features, the unique vocal signature and the genital hypotrophy, are mentioned for the first time in the *Callibella* redescription without the most useful supporting evidence, namely comparative sonograms and anatomical illustrations. From the perspective of morphology and behavior, then, evaluating the species' potential status as a new genus is difficult with the information provided in its description and redescription alone.

The van Roosmalens' reliance on one subsection of mitochondrial DNA for their genetic analyses also raises questions. Their conclusions do not correspond with the results of other molecular analyses, in particular Tagliaro *et al.* (1997) and Schneider (2000), who argue that *Cebuella* is not a discrete genus, but rather part of a broadly interpreted genus *Callithrix*, which would also include the Atlantic Forest marmosets (*Callithrix*) and the Amazonian species (*Mico*)[16]. These latter authors were unable to include samples of *Callibella* in their analyses – but if *Cebuella* is subsumed into *Callithrix*, this might question the independence of *Callibella* as well. Here I do not

---

[16] Together with Marroig and Cheverud (2009), I am not convinced that the Amazonian marmosets merit a separate genus, but I use "Mico" as a term of convenience to distinguish the Amazonian marmosets.

address the conflicting molecular results, but focus only on the morphological aspects of the issue.

The redescription of *Callibella* was followed by a short paper in which I analyzed the cranial morphology of the dwarf marmoset, comparing *Callibella* with several other species of marmosets and tamarins (Aguiar and Lacher, 2003). Although preliminary and based on a limited sample set, my analysis demonstrated that *Callibella* is distinct from other callitrichids, especially in the structure of its jaw. I was only able to include measurements from three specimens of *Callibella*, the holotype and two paratypes, which so far remain the only specimens available. The van Roosmalens had at least five other dwarf marmosets in their private facility in Manaus, but the remainder of this group fell victim to an outbreak of yellow fever, which decimated the monkeys living there (M. van Roosmalen, pers. comm.). Until these or other specimens become available, further morphological analyses will be restricted to the three individuals already examined.

Methods

I examined the extant specimens of *Callibella* in the context of a wider study involving callitrichid morphology and biogeography. The holotype of *Callibella humilis* is housed at the Museu Paraense Emílio Goeldi in Belém, Pará, where it was first catalogued with the name *Callithrix humilis*. The two paratypes are at the Instituto Nacional de Pesquisas Amazônicas in Manaus, Amazônas. The specimens representing the other genera analyzed here are kept at the American Museum of Natural History in

New York, New York; the Field Museum of Natural History in Chicago, Illinois; the National Museum of Natural History in Washington, D.C.; the Los Angeles County Museum in Los Angeles, California; the Harvard Museum of Comparative Zoology in Cambridge, Massachusetts; the Museu Nacional de Rio de Janeiro and the Museu de Zoologia da Universidade de São Paulo, in Brazil; the Naturhistoriska Riksmuseet in Stockholm, Sweden; the Humboldt Museum für Naturkunde in Berlin, Germany; the Naturalis/Nationaal Natuurhistorisch Museum in Leiden, the Netherlands; and the Museum National de Histoire Naturelle in Paris, France. A full list of specimens and localities is available upon request.

I measured all specimens to the nearest 0.01 mm with Mitutoyo Digimatic digital calipers, series/model 500-196. I chose a total of 32 standardized characters to measure from each specimen, although the actual number of data points often varied with damage, since I did not take partial measurements on damaged features. In order to avoid the complications of ontogenetic change, I only examined adult specimens; my criteria for determining adulthood were fully fused cranial sutures and completely descended upper canines, together with sharply defined superior temporal ridges. I analyzed the data using the Discriminant Analysis module of SPSS 13.0 (SPSS, Inc. 2003). For these analyses I chose not to substitute values for missing data; instead I removed those variables with less than 80% of the cases available, which I believe

Table 3. Cranial and mandibular variables used in the morphological analyses of callitrichid genera.

Variable	**Description**
Cranial	
CL	Cranial length, as measured from prosthion (foremost tip between inner incisors) to the furthest reach of the skull's aft curvature
OCP	Distance from the left occipital condylion to the prosthion: essentially a measure of the underside of the skull.
SKW	Skull width at the broadest span, usually far aft along the temporal flanges.
OWC	Width across the eyes at the cyclosions, the widest span of the orbits.
BL	Bregma to lambda: distance from the tripoint intersection of the parietals with occipital, at the aft of the skull to the bregma, or intersection of frontal and parietals.
CONW	Width of the cranium at the condyles.
CW	Canine width of the maxillary C1s.
PBG	Prosthion to bregma – from the front tip of the skull to the top of the skull.
NP	Nasion to prosthion – from the feature above the nares to the front tip of the skull.
PL	Prosthion to lambda – from the foretip of the skull, between the front incisors, to the aft tripoint feature.
Mandibular	
CWJ	Width across the molars and the canines of the lower jaw; parallel to CW.
SGL-L	Measured from the symphysion (the mandibular equivalent of the prosthion) to the far edge of the gonion, the aft curve of the jaw.
CJB-L	Condylion height as measured to the jaw base.
COR-L	Height from the tip of the coronion to the jaw base.
SCN-L	Symphysion to condylion: from the front tip of the jaw to the aft end of the right or left mandibular condyle.
SCOR-L	Symphysion to coronion.
JWCY	Jaw width measured across the condylia.

provides a cleaner dataset than using routines for missing value estimation. This resulted in a large dataset with specimens of all genera available for analysis.

For my analyses, I used measurements for the following variables: CL, OCP, SKW, OWC, BL, CONW, CW, PBG, NP, NL, CWJ, SGL-L, CJB-L, COR-L, SCN-L, SCOR-L and JWCY (Table 3; see also Aguiar and Lacher, 2003). I used direct entry of all variables. Whenever two paired variables were symmetrical, I used the measurements from the left side. The classification procedure used the same cases; missing values were not substituted with mean samples, and the classification plots show the same cases as were used when deriving the discriminant functions.

All the specimens included in this analysis were wild-caught, either shot by professional collectors or, in the case of *Callibella*, taken alive from their captivity as pets in riverside communities. (A list of species and sample sizes is given in Table 4.) The only exceptions are the specimen-sets of *Callimico* (callimicos) and *Leontopithecus* (lion tamarins), in which I have included a mixture of wild-sourced and zoo-bred individuals. The scarcity of wild-sourced specimens for these genera, especially *Callimico*, necessitated the use of captive-born animals which I would have ordinarily rejected. For the same reason, my set of *Leontopithecus* is comprised of individuals from all four species; the cranial morphology of lion tamarins is distinctive enough that for purposes of a genus-level comparison, I expect any interspecific variation will be overshadowed by the differences between genera.

Table 4. Number of cases per taxon for the discriminant and cluster analyses.

Species	**All Variables**	**Skull only**	**Mandible only**
Callimico goeldii	6	7	9
Cebuella pygmaea	8	9	11
Mico chrysoleucus	15	24	33
Callibella humilis	2	3	2
Leontopithecus spp.	2	2	11
Callithrix penicillata	11	16	20
Saguinus midas	14	18	20
Total	**58**	**79**	**106**

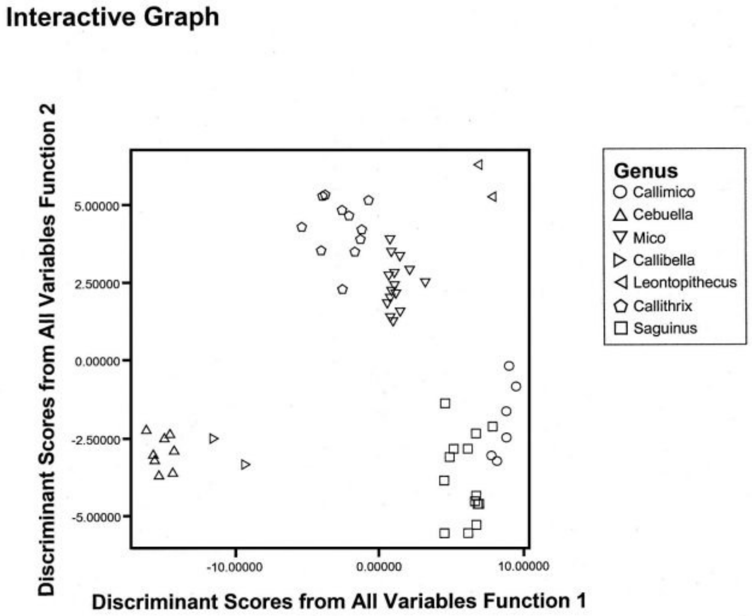

Figure 14. The plot of cases for the seven genera of callitrichids, for discriminant functions 1 and 2 for all cranial and mandibular variables.

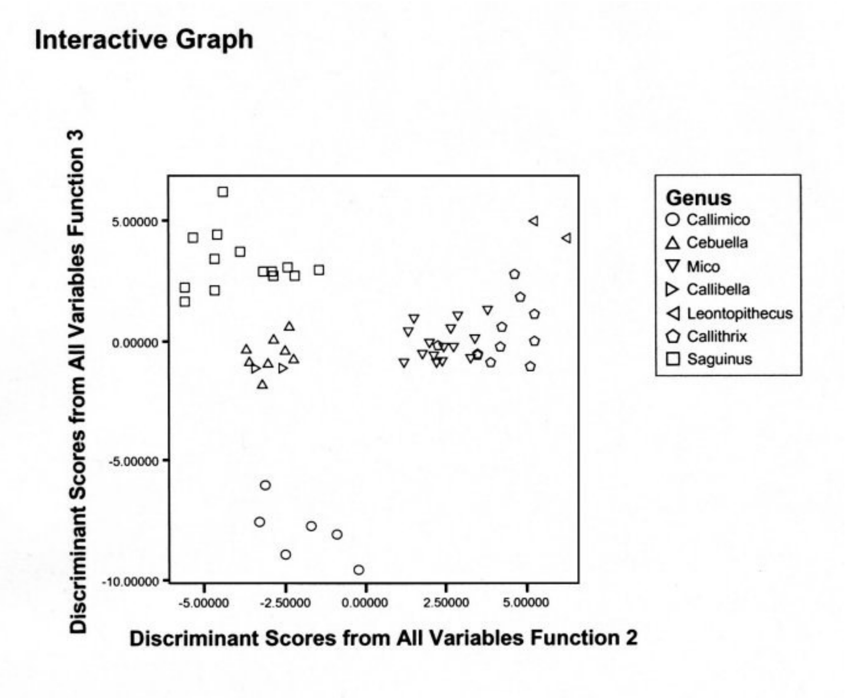

Figure 15. The plot of cases for the seven genera of callitrichids, for discriminant functions 2 and 3 for all cranial and mandibular variables.

Results

I compared the cranial and mandibular morphology of *Callibella humilis* with representatives of the other six recognized callitrichid genera: *Callimico*, *Cebuella*, *Leontopithecus*, *Saguinus* and both the Atlantic (*Callithrix*) and Amazonian (*Mico*) clades of marmosets (Table 4). In these analyses my main interest was to evaluate morphological variation in the Callitrichidae at the generic level, with a particular emphasis on whether *Callibella* would stand out as equally distinct among the other genera, based upon the selected cranial and mandibular morphological variables.

I performed a discriminant analysis using a total of 17 cranial and mandibular characters to generate a classification matrix among the genera (Figs. 14, 15; Tables 5, 6). The first three discriminant functions accounted for 93.8% of the total variance among groups. The first function, accounting for 67.4% of the variance, separated genera largely on the basis of size, with larger taxa scoring higher on the positive side of Function 1 and the two smallest marmosets (*Cebuella* and *Callibella*) scoring on the negative side. This was not exclusively a size function, however, and coefficients indicated significant allometry as well (Table 6). Function 2, which accounted for an additional 14.1% of the variance, separated *Mico*, *Callithrix*, and *Leontopithecus* from the other genera. The combination of these two axes clearly separates the non-gougers (*Leontopithecus*, *Saguinus* and *Callimico*) from the gougers (*Callithrix*, *Mico, Callibella* and *Cebuella*). Function 3 accounted for 12.2% of the total variance. Both Functions 2 and 3 separate the genera on the basis of form, and the plot of Functions 2 versus 3 (Fig. 15) shows strong separation among genera, especially of *Callimico* from all other

Table 5. Results of the discriminant analyses for the comparisons among genera.

Skull Only

Function	Eigenvalue	% of Variance	Cumulative %
1	33.697	71.2	71.2
2	6.272	13.2	84.5
3	5.432	11.5	96
4	1.639	3.5	99.5
5	0.167	0.4	99.8
6	0.091	0.2	100

Mandible Only

Function	Eigenvalue	% of Variance	Cumulative %
1	28.664	87.9	87.9
2	2.615	8	95.9
3	0.919	2.8	98.7
4	0.314	1	99.7
5	0.058	0.2	99.9
6	0.044	0.1	100

All Variables

Function	Eigenvalue	% of Variance	Cumulative %
1	62.325	67.4	67.4
2	13.004	14.1	81.5
3	11.317	12.2	93.8
4	4.952	5.4	99.1
5	0.571	0.6	99.7
6	0.243	0.3	100

Table 6. Standardized discriminant function coefficients for the generic comparisons. See Table 3 for variable codes.

Cranial Variables

Variable	Function 1	Function 2	Function 3
CL	-0.199	0.932	-3.110
OCP	-0.399	0.267	1.440
SKW	-0.059	-0.309	-0.275
OWC	0.438	0.283	-0.942
BL	0.225	0.184	-0.319
CONW	0.192	0.139	0.018
CW	0.424	-1.106	0.179
PBG	0.488	0.688	0.001
NP	-0.644	0.215	0.308
PL	0.817	-0.897	2.718

Mandibular Variables

Variable	Function 1	Function 2	Function 3
CMJ	0.344	0.432	0.809
SGLL	-0.109	-0.159	0.210
CJBL	0.1	-0.62	0.608
CORL	-0.041	0.703	-0.712
SCNL	0.117	-1.114	0.451
SCORL	0.517	0.742	-0.356
JWCY	0.521	0.038	-0.538

All Variables

Variable	Function 1	Function 2	Function 3
CL	-1.428	-2.031	-2.334
OCP	0.179	0.862	1.641
SKW	-0.017	-0.105	-0.287
OWC	0.462	-0.437	-0.962
BL	0.433	-0.168	-0.034
CONW	-0.029	0.146	0.035
CW	-0.173	-0.992	0.985
PBG	0.766	0.548	0.032
NP	-0.736	0.483	-0.119
PL	1.292	1.471	2.001
CWJ	0.113	-0.277	0.086
SGLL	0.169	0.119	0.481
CJBL	0.012	0.190	0.499
CORL	0.042	-0.105	-0.670
SCNL	-0.072	0.469	-1.027
SCORL	0.301	-0.441	-0.598
JWCY	0.336	0.300	0.287

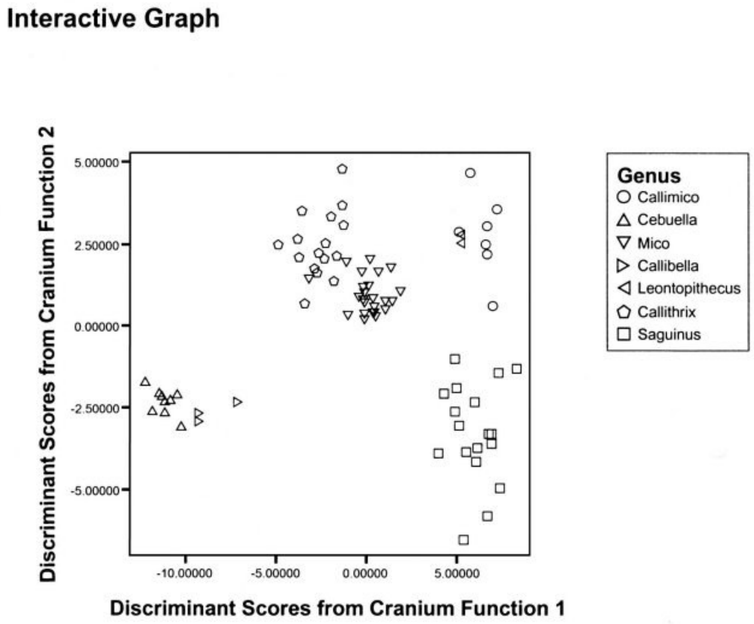

Figure 16. The plot of cases for the seven genera of callitrichids, for discriminant functions 1 and 2 for all cranial variables.

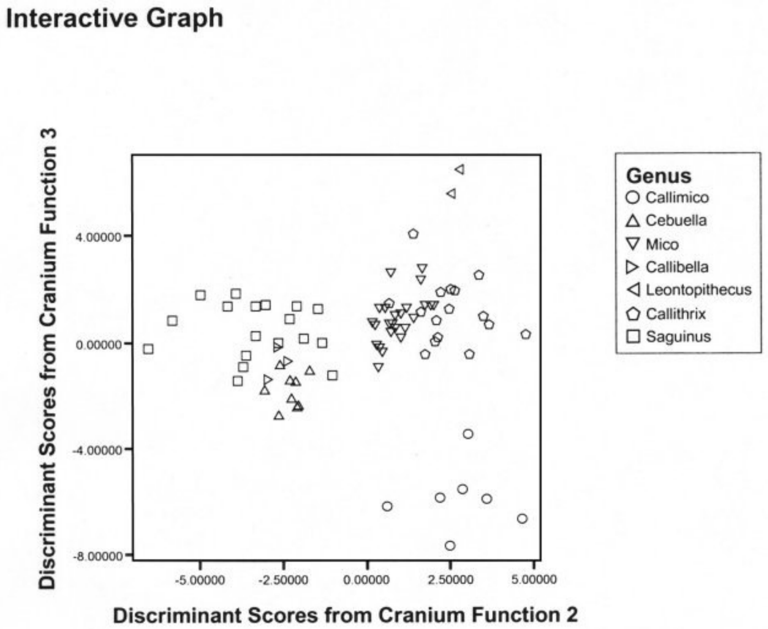

Figure 17. The plot of cases for the seven genera of callitrichids, for discriminant functions 2 and 3 for all cranial variables.

genera. In the classification matrix, *Callibella* returned a 100% correct classification – as did all seven genera – showing no overlap with any other taxon in the full comparison. This strongly supports the classification of *Callibella* as a full and distinct genus, based on its clearly distinct morphology.

My second discriminant analysis examined ten characters measured from the cranium alone (Figs. 16, 17; Tables 5, 6). The first three eigenvalues accounted for 96.0% of the variance, and from this perspective the relative overlap of the genera shifted most dramatically in *Callimico* and *Saguinus*. Here this pair overlaps completely on Function 1 but is now widely separated along Function 2, and *Callimico* shows no classification overlap with *Saguinus*. There is a size component on Function 2, but the key morphological traits involved in the separation appear to be larger canine width in *Saguinus* and a larger prosthion-to-bregma measure in *Callimico*. The plot of Function 2 versus Function 3 shows a clear and complete separation of *Saguinus* and *Callimico*, based upon cranial form. *Callibella* remains 100% distinct from the other genera, but now plots more closely to *Cebuella* in both Figures 16 and 17 – suggesting that the cranial differences between the two smallest marmosets are slight, and due more to size than any divergent functional pressures. In Fig. 17, where both Functions 2 and 3 represent differences in cranial form, *Saguinus* shows strong overlap with *Callibella* and *Cebuella*, even though there are significant size differences among the three genera.

My third discriminant analysis used seven characters to compare features of the lower jaw (Fig. 18; Tables 5, 6), with the first two functions accounting for 95.9% of the variance. Function 3 was not used in the analysis, accounting for only 2.8% of the

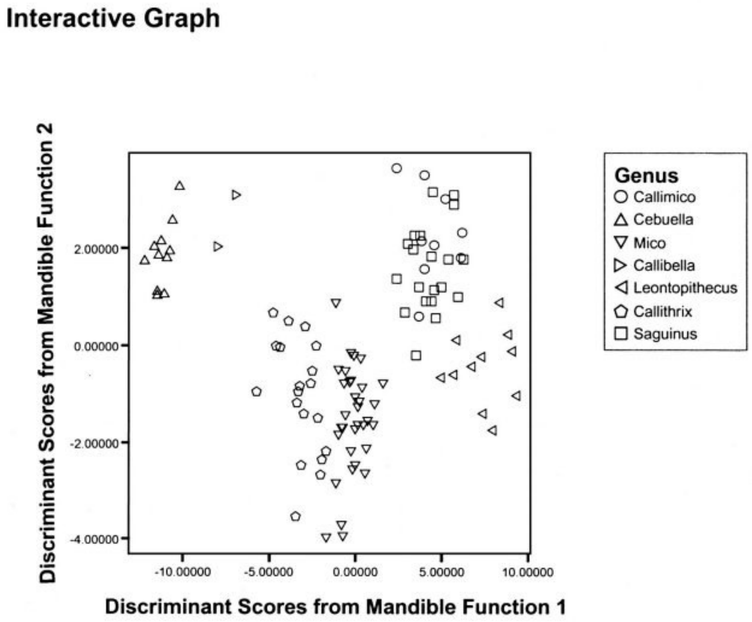

Figure 18. The plot of cases for the seven genera of callitrichids, for discriminant functions 1 and 2 for all mandibular variables.

variance among groups. Here the strong separation of *Callimico* and *Saguinus* is reversed: callimicos, together with the lion tamarins, overlap with *Saguinus* (11.1% and 9.1% misclassifications, respectively). *Mico* and *Callithrix* also show a small degree of mutual misclassification (between 3 and 10%), while *Cebuella* and *Callibella* are both classified as 100% distinct.

In all three discriminant analyses, the genera follow a strong gradient of size, with *Cebuella* and *Callibella* distinct but closely paired in every case. The Atlantic and Amazonian marmosets consistently appear as two well-defined but overlapping clouds, with *Mico chrysoleucus* reliably larger than *Callithrix penicillata*. Both genera do show a greater degree of separation on the plots of Function 2 versus 3 for both the combined analysis (Fig. 15) and the cranial variables only (Fig. 17). *Callimico*, *Saguinus* and *Leontopithecus* show a great deal of coarse overlap on Function 1, with a strong separation of *Leontopithecus* on Function 2; there is also a clear separation of *Callimico* and *Saguinus* on the plots of Functions 2 and 3 that separate the genera on the basis of shape (Figs. 15, 17).

The strong separation of *Callimico* and *Saguinus* in cranial but not mandibular features in the overall comparison is one of the most interesting results from our discriminant analyses – suggesting that the primary differences in their skull morphology might stem from selective forces other than those involved in feeding behavior. Although completely overlapping on the axis of Function 1 for cranial variables (Fig. 16), showing a congruence of size, *Callimico* and *Saguinus* are completely separated in the plots of Functions 2 and 3 (Fig. 17), reflecting a strong disparity in cranial shape.

Primarily plotting on the positive axis of Function 2, *Callimico*'s divergence in shape is driven by the strongest positive canonical coefficients, with a larger overall cranial length (CL, 0.932) and a greater distance from prosthion to bregma (PBG, 0.688). *Saguinus*, set apart by strongly negative values, is distinguished by the larger width across its upper canines (CW, -1.106) and the larger distance from prosthion to lambda (PL, -0.897). Taken together, these features indicate that the skull of *Callimico* is larger and higher in the crown, and more bulbous in the occipital region, while that of *Saguinus* is longer overall and wider in the front of its face. The skull of *Callimico* also appears to be broader across the cyclosia, perhaps indicating its eyes are more widely set apart.

A second gradient is clear in each of the discriminant plots, however, which is directly linked to feeding ecology: the sharp division between those species which gouge for exudates and those which do not. Easily seen in the overall comparison, the division between gouging and non-gouging species is less evident in the analysis of cranial features alone. But the separation is stark in the structure of the jaws, as seen in the plot of Functions 1 and 2 (Fig. 18): a diagonal runs from the positive quadrant of Function 2 down to the positive quadrant of Function 1, evenly dividing *Cebuella*, *Callibella* and both *Mico* and *Callithrix* from *Saguinus*, *Callimico* and *Leontopithecus*. Along this diagonal, *Mico* is the least specialized for gouging, and *Callibella* and *Cebuella* the most. This is largely a size function, and might relate to size restrictions in the ability to use gums as a food resource, as recently suggested by Marroig and Cheverud (2005, 2009).

Discussion

In Aguiar and Lacher (2003), I compared *Callibella* with representatives from four other callitrichid genera. In that limited dataset, all five groups returned 100% correct classification in my discriminant analyses, which was convincing evidence that the dwarf marmoset deserved recognition as a unique genus. Here I have analyzed *Callibella* in the context of all the callitrichid genera, including *Callimico goeldii*, and have added *Callithrix penicillata* to represent the Atlantic clade of marmosets.

In both my prior and current analyses, *Callibella* emerged as sharply distinct – but always closely associated with *Cebuella*, both of which were strongly separated from all other genera in my discriminant analyses. This is due primarily to their similarity in size, which is the major influence on Function 1 of all my discriminant analyses, and which appears as the most obvious gradient in the discriminant plots.

But *Callibella* and *Cebuella* share more than a coincidental perch as the world's two smallest anthropoids. They are similar enough, in fact, that when Marc van Roosmalen first saw the infant *Callibella* which the *caboclo* brought to his door, he thought it was simply another species of *Cebuella*. This was no momentary *deja vú*: the preliminary label on the holotype of *Callibella*, at the Museu Goeldi, was neatly pencilled "Cebuella humilii." During the initial search for groups in the wild, the underlying assumption was that this was an exceptional *Cebuella* (Quammen, 1997), and even after the monkey was announced to the press, there were many who imagined it was a second pygmy marmoset. The creature's presumed identity as a new species of

Cebuella only faded as the first specimen grew into adulthood, passing through a striking sequence of color patterns which helped mark it as unique.

Despite its differences in pelage, however, and its large half-bare ears, the dwarf marmoset is much like *Cebuella* in some respects. Like *Cebuella*, the dwarf marmoset is known from riparian areas; like *Cebuella*, it is not hunted intensively, but is still vulnerable to random target practice or live capture as a household pet. And like *Cebuella*, the dwarf marmoset apparently specializes in exudate-feeding to an extent unmatched by other Amazonian callitrichids – a habit made possible by the jaw structures of both species, and which speaks of either a close kinship or a remarkable convergence.

In my prior analysis of *Callibella*, I noted a second gradient in the discriminant plots, more subtle than the size gradient of Function 1, but not precisely following the shape-influenced pattern spread along Function 2 (Aguiar and Lacher, 2003: 12). This gradient appeared most clearly in the comparison of mandibular features: a sharp boundary between the callitrichids which gouge trees and vines for exudates and those which do not. The latter genera, *Saguinus* and *Leontopithecus*, are joined in the present analyses by the enigmatic *Callimico*, which was poorly discriminated from *Saguinus* in the shape and size of its jaw. Whatever their other differences, callimicos and at least some tamarins share a jaw structure which, aside from the matter of the third molar, is almost identical in its proportions. This, in turn, would suggest a lack of differential selective pressure on feeding behavior and the relevant anatomy, despite a strong separation in the design of their respective crania.

In the overall analysis of both cranial and mandibular characters, the third function accounted for 12.2% of the variance, which was substantial enough to justify plotting Functions 2 and 3 together. While Function 1 typically has a large size component, Functions 2 and 3 are principally driven by shape, and the results in this case were both surprising and challenging to interpret. *Cebuella* and *Callibella* overlapped completely, while *Callithrix* and *Mico* were fused against each other with some degree of overlap. *Saguinus* and *Callimico* also overlap strongly on Function 2 – but they are overwhelmingly separate on Function 3, and in fact *Callimico* is fundamentally removed from all other callitrichids on this axis. This division seems to be driven by three features in particular: the overall length of the skull, the width of the eyes, and the proportions of the posterior region of the jaw. The other callitrichids range from strongly positive to weakly negative on the axis of Function 3, but a well-defined lower limit keeps them firmly apart from *Callimico*.

When plotting the same functions derived from only cranial variables, the division between *Callimico* and *Saguinus* becomes absolute. Among all the callitrichids, the cranial shape of *Callimico* is at the furthest remove. Distinctions are less sharp-edged among the other genera on the plot of Function 2 against Function 3, and there is extensive overlap among the other callitrichids on Function 3. On Function 3, *Saguinus* overlaps with *Cebuella*, *Callibella*, *Callithrix* and *Mico*, but is entirely separate from *Callimico* – and *Callimico* is entirely distinct from all other callitrichids on this axis.

The strong positive vector for *Callimico* on Function 2, and its equally strong negative vector on Function 3, are both driven by the corresponding loadings for the variable CL, which represents overall cranial length. This is in strong opposition to PL, the distance between prosthion and lambda, which tracks a subtly different aspect of skull length and shows inverse loadings in *Saguinus*. The cumulative message of these results, then, is that *Saguinus* and *Callimico* are powerfully distinguished by differences in the shape of the lower skull – reflecting either a difference in the posterior curve of the skull, prognathism in the maxilla, or some unknown combination of the two.

Callimico and the tamarins, together with *Leontopithecus*, are strongly separated from the other callitrichids in these analyses, most dramatically in the shape of their lower jaws. Although not above collecting exudates from the wounds of trees caused by other organisms (or, in the case of saddleback tamarins, filching the efforts of true gougers), these three genera will not gouge trees themselves. In this they stand apart from the marmosets – pygmy, dwarf, Atlantic and Amazonian – who actively gouge for exudates and rely on them to greater or lesser degree (see reviews, Taylor *et al.*, 2009; Vinyard *et al.*, 2009). Of these, *Cebuella* is known for its dependence on exudates as the staple carbohydrates in its diet (Soini, 1988), while the Amazonian marmosets – preferring areas of secondary forest dense with small fruits, large insects and opportune vertebrates – are much less reliant on exudates for their primary nutrition, approaching them less as a staple and more of a last resort.

It would seem to be no coincidence that *Cebuella* and the Amazonian marmosets occupy the opposite endpoints of a continuum of gouging behavior which is reflected in their mandibular morphology (Fig. 18). Much closer to the Amazonian marmosets behaviorally and morphologically, and overlapping them at their fringes, are the Atlantic marmosets – represented here by *Callithrix penicillata*, one of the most adaptable and widespread of all the marmosets, and one of the most exudate-dependent of the Atlantic clade (Rylands and de Faria, 1987, 1993). These three marmoset groups are arranged along the diagonal continuum in the discriminant plots (Fig. 18) – *Cebuella* the most specialized gouger, *Callithrix penicillata* less so but still adept, and *Mico chrysoleucus* at the edge of the non-gouging condition.

This continuum is also apparent in the plot of combined variables for Functions 1 and 2 (Fig. 14). When the results from the combined variables are plotted on Functions 2 and 3 – effectively viewing the dataplot from an orthogonal perspective – this continuum alters its order but not its composition (Fig. 15). The more intensively gouging marmosets – *Cebuella*, *Callibella* and *Callithrix* – now lie on either side of *Mico*, which might suggest that pure size was driving the gradient seen before; but although the positions of the non-gouging callitrichids have shifted dramatically, *Mico* and *Callithrix* remain so tightly clustered that they should be considered as two lobes of the same datacloud. This suggests that the morphological support for the genus *Mico*, at least in its cranial and mandibular features, is tenuous at best (but see Ford and Davis, 2009, for an alternative view from postcranial data).

In my first examination of the type and paratypes of *Callibella humilis*, I noted that aside from its size – substantially smaller than *Callithrix* or *Mico*, and only slightly larger than *Cebuella* – there were no features of the dwarf marmoset's cranium that definitively set it apart. In both my current and prior discriminant plots of cranial characters, as expected, *Callibella* and *Cebuella* are barely divided on the size axis and essentially indistinguishable in shape. This would suggest, among other things, that equivalent pressures have molded equivalent skulls – or else an ancestral design has found no reason to change. This tight similarity makes it difficult to define either one in the context of the other. Hershkovitz (1977) relied on *Cebuella*'s small size to distinguish it from the other callitrichids; but with a second marmoset now in the same size range, some other physical characteristic is needed to separate the pair.

Although their cranial morphology is virtually identical, the structure of the mandible is clearly distinct between *Callibella* and *Cebuella*, as detailed in my initial assessment. The mandible of *Cebuella* is a delicate thing, a wisp of recurved bone lighter than a paperclip yet strong enough to cut through the bark of a tropical tree. Unlike the jaws of the seed-predator sakis (*Pithecia* and kin), whose deep mandibles support the muscle mass needed to deliver their crushing force, the jaw of *Cebuella* is leaned out to the extreme, optimized to concentrate strength at the tips of the incisors. In this design, the pygmy marmoset's jaw occupies the endpoint of a trend seen across the callitrichid genera: a reduction in the size of the ascending ramus and a lowering of the coronial and condylar processes. In *Cebuella*, this results in the condylion – the jaw's point of articulation with the cranium, and its natural pivot – lying directly in line with the tops of the molar and premolar teeth, resting within their occlusal plane. This design in *Cebuella* is far different from the arrangement of *Saguinus* and *Leontopithecus*, whose condylia rest at a high distance above the occlusal plane, with their coronia swept up like brandished scimitars.

The jaw of *Callithrix*, by contrast, shows a less aggressive coronion and a condylar pivot which lies nearer to the occlusal plane, reflecting the marmosets' greater emphasis on exudate-gouging, although not to *Cebuella*'s extreme. Unlike *Leontopithecus* and *Saguinus*, whose jaw base is relatively flat, the angular process of *Callithrix* often extends below the lower jawline as a rounded lobe. In *Cebuella* this lobe is much leaner, but proportionally projects far deeper, and overall the ramal assembly seems dorsally compressed and rotated back when compared to the *Saguinus* design.

In this context, *Callibella* appears intermediate between the moderate shape of *Callithrix* and *Cebuella*'s radical design, with a condylion which lies marginally above (but not precisely on) the occlusal plane; the coronion is not as bold and high as *Callithrix*, but fuller and more developed than the sharp light hook of *Cebuella*. This intermediate shape of the coronoid and condylar processes is combined with a uniquely protruding angular process, which projects even broader and deeper than in *Cebuella*.

As a unique morphological suite, these proportions of the aft mandible serve to isolate *Callibella* unmistakably from both pygmy and conventional marmosets. This design provokes a number of questions, however, as to the dwarf marmoset's evolutionary history and feeding ecology. From its position in the discriminant plots, lying between *Cebuella* and the Atlantic marmosets, the easy prediction is that *Callibella* is likewise specialized for intensive exudate-gouging, but perhaps to a lesser degree than *Cebuella*.

On the face of it, this fits well with what little has been reported of the dwarf marmosets' feeding behavior. Although the van Roosmalens kept several individuals at their primate facility in Manaus – both in cages and free in the house – they did not publish their feeding protocols, and thus the diet they used to raise these marmosets cannot be evaluated.

Moreover, the feeding behavior of dwarf marmosets in the wild has never been systematically documented. In their original description of *Callithrix humilis*, van Roosmalen *et al.* (1998) offered only hints of its diet and habits. Although they named half a dozen species of gum-producing trees growing around the human settlements, close to where the first semi-wild groups were found, the authors did not present observational data on feeding behavior. In their account of its discovery, echoed by David Quammen's earlier article, they noted that the dwarf marmosets gouged and fed from the morototó, *Didymopanax morototoni*. Relaying the observations of local people, Van Roosmalen *et al.* (1998: 8) claimed that this species was the most important of the potential feeding trees in the area: "This tree is said to be [*Callibella*'s] principal exudate source all year round." But it is not clear whether these comments, presumably from Senhor Antônio's family, referred to the species in general or just the one group feeding on that one tree – and the authors did not present a feeding budget or other behavioral data. The authors did claim to have seen the marmosets feeding on fruit from trees around human houses, but without more detailed information, it is difficult to estimate the relative importance of fruit and gum in *Callibella*'s diet.

In their 2003 redescription of *Callibella* née *Callithrix*, the van Roosmalens make no mention of specific feeding behavior, except in a passing comment on the importance of exudate-gouging as a "keystone resource" for *Callibella*, and its lesser importance to the sympatric Manicoré marmoset, *Mico manicorensis*. The morototó appears only once, in a species list of available fruit and exudate sources presented in their Appendix, and the authors no longer give it any special importance.

They do, however, make the new claim that *Callibella* is "almost totally dependent for survival on multi-species managed forests, fruit orchards and gardens" established and maintained by the *caboclos* who have settled the fertile riverbanks (Van Roosmalen *et al.,* 2003: 5). Marc van Roosmalen made the additional claim, during a presentation at the 2002 IPS congress in Beijing, that the dwarf marmoset would have gone extinct some four thousand years ago had it not developed a commensal relationship with humans in the Amazon. No evidence for this theory was offered, nor an explanation as to why *Callibella* as a species should be dependent on the proceeds of human cultivation, when the entire region is apparently suffused with *Inga*, *Spondias*, *Parkia*, *Enterolobium* and *Didymopanax* itself.

This proposal also raises the question of why, if *Callibella* is a successful commensal of human settlements, it has not spread with them throughout the Amazon in its several thousand years of potential coexistence. Apart from the easy access to gardens and orchards, the prime draw for *Callibella* in this theory would be the ultrafertile soils of the *terra pretas* – the anthrosols of lost antiquity, which early Amazonians are thought to have created during thousands of years of small-scale occupation (Mann, 2002; Lehmann *et al.*, 2004). The *terra pretas* may occupy as much as 10% of the entire Amazon basin, representing the culmination of agricultural practices which were cut off abruptly with the European arrival (W. Sombroek, pers. comm.).

The issue of *Callibella*'s affinity for *terra pretas* is tied to the general assumption of its restricted range, which the van Roosmalens based on their having sighted the species primarily in a narrow corridor along the west bank of the Rio Aripuanã, extending some 65 km south of its confluence with the Rio Madeira (see Fig. 12). During their search for the dwarf marmoset, the van Roosmalens concentrated on the Rio Aripuanã, as well as nearby territory on the northern margins of the Rio Madeira – where a trip to the Lago Matupiri, some 80 km southwest of Novo Aripuanã (Fig. 12, Loc. L), revealed *Cebuella* but no *Callibella*.

In their original description, they report no explorations other than along the margins of the Rios Madeira and Aripuanã, apart from what seem to have been brief forays into the mouths of the Rios Mariepauá and Mataurá. In a proof note to the original description, Van Roosmalen *et al.* (1998: 13) reported finding a "geographically isolated population" along the Rio Atininga, a small tributary to the immediate east of Manicoré. They claimed this population was set apart from other dwarf marmosets by differences in fur color – in particular, "a more orange-ochraceous ventral coloration." They gave no information on how many individuals they had seen, nor exactly where on the Atininga they had been sighted, but they raised the possibility that this population was "yet another new taxon" of callitrichid.

In their 2003 redescription of *Callibella*, the location was narrowed to "ca. 10 km. east of the town of Manicoré," at 05º54'S, 61º15'W (Van Roosmalen and Van Roosmalen, 2003: 3.). (These coordinates plot to an area some 15 km south-southeast of Manicoré, although on their Fig. 1 this point is shown 20 km to the town's southwest.) According to the redescription, local people apparently captured a young female from this area and gave it to Marc van Roosmalen. On the female's death in captivity two years later, the remains became INPA 4090, which serves as the only representative of the Atininga population.

I had the opportunity to examine INPA 4090 and to compare it with INPA 4091, another *Callibella* from the van Roosmalens' private facility, which presumably represents the baseline population of dwarf marmosets. Apart from a faint orange tinge to the ventral fur, the Atininga specimen is essentially identical to baseline *Callibella*, and the slight differences in color may be due to individual variation rather than the isolation of a breakaway population. No other information is available on this population, and a brief exploration of the region (Aguiar, 2001) yielded no sightings.

By the time of their 2003 redescription, the van Roosmalens had made additional surveys at two sites along the west bank of the upper Aripuanã – approximately 100 and 150 km south of Novo Aripuanã – as well as at a site on the eastern bank of the Rio Manicoré, some 20 kilometers southwest of the reported population at Atininga and approximately 130 km southwest of Novo Aripuanã. None of these surveys (cited as "Van Roosmalen and Peres, in prep.") revealed any trace of *Callibella*, not even gouge-marks, which convinced the van Roosmalens that the new genus did not occupy undisturbed forest or *igapó*. In the original description, they claimed the distinctive Atininga population occurred exclusively in *igapó*, but in 2003 they reported it from both *terra firme* and *igapó* habitat.

They did not, however, report surveys along the Rio Mariepauá beyond its mouth, nor anywhere along the Rios Uruá and Mataurá, which lie between the Aripuanã and the Atininga, and which – at least at some point in the past – dwarf marmosets must have occupied in order to diffuse from one area to the other. Why the van Roosmalens did not explore these rivers is not clear from their writings, although their efforts in searching the Aripuanã may have been daunting enough. More probably, though, they passed over the other three rivers because their upper reaches, in human terms, are thinly populated or completely uninhabited – making the surrounding forest uninviting to a species which, they believed, was dependent upon *terra pretas* and the human settlements which are often built on them. This conviction is firmly presented in the *Callibella* redescription: "We assume that *Callibella* nowadays occurs almost exclusively on bluffs along blackwater and clearwater streams and lakes, where generations of ancient Indian farmers once lived" – and who, intentionally or not, generated the *terra preta* anthrosols (Van Roosmalen and Van Roosmalen, 2003: 4). The evidence for this association is not presented, other than the fact that *Callibella* was easily found close to human settlements (with their tempting concentration of fruit trees), and was not seen at three points in unoccupied forest.

While undoubtedly true, this by itself hardly precludes dwarf marmosets from living quietly throughout the region and beyond, and – like *Cebuella* – skittishly avoiding human intruders, at least wherever there is no lure of planted fruit to lower their suspicions. Until more thorough and systematic surveys are conducted along all the small rivers and *igarapés* of the region, we cannot be certain that dwarf marmosets are so tightly confined as previously assumed.

In addition to its extraordinary morphology, *Callibella* is also unique in that it apparently shares its range with another marmoset, *Mico manicorensis*, discovered by the van Roosmalens in 1996 during their early search for the dwarf marmoset. Sympatry is known in rare cases between marmosets and other callitrichids, in particular between *Callithrix kuhlii* and *Leontopithecus chrysomelas* in Bahia (Rylands *et al.,* 1993; Rylands *et al.*, 2009). Ferrari *et al.* (1999; in press) have also reported sympatry between the Rondônia marmoset (*Mico* cf. *emiliae*) and *Saguinus fuscicollis weddelli* (Weddell's saddle-back tamarin), although their respective ranges may be different than first expected (Rylands *et al.*, 2009). Sympatry among tamarins, by contrast, is widespread and well-documented (Rylands *et al.,* 1993), as well as between *Cebuella* and several species of tamarins (Soini, 1988; Rylands *et al.,* 2009). But the apparent coexistence of *Callibella* with *M. manicorensis* is the first known instance of a marmoset sympatric with another marmoset – all the more interesting because, unlike the cases above, both species are adapted to actively gouge trees for exudates.

Like other recently discovered marmosets, such as *Mico acariensis* (the Rio Acarí marmoset), *M. mauesi* (the Maués marmoset) and *M. saterei* (the Saterê marmoset), the Manicoré marmoset is known from only a bare handful of sites and specimens – and like these others, its geographic range has been projected far beyond the current evidence. The holotype of *M. manicorensis*, INPA 2511, was taken alive from the "Seringal São Luis," a small patch of semi-managed forest on the outskirts of the river-town of Manicoré (Van Roosmalen *et al.,* 2000). A second individual, taken together with the holotype, was reported as a living paratype in the species description; no accession number was included and the whereabouts of this specimen, dead or alive, are unknown. A third specimen, INPA 2512, was reportedly from Santa Cruz, a settlement near the mouth of the Rio Mariepauá; this individual was kept by local residents for an unknown time and then acquired by van Roosmalen. A fourth specimen, INPA 3930, is also problematic: an adult female which the van Roosmalens claim had been kept in their private facility "for several years." Although their text gives no further details, the specimen tag at INPA lists the female's origin as the Seringal São Luis.

Thus this species is known from only two points along the Rio Madeira: the type locality, in the intensively modified vicinity of Manicoré; and the tiny community of Santa Cruz, located some 95 kilometers to the northeast of Manicoré and approximately ten kilometers upstream on the Rio Mariepauá. This latter locality is not entirely certain; it is unclear whether the van Roosmalens visited the community themselves, and since the marmoset was being kept as a pet, it could have come from anywhere in the region.

In their description of the Manicoré marmoset, Van Roosmalen *et al.* (2000: 6) mention "various groups observed in the wild" but give no information on *where* they were observed nor on their group size, composition or behavior. On the same page, the authors claim that the species is known from the mouth of the Rio Aripuanã "south to the confluence with the Rio Roosevelt" – a distance of over 270 kilometers – but they provide no field observations, interviews or other supporting evidence. In their redescription of *Callibella*, the van Roosmalens (2003) mention sightings of *Mico manicorensis* during surveys they conducted on the west bank of the Rio Aripuanã, at two sites some 50 and 65 kilometers south of its confluence with the Rio Madeira, but they give no information on group size or other aspects of the species' behavior and ecology. Given this, the range maps for *Mico manicorensis* presented in its description (Figs. 1 and 2, Van Roosmalen *et al.,* 2000) appear to be based on inference rather than evidence. The most that can be said from what has been published to date, together with the three available specimens, is that the species occurs at two points on the southeast bank of the Rio Madeira, and has been observed at two sites on the west bank of the Rio Aripuanã.

However, it does follow that *Mico manicorensis* is sympatric with *Callibella*, since the one is known almost entirely from within the range of the other. But it is unclear whether the two species share specific habitats, and whether or not they interact directly – a key issue for evaluating the ecology and behavior of both.

In the original description of the dwarf marmoset, Van Roosmalen *et al.* (1998) mentioned that *C. humilis* had been seen in both dense primary *terra firme* rainforest as well as the secondary disturbed forest around human settlements, known locally as *capoeira*. They also noted that the dwarf marmoset was sympatric with another species of *Callithrix*, but gave no further details. When that new species was named *Callithrix manicorensis* (now considered *Mico manicorensis*) by Van Roosmalen *et al.* (2000), its habitat was described as dense primary *terra firme* rainforest and secondary disturbed forest. They also noted “very high densities” of *C. manicorensis* in *seringal* forest, and commented that these stands of rubber trees “appear to offer optimal habitat and a year-round food supply for small monkeys, such as marmosets, pygmy marmosets, dwarf marmosets, titi and night monkeys” (Van Roosmalen *et al.,* 2000: 6). They repeated the assertion that *C. humilis* was sympatric with *C. manicorensis*, but cited no survey data or other supporting evidence.

In their redescription of *Callibella*, the van Roosmalens (2003: 3) stated that they had seen dwarf marmosets “in disturbed primary and secondary *terra firme* rain forest” directly adjacent to human fields and gardens, and that their earlier report of *Callibella* in dense, distant primary rainforest was based on assumptions alone. After conducting the surveys at the two sites on the Rio Aripuanã, they reported “not a single sighting” of *Callibella* in pristine *terra firme* rainforest (Van Roosmalen and Van Roosmalen, 2003: 3). They did, however, claim to see gouge-marks made by *Mico manicorensis* at their survey sites in primary forest. They also noted that the Manicoré marmoset “share[s] with *Callibella humilis* a preference for disturbed forest near human settlements,” but went on to say that they had seen *M. manicorensis* in secondary forest clearings well removed from human communities (Van Roosmalen and Van Roosmalen, 2003: 4).

From the sum of their comments, it seems clear that *Mico manicorensis* is smoothly adaptable to a spectrum of forest types, from pristine *terra firme* rainforest to anthropogenic *seringal*. Given this ecological malleability, and its presumed affinity for *capoeira*, it seems strange that *M. manicorensis* has apparently never been sighted together with *Callibella* – especially if *Callibella*, as they claim, is found overwhelmingly in *capoeira* and *seringal* habitats. In 1999, Marc van Roosmalen indicated that *Callibella* could be seen together with *M. manicorensis* at the Seringal São Luis (pers. comm.), but there are no published observations to support this. The question of their coexistence bears directly on issues of niche overlap and potential competitive exclusion, which in turn may be central to an understanding of *Callibella*'s evolution. Until additional fieldwork can clarify their distribution, however, their mutual ecology will remain impossible to evaluate.

The dwarf marmoset presents a unique array of morphological features, in particular the distinctive structure of its lower jaw, which separates it from all other callitrichids. However, this structure does not exist in isolation, but rather in the context of a continuum of feeding behavior, with *Cebuella* most adapted for gouging exudates and the Amazonian marmosets least so. This potential difference in feeding ecology between *Callibella* and *Mico manicorensis* may explain their apparent sympatry in terms of niche partitioning, but confirming this will require additional evidence from field research.

CHAPTER IV

RIVER-BARRIERS AND CRANIAL MORPHOLOGY IN AMAZONIAN MARMOSETS

Introduction

Burning Ships and Distant Rivers

In May of 1848, two young Englishmen arrived at the southern mouth of the Amazon, intending to follow the example of Humboldt, Spix, Natterer and the other great naturalist-explorers of the previous generation. The two naturalists, Henry Bates and Alfred Wallace, had met in Leicester several years earlier, the former a passionate entomologist and the latter a devoted collector of plants. Neither had set foot in the tropics before; Wallace had barely ventured across the English Channel. Inspired by the narratives of prior explorers, they were fascinated by “the luxuriance of animal and vegetable life said to exist” in the American tropics, and they resolved to experience it for themselves. But the purpose of their journey was not simply to wander unguided, nor only to amass a great collection of specimens; rather they had decided, well before their departure, that they should undertake their expedition to gather evidence “towards solving the problem of the origin of species,” as Wallace had earlier written to Bates.

Embarking from the town of Pará (now Belém) on the southern mouth of the Amazon, the two naturalists began an exploration of the great river and its tributaries which would take them across thousands of miles over the course of several years. Enthusiastic and omnivorous collectors, especially of birds and beetles, they built up a substantial library of specimens, as well as sketches, notebooks and maps; Wallace meticulously prepared and tagged the proceeds of each day for detailed analysis once he returned to England. For the first two years they traveled together, quickly learning Portuguese and confronting the challenges of work, travel and simple existence in the world of forest and river, where climate, fauna and other humans could be contrary at best, and where the only solution was often, as Wallace wearily noted, "paciencia."

In 1850 they parted ways to explore different regions; Wallace continued for two more years, while Bates remained for seven years beyond that, taking full advantage of an entomologist's paradise. Wallace estimated that he had collected nine hundred species of butterflies alone during the course of his sojourn; Bates had over twelve hundred, and the both of them wondered at such extraordinary diversity "in a country without any variation of climate or of physical features, and no part of it elevated five hundred feet above the level of the sea."

Wallace returned to Pará in July of 1852, and shortly thereafter he took passage on a brig bound for England, carrying with him the great majority of his notes, sketches and collections from the past four years. All of it burned in the mid-Atlantic, along with the ship, the other cargo and a number of unfortunate monkeys and birds, which Wallace had hoped to bring back to England alive. Like Marcgrave two centuries before, a phoenomenal amount of work was lost to fire and shipwreck, and Wallace spent ten days adrift with the captain and crew before their ship's gig and longboat were rescued. He had only been able to salvage a handful of notebooks and sketches from his berth.

But not yet thirty and evidently quite resilient, before the end of the year he had published a four-page note, “On the Monkeys of the Amazon,” which contained the first seeds of his nascent theory of Amazonian biogeography. Much of the note is a brief survey of the twenty-one primate species he had seen, but he finished with a few lines of crystalline commentary on their distributions. “During my residence in the Amazon district,” he wrote, “I took every opportunity of determining the limits of species, and I soon found that the Amazon, the Rio Negro and the Madeira formed the limits beyond which certain species never passed.”

At their headwaters, he noted, the rivers no longer held the species apart, but along their main channels they served as powerful barriers. Between them, these three rivers – the Amazon and its two greatest tributaries – divided the Amazon basin into discrete regions: “Thus there are four districts, the Guiana, the Ecuador, the Peru and the Brazil districts, whose boundaries on one side are determined by the rivers I have mentioned.”

This was perhaps the first instance in which the distributions of Amazonian mammals were compared to large-scale features of the landscape, and had both Wallace and his collection returned to England intact, he would no doubt have painstakingly described each of these biogeographic units based on their distinctive fauna. He did not yet develop this into a theory of origins by diversification per se; in his first note he commented mainly on the general want of knowledge for distributions – “there is scarcely an animal whose exact geographical limits we can mark out on the map” – in the context of its importance to the questions raised by the prospect of riverine divisions.

The following year Wallace published *A Narrative of Travels on the Amazon and Rio Negro*, which he compiled from the journals he had sent on before his departure, as well as his recent and detailed memories. The travelogue begins with his arrival in Pará and concludes with his escape from the burning ship on the journey home. Much of the book details his experiences while exploring and collecting, from the mouth of the Amazon to the upper Rio Negro; but several chapters at the end provide commentary and insights on the fauna, especially mammals and birds, and the indigenous peoples whose forests he passed through. Wallace had originally planned to present these last four chapters as a separate book on the natural history and native peoples of the Amazon, based on an extensive analysis of his zoological and cultural collections. Those having been lost, he wrote what he could and appended his observations to his general narrative.

In Chapter XVI, "Observations on the Zoology of the Amazon District," Wallace laid out a more detailed case for the division of the forest landscape by its major rivers. Starting out with the example of oceans between continents, he acknowledged that geographic barriers prevented intermixing on the broadest scale, and compared mountain chains such as the American Rockies, which had distinct "sets of animals" on either side. "But there must be many other kinds of boundaries besides these," he wrote, "which, independently of climate, limit the range of animals." He continued, "There must be some boundary which determines the range of each species; some external peculiarity to mark the line which each one does not pass."

Wallace was careful to note the interplay between the size of a river and the animals it might deter:

> Rivers generally do not determine the distribution of species, because, when small, there are few animals which cannot pass them; but in very large rivers the case is different, and they will, it is believed, be found to be the limits, determining the range of many animals of all orders.

For Wallace, smaller tributaries and the countless igarapés posed no issue; only the largest rivers left their imprint on the biota. To support this notion, Wallace gave the examples of a number of primate species, which he considered the best-suited for illustrating the concept. In his experience, they were "almost the only animals found in any numbers" in the dense rainforest, and he also noted they were not at all good swimmers, "so that this kind of boundary might be expected to be more definite in their case than in that of other quadrupeds, most of which readily take to the water."

Beyond the observations he had made himself, he also invoked the testimony of native hunters, whose interest in pursuing the monkeys made them natural experts on their distributions. The monkeys, he wrote,

> …are so much sought after for food, and all their haunts are so thoroughly searched, and the localities for the separate kinds are so often the subject of communication from one hunter to another, that it is quite impossible that any well-known species can exist in a particular district, unknown to men whose lives are occupied in forming an acquaintance with the various tenants of the forests.[17]

Wallace also predicted an important corollary of separation by rivers: "Towards their sources, rivers do not form a boundary between distinct species; but those found there, though ranging on both sides of the stream, do not often extend down to the

---

[17] Wallace may have slightly overstated the case to bolster his point, but he was one of the few naturalists of his day who was willing to listen to native people and respect their observations and field experience.

mouth." He acknowledged that rivers would not be expected to have the same effect on birds, but went on to give an example from three species of *Psophia*, the trumpeters (Aves: Psophiidae), which he noted "are inhabitants of the dense forests, and scarcely ever fly" – making them more susceptible to riverine effects.

Despite fire, shipwreck and the loss of four years' determined collecting effort, Wallace had not given up on the tropics, even though the toll had been terrible in personal terms: his younger brother Herbert, who had joined him for the latter part of his explorations, had died in a general wave of yellow fever in Pará. But in July of 1854, following the publication of his *Travels*, Wallace arrived in Singapore to begin a prolonged and superbly productive tour of Malaysia. This culminated in his describing a fundamental biogeographic division between the islands of the Celebes (now Sulawesi) and Borneo, which quickly became known as Wallace's Line.

Soon after his arrival in Malaysia, he began a long-distance correspondence with another Englishman concerned with the origin of species, which eventually resulted in the latter's publication of a modest but extremely popular book on the topic. For his part, Wallace continued his biogeographical explorations, and in 1876 published the first volume of *The Geographical Distribution of Animals*, in which he elaborated his observations from Malaysia and the Amazon.

Had the hold of the *Helen* not smouldered into flame in the mid-Atlantic, Wallace might well have remained in England to process and analyze the immense collection of specimens which he had so vigorously collected. Armed with his meticulous data on localities – as well as the specimens themselves for morphological comparison – Wallace might have been able to produce a detailed, quantified characterization of the great interfluvial divisions he had recognized – and, given that his theoretical interest had always been the origins and diversification of species, he would have been well-positioned to write a definitive, seminal work of his own. Malaysia's loss would have been South America's gain, and the biogeography of the Amazon might have been characterized many decades earlier; but like Darwin's exploration of the emotions of animals, Wallace's latent theory of rivers as active barriers lay fallow for nearly a century more.

Hershkovitz

The modern conception of rivers as barriers to faunal interchange, especially in the primate context, stems from the immense body of writing by Philip Hershkovitz, for decades the doyen of platyrrhine taxonomy and a curator for life at the Field Museum of Natural History. Hershkovitz had many years' field experience in the Neotropics, principally in Colombia and northwestern South America, but also in Surinam, Bolivia and Brazil. His ferocious productivity generated over three hundred publications, including the landmark *Living New World Monkeys*, as well as the description of at least 75 new species (Coimbra-Filho, 1997).

Although much of his work focused on rodents and marsupials, he published extensively on primates over a period of more than forty years. This great depth of experience – coupled with a phoenomenal breadth of knowledge on South American mammals, both living and extinct – informed and enriched all his work, but also led to a certain rigidity of perspective, and an adamant conviction of his own inerrancy. His opinions towards his colleagues were rarely favorable, and often expressed in terms which one of them described as “jaw-droppingly savage.” George Gaylord Simpson, a frequent target of these barbs, noted with civil understatement that Hershkovitz held views which were “often quite idiosyncratic” – and he had no patience for critics and fools, who for him were essentially synonymous.

But despite his contrarian views and his caustic pen, Hershkovitz was a meticulous and exhaustive researcher, and to him is given full credit for having untangled the sticky skein of marmoset taxonomy that had accumulated by his time. In 1977, after decades of research, Hershkovitz published the first volume of what was intended to be a definitive revision of the New World monkeys. The traditional view of the platyrrhines divided them into two major groups: the callitrichids on the one hand – the marmosets and tamarins – and the cebids on the other, being everything else. The callitrichids, which Hershkovitz viewed as inarguably the most primitive anthropoids, were the logical place to begin, and through the course of more than a thousand pages he compiled an exhaustive tally of every publication for every taxon since its discovery and description. Reinforced by his years of fieldwork and decades of museum experience, his volume on the callitrichids – only the first of the platyrrhines, and the first of many others he intended to write – stands as the most comprehensive work ever published on this group, and will likely remain so for decades if not centuries to come.

In *Living New World Monkeys, Vol. 1*, Hershkovitz first mentions rivers as barriers on p. 97, in the context of the many subspecies of *Saguinus fuscicollis*, the saddleback tamarin. This challenging, diverse species (or species complex) ranges across a vast area of the western Amazon, from central Bolivia through Peru, Ecuador and Colombia, and deep into Brazil almost to the Rio Negro. For Hershkovitz, the arrangement was simple: "Rivers form the boundaries between each of the thirteen well-differentiated races of *Saguinus fuscicollis*," he wrote, adding that each race "remains sharply defined by color or color pattern" throughout a broad range. Much later, in a discussion of dispersal on p. 413, he comments on the proposal by Haffer (1969) that the ebb and flow of forest and savanna, driven by climatic fluctuations, had helped to generate species confined to forest patches; this would later become known as the hypothesis of Pleistocene refugia. Hershkovitz, characteristically, was an early doubter. He acknowledged that forest refugia might have generated some species, but he went on to add:

> Barrier rivers, however, appear to be the primary isolating factor in the case of callitrichids. Shifting of river courses…was probably more effective in promoting speciation among Amazonian callitrichids during any one climatic regime than shifting climates during the entire Pleistocene.

These two comments are most of what Hershkovitz has to say about river-barriers in his monograph, but he had been considering the matter long before this. Nearly a decade earlier, in a comprehensive review of Neotropical zoogeography, Hershkovitz (1969) had alluded to the importance of rivers in general terms, allowing for their effects as barriers on lowland tropical species. His exemplars were two primate genera, the tamarins (*Saguinus*) and the titi monkeys (*Callicebus*), which in his view had been differentiated by rivers as part of their respective expansions. The titis, he believed, had arisen in the northern Andean piedmont, and had dispersed south and east thereafter, dividing into separate interfluvial populations as they went. For Hershkovitz, the highlands surrounding the Amazon basin were the ultimate source of new taxa, not the basin itself:

> Mammalian evolution within the Amazonian valley has been of low taxonomic grade. Indeed, much of the speciation had already been accomplished in the uplands before the invaders converged on the bottom lands.

Several years earlier, Hershkovitz (1966b) had described four new subspecies of *Saguinus*, in order for the names to be available for his subsequent work. Soon thereafter, Hershkovitz (1968) introduced his theory of metachromatic evolution, or "metachromism," for much the same purpose. This theory – surely one of his more idiosyncratic views – held that the patterns of mammalian pelage changed over the course of a species' evolution, not at random but along a predetermined trajectory, beginning with agouti banding and moving inexorably towards a final albinotic state. "Ultimately," he wrote, "all color fields fade into a more or less uniformly whitish coat."

For Hershkovitz, the marmosets and tamarins were a classic example of this tendency, and *Saguinus fuscicollis* presented an ideal study of the different stages of chromatic evolution. Here, in the context of this discussion, he first clearly presented his belief that rivers served to separate chromatic races: "Rivers form the boundaries between each of the thirteen well-differentiated races of *Saguinus fuscicollis*."[18] Hershkovitz contrasted these clear-cut differences with what he felt were clinal variations in the pelage of the eastern common marmoset, *Callithrix jacchus*, the various "races" of which were not separated by rivers of the same magnitude. (These regional

---

[18] This and a number of other passages from his 1968 paper are recycled verbatim in his 1977 monograph, and many of the illustrations recur as well.

variants were elevated to species status by Mittermeier and Coimbra-Filho (1981), Mittermeier *et al.* (1988) and de Vivo (1991), and are now considered the six species of the *jacchus* group.)

Hershkovitz (1968) believed that pelage coloration in certain marmosets was correlated with rainfall, but he was hard-pressed to explain how an albinotic race such as *Saguinus fuscicollis melanoleucus* could coexist across the same river from much darker forms, beneath the same clouds and rain. As he presented it, the trajectory of pelage coloration was a process of degeneration, or "bleaching," leading irreversibly to wholesale albinism – and afterwards, extinction. For him, this was not confined to primates, but was an inescapable, universal phoenomenon:

> Metachromism is the principle of saturation, bleaching (or reduction), and elimination of integumental pigments along similar and irreversible pathways, in all mammals, irrespective of the environment.

Here he also presented an overview of the Amazonian marmosets, for him entirely represented by *Callithrix humeralifer* and *C. argentata*. In his view, these two species had originated in the Brazilian highlands and spread north, funneled up between the Rios Tocantins, Tapajós and Madeira, and halted at the southern banks of the main-channel Amazon. Here he presented two subspecies for the former, *C. h. humeralifer* and *C. h. chrysoleuca*, and three for the latter: *C. a. argentata*, *C. a. leucippe* and the melanistic *C. a. melanura*, which for him had clearly been an early detour from the inexorable expansion to the north. For him, the lighter forms – *C. h. chrysoleuca* and *C. a. leucippe* – provided a tidy parallel between two closely related species, which he took as evidence for the universal tendency towards ultimate bleaching.

The remainder of his 1968 paper is given over to a detailed consideration of the eastern marmosets and a comparison with desert mice of the Tularosa Basin in New Mexico. For the eastern marmosets, whose variation is much more complex, Hershkovitz believed that the barriers were climatic and anthropogenic, given that this region of Brazil had been under cultivation and pasture for nearly five centuries. But he believed that the barriers themselves were mere gateways to successive stages of bleaching: "Whatever the ecology, as each barrier is breached, each successive colonization produces a population a tone or grade nearer the end of its chromatic evolution." For Hershkovitz, then, rivers and other barriers were only the facilitators of a grander scheme.

This scheme, as outlined in his theory of metachromism, met with less than universal agreement. A number of objections were immediately raised, and Lawlor (1969) delivered a thorough refutation of what he believed were discrepancies and logical gaffes in the metachromatic approach. Lawlor criticized what he called "a rather improbable scheme of color change in mammals," and objected in particular to Hershkovitz's insistence that the stages of bleaching were both irreversible and unmoored to the marmosets' physical environment. "Color of pelage in marmosets is almost certainly highly adaptive, not inadaptive as Hershkovitz states," he wrote, and delivered a condensed summary of current research on genetics and coat coloration. Lawlor also objected to how Hershkovitz had so easily extrapolated from a handful of marmosets to all mammals everywhere: "Generalization to other mammals from one or a few examples of color change in marmosets is unwarranted," he wrote – and although he allowed that a handful of marmosets may have conformed to the pattern, “it does not follow unequivocally that other mammalian species or even other marmosets also exhibit the same or similar trends as Hershkovitz infers.”

Hershkovitz had little use for this criticism, and his rebuttal the following year brushed aside most of Lawlor’s pointed critiques as “hypothetical side issues.” Hershkovitz (1970) cited “errors of omission” for any confusion on the part of his readers, and insisted that “metachromism is a highly visible phenomenon, easily verified without aid of special equipment, or explanations in terms of mathematics, biochemistry, genetics, or ecology.” He went on to give a revised summary of the theory, in which each band of color on a hair “is an independently controlled chromogenetic field,” all of which somehow interacted according to “the presumed master control system” which determined color patterns on the scale of individuals, demes and geographic regions.

How this would operate without recourse to genetics is unclear, but he reiterated that the overall trend “is for all fields to ultimately resolve into a uniformly white coat.” Despite the “present ignorance of the mechanics of metachromic programming,” he insisted that the theory still had both descriptive and phylogenetic value, and could be used to reconstruct routes of dispersal. As for its trajectory, Hershkovitz brooked no compromise: “Irreversability of evolutionary processes is axiomatic and needs no further comment.”

Hershkovitz (1970) gave no further mention to rivers as barriers, and in neither paper did he cite Wallace’s work. In his rebuttal to Lawlor, he referred certain “tangential matters” from various critiques to his forthcoming monograph, which was a further seven years to come. When Volume 1 of *Living New World Monkeys* finally appeared, Hershkovitz devoted a short chapter to metachromism, peppered with passages from his 1968 and 1970 articles. Never one to modify his views on account of mere detractors, Hershkovitz (1977) reiterated his core theme: pelage coloration inevitably followed a progression towards a purely bleached white, and it was universal: "Metachromism applies to all species of mammals whether terrestrial, arboreal, subterranean, aquatic, or volant, and to all color changes in hair and skin whether ontogenetic, phylogenetic, geographical, seasonal, sexual, or individual."[19] Much of the chapter repeats what Hershkovitz (1968, 1970) had already presented, reiterating his views on the thirteen subspecies of *Saguinus fuscicollis*, the two species of Amazonian marmoset and the complex situation of the eastern Brazilian marmosets.[20]

As already noted, Hershkovitz (1977) spent little time on the theory of rivers as barriers; virtually all of what he presented had been published some years before. His taxonomic arrangement of the marmosets likewise had not changed; he recognized a single, complex species for the eastern Brazilian marmosets (*Callithrix jacchus*) and two species from the Amazon, *Callithrix argentata* and *C. humeralifer*. The only addition was a new subspecies of the latter, *C. h. intermedius*, which he considered "an offshoot of ancestral *humeralifer* stock," and which he characterized as "well-bleached." For Hershkovitz, the tale of the Amazonian marmosets was a simple one: two species, with

---

[19] The same passage appears, nearly word for word, in Hershkovitz (1968:558).

[20] Hershkovitz (1970) ventured into perilous territory when he listed a series of albinotic mammals – beluga whales, polar bears, white mice, white bats, white goats – and included "the blond norseman" among his company of "advanced examples of metachromism," which might well have been misunderstood. Hershkovitz (1977) reproduced and expanded this list, which now included "the blond Norsemen [and] the albinotic San Blas tribesmen of Panamá," now presented as exemplars of "dead-end white or whitish animals," which hardly seems to be an improvement.

three subspecies apiece, each in its well-defined position along the predestined, irreversible trajectory of metachromatic bleaching. His 1977 monograph is taken as the starting point for modern callitrichid taxonomy, and rightly so; but his views on the Amazonian marmosets had been essentially fixed many years earlier, and remained unchanged thereafter.

Discoveries and Assumptions

Prior to the 1990s, the taxonomy of the Amazonian marmosets had mainly involved well-established names for long-recognized forms, with the principal question being which of them merited species or subspecies status. The impact of Hershkovitz's monograph left an echoing silence for years afterward; according to Mittermeier and Coimbra-Filho (1981), "his papers should be considered the standard references on species and subspecies level taxonomy of New World monkeys." They differed with Hershkovitz primarily on the eastern Brazilian marmosets, preferring to recognize as five species what Hershkovitz considered one, but the taxonomy of the Amazonian species appeared to be settled. In their update near the end of the decade, Mittermeier *et al.* (1988) retained the arrangement which Hershkovitz had laid down for the Amazonian marmosets, but they included another form, *Callithrix emiliae*, originally described by Thomas (1920). Hershkovitz had dismissed this as a darker form of *Callithrix argentata argentata*, but Ávila-Pires (1986) recognized it as a subspecies, while de Vivo (1985) acknowledged it as a full species.

De Vivo's recognition came as a part of his dissertation research, acknowledged by Mittermeier *et al.* (1988) as de Vivo (1988); at the time, Mittermeier *et al.* noted that de Vivo had re-evaluated *Callithrix* but had yet to publish his results. In 1991, he produced a slim volume, "*Taxonomia de* Callithrix," in which he presented a craniometric analysis of all the known taxa of marmosets. Apart from this analysis, de Vivo's main contribution was to provoke a paradigm shift in marmoset taxonomy. Hershkovitz had never explicitly defined his species concept in his monograph – perhaps for him it was another self-evident axiom – but de Vivo did, choosing the phylogenetic species concept of Cracraft (1983), which considers the smallest diagnosable cluster of organisms to be a species (*sensu* Groves, 2001). As interpreted by de Vivo, this allowed the recognition of all terminal taxa as species; and so in his revision, there were seven marmoset species known from the Amazon: all six taxa recognized by Hershkovitz, plus the seventh, *Callithrix emiliae*. Thus at the start of the decade, de Vivo (1991) presented a rationale to consider all taxa as full species – and no sooner had he done so than a series of new discoveries put this concept into practice.

In early 1992, Ferrari and Lopes described *Callithrix nigriceps*, a black-faced, grey-furred marmoset from the vicinity of Humaitá in the Brazilian state of Amazonas. This region had been assumed to contain only a single marmoset species, *Callithrix emiliae*, which Ferrari and Lopes presumed was held apart from *C. nigriceps* by one of the tributaries of the Madeira.[21] Their new species, like both forms of *C. emiliae*, lacked

---

[21] Ferrari and Lopes (1992) referred to this form as *Callithrix emiliae*, following de Vivo (1985, 1991), who had aligned the marmosets he observed in Rondônia with the species which Oldfield Thomas (1920) had named for the collector Emilia Snethlage. Physically distinct and separated by hundreds of miles of rainforest, these two forms have since been recognized as discrete taxa (Rylands, 1993; Ferrari *et al.*,

the dramatic ear-tufts of *Callithrix humeralifer* and *Callithrix chrysoleuca*, and so they grouped it with the "bare-eared" species, which also included *C. melanura*, *C. argentata* and *C. leucippe*. Apart from this feature, and the new monkey's deeply melanistic face, the only characters they used to describe it were details of its pelage.[22]

At the time of its description, *Callithrix nigriceps* was known only from two localities across the Madeira from the town of Humaitá. Ferrari and Lopes (1992) presumed that a river, perhaps in conjunction with a nearby region of cerrado, "may constitute an effective barrier to the dispersal of callitrichids." Their estimate of the size of its distribution (10,000 km^2) was based on potential habitat between presumed river-barriers.

Later in 1992, Mittermeier *et al.* described *Callithrix mauesi*, a species with densely tufted ears which they allied with *C. humeralifer* and *C. chrysoleuca*. Mittermeier *et al.* (1992), like Ferrari and Lopes (1992), acknowledged de Vivo's (1991) revision of the marmosets and followed his lead, but did not dwell on species concepts nor cite Cracraft (1983). In addition to describing *C. mauesi*, Mittermeier *et al.* (1992) provided a brief review of *Callithrix* taxonomy, recognizing both *Callithrix nigriceps* and *Callithrix intermedia*, a subspecies described by Hershkovitz (on the basis of its "intermediate" pelage) and later recognized by de Vivo (1991).[23] Including their new

---

1999), and the Rondônian form has more recently been referred to as *Callithrix* aff. *emiliae* (e.g. Rylands, 1993; Van Roosmalen *et al.*, 2000). Ferrari *et al.* (in press), at long last, have rechristened this taxon as *Mico rondoni*.

[22] Ferrari and Lopes (1992) provided a series of gross body measurements, as well as a list of means for craniometric variables for the bare-eared marmosets, but performed no analyses thereon.

[23] Hershkovitz had described the subspecies as *Callithrix humeralifer intermedius*, but when de Vivo (1991) elevated it to full species, he noted that *Callithrix* is a feminine word and emended the species names to *Callithrix humeralifera* and *Callithrix intermedia*, which Mittermeier *et al.* (1992) noted and

species, Mittermeier *et al.* (1992) recognized a total of fourteen species of *Callithrix*, nine of which were Amazonian.

Like *Callithrix nigriceps*, the Maués marmoset was described entirely on the basis of ear-tufts and pelage differentiation, and like the black-faced marmoset, *C. mauesi* was known only from the type locality. Despite this, Mittermeier *et al.* (1992: 10) provided a map of the presumed distribution of the new species, based on the assumption that it would be bounded by two major rivers, the Rio Maués and the Rio Abacaxis, which converge just north of the type locality. Together these rivers neatly enclose a compact region which, judging from the map, is custom-made to contain a species in tidy isolation. (Given Mittermeier's position, then as now, as the chair of the IUCN/SSC Primate Specialist Group, the authors also took the opportunity to sketch out the numbers for primate diversity in Brazil.)

The following year, as part of an assessment of *Callithrix argentata*, Ronaldo Alperin described a new subspecies, *Callithrix argentata marcai*, based on three disheveled specimens in the Museu Nacional in Rio de Janeiro (Alperin, 1993). These specimens had been collected by Theodore Roosevelt in his expedition down the Rio da Dúvida (the River of Doubt, renamed the Rio Roosevelt in his honor) and had been referred to *Callithrix argentata melanura* by Allen (1916) in his tally of the expedition's collections. Alperin (1993) gave a very brief diagnosis of the new subspecies, based on

---

followed. In truth, *Callithrix* may be interpreted as *either* masculine or feminine, rendering the decision largely a matter of personal preference.

what he considered to be strong differences in its pelage from the other taxa in the bare-eared *argentata* group, all of which he treated as subspecies.[24]

Alperin's notion of the bare-eared marmosets, including *C. emiliae sensu* de Vivo, as far-flung subspecies of *C. argentata* was based on what he believed to be substantial gene flow between the "races," evidenced by individuals which showed intermediate characteristics. One of the few proponents of marmoset subspecies after Hershkovitz, Alperin believed that these geographic forms, although distinct in their coloration, were not entirely isolated from each other, owing to the "apparent absence of geographic barriers to isolate the taxa definitively."[25] Alperin's note was comparatively brief and contained no measurements.

During this same time several other marmoset species had been identified in the field, most of them by Marc van Roosmalen and his son Tomas. The exception was the Saterê marmoset, *Callithrix saterei*, another bare-eared species originally announced in 1996 and described by Silva Júnior and Noronha (1998). In a much more thorough and careful description than the previous three, the authors diagnosed their new species based not only on its strikingly different pelage, but on a unique feature of the genitalia: both males and females possess a long pair of fleshy lobes, pigmented orange with the rest of the anogenital skin, the function of which remains unknown. Although much of the description involves a meticulous description of skin and pelage coloration, this was

---

[24] Alperin (1993) also included the black-faced marmoset as *Callithrix argentata nigriceps*, the first author to do so. Rylands *et al*. (1993) did the same, but Van Roosmalen *et al*. (1998, 2000) and Rylands *et al*. (2000) again treated it as a full species, which subsequent authors have upheld.

[25] In the original: "Esta idéia é reforçada pela aparente inexistência de barreiras geográficas a isolarem os taxa de forma definitiva."

the first time such an accessory structure was described for a marmoset species, and it remains unique to *C. saterei* among the callitrichids and all platyrrhines.

In their description, Silva Júnior and Noronha presented craniometric data for the adults in the type series, represented by one male and two females. The male's larger values prompted them to suggest that the Saterê marmoset demonstrated some sexual dimorphism, although this has not been reported from other species of *Callithrix* (Hershkovitz, 1977; Aguiar, unpubl. data). They also presented a comparison of cranial measurements with the other bare-eared marmosets – a rapidly expanding clan, now including *C. argentata*, *C. leucippe*, *C. melanura*, *C. emiliae* (presumably from Rondônia) and *C. nigriceps* – and they noted that for many of these measurements, "*C. saterei* sp.n. also presented high values surpassing those of the majority of the other species." This, in their view, combined with its heavier weight, contributed to its greater "robusticity" compared to other Amazonian marmosets.

The authors, in what was becoming a marmoset tradition, presented a map with the type locality near the confluence of two major rivers, the Rio Abacaxis and the Rio Canumã, and its "presumed geographical distribution" shaded across all the territory which they enclosed. Unlike most of the previous descriptions, Silva Júnior and Noronha (1998) noted the potential of rivers as barriers, and then supported the theory with testimony from local hunters – in this case regarding the Rio Canumã, the hunters insisting that *Callithrix saterei* was found only to its east and *Callithrix chrysoleuca* only to the west.

As with the previous descriptions, Silva Júnior and Noronha (1998) kept a running tally of Amazonian marmosets, recognizing those described earlier as full species – with the curious omission of *Callithrix argentata marcai*, which they did not acknowledge in any form. In the description of yet another marmoset species, however, dated only a week after the publication of *Callithrix saterei*, Van Roosmalen *et al.* (1998) recognized "*C. marcai* Alperin, 1993" alongside the other marmoset species, old and new, and included *Callithrix marcai* in several tallies of primate diversity without further comment.

Van Roosmalen *et al.* (1998) were describing "a new and distinctive species of marmoset," originally named *Callithrix humilis*, but soon re-evaluated as *Callibella humilis* by Van Roosmalen and Van Roosmalen (2003)[26]. Immediately recognized as unique among all callitrichids, the dwarf marmoset had other features to distinguish it besides simple patterns of pelage. Chief among these was its exceptionally small size, between *Cebuella* and the conventional *Callithrix*; this alone separated it from either existing genus, although the authors initially described it as a *Callithrix*, "a conservative stance," given its peculiar intermediate form.

In addition to its size and pelage, the authors also presented a list of behavioral comparisons between *Callithrix*, *Cebuella* and the new marmoset; these were not included in the strict diagnosis, but this marked the first time that behavioral features

---

[26] This reassignment to generic status was upheld by Aguiar and Lacher (2003, 2005, 2009) and Ford and Davis (2005, 2009) and has since been generally accepted (e.g. dos Reis *et al*., 2008; Rylands and Mittermeier, 2009; Rylands *et al*., 2009).

were considered in the description of a new marmoset species.[27] The authors also gave detailed information on its habitat, another departure from the previous descriptions, which generally limited themselves to one-line comments on secondary forest. Likewise the authors provided a more detailed map of distributions, based on a series of field surveys conducted the year before. (A full account of the discovery is presented in Chapter III.) Rather than simply presuming a distribution, the authors made a series of sightings along the west bank of the Rio Aripuanã and limited their comments to that region alone.

The final two marmosets of the decade, described by Van Roosmalen *et al.* (2000), first came to the attention of the van Roosmalens in 1996, as they searched the region surrounding the Rio Aripuanã for populations of the dwarf marmoset. From the river-town of Manicoré, the van Roosmalens acquired two captive marmosets which became the type series for *Callithrix manicorensis*, although it is not clear whether these individuals had been captured in the immediate vicinity or if they had been transported some distance before.[28] As Manicoré sits in the interfluvium between the Rios Manicoré and Aripuanã, Van Roosmalen *et al.* (2000) took this entire area to be its range, and in classic form they presented a map of the type locality with the range shaded for at least 250 km further south. (More details on the assumptions concerning *C. manicorensis* are

---

[27] Several of these features, in particular the lack of scent-marking or other territorial behavior, would be exceptional for a callitrichid and still require a more rigorous verification from the field.

[28] Keeping monkeys as pets, often in wretched conditions, is common throughout the region, and people will trade them or carry their pets with them as they travel. In one home in Manicoré, I found a red-chested tamarin (*Saguinus labiatus thomasi*), which is native to a swathe of forest northwest of the Rio Madeira. Manicoré is on the southeastern bank of the Madeira, so the current home of a captive monkey may say very little about its origins.

presented in Chapter III.) This region, it should be noted, also contains the putative type locality for *C. marcai*, which has yet to be located in the wild.

As with most of the other new species, Van Roosmalen *et al.* (2000) diagnosed *Callithrix manicorensis* entirely on the basis of its fur and facial pigmentation, and they followed this pattern for their other new marmoset, *Callithrix acariensis*. The holotype, and thus far the sole extant specimen, was a juvenile female kept as a pet in the interfluvium of the Rios Acarí and Sucundurí. Although the authors observed several groups of *C. manicorensis* in the vicinity of Manicoré, they were unable to locate wild groups of *C. acariensis* in the region where they found their captive. Nonetheless, they presented the Acarí-Sucundurí interfluvium as the distribution of the species, based on a single specimen of uncertain provenance. Its one other distinguishing feature was its hypertrophied genitalia, although they did not possess the same ancillary lobes as *C. saterei*.

Van Roosmalen *et al*. (2000) also presented cranial measurements for the holotype of each species, but gave no comparisons with other taxa. They did, however, provide a new type of analysis for a marmoset description: a preliminary phylogeny based on nuclear and mitochondrial DNA, in which *C. manicorensis* grouped most closely with *C. argentata*, and *C. acariensis* joined with *C. humeralifer* and *C. mauesi*. The authors presented a number of scenarios of possible dispersal and radiation, and for the first time included a discussion of Wallace and river-barriers, contrasting what they believed to be the more strongly separated marmoset species with the less discrete tamarins. An excellent schematic summarized the thinking for the Amazonian marmosets (Fig. 19).

In their taxonomic summary of recent discoveries, Van Roosmalen *et al.* (2000) acknowledged all the forms described to date, for a tally of fourteen Amazonian *Callithrix* and six more from the Atlantic Forest, in addition to *Cebuella pygmaea* and the dwarf marmoset *C. humilis*, which was shortly to be renamed *Callibella*. Rylands *et al*. (2000), writing only a few months afterward, acknowledged the same tally of Amazonian species, but reallocated them to the genus *Mico*, on account of recent molecular research suggesting that *Cebuella*, the monotypic pygmy marmoset, was more closely related to the Amazonian marmosets. Groves (2001), appearing shortly thereafter, had not been able to include the comments of Rylands *et al*. (2000) nor the most recent discoveries, and thus omitted *Callithrix saterei*, *C. manicorensis* and *C. acariensis*. The remaining taxa he considered to be full species (albeit of the subgenus *Mico* within *Callithrix*), but his diagnoses were based almost entirely on an overview of their pelage.

Subsequent assessments have universally retained the Amazonian marmosets as full species; the section on primates in Wilson and Reeder (2005) was written by Colin Groves and follows his 2001 arrangement, with the addition of *Callithrix saterei*, *C.*

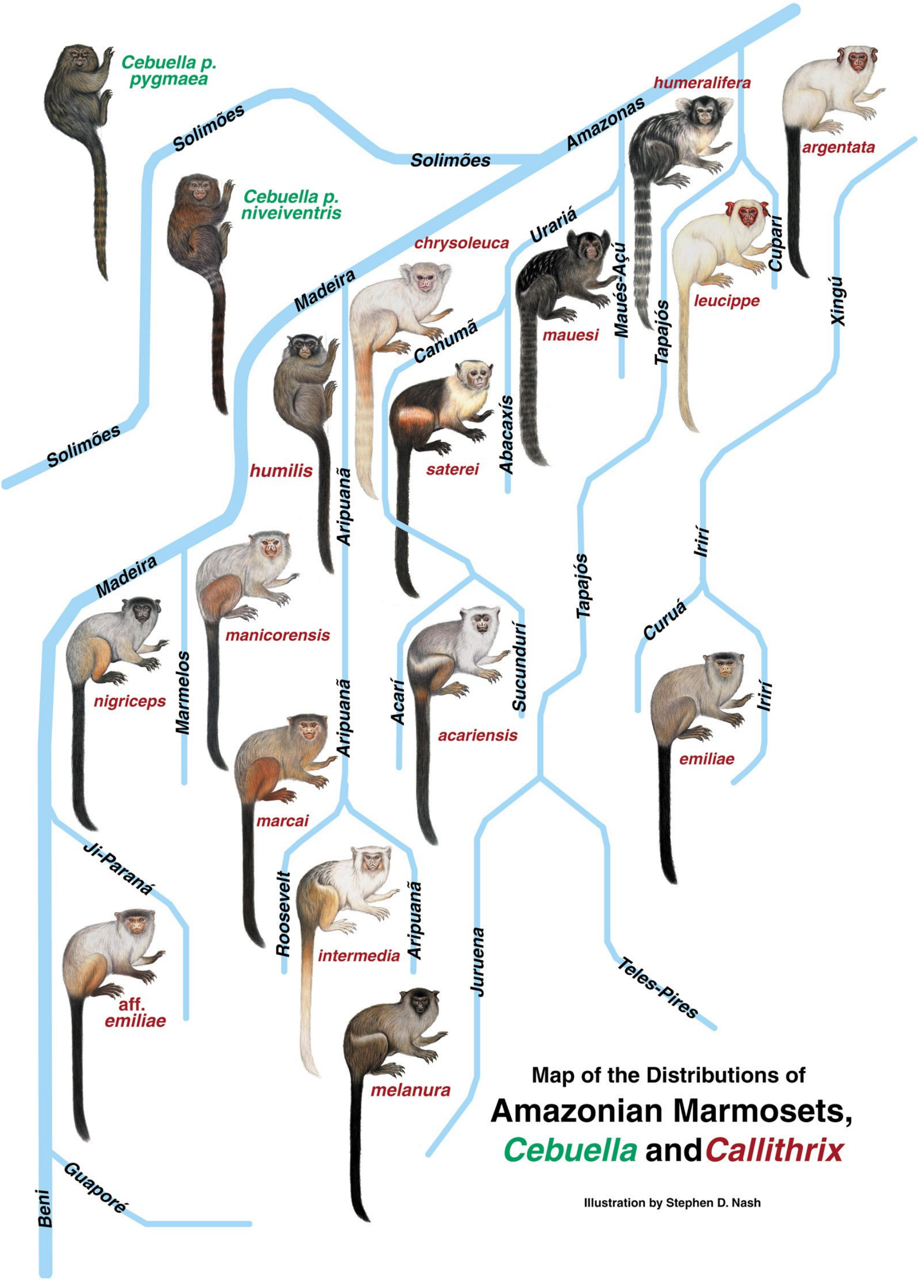

Figure 19. The Amazonian species of *Callithrix*, together with *Callibella* and *Cebuella*, in a schematic illustrating their presumed separation by major rivers of the Amazon basin. Artwork by Stephen J. Nash and used by permission.

acariensis and *C. manicorensis*. The most recent reviews of callitrichid taxonomy (dos Reis *et al*., 2006; dos Reis *et al*., 2008; Rylands and Mittermeier, 2009; Rylands *et al*., 2009) continue to recognize the full list of species presented in Van Roosmalen *et al*. (2000), with *C*. aff. *emiliae* treated as a separate, as-yet-unnamed species. These reviews tend to focus on very recent publications, and make little mention of biogeography or species theory. Stephen Ferrari (2008), writing in dos Reis *et al*. (2008), claims that the Amazonian marmosets "may be divided into two morphological groups, based on the presence (humeralifer group) or absence (argentatus group) of auricular tufts, and the presence or absence, respectively, of rings on the tail," despite the fact that neither molecular nor morphological evidence supports these groupings (e.g. Barros *et al*., 1996; Sena, 1998; Sena *et al*., 2002; Aguiar, unpubl. data)[29]. Much of the taxonomic thinking regarding these species, then, remains based on essentially the same characters which Hershkovitz used over forty years ago.

Methods

Given the scant attention paid to morphological variables in determining species status among the Amazonian marmosets, I performed an analysis of standard craniometric variables by taxa and by river basins, in order to determine if there are significant cranial distinctions between taxa separated by rivers. I examined specimens representing all fourteen described species of Amazonian marmosets, drawn from

---

[29] Writing in Portuguese, his original sentence runs as follows: "As espécies podem ser divididas em dois grupos morfológicos, baseado na presença (grupo humeralifer) ou ausência (grupo argentatus) de tufos de pêlo auriculares, e a presença ou ausência, respectivamente, de anelação na cauda, semelante àquela observada no gênero *Callithrix*." The final phrase says that the same is seen in the eastern Brazilian marmosets, which he considers as a separate genus.

collections made throughout the twentieth century. Many of the series now held at separate institutions were collected together in the field and then dispersed. A large number are held in natural history collections in the United States, including the American Museum of Natural History in New York, New York; the Field Museum of Natural History in Chicago, Illinois; the National Museum of Natural History in Washington, D.C.; the Los Angeles County Museum in Los Angeles, California; and the Harvard Museum of Comparative Zoology in Cambridge, Massachusetts. Some of the best series are kept in Brazil, at the Museu Nacional de Rio de Janeiro; the Museu de Zoologia da Universidade de São Paulo; the Museu Paraense Emílio Goeldi in Belém; and the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus. Additional specimens were examined in the care of the Naturhistoriska Riksmuseet in Stockholm, Sweden; the Humboldt Museum für Naturkunde in Berlin, Germany; the Naturalis/Nationaal Natuurhistorisch Museum in Leiden, the Netherlands; the Museum National de Histoire Naturelle in Paris, France; and the British Museum (Natural History) in London, England (see Appendix 2). Almost all specimens included in these analyses were wild-sourced, either shot by professional collectors or taken as part of a type series; the exceptions are *Callithrix acariensis* and *C. manicorensis*, the types of which were collected alive by the van Roosmalens and kept in captivity until they died.

I measured all specimens to the nearest 0.01 mm with Mitutoyo Digimatic digital calipers, series/model 500-196. I chose a total of 32 standardized characters to measure from each specimen (Table 7), although the actual number of data points often varied

Table 7. Cranial and mandibular variables measured for river-barrier analyses.

CL	cranial length	prosthion to rearmost point of cranium
OCP	occipital condyle-prosthion	rear of left occipital condyle to prosthion
ZAZ	zygomatics at zygions	width of zygomatic arches at zygions
SKW	skull width	maximum skull width, at temporal ridges
OWC	orbital width at cyclosions	maximum orbital width at cyclosions
BL	bregma-lambda	distance from tripoint bregma to tripoint lambda
CONW	condylar width	distance across base of occipital condyles
MW	molar width	maximum width of upper molars, M1L-M1R
CW	canine width	maximum width of upper canines, C1L-C1R
MSL-L	molar series length, left	length of left upper molar/premolar row
MSL-R	molar series length, right	length of right upper molar/premolar row
BN	bregma-nasion	distance from tripoint bregma to tripoint nasion
PBG	prosthion-bregma	distance from prosthion to tripoint bregma
NP	nasion-prosthion	distance from prosthion to tripoint nasion
NL	nasion-lambda	distance from tripoint nasion to tripoint lambda
PL	prosthion-lambda	distance from prosthion to tripoint lambda
MWJ	molar width, jaw	maximum width of lower molars, M2L-M2R
CWJ	canine width, jaw	maximum width of lower canines, C1L-C1R
MSLJ-L	molar series length, jaw, left	length of left lower molar/premolar row
MSLJ-R	molar series length, jaw, right	length of right lower molar/premolar row
SGL-L	symphysion-gonion, left	distance from symphysion to rearmost left gonial point
SGL-R	symphysion-gonion, right	distance from symphysion to rearmost right gonial point
CJB-L	condylion-jaw base, left	height from condylar knob to base of left jaw flange
CJB-R	condylion-jaw base, right	height from condylar knob to base of right jaw flange
COR-L	coronion-jaw base, left	height from coronion tip to base of left jaw flange
COR-R	coronion-jaw base, right	height from coronion tip to base of right jaw flange
SCN-L	symphysion-condylion, left	distance from symphysion to rearmost left condylion
SCOR-L	symphysion-coronion, left	distance from symphysion to left coronial tip
SCN-R	symphysion-condylion, right	distance from symphysion to rearmost right condylion
SCOR-L	symphysion-coronion, right	distance from symphysion to right coronial tip
JWCR	jaw width, coronia	maximum width between outer coronial tips
JWCY	jaw width, condylia	maximum width between outer condylar knobs

with damage, since I did not take partial measurements on damaged features. In order to avoid the complications of ontogenetic change, I only examined adult specimens; my criteria for determining adulthood were fully fused cranial sutures and completely descended upper canines, together with sharply defined superior temporal ridges.

To assemble the dataset for analysis, I made a case-by-case assessment of the degree of damage. I removed all variables with less than 80% of all cases intact. Once I removed all variables which were disqualified for excessive damage, I winnowed the dataset for cases in other categories which I considered to be problematic; these included cases with vague or undocumented localities, cases which were juveniles or subadults[30], and any other specimens which seemed questionable. Once I had my final tally of cases, I prepared the dataset by removing extraneous information (museum codes, names of collectors, body measurements and other notes) and added codes for gender, for species and for basins. Since many of the remaining specimens still had missing measurements due to damage, I converted the damage descriptors to a numerical code which could be read by the imputation software.[31]

Once the base dataset was ready, I divided it into separate datasheets for each species, and prepared them individually for data imputation in SOLAS for missing data analysis (SOLAS v. 3.2). I ran multiple imputation procedures on each species, and afterwards re-saved each individually imputed species file to SPSS format, and then log-

---

[30] Although most juvenile specimens could be sorted out on the trays before measuring, there was a learning curve on my part when going through the collections, and afterwards I realized that some of the specimens I had originally been uncertain about were undeniably subadult.

[31] When I was measuring and describing specimens in the collections, I made notes on the type and extent of damage for each variable. These ranged from “broken” and “missing,” for the more common types of damage, to “sawn,” “sprung” or “soaked” for more unusual forms of abuse.

transformed the data to log-natural format. Once this was done for all the individual species datasets, I recombined them into a single fourteen-species datasheet for further analysis. Even with imputation, I could not resolve the missing values for several species with small sample sizes, which prohibited the use of the imputation procedure.

I chose to analyze the log-transformed variables with a multiple analysis of variance (MANOVA) to search for any significant differences between any of the twenty-eight potential species pairs.[32] All variables were subjected to post-hoc multiple comparisons using both Tukey's HSD and Tamhane's for unequal variances. Once I detected significant differences with the overall MANOVA, I examined the trends and driving variables with a discriminant analysis. To explore the potential effects of rivers in more detail, I divided the overall range of the Amazonian marmosets into four major basins, as defined by major tributaries of the Amazon (Fig. 20), and analyzed the species with two approaches. In order to include cases from as many species as possible, I merged the species within each basin, treating them as a basin-wide population, and then compared the four merged populations with MANOVA and discriminant analysis. I also selected one well-represented species from each of the basins (a "proxy" for the basin at large) and repeated the MANOVA and discriminant analysis to determine if certain species might be driving the merged-basin analysis.

I analyzed the data using the General Linear Model and Discriminant Analysis modules of SPSS 15.0 (SPSS, Inc., 2007). For my analyses, I used measurements for the

---

[32] *Callithrix acariensis* and *C. emiliae* (*sensu* Oldfield Thomas, 1920) are only represented by a single specimen apiece – the type specimen, in both cases – and could not be included in these analyses, as a sample of 1 has no variance.

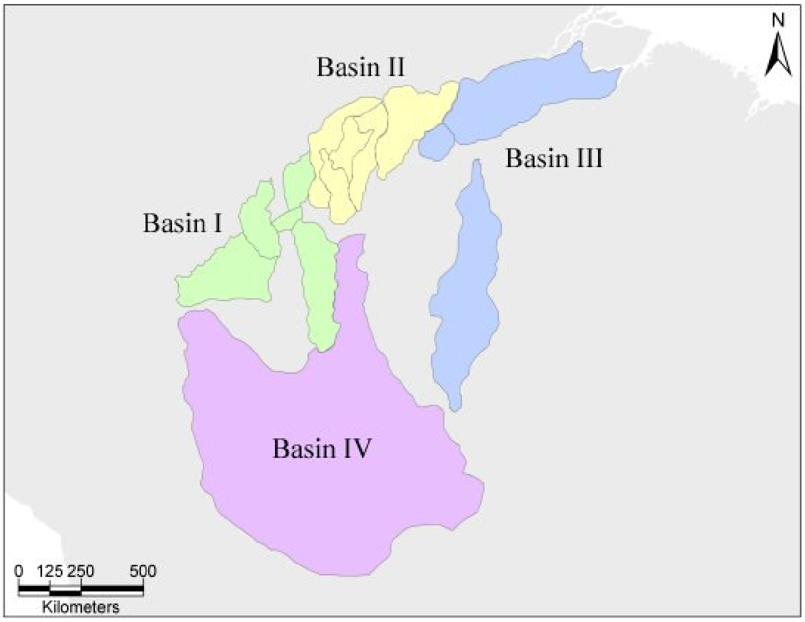

Figure 20. The Amazonian species of *Callithrix* grouped by major river-basins. Basin I extends from the Rio Madeira to the Rio Aripuanã, and includes the species *rondoni, nigriceps, marcai, intermedia,* and *manicorensis*. Basin II extends from the Rio Aripuanã to the Rio Tapajós, and includes *chrysoleuca, acariensis, mauesi, saterei* and *humeralifer*. Basin III extends from the Rio Tapajós to the Rio Tocantins, and includes *leucippe, emiliae* and *argentata*. Basin IV extends from the Río Mamoré to the Rio Guaporé, and includes only *melanura*. Map by Krista Adamek, Department of Wildlife and Fisheries Sciences.

following variables: CL, OCP, SKW, OWC, BL, CONW, BN, PBG, NP, NL, PL, SGL-L, SGL-R, CJB-L, CJB-R, SCN-L, SCN-R and JWCY (Table 7). I used direct entry of all variables. The classification procedure used the same cases, and the classification plots show the same cases as were used when deriving the discriminant functions.

Results

For each analysis, I first ran a MANOVA to detect any significant differences in morphological variables, and then a discriminant analysis to explore any resulting trends. For each analysis, the results of the MANOVA are considered first, followed by the discriminant analysis, in the following sequence:

- All-Species Comparisons
    - All-Species MANOVA
    - All-Species Discriminant Analysis
- Four-Species Basin Proxy Comparisons
    - Four-Species Basin Proxy MANOVA
    - Four-Species Basin Proxy Discriminant Analysis
- Four-Basin Merged Comparisons
    - Four-Basin Merged MANOVA
    - Four-Basin Merged Discriminant Analysis

All-Species Comparisons: All-Species MANOVA

Of the fourteen Amazonian marmoset species, only eight are well-enough represented in museum collections to support a MANOVA procedure. Among these eight species, there are twenty-eight potential species-to-species comparisons. Among these twenty-eight potential species dyads, fifteen species pairs returned significant differences on at least one variable. Of those species pairs, *Callithrix chrysoleuca* and *C. argentata* had the greatest number of differences; virtually every variable returned a significant difference, including CL, SKW, OCP, OWC, BL, BN, NP, PL, SGLL, SGLR, CJBL, CJBR, SCNL, SCNR and JWCY (Appendix I, Table 4).

Callithrix argentata was almost as strongly differentiated from *Callithrix melanura*, with 12 variables returning as significantly different: CL, OCP, OWC, BL, CONW, BN, PBG, NL, PL, SGLL, SGLR and CJBL. Also showing a strong separation were *C. chrysoleuca* and *C. humeralifer*, with ten variables distinct: OCP, SKW, OWC, SGLL, SGLR, CJBL, CJBR, SCNL, SCNR and JWCY. Several other species pairs showed a more moderate separation: *C. humeralifer* and *C. argentata* were set apart by eight variables (CL, OCP, OWC, BN, PL, SGLL, SGLR, SCNL), as were *C. melanura* and *C. chrysoleuca* (OWC, PBG, NP, SGLL, SGLR, SCNL, SCNR, JWCY). *Callithrix chrysoleuca* was also strongly separated from *C. rondoni* and *C. leucippe* by seven variables apiece (OCP, OWC, PL, SGLL, SGLR, SCNL, SCNR and OCP, OWC, SGLL, SGLR, SCNL, SCNR, JWCY, respectively), while *C. melanura* and *C. humeralifer* were distinguished by six variables (BL, CONW, PBG, NL, CJBL and CJBR).

Other species pairs showed weaker distinctions, such as *C. leucippe* vs. *C. argentata* and *C. saterei* vs. *C. argentata*, with four variables distinct for each (SKW, BL, BN, SCNL and OWC, SGLR, SCNL, JWCY, respectively). Several other pairings were distinguished by only two variables (*C. humeralifer* vs. *C. leucippe*, *C. melanura* vs. *C. saterei*) or only by a single significant difference (*nigriceps* vs. *argentata*, *saterei* vs. *leucippe*, and *rondoni* vs. *argentata*). Among the species showing significant differences, *C. argentata* differed more often in cranial than mandibular characters, while *C. chrysoleuca* was more often set apart by mandibular features.

Each of the eight species used in this analysis had the possibility for significant differences with as many as seven other species. All eight species had at least one significant difference with one other species, although the pattern varied widely. Based on the number of significantly different species-pairs, *Callithrix argentata* was the most distinctive overall, returning significant differences with each of the other seven species. *C. chrysoleuca* was nearly as well-defined, differing from five of seven species. *C. melanura*, *C. leucippe* and *C. humeralifer* each differed from four other species; *C. saterei* resolved as distinct from three others, while *C. rondoni* was distinguished from just two other species and *C. nigriceps* from only one.

As important as those species pairs which returned significant differences were those which did not. *C. melanura*, *C. rondoni* and *C. nigriceps* showed no significant differences among themselves; these are the three westernmost species in the Brazilian Amazon. Likewise *C. chrysoleuca* and *C. saterei* returned no differences between each other; they are allopatric in the midst of the overall species group. *C. nigriceps* returned only a single distinct variable (OWC) with one other species (*C. argentata*), and was otherwise indistinguishable from all other species.

All-Species Discriminant Analysis

In the discriminant analysis for all Amazonian marmosets (less those species with inadequate samples) a complex situation emerges. In the all-species analysis, Function 1 accounted for 46.6% of the variance, with the strongest negative loading on CL at -0.940, followed by OWC at -0.606 (Appendix I, Tables 5 and 7). The strongest positive loadings were for BN at 0.663 and SCNR at 0.624. In the plot for this analysis (Fig. 21), *C. melanura* plots only moderately negative on Function 1; the species trending most strongly negative are *C. chrysoleuca* and *C. saterei*, suggesting a greater overall skull length for the latter pair. *C. argentata* again plots the most strongly positive along the axis of Function 1, together with *C. leucippe*, suggesting these two species present the smallest overall skull length among the group as a whole. These results correspond to those in the four-species analysis – and again, in a curious anomaly, *C. rondoni* plots closer to these two easternmost species than to any of its allopatric congeners in the west. The strong positive loading for BN, the bregma-to-nasion length, suggests that *C. argentata* and *C. leucippe* present a subtly higher forehead or a slightly smaller facial complex.

Function 2 accounted for 27.2% of the remaining variance; the greatest negative loading was -1.030 for NL, the nasion-to-lambda length, followed by -0.701 for SGLR, while SCNR and SCNL represented the greatest positive loadings, at 0.929 and 0.895 respectively (Appendix I, Tables 5 and 7). *C. melanura* plots overwhelmingly negative on this axis, strongly suggesting that this species has the greatest nasion-to-lambda length of all the Amazonian marmosets. The *chrysoleuca-saterei* pair plots strongly

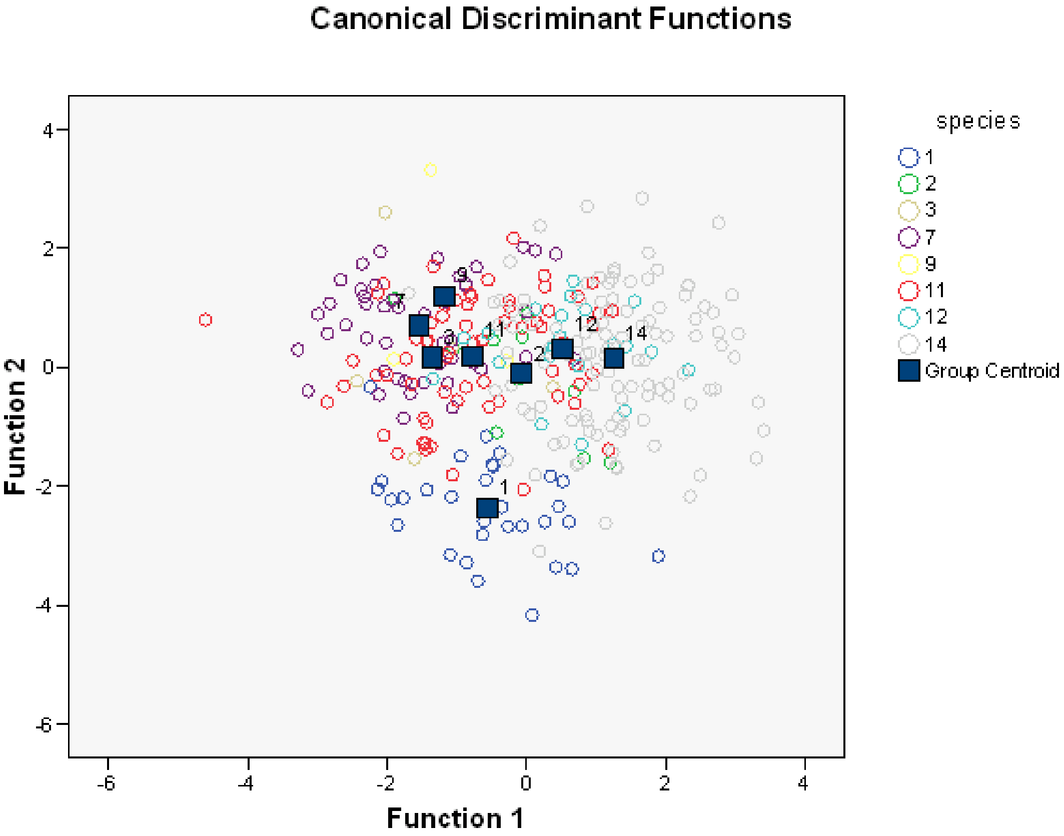

Figure 21. Discriminant analysis of all species in river-barrier analysis. 1 = *melanura*, 2 = *rondoni*, 3 = *nigriceps*, 7 = *chrysoleuca*, 9 = *saterei*, 11 = *humeralifer*, 12 = *leucippe* and 14 = *argentata*

positive, driven by a greater length in the symmetrical SCNL/SCNR variables, while *argentata-leucippe* and the remaining species are intermediate. Function 3 adds another 12.7% of total variance, with SGLL the strongest negative at -1.160, followed by CL at -0.743; the strongest positive is SCNL at 0.695 (Appendix I, Tables 5 and 7). The loadings on this axis show another peculiar asymmetry in SGLL and SGLR, loading at -1.160 and 0.523 respectively, despite their being mirrored measurements on the lower jaw.

These results show three strong groupings of species. *C. chrysoleuca* and *C. saterei* plot as a unit to one side, distinguished by the greater overall length of their lower jaw; *C. argentata* and *C. leucippe*, loosely joined by *C. rondoni*, are distinguished by their smaller overall skull lengths and smaller cyclosial width, and perhaps by a higher forehead, as evinced by the greater bregma-to-nasion length. *C. melanura* is overwhelmingly distinct in a space of its own, driven by a much greater nasion-to-lambda length, while *C. humeralifer* and *C. nigriceps* are only mildly negative on Function 1 and blandly intermediate on Function 2.

Taken together, the results of these two discriminant analyses suggest an eastern node (*C. argentata* and *C. leucippe*), with relatively smaller faces and absolutely smaller skulls; a central node (*C. chrysoleuca* and *C. saterei*) with larger skulls and longer lower jaws; and *C. melanura* as a node of its own, slightly larger than intermediate in skull length but overwhelmingly larger in its nasion-to-lambda length.

Four-Species Basin Proxy MANOVA

Because some species are only represented by very small samples – in some cases, only the type series – I apportioned the total distribution of the Amazonian marmosets into four major basins, and chose one species with adequate sample size as a representative for each of these basins (see Fig. 20). I chose *Callithrix rondoni* as a representative for Basin I, *C. humeralifer* for Basin II, *C. argentata* for Basin III, and *C. melanura* for Basin IV.

In this analysis the MANOVA detected significant differences between species for the majority of variables (Appendix I, Table 11), although the number of variables separating species pairs varied tremendously – from virtually all variables between *Callithrix melanura* and *C. argentata* to only a single significant variable between *C. melanura* and *C. rondoni*, and between *C. rondoni* and *C. argentata*. *Callithrix melanura* and *C. argentata*, separated by hundreds of miles of lowland rainforest, proved to be distinct on the greatest number of variables: CL, OCP, OWC, BL, CONW, BN, PBG, NL, PL, SGLL, SGLR, CJBL and CJBR, comprising nearly every analyzed variable of the mandible and skull.

C. humeralifer and *C. argentata* were separated by a smaller number of variables – CL, OCP, OWC, BN, PL, SGLL, SGLR, SCNL and JWCY – representing a nearly even split between cranial and mandibular characters, while *C. melanura* and *C. humeralifer* were separated by a slightly smaller subset (BL, CONW, PBG, NL, CJBL, CJBR), which included more cranial than mandibular features. *Callithrix rondoni*, oddly enough, was set apart from *C. melanura* and *C. argentata* by only a single variable apiece, CONW and JWCY respectively – the former a cranial measurement and the latter mandibular. Only *C. rondoni* and *C. humeralifer* showed no significant differences, likely owing to the comparatively indistinct morphology of the former, and only three variables (SKW, NP and SCNR) returned no significant differences between any species pair.

Four-Species Basin Proxy Discriminant Analysis

I chose one species as a representative from each of the four major interfluves, selecting *Callithrix melanura*, *C. rondoni*, *C. humeralifer* and *C. argentata* for their large sample sizes. In the discriminant analysis comparing these four species, Function 1 accounted for 56% of the total variance (Appendix I, Table 12). The greatest positive loading, 1.225, registered for the variable SCNR; the variable CL had the greatest negative loading at -1.322 (Appendix I, Table 14). On the axis of Function 1, the centroid for *C. melanura* is strongly negative, indicating that *melanura* is distinguished by the largest value of CL among these four species (Fig. 22). *C. argentata* plots the most strongly positive on this axis, demonstrating the largest values for SCNR.

On Function 2, which accounted for 35.3% of the total variance, the variable PL had the greatest negative loading (-1.124) and NL had the highest positive score (1.281) (Appendix I, Tables 12 and 14). *C. melanura* plotted strongly positive on this axis, indicating a greater nasion-to-lambda length, while *C. humeralifer* shows the strongest negative trend for Function 2, apparently driven by a greater distance from prosthion to lambda. Function 3 accounted for only 8.7% of the total variance, but was marked by

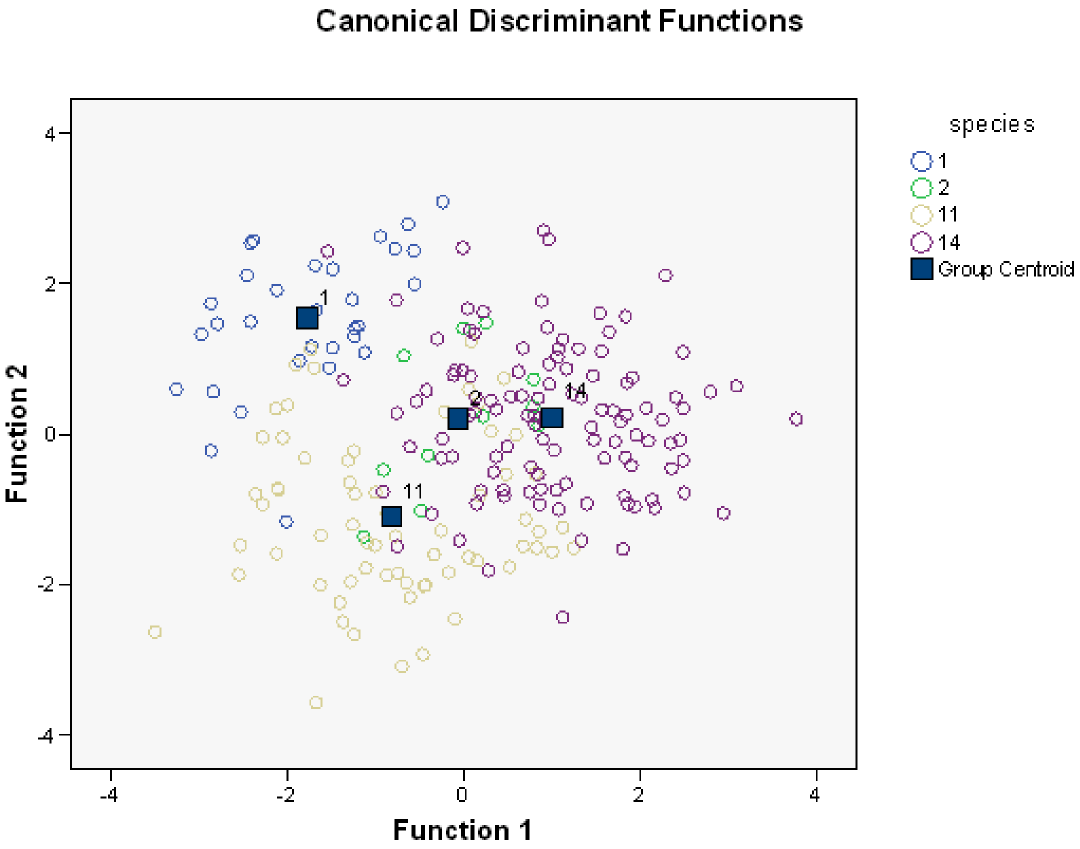

Figure 22. Discriminant analysis of representative species for river-barrier analysis. 1 = *melanura*, 2 = *rondoni*, 11 = *humeralifer* and 14 = *argentata*.

several exceptionally strong loadings: PL scored at 3.726 and CL at -2.810, while SCNL and SCNR – symmetrical measurements of mandible length – showed strongly divergent scores of 1.234 and -1.465 respectively (Appendix I, Tables 12 and 14).

In this analysis, *C. melanura* is distinguished by greater overall skull length and a relatively larger symphysion-to-gonion length in the lower jaw (SGL), while *C. argentata* presents with the smallest overall values on those dimensions. *C. melanura* also presents with the largest nasion-to-lambda length (NL), *C. humeralifer* the greatest prosthion-to-lambda distance, and *C. argentata* midway between the two for both features. *C. rondoni* trends more positively in Function 1 than *melanura*, suggesting an smaller overall size of the skull, but shows almost complete overlap on Function 2, suggesting that like *C. argentata*, the Rondônian marmoset is also intermediate between *melanura* and *humeralifer*. In this, and in its smaller overall length, *C. rondoni* is more similar in cranial and mandibular morphology to *C. argentata* – a surprising anomaly given its separation from *C. argentata* by hundreds of miles and half a dozen substantial rivers.

Four-Basin Merged MANOVA

The MANOVA detected significant differences between basins for virtually every variable, although the basins varied widely in the number of features which set them apart. Basins 2 and 3 differed on the greatest number of variables: CL, OCP, SKW, OWC, BN, NP, PL, SGLL, SGLR, CJBL, SCNL, SCNR and JWCY were all distinct between these two species groups (Appendix I, Table 18). Basins 3 and 4 were set apart by some of the same variables (CL, OCP, OWC, BL, CONW, BN, PBG, NL, PL, SGLL, SGLR and CJBL), while Basins 2 and 4 were differentiated by a smaller subset of features (OWC, BL, CONW, PBG, NP, NL, SCNL, SCNR and JWCY). Basins 1 and 3 were only set apart by a handful of variables (OWC, BL, BN, SGLL, SGLR and JWCY), while Basins 1 and 4, unexpectedly, differed only by the single variable CONW, which was also significant for the 2 vs. 4 and 3 vs. 4 basin-pairs.

The merged basins show a pattern of separation which echoes that of the species-proxy comparisons. The strong separation of Basins 2 and 3 may well reflect the differences between *Callithrix chrysoleuca* and *C. argentata*, combined with the lesser differentiation between *C. humeralifer* (also in Basin 2) and *C. argentata*. Basins 3 vs. 4 represent *C. argentata* and *C. leucippe* in opposition to *C. melanura*, and reflect the geographical distance between these two groups. The absence of any strong differentiation of Basin 1 from the other basins may be caused, in part, by the strong effects of *C. rondoni*, which the previous analyses have shown is only faintly distinct from other taxa in the variables considered.

Four-Basin Merged Discriminant Analysis

In this analysis, Factor 1 accounted for 59% of the variance between basins (Appendix I, Table 19). The greatest function loading was –1.272 for the variable CL, followed by –0.609 for OWC on the negative axis (Appendix I, Table 21). The greatest positive loading was 0.854 for NB, closely followed by 0.805 for SCNR. On Function 2, which accounted for another 36.7% of the total variance, the greatest loading was –

1.124 for NL; the next largest negative loading was –0.849 for SGLR (Appendix I, Tables 19 and 21). The two greatest positive loadings on Function 2 were 0.897 for SCNR and 0.784 for SCNL. Together these two functions accounted for over 95% of the total variance, and the third function – essentially statistical noise – is not considered here.

The plot of this discriminant analysis (Fig. 23) shows broad overlap between the first three basins, but they do group into recognizable regions: Basins 2 and 3 show a strong segregation within the overall cloud, with the centroid of Basin 2 trending strongly negative on the axis of Function 1. This suggests that the species in Basin 2 have the greatest overall skull length, while the species in Basin 3 would have the smallest skull length. Basin 4, the stand-alone *Callithrix melanura*, shows only a moderate negative trend on Function 1, but a profoundly negative alignment on Function 2. This is driven by NL, the nasion-to-lambda length, which is a slightly different measurement from overall skull length. Basins 1 and 3 are virtually neutral on the y-axis, and Basin 2 is only slightly positive; the positive loading here is driven by the mirrored measurements of SCNL and SCNR, bellwethers of jaw length, suggesting that the species of Basin 2 have the longest jaws of the species analyzed.

Basin 1, comprised of small-sample species, shows total overlap with the other basins on Function 1, and its cases are scattered widely throughout the cloud. The exception lies in the negative reaches of Function 2, where the bases of Basin 1 form a "snow line" which touches, but does not cross over, the northern borders of Basin 4, which is *Callithrix melanura*. (A single outlier of *C. melanura* rests at the midline of

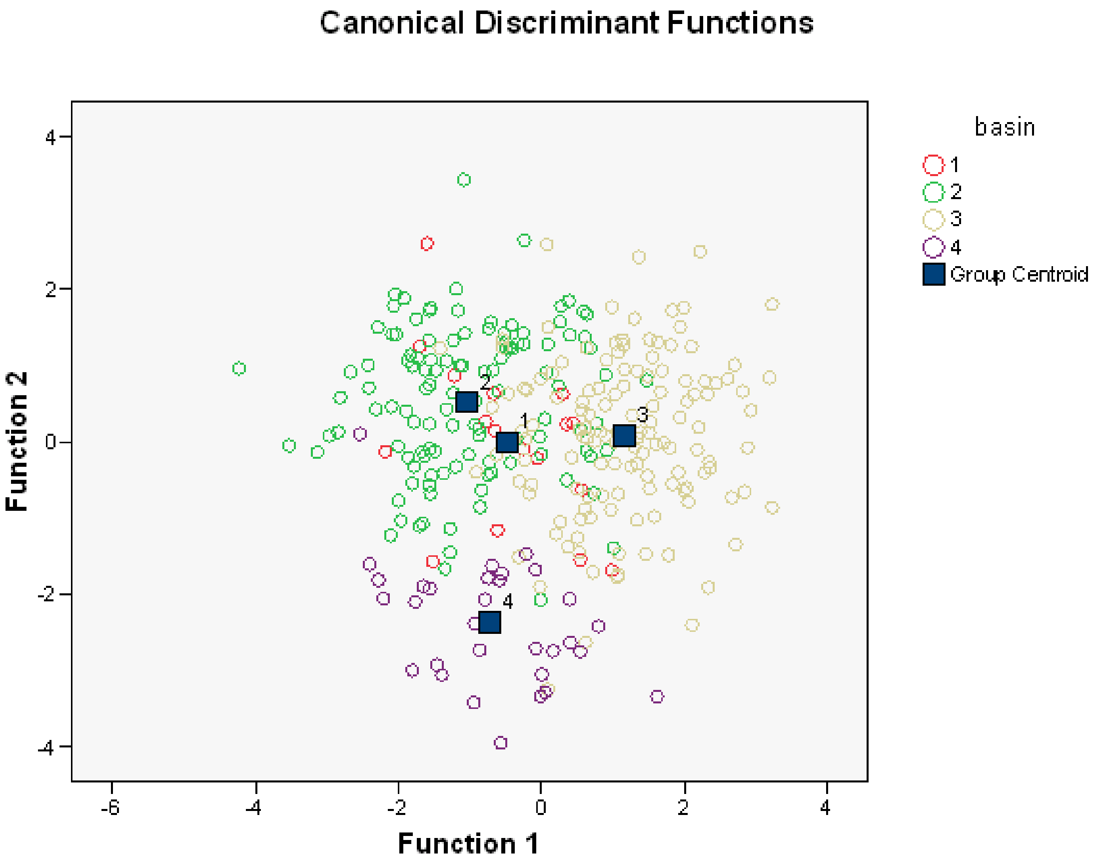

Figure 23. Discriminant analysis of all species merged into basins for river-barrier analysis. For definitions of the basins and their constituent species, please see Fig. 20.

Function 2, but none of the cases from Basin 1 extend below the upper margin of the main *melanura* cloud.) The relatively undifferentiated scatter of the Basin 1 species may be a reflection of the very small *n* which several of them contribute, or may represent an intermediate morphology compared to the upland *melanura* and the other lowland rainforest species.

Discussion

Although the above analyses examined different groups of taxa from different perspectives, several common patterns emerged, focused on a number of species which were in some cases strikingly distinct. In the all-species comparison, fifteen of the potential species pairs demonstrated a significant difference on at least one variable; the greatest differences here were between *Callithrix argentata* and *C. chrysoleuca*, whose ranges are separated by several different rivers over some 500 kilometers. The differences between these species were evenly split between cranial and mandibular features. *C. argentata* was also strongly distinct from *C. melanura*, which was expected from the most widely separated species pair: at least a thousand kilometers separate the bulk of their two ranges, with the most of the central Amazon basin lying between them. These species were distinct on three times as many cranial than mandibular variables, suggesting that differences in the cranium are driving this morphological separation (Table 8).

Callithrix argentata is also relatively distinct from a much closer neighbor: *C. humeralifer*, parapatric across the Rio Tapajós, which for much of its lower reaches is

Table 8. A comparison of significant differences returned by a MANOVA on representative species of Amazonian marmosets. 🛇 indicates no significant differences between the given species pair; the numbers indicate the number of variables returning a significant difference, with red indicating cranial variables and blue denoting mandibular. 1= *melanura*, 2 = *rondoni*, 3 = *nigriceps*, 7 = *chrysoleuca*, 9 = *saterei*, 11 = *humeralifer*, 12 = *leucippe* and 14 = *argentata*.

	1	**2**	**3**	**7**	**9**	**11**	**12**	**14**
1	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**
2	🛇	**-**	**-**	**-**	**-**	**-**	**-**	**-**
3	🛇	🛇	**-**	**-**	**-**	**-**	**-**	**-**
7	**3/5**	**3/4**	🛇	**-**	**-**	**-**	**-**	**-**
9	**1/1**	🛇	🛇	🛇	**-**	**-**	**-**	**-**
11	**4/2**	🛇	🛇	**3/7**	🛇	**-**	**-**	**-**
12	🛇	🛇	🛇	**2/5**	**1/0**	**2/0**	**-**	**-**
14	**9/3**	**0/1**	**1/0**	**8/7**	**1/3**	**5/3**	**3/1**	**-**

the broadest river within the distribution of the Amazonian marmosets. Here the differences between cranial measurements again dominated, suggesting something unique in the skull of *C. argentata*. *Callithrix chrysoleuca* is also strongly distinct from *C. humeralifer* – this time more powerfully in the mandible – and also from *C. melanura*, again in features of the mandible. *C. chrysoleuca* is less powerfully separated from *C. leucippe* and *C. rondoni*, but again the mandible is more often distinct.

These differences are reported from the MANOVA without polarity, but the discriminant analysis provides a strength and direction for each variable. The sharp distinctions between *Callithrix argentata* and *C. chrysoleuca* are driven by disparities in size of both skull and mandibles: the former with the smallest overall skull length of the Amazonian marmosets, and the latter with the longest lower jaw. *C. melanura* has the largest skull on another dimension, the nasion-to-lambda distance, which on first approximation might suggest a more protruding forehead.

The patterns of distinction, and also of similarity, suggest three regional groupings of species. The easternmost species, *Callithrix argentata* and *C. leucippe*, are assumed to be closely related; with the exception of *argentata*'s black tail, they are almost visually identical, and *leucippe*'s range is effectively one lobe of *argentata*'s greater extent. These two species form an "eastern node" among the Amazonian marmosets, set apart by cranial features which suggest smaller faces and smaller skulls overall.

At the opposite end of the marmosets' distribution is *Callithrix melanura*, with by far the largest range of any species in its genus. *C. melanura* is the most southerly of the group, and often occupies slightly higher-elevation scrubland, as opposed to the lowlands rainforest occupied by the other Amazonian marmosets. *C. melanura* is distinguished most strongly by its nasion-to-lambda length, but not from its nearest neighbors: *C. rondoni* and *C. nigriceps* had no significant differences with *melanura* nor with each other. This may be due less to a similarity with *C. melanura* than to an absence of distinguishing features of their own; in the discriminant plots they are undifferentiated and scattered widely throughout the datacloud. Together these three species are the westernmost of the Amazonian marmosets, and their overlap suggests a "western node" of potentially interbreeding forms.

Positioned directly between these two is a "central node" comprised of *Callithrix chrysoleuca* and *C. saterei*, which were consistently distinguished by the largest overall skull length as well as the longest lower jaws. In every analysis, these two species (or *C. chrysoleuca*, when alone) presented the largest craniometric dimensions. Silva Júnior and Noronha (1998) had noted this when they first described *C. saterei*, and suggested that its larger cranial measurements, together with the heavier bodies of the type specimens, helped define its "robusticity" as compared to other species of marmosets.

Although there is substantial overlap and misclassification in the discriminant analyses, the patterns of similarity suggest a clear segregation of a number of species into distinct geographic regions. A strong association between pairs or groups of species, without regard to the landscape, might suggest either a parallel drift in certain characters, or else a parallel selection for features which might be adaptive in similar habitats. The majority of the Amazonian marmosets, however, inhabit the same nearly continuous, virtually level lowlands rainforest extending from the southern mouth of the Amazon to the middle reaches of the Madeira.

The simplest explanation for the close similarity of these three species nodes is that they are isolated from other taxa but not from each other, and the most obvious agents of separation – as Wallace (1852) first noted, and Hershkovitz (1977) independently believed – are the large rivers which flow roughly north from the Brazilian highlands into the Madeira and the main Amazon. Ideally a detailed analysis would take into account the width and volume of each tributary, but for many of the newly described species there are not nearly enough specimens available.

These results align remarkably well, however, with a recent analysis of marmoset phylogeny by Sena *et al.* (2002), who compared the mitochondrial COII gene for twelve species of Atlantic and Amazonian marmosets. From this widespread sample, Sena *et al.* identified three species clusters which were clearly assorted by geography. As expected, the Atlantic Forest marmosets grouped as a monophyletic clade, but Sena *et al.* also found subdivisions among the Amazonian species, with the representatives of the eastern Amazon (*Callithrix argentata* and *C. emiliae*) strongly distinct from the remaining taxa, further west and south across the Rio Tapajós.

This division, which parallels my own findings, represents an unusual convergence of molecular and morphological data, and reinforces the evident strong divergence between these two eastern species and the remainder of the Amazonian clade. The remaining species analyzed by Sena *et al.* – *humeralifer*, *mauesi*, *saterei*, *melanura* and aff. *emiliae* – formed a cohesive cluster, but Sena *et al.* noted that *C.* aff.

emiliae, the Rondônia marmoset, "was peripheral to this cluster," with a weak bootstrap value indicating uncertain affinities. For Sena *et al.*, this was additional proof that the Rondônia marmoset, previously allied with *C. emiliae* (*sensu* de Vivo, 1985, 1991), was in fact powerfully distinct from both *emiliae* and *argentata*, occurring as it did far across the Tapajós and several other intervening rivers. Sena (1998) and Ferrari *et al.* (1999) had earlier emphasized this division, and Sena (1998) explicitly noted the importance of the Rio Tapajós as a geographic barrier which, according to him, was responsible for the fundamental division between the two main clades of Amazonian marmosets. The research presented by Sena (1998), Ferrari *et al.* (1999) and Sena *et al.* (2002) laid the molecular foundation for the redescription of the Rondônia marmoset as *Mico rondoni* (Ferrari *et al.*, in press).

Many other Brazilian researchers have developed a substantial body of work on platyrrhine genetics (e.g. Schneider *et al*., 1996; Barroso *et al*., 1997; Tagliaro *et al*., 1997, 2005; Canavez *et al*., 1999), but very little has been done to explicitly test the theory of river-barriers for callitrichids. A significant exception is the work by Vallinoto *et al.* (2006) on several species of *Saguinus* in the eastern Brazilian Amazon. In an analysis of the mitochondrial D-loop region, Vallinoto *et al.* found that individuals of *Saguinus niger* from opposite banks of the Rio Tocantins were more divergent from each other than from the closely related *S. midas*. Moreover, populations from the eastern bank of the Rio Xingú and the western bank of the Tocantins, separated by several hundred kilometers, were more closely related to each other than to the eastern Tocantins population, which strongly implies that genes flow more easily within the

Tocantins-Xingú interfluvium than across the Tocantins itself. "These results strongly suggest that *S. niger* populations from different banks of the Tocantins river have been isolated for a long time," they concluded, "and are consequently undergoing a process of differentiation driven by geographical isolation." This had been previously implied by Tagliaro *et al.* (2005), and Vallinoto *et al.* (2006) suggested that these populations might be distinctive at the subspecies or even species level.

A handful of other studies have examined the genetics of callitrichids at the local level, often in the context of fragmentation (e.g. Marsh, 2003; Veracini *et al*., 2009), but only one research project has addressed the issue of river-barriers in *Saguinus fuscicollis*, the species which Hershkovitz (1977) used as a ready-made exemplar of the theory. In a now-classic study, Peres *et al.* (1996) analyzed both coat pattern and mitochondrial cytochrome *b* from 18 specimens of *S. fuscicollis* collected along both banks of the Rio Juruá, a major tributary of the Amazon in the southwestern Amazon basin. Despite the small sample size, Peres *et al.* demonstrated a genetic difference between the two putative subspecies, *S. f. fuscicollis* and *S. f. melanoleucus*, which are also fundamentally different in the pattern and color of their coats. Most intriguingly, the authors also reported an apparent hybrid population near the headwaters of the river, sporting an intermediate coat pattern which Peres *et al.* took as proof of the recent vicariant transfer of a small founder population. This population, which was found near the headwaters of the Rio Juruá, would support an important corollary of the original river-barrier theory, as Wallace (1852) had predicted greater differentiation along the lower reaches of a river, as compared with the narrower span closer to its source.

Other taxa besides primates have been examined for evidence of isolation by Amazonian rivers, and the results have often been equivocal at best. One of the strongest genetic challenges to the river-barrier theory resulted from an extensive faunal survey of the Rio Juruá in the southwestern Brazilian Amazon. From July 1991 to June 1992, Claude Gascon and his collaborators sampled frogs and small mammals at paired sites on either side of the Rio Juruá, traversing nearly a thousand kilometers of its course, from its headwaters near the western border of Brazil to its debouchment with the main-channel Amazon. Gascon *et al.* (1996) reported on samples of a single leptodactylid frog, *Vanzolinius discodactylus*, collected from both sides of the Rio Juruá. Although their samples showed substantial genetic variation between populations, Gascon *et al.* wrote that "we can find no evidence that the river has had an impact on the genetic structure" of those populations, and in fact several populations showed a strong divergence despite being on the same side of the river and only a short distance apart.

Working with an additional four species of frogs, Gascon *et al.* (1998) again found no evidence of isolation by the Rio Juruá; all four species had strongly differentiated populations, but without presenting an overall pattern which might indicate a river's imprint. Drawing on the same dataset, Lougheed *et al.* (1999) analyzed mitochondrial cytochrome *b* from a poison-dart frog, *Epipedobates femoralis*, but found no clustering of haplotypes along common riverbanks. Instead, they found cladistic divisions on either side of the proposed Iquitos Arch – an ancient, now-eroded ridge that once separated two geological basins. Lougheed *et al.* proposed that remnant ridges, relics of distant orogeny, may have exerted a more powerful effect on speciation than ephemeral modern rivers. And, in a full synthesis of community structure of both small mammals and frogs, Gascon *et al.* (2000) reiterated the apparent lack of effect on any of the taxa by the Rio Juruá, which seemed to be a death-knell for the theory of riverine barriers. Although the authors acknowledged that rivers might play some role in generating diversity, perhaps by creating floodplain and successional habitats, they proposed that the underlying geology of the region had more of an effect on speciation than the rivers which lay above.

But more recent research on a variety of Amazonian taxa has provided new perspectives on the issue, and a very recent study from the upper Rio Madeira offers countervailing evidence from *Allobates femoralis*, the same species (allocated to a new genus) which Lougheed *et al.* (1999) had examined. Working several hundred kilometers to the east of the Rio Juruá, Simões *et al.* (2008) sampled 17 populations from the upper reaches of the Rio Madeira in Rondônia, analyzing both external morphology and acoustic profiles of calling frogs. Simões *et al.* found a unique acoustic signature from populations on one side of the river which did not occur on the other, and which – together with consistent differences in color and morphology – they interpreted as evidence that the river did serve as an effective barrier, even along its narrow upper reaches.

In a well-publicized study on leafcutter ants, Solomon (2007) and Solomon *et al.* (2008) analyzed the phylogeography of three species of *Atta* to test predictions of the river-barrier hypothesis, as well as two other theories of diversification, the marine incursion and Pleistocene refugia hypotheses. Although Solomon and his colleagues found some support for the refugia theory, they found no evidence for river-barrier effects on leafcutter ants. (This is not at all surprising, however, given that, as Solomon *et al.* acknowledged, *Atta* queens may travel over a kilometer on their mating flights, and a windblown queen might safely traverse even the main-channel Amazon itself.)

In first elaborating the river-barrier theory, Wallace (1853) suggested that while most birds could easily cross any river, those which were weak or reluctant fliers might well be influenced; he chose as one "very remarkable instance" the example of the trumpeters of the genus *Psophia*, "the three species of which are separated by rivers," the Madeira and the main-channel Amazon. Another group of birds, the woodcreepers of the genus *Xiphorhynchus*, are stronger fliers than the trumpeters, but specialized for insect-gleaning on the trunks of forest trees. In a dissertation on the phylogeography of Amazonian woodcreepers, Aleixo (2002) found some evidence that major rivers served to shape the distribution of certain species. Although not every river seemed to exert this effect, Aleixo's results showed that the Xingú and Tapajós, together with the upper Amazon, did present significant barriers to gene flow. The Rio Tapajós in particular, according to Aleixo's analyses, divides the sister species *Xiphorhynchus spixii* and *X. elegans*, which Aleixo believes is evidence that the river contributed directly to their speciation.

These analyses provide phylogeographic evidence for several of the areas of avian endemism which Cracraft (1985: 67) proposed for the central Amazon basin. Aleixo's findings provide an intriguing parallel to my own results, in which the species to the east of the Tapajós (*argentata* and *leucippe*) are powerfully distinct from those to the west. Both my results from cranial morphology and Sena's (1998) molecular analyses suggest a correspondence of marmoset biogeography with the Rondônia and Pará centers of endemism which Cracraft (1985) proposed, and which Aleixo's (2002) results further support. (Intriguingly enough, the division in populations of *Saguinus niger* reported by Vallinoto *et al.* (2006) aligns with Cracraft's Pará and Belém bioregions, which are separated by the Rio Tocantins.) Aleixo (2002) noted that river-barrier effects did not appear for several large white-water rivers, including the Rios Madeira and Juruá. Aleixo suggested that the relatively younger western Amazonian rivers are more likely to change their courses, providing a greater opportunity for vicariant transfer. Aleixo (2002) and Aleixo *et al.* (2004) also noted that the Rios Xingú and Tapajós have both their headwaters and most of their courses rooted in the Brazilian shield, with channels relatively permanent and fixed.

The theory of riverine barriers was born in Amazonia, and for much of its history the pertinent research has been conducted in the Amazon; but more recently the concept has been explored in the context of other landscapes and biota. In Madagascar, several research groups across several decades have suggested that rivers might curtail the distribution of various lemur species (Petter *et al.*, 1977; Tattersall, 1982; Mittermeier *et al.*, 1994, 2006, in press). Recently Goodman and Ganzhorn (2004) tested these hypotheses with a novel approach uniquely suited to the Malagasy terrain. Unlike the Amazon basin, with its almost imperceptible grade across thousands of miles, the rainforests of eastern Madagascar follow a steep elevational gradient, presenting the eastern lemurs with an altitudinal range which most marmosets could scarcely imagine.

Goodman and Ganzhorn reasoned that any river with a source higher than a lemur's maximum elevation must, by default, serve as a barrier to that species. Their analysis of lemur ranges in relation to these steeply-flowing rivers uncovered a complex scenario, in which some rivers originated at higher elevations than the lemurs were known to occur, which the authors took as support of the theory. Other rivers, however, had their sources much lower than the lemurs' maximum elevations, and were presumed not to be effective as barriers.

It should be noted, however, that this study involved a review of distributional reports, rather than conducting morphological or molecular comparisons, and thus the results must be considered circumstantial at best. The authors note that "in numerous cases dispersal occurred around the sources or in the upper regions of the headwaters" of the rivers in question, but this assumes not only the mechanism for dispersal, but also seems to take as granted that the lower reaches will automatically serve as barriers. The authors claim that "at lower elevations even small rivers can act as efficient barriers," but without a direct test of this assumption – not to mention acknowledging contrary evidence from other systems – their results remain unverifiable, and other factors cannot be ruled out.

A handful of other studies have examined the issue with other primate taxa in Africa and Asia, almost all of them using molecular techniques and often with compelling results. Telfer *et al.* (2003) analyzed cytochrome *b* in mandrills (*Mandrillus leucophaeus*) in western equatorial Africa, and found two strongly divergent haplogroups occurring on opposite sides of the Ogooúe River. Each of these two haplotypes, representing a northern and a southern population, is infected with a unique strain of SIV – each of which appears to have entered its respective hosts independently, from different species of *Cercopithecus*. Telfer *et al.* invoke models of Pleistocene refugia to explain this exceptional double divergence, with the Ogooúe River serving as a barrier to mandrill populations as the postglacial forests expanded. This river has been noted as a barrier between other West African species as well, in particular the two populations of talapoins (*Miopithecus talapoin* and *M. ogouensis*), which Kingdon (1997) treated as distinct species.

The great apes have also long been considered to be constrained by rivers, in large part because most great apes are neither strong nor willing swimmers, and thus rivers are expected to serve as powerful inhibitors of gene flow. In Africa, this expectation is reinforced by the overall distribution of chimpanzees and bonobos, with the latter species definitively separated to the south of the Congo. In an attempt to determine if smaller rivers influenced the population structure of bonobos, Eriksson *et al.* (2004) analyzed the mitochondrial control loop of samples taken throughout the bonobos' range. Although the differing haplotypes were not as powerfully distinct as those from the mandrills, Eriksson *et al.* found "intriguing hints" of riverine influence, manifesting in a much greater distance index than could be explained by straight-line distances alone – but which, they believed, could be accounted for as the distance required to circumvent the full length of the river. Not all the rivers appeared to present strong barriers, however, and Eriksson *et al.* suggest that the slow, meandering rivers of the Congo Basin may change their courses and allow for vicariant transfer.

Although less chary of water than their African cousins, orangutans may also be limited by the courses of some rivers. Jalil *et al.* (2008), working with orangutans in northeastern Borneo, compared sequences of the mitochondrial control loop from 73 individuals from both sides of the Kinabatangan River. The sequences were strongly distinct, indicating “two major genetic groups of orang-utans on either side of the Kinabatangan River,” and the authors postulated that rivers in Borneo are responsible for separating identifiable orangutan populations.

In perhaps the most extensive survey of primate phylogeography to date, Anthony *et al.* (2007) examined mitochondrial haplotypes of gorilla populations throughout central Africa in an explicit test of both the river-barrier and Pleistocene refugia hypotheses of speciation. Rather than negating one or the other, the authors found support for both paradigms acting together, much as Eriksson *et al.* (2004) had proposed. And likewise, Anthony *et al.* found that rivers exerted an influence on genetic distance between mitochondrial haplotypes, which were separated not by straight-line distances, but by the distance required to circumvent the river entirely. Although not as definitive as the dramatic separations shown by Sena (1998), Sena *et al.* (2002) and Vallinoto *et al.* (2006), these results do strongly suggest that rivers have served as some degree of barrier to virtually all species of the great apes.

Although the effects of rivers on primate populations must vary broadly with both taxonomy and geography, it is possible to make some assumptions about how river-barriers may operate in the Amazon, and what effects they may have on marmoset distribution. The species with the largest range, *Callithrix melanura*, occupies drier and slightly more elevated habitat than the other Amazonian marmosets, and it has evidently crossed a number of rivers, including the Río Guaporé. The rivers in this region are in drier biomes, where seasonal effects on river flow can be dramatic; Hershkovitz (1968) noted a similar situation with the seasonally dry riverbeds in some parts of eastern Brazil. In addition, *C. melanura* occupies higher-elevation scrublands, where the rivers are narrower and more easily circumvented.

In the lowlands, by contrast, the rivers flowing north have grown broad and heavy, and as Wallace noted they offer nearly insuperable barriers to primates in particular – among the least-suited of Amazonian mammals for surviving an accidental immersion. (Van Roosmalen *et al.* (2000) noted that smaller primates, and marmosets in particular, tend to "drown at the spot when fallen into water.") Lacking any active method for crossing even a small stream, marmosets and other small primates have only two options for transport across flowing water, both of them passive.

Hershkovitz (1977) only mentioned these briefly, during a discussion of callitrichid radiation and dispersal: "Waifing across barrier rivers or passive translation by operation of a river bend cutoff…may be occasional phoenomena." His term "waifing" means the lucky transport of a group of marmosets across a river by riding along a fallen tree. David Quammen (1997), in his article on the discovery of *Callithrix humilis*, describes it like so:

> If a family of pygmy marmosets were sleeping in a tree hollow on the Madeira's west bank when that tree toppled into the current, they would wake to find themselves waiflike castaways on a floating log. If the log later washed up against another bank, they probably would jump ashore. If it happened to be the east bank, they would have achieved a safe crossing of that seemingly merciless river.

In reality, the odds of a safe crossing are exceptionally slim. Trees fall from riverbanks at a certain rate, but marmosets would only rarely be in them at the time, and more often than not the impact would throw them into the water. Those able to cling to the branches – and who survived the tilting and rolling of the fallen tree in the current – would be easy prey for any raptors cruising overhead, and would also have to survive an uncertain time on the water, with little food to carry them through. And, should the dead tree actually touch shore with its helpless cargo still alive, there is only a fifty-fifty chance that the tree would actually reach the *opposite* riverbank. Quammen (1997) reported that the waifing hypothesis was the favored explanation for the distribution of *Callithrix humilis*, but Hershkovitz (1977: 413) acknowledges that any colonizations resulting from this would be "extremely rare."

The more likely mechanism for river-crossings is the classic example of vicariant dispersal, in which a tight loop of a meandering lowland river is worn through by the current and isolated as an oxbow lake. This has important consequences for the piscine fauna, which rapidly changes from a lentic-dominated to lotic-dominated species assemblage (Winemiller, pers. comm.), but also serves to effortlessly transfer the enclosed forest from one side of the river to the other. For a brief period, the enclosed pocket of forest would effectively be an island, especially for arboreal primates which are chary of crossing open ground; but after a few months or years enough vegetation would have grown up around the edges of the new oxbow to allow the marmosets to escape. An "oxbow pocket" of forest comprising even a few dozen hectares would be enough to sustain a family group, allowing for some fortune in surviving predators; an enclosed forest of several hundred hectares might sustain a small population, which would be ready to expand into new territory once the margins of the new oxbow lake had grown up enough to allow them access to the forest beyond.

This was essentially the scenario which Hershkovitz (1977: 97) presented in his brief comments on river cutoffs and passive transport, and this has been cited as an authority ever since. Hershkovitz made no distinction between these effects in various regions within the Amazon, but Van Roosmalen *et al.* (2000) noted that the classic example of *Saguinus fuscicollis* occurs in Western Amazonia, and commented that "the greater slope of rivers coming from the Brazilian Shield in Eastern Amazonia…precludes such meandering and, with it, passive cross-river migration of breeding primate populations."

This caveat may hold true for the southern reaches of many of these rivers, but one look at a satellite photograph reveals the exceptional meanderings of many of the smaller rivers – in the region of *Callibella humilis*, these include the Rios Mariepauá, Uruá and Mataurá – which must waver constantly across the forested landscape, effectively serving as a series of semipermeable membranes, allowing for a slow and steady diffusion of individuals and family groups in both directions.

Larger rivers in this region must have much slower rates of oxbow cutoffs, but they too show pronounced meanders which may eventually separate, such as on the Rio Abacaxis, which serves as the putative western boundary for the range of *Callithrix mauesi*. Other mechanisms may also serve to change channels and boundaries, depending on the particular rivers in question. The Rio Aripuanã is well-known for its multiple channels and long, sinuous islands, eeling their way alongside each other for many miles. These islands support a substantial mass of forest, which might serve as transitional habitat if the river-channels shift and sediments link the islands to one river-bank or the other. This would be another form of passive transport, operating by a separate mechanism, but with the same ultimate effect: the transfer of small breeding populations from one riverbank to the other.

Other mechanisms may also be possible, such as tributary capture or redirection, perhaps owing to the annual floods of the main-channel Amazon. The question for all of these mechanisms is the rates at which they operate, and the effects of potential transmigrations between different breeding populations. Peres *et al.* (1996) were able to demonstrate genetic introgression and gradation between two subspecies of *Saguinus fuscicollis*, and noted a recent oxbow formation in the vicinity of their study, but a thorough analysis would require a direct estimate of the rates of oxbow formation (through a time-series of aerial photographs and satellite images) and a correlation with gene flow among populations on both sides of a putative barrier river.

Without this level of detail, however, it is still reasonable to suggest that larger rivers exert a greater separation effect, up to the nearly insurmountable barriers of massive rivers such as the Río Negro, Rio Amazonas and Rio Madeira. The effects at this scale were dramatic enough to impress themselves on Wallace, and a classic analysis by Ayres and Clutton-Brock (1992) demonstrated that the main-channel Amazon has a powerful separation effect on primate ranges, most strongly in its middle reaches. The separation effect tails off somewhat at either end: both in the upper reaches, because the width of the river is less, and also at the mouths of the Amazon, where the many channel islands seem to allow for a stepping-stone effect.

Hershkovitz (1977: 413) alluded to something of the sort in his musings on the evolution and radiation of *Saguinus*, the true tamarins, which he considered to have sprung from the (ostensibly more primitive) marmosets of the genus *Callithrix*: "Tamarins of the genus *Saguinus* must have evolved directly from a colony of prototypes of the *Callithrix argentata* group that breached the Rio Madeira barrier and established itself on the west bank [of the Madeira]." How they would have breached this barrier is unclear, but Hershkovitz seems to feel the Rio Madeira would have made for an easier crossing than the main-channel Amazon, which is miles wide in many places.[33]

The tributary rivers of the Rio Madeira and the main-channel Amazon may exert a moderate separation effect, serving to hold species generally apart while allowing for rare transmigrations and limited gene flow. The largest tributary of the main-channel Amazon is the Rio Tapajós, which divides *Callithrix argentata* and *leucippe* on the east from *C. humeralifer* and (more distantly) *mauesi*, *saterei* and *chrysoleuca* to the west. The strong separation of these two groups – and in particular the clear distinction of *C. argentata* from many other species, both near and far – suggests that the Tapajós exerts a powerful separation effect, as demonstrated for other taxa of primates and birds (e.g.

---

[33] For Hershkovitz, as noted previously, the callitrichids represented the most primitive of all platyrrhines, and within the Callitrichidae the genera were assorted in an ascending hierarchy of advancement. *Cebuella* was absolutely the most primitive of the group – just a hop, skip and vertical cling from the indisputably ancestral tarsiers – and thus the clear progenitor of the slightly more advanced marmosets, who in turn gave rise to the more advanced tamarins. More recent reassessments have suggested that the callitrichids are a secondarily dwarfed radiation, and thus their small stature and clinging ways are synapomorphic adaptations rather than clues to a plesiomorphic base.

Sena *et al.*, 2002; Aleixo *et al.*, 2004; Vallinoto *et al.*, 2006). Smaller rivers may have less of an effect, as suggested by the close similarity of *C. chrysoleuca* and *C. saterei* in cranial dimensions; these species are separated by the smaller Rio Canumã, but the combined mouths of the Rios Canumã and Abacaxis are a complex affair, and the same stepping-stone effect which Ayres and Clutton-Brock (1992) noted for the mouths of the main Amazon may also operate, more swiftly and locally, for these tributaries as well. In addition, the ranges of *C. chrysoleuca* and *C. saterei* are separated, at least in theory, by the shaded area postulated for the range of *C. acariensis* (Van Roosmalen *et al.*, 2000), which as noted above is known from a single captive individual of dubious locality, as well as secondhand reports from local *caboclos*. The putative range for *C. acariensis*, by definition enclosed by the Rios Acarí and Sucundurí, has not been surveyed since the original description, and the local biogeography may be more complex than their maps would suggest.

There is no large river comparable to the Tapajós to separate the central and western nodes – the *chrysoleuca*/*saterei* group and the *melanura* clan – but the distinction of *melanura*'s slightly drier, more upland habitat may serve as a separating influence on its cranial morphology. The question here would be why *Callithrix nigriceps* and *C. rondoni*, which occupy more classic lowlands rainforest, would map so closely with *C. melanura*. In fact, although they show no significant differences in the MANOVA results, they do demonstrate the "snow line" effect in the discriminant analyses, where *C. rondoni* in particular is clearly divided from *C. melanura* on Function

2 (Fig. 23). The question then becomes why *C. rondoni*, which does not overlap with *C. melanura*, is so broadly scattered across the rest of the plot.

Several species were too poorly represented in the collections for MANOVA analysis, and two of these in particular may have a direct bearing on the question of rivers and barriers; like old friends at a long-planned party, their absence is keenly felt. These are two of the recently described species, *Callithrix marcai* (née *Callithrix argentata marcai*) and *C. manicorensis*, both apparently from the interfluvium of the Rios Aripuanã and Manicoré. As with the majority of the new species, these were described almost entirely on the basis of pelage, and neither has been rigorously observed in the wild. When describing *C. manicorensis*, Van Roosmalen *et al.* (2000) noted "various groups observed in the wild," but gave no coordinates or other information. In the course of their redescription of *Callibella humilis*, Van Roosmalen and Van Roosmalen (2003) offered slightly more information on the range of *C. manicorensis*, but their surveys were not reported in detail, and apart from two or three localities along the Rios Madeira and Aripuanã, nothing else is reliably known of this species' distribution.[34]

Alperin (1993) described *C. marcai* on the basis of three faded and tattered skins which had been collected nearly eighty years before, and which Allen (1916) had provisionally but reasonably assigned to *Callithrix argentata melanura*. Alperin considered the skins to be distinct enough to warrant description at the subspecies level, although based on only minor differences in pelage coloration. His *Callithrix argentata*

---

[34] A more detailed discussion of the assumptions about the Manicoré marmoset's range is given in Chapter III, as part of the discussion of the distribution of *Callibella humilis*.

marcai was swept up in the general elevation of all marmosets to species level (Rylands *et al.*, 2000, following de Vivo, 1991) without a careful consideration of the distinguishing merits of this particular taxon – in essence, elevated by a shift in philosophy rather than a critical re-examination of its native features.

From a certain point of view, this could be seen as usefully conservative, since its inclusion as a full species might confer conservation benefits not so readily available to an obscure and dubious subspecies (following Kleiman and Rylands, 2002). Moreover, *Callithrix marcai* is the only described taxon of marmoset which has never been observed in the wild, and its type locality was the topic of brief dispute.[35] Although this topic seems to have been settled (Alperin, 2002), the fact remains that there is no verifiable information on which to base estimates of its potential range, and the presumed distribution provided in the IUCN Red List (IUCN, 2008) is absolute speculation.

As noted above, this has not always prevented authors from shading across an entire interfluvium based on one or two specimens collected from one corner, as witness the published distributions for *Callithrix saterei*, *C. mauesi*, *C. acariensis*, *C. manicorensis* and *C. nigriceps*. These, however, generally have the advantage of being the only marmosets known from their respective river-basins (although see Noronha *et al.*, 2008 for new localities of *C. mauesi* in a region where *C. saterei* had been expected).

In the case of *C. marcai*, its presumed (and never verified) type locality lies to the south of the presumed (and never verified) distribution of *C. manicorensis*, at the

---

[35] Several subspecies of *Saguinus fuscicollis* also remain unknown from the wild, with no clear provenance for the specimens which Hershkovitz (1977) included in his example.

southern tip of the interfluvium between the Rios Manicoré and Aripuanã. If both are full species, these would be the only two taxa of *Callithrix* which are not separated by a river of even modest stature. Two of the most closely similar Amazonian marmosets, *Callithrix argentata* and *C. leucippe* – the "eastern node," and almost certainly sibling species – are separated by a small eastern tributary of the Tapajós, the very minor Rio Cuparí. That no similar river separates the assumed ranges of *C. marcai* and *C. manicorensis* would seem to violate one of the founding assumptions of marmoset biogeography. If so many of the new species have been described on the assumption, explicit or otherwise, that they are separated by rivers from their nearest kindred, what is the rationale for retaining the distinction of these two taxa, which appear to have no separation whatsoever?

A comparison of the illustrations for these two species, as rendered by Stephen D. Nash and published in Van Roosmalen *et al.* (2000), finds very little grounds for distinction in their pelage or pigmentation. As illustrated, *C. marcai* is only slightly darker than *C. manicorensis*, and of all the Amazonian marmosets these two – without any evident barrier between their presumed distributions – are the best candidates for color morphs of a single species, with the *marcai* form perhaps only a southern clinal variant. Were this found to be the case, the epithet *marcai* should take priority, as this taxon was published first by Alperin (1993), and was recognized as a full species by Van Roosmalen *et al.* (1998) before the publication of *C. manicorensis* by Van Roosmalen *et al.* (2000).

One other quandary of river-barriers, involving another pair of marmosets, has more to do with a disparity of dispersal than an imperfect knowledge of distributions. The range of the pygmy marmoset, *Cebuella pygmaea*, is reasonably well understood; it is the largest distribution of any callitrichid, extending from the northwestern banks of the Rio Madeira (directly across from the territory of *C. nigriceps*, *manicorensis* and *chrysoleuca*) into the Peruvian and Ecuadorean Amazon. This is itself somewhat peculiar, since *Cebuella* is the smallest of all the marmosets, and thus the smallest living anthropoid primate. The majority of the Amazonian marmosets have far smaller ranges, and are typically three or four times *Cebuella*'s body mass; if nothing else, they should be able to jump slightly farther across a narrow stream.

But in fact, *Cebuella*'s minuscule size may aid its dispersal in several ways. Quammen's use of the *Cebuella* family as an example of waifing may not be so far-fetched for a number of reasons. First, pygmy marmosets are much more commonly found in riparian habitat, with far greater densities than in upland primary forest (Soini, 1988). Thus pygmy marmosets are far more likely to be in riverbank trees than their larger kin from *Callithrix*, and a greater proportion of their total population is found directly beside the rivers. Moreover, the pygmy marmosets may well have a better chance of surviving a tree-fall into the water: their tiny size means less mass and less momentum on the way down, which in turn means that a slender branch would be more likely to hold their weight than that of a marmoset or larger monkey, which might simply snap the branch and continue underwater. Once on a floating tree, their small size – as well as their naturally cryptic coloration and behavior – would serve to protect them against predators from above. And, although smaller bodies might mean a faster metabolism, a family of pygmy marmosets would likely be able to survive longer on the clinging insects and residual gums than an equal number of full-sized *Callithrix*.

Some of these same factors might also improve their ability to colonize new habitat following a riverbend cutoff and oxbow formation. For one thing, their exceptionally small range size – sometimes only 0.4 hectare (Soini, 1988) – would mean that even the smallest forest-pocket could potentially hold a viable founder population, meaning a greater proportion of oxbows would successfully transfer groups from side to side. And their small body size might facilitate water crossings in a simpler way: by more easily exploiting the slender twigs at the tips of branches, pygmy marmosets might be able to cross smaller streams directly, where the crowns of opposing trees brush against each other, and where the heavier, full-sized marmosets would fear to cling.[36]

Many of these factors must have influenced the pygmy marmosets' ability to colonize vast areas of suitable habitat, and so considering them all together, it may be no particular surprise that *Cebuella* has been able to expand across much of the western Amazon. The real question here is why none of this seems to have had a parallel effect on *Callibella humilis*, the dwarf marmoset – almost as small as *Cebuella*, but apparently confined to a tiny wedge of forest in one corner near the mouth of the Rio Aripuanã, in an area of perhaps less than six thousand square kilometers. If *Cebuella*'s small size gives it an edge in large-scale colonization, why not for *Callibella* as well?

---

[36] Full credit for this last idea should go to Tom Lacher.

As Van Roosmalen *et al.* (2000) noted, there may indeed be innate features of the western Amazonian rivers which make them more amenable to passive colonization, although as noted above this would seem unlikely. What may, in fact, be a far greater constraint on *Callibella*'s ability to expand, either now or in the past, is the presence of closely related callitrichids who compete for many of the same resources. *Callibella*, like *Cebuella*, appears to be an intensive exudate-feeder, as suggested both by observations from the field (Van Roosmalen *et al.*, 1998, 2003) and comparisons of its mandibular anatomy (Aguiar and Lacher, 2003, 2005, 2009). In the northwestern Amazon, *Cebuella* is sympatric with a variety of other callitrichids – but all of them tamarins, which are only opportunistic gum-feeders; they will feed on any gums they happen across, but lack the specialized anatomy or behavior to stimulate the flow of exudates themselves.

South and west of the Rio Madeira, however, are the many species of Amazonian *Callithrix*, which by definition are specialized to gouge for gums and other exudates. *Cebuella* may have been free to expand so widely precisely because the tamarins were not effective competitors for exudates. *Callibella*, by contrast, may have been confined to its current distribution on account of hard competition from its erstwhile congeners. The question then would be how *Callibella* has managed to survive the sympatry with *Callithrix manicorensis*, whose only concrete localities are syntopic with *Callibella*. (Van Roosmalen and Van Roosmalen (2003) reported a series of surveys further down the western bank of the Rio Aripuanã, but gave no details of their observations.)

It may be that *Callibella* is in a parallel situation to *Saguinus bicolor*, an endangered tamarin which is now found only in the immediate environs of the city of Manaus. Wallace (1853) noted this species along the eastern bank of the lower Rio Negro, in the vicinity of the town of Barra (the precursor to Manaus), but made no particular mention of its rarity; his surveys in this area were limited to the river, so the "*Jacchus bicolor*" must have been common and easy to see. In the past century, however, this species has apparently been the loser in a competitive struggle with *Saguinus midas*, which has extended its range to encompass all the region save Manaus itself. Although the expansion of *S. midas* may have been partly facilitated by human activity – and the growth of Manaus itself was certainly no favor – for the most part this may have been a natural case of competitive exclusion (Ayres *et al.*, 1982; Egler, 1992).

Callibella humilis may have experienced a similar pressure from *Callithrix manicorensis*, and perhaps other callitrichids as well, although the details of its sympatry with the former are unclear. Van Roosmalen (2002) and Van Roosmalen and Van Roosmalen (2003) claimed that *Callibella* was in fact commensal with local humans, apparently owing to the fact that both humans and dwarf marmosets could be found on *terra pretas* – the exceptionally rich anthrosols which are thought to have been developed by a previous indigenous culture spread throughout the Amazon basin.[37] This argument is unconvincing, however, as an explanation for the restricted distribution of the dwarf marmosets. The *terra pretas* are widely distributed throughout the lower

---

[37] Based on the agricultural potential of the *terra pretas*, this civilization may have supported a greater population in the 15th century than now exists in the 21st. One bit of circumstantial evidence for this civilization is the fact that many of the indigenous peoples living in the region today still have a system of hereditary titles – entirely unknown for nomadic peoples outside of the Amazon.

Amazon, both north and south of the main channel – and if dwarf marmosets are truly tied to these anthrosols, or the humans inhabiting them now, then they should be widely distributed as well.

Perhaps the most optimistic interpretation, although speculative, is that the dwarf marmosets were once more broadly distributed, and competition with other marmosets – perhaps spurred by a recent expansion – has slowly whittled the dwarf marmosets into small pockets and corners throughout the Amazon. A hopscotch distribution would not be implausible; the peculiar quasi-marmoset known as the Goeldi's monkey, *Callimico goeldii*, seems to have a similarly spotty distribution along the inner arc of the Andes, from Bolivia around to Ecuador (Porter, 2007). As the authors of virtually every new species of marmoset have noted, much of the south-central Amazon remains sparsely inhabited and virtually unexplored, and a map of marmoset distributions based on known specimens would have many more question marks than localities, especially in the deep basins far from major rivers. The dwarf marmoset itself managed to avoid notice by two centuries' worth of avid naturalists and collectors; it was only because a *caboclo* brought a newborn *Callibella* to the van Roosmalens' front door that they learned of its existence at all – and the dwarf marmoset occupies a region at the confluence of the Rios Madeira and Aripuanã, two heavily traveled and relatively well-settled rivers. Other pockets of *Callibella* may yet survive – either *humilis*, or perhaps another species – in the deeper reaches of the Amazon basin, waiting discoveries of their own.

CHAPTER V

CONCLUSION:

CONSERVATION OF CALLITRICHIDS IN THE BRAZILIAN AMAZON

When Alfred Wallace and Henry Bates made their excursions across the Amazon, they were exploring a world of river and forest which, although new to them, had been scouted and claimed many decades before by Portuguese and Brazilian settlers – and which had originally been peopled many thousands of years before the European arrival. Prior to 1500, the Amazon basin supported a population which may well have exceeded the total today, owing in part to the exceptionally fertile terra preta soils which the native peoples developed (W. Sombroek, pers. comm.).

Such a population would have had its own impacts on native primate species, which are hunted throughout the Neotropics; the larger-bodied species, such as howlers and spider monkeys, are often preferred and likely always have been. Apart from hunting pressure, however, a substantial indigenous presence would have had another impact on primate species: their capture and transport, possibly over long distances. Primates have always been favorite pets in the region; Bates (1863) commented on several species which he had seen in local homes, "and heard that there were many so kept, and that they were esteemed as great treasures."

The esteem may be less today, but both birds and primates are common pets in the modern Amazon. During one impromptu survey of a small river-town, I found at least ten species of monkeys being kept in (or under) various homes, most of them in

Figure 24. An individual of the recently discovered species *Callithrix manicorensis*, kept in semi-captivity by a family of *ribeirinhos* in the vicinity of Manicoré. Photo by J. M. Aguiar.

miserable condition. Marmosets are popular pets in rural settings as well; they are easily captured from the forest, and often adapt to a semi-tame lifestyle (Fig. 24). Two of the most recently described species, *Callithrix acariensis* and *C. manicorensis*, were first noted from captive individuals (Van Roosmalen *et al.*, 2000); the holotype of the former, the only extant specimen, was being kept as a pet, and without this custom it might have gone unnoticed.

Very little is known of the indigenous population of pre-contact Amazonia, but primates must have been a part of their many cultures, and they were almost certainly traded back and forth. Bates (1863) noted a local official who sent twelve rare uakari monkeys – the crimson-faced, white-furred *Cacajao calvus* – to a ranking patron in the capital of Rio de Janeiro, in recognition of a political appointment; it took six experienced native hunters more than three weeks to secure this “unique and princely gift.” Bates went on to note that “scarcely one in a dozen succeeds in reaching Rio [de] Janeiro alive,” this species having been known to be “of delicate constitution” and rarely surviving even a gentle captivity. Marmosets, by contrast, adapt well enough that in pre-contact Amazonia they may have been commonly traded up and down the rivers – not as princely gifts, but likely as casual presents between family and friends. Some of these may well have absconded from their new homes – and, if those homes were across rivers, the indigenous peoples may have helped the marmosets to circumvent natural barriers.

The direct impact of the original Amazonian cultures on primate populations is, by definition, impossible to quantify, and researchers can only make inferences based on present-day communities (e.g. Silva *et al.*, 2005). An easy assumption is that these pre-contact hunting pressures must have been sustainable, as otherwise the Amazonian primate fauna would not have survived to the present day. This possibility, sometimes caricatured as the "noble savage" theory (Redford, 1991), has been widely debated (e.g. Redford and Stearman, 1993; Schwartzmann *et al.*, 2000) but depends on the assumption that native peoples have not already driven certain species to extinction, species whose existence we have never known.

This is entirely possible, given the experience of the many unique lemurs of Madagascar. The lemur fauna of this miniature continent is now estimated at over 100 taxa (Mittermeier *et al.*, 2009a,b), but many more forms had evolved during Madagascar's tens of millions of years of isolation, taking advantage of a diversity of habitats to radiate into a plethora of unique designs (Mittermeier *et al.*, in prep.; Fig. 25). Among these were several species in the genus *Archaeolemur*, which were evidently adapted to a terrestrial lifestyle in ancient grasslands, much as the baboons (*Papio* spp.) of Africa are today. A second closely related genus, *Hadropithecus*, may have been semi-terrestrial. The more distantly allied *Archaeoindris* was apparently terrestrial, owing to its enormous size – up to 160 kg, nearly as large as modern gorillas, and the largest known lemur from any age; its postcranial anatomy, however, hints at arboreal adaptations as well (Jungers *et al.*, 2002). Another form, *Megaladapis*, the "koala lemur," may have been a slow-moving arboreal herbivore; its skull was elongated to a greater degree than any other known primate, and it may have had a flexible snout, enabling it to crop a broad radius of leaves from a sitting position. Most intriguingly, the

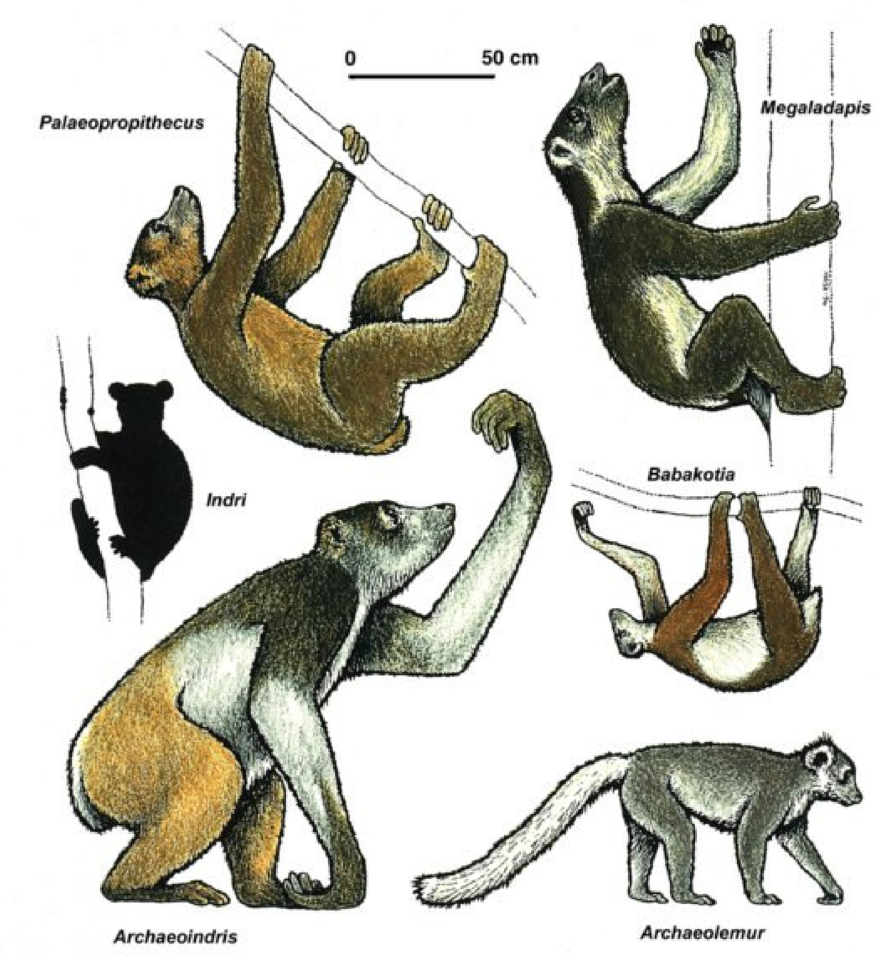

Figure 25. Reconstructions of several of the extinct lemur species of Madagascar, representing some of the many unusual adaptations in the lost megafauna. These and all others of the extinct forms were as large as or larger than the indri (silhouetted at left), the largest lemur species which survives today. Artwork by Stephen J. Nash and used by permission.

long arms and hooked forehands of *Paleopropithecus*, together with aspects of its dentition and spinal column, suggest that it was a suspensory feeder – in essence, a lemur which evolved a quintessentially slothlike way of life.

These and other fossil lemurs – at least eight genera and 16 species – went extinct over the past 1600 years, the same timeframe in which modern humans first settled Madagascar and burgeoned into the twenty million Malagasy of today (Mittermeier *et al.*, in prep.). Virtually all of the extinct lemurs were larger than the surviving species, which suggests a classic pattern of naïve, slow-moving megafauna being exterminated by a novel and cunning predator. The greatest diversity of lemurs today is among the smaller forms, such as the mouse lemurs (*Microcebus*) and sportive lemurs (*Lepilemur*), none of which are heavily hunted (Andriantompohavana *et al.*, 2006; Louis Jr. *et al.*, 2006, 2008; IUCN, 2008). Although changes in climate and habitat may have been part of the relatively sudden disappearance of the largest lemurs, the consensus is that the recent wave of extinctions, spanning roughly the years 400 – 1600 AD, was owing primarily to direct consumption by an ever-expanding human population (Mittermeier *et al.*, in prep.).

This pattern, if it occurred in Amazonia, must have unfolded many thousands of years before the events in Madagascar, and without European observers to record tantalizing glimpses of a species' final days. Whatever the species composition of the Amazonian pre-contact primate fauna, it was unlikely to have radiated into such an exceptional variety of niches; the early lemurs of Madagascar had virtually no competitors, while the ancestral platyrrhines arrived in a landscape already filled with strange mammalian forms, owing to South America's own period of long isolation (Simpson, 1980). The niche of the suspensory folivores has long been occupied by the sloths themselves, and broad areas of open savanna, although perhaps sporadically available during the Pleistocene fluctuations (e.g. Haffer, 1969), have never been a major feature of the Amazon valley, as Wallace (1853, 1876) and others noted early on.

A few hints of a prior large-bodied fauna have appeared, however, and in much the same way as the evidence for many paleolemurs: by way of subfossil remains in limestone caves. Hartwig (1995) reanalyzed a set of fossils from the caves of Lagoa Santa, in southeastern Brazil, which had been described in 1838 as *Protopithecus brasiliensis* by Peter Wilhelm Lund, the Danish naturalist who first discovered them. Based on the anatomy of the femur, Hartwig (1995) proposed that *Protopithecus* had been closely related to the muriquis, *Brachyteles*, currently the largest platyrrhine at 12-15 kg. Hartwig believed that *Protopithecus* was nearly twice that mass, at 23-24 kg, although according to him it was still a capable brachiator and fully arboreal. Hartwig and Cartelle (1996) reported a nearly complete skeleton, which they estimated at 25 kg, showing features of both howler (*Alouatta*) and spider monkeys (*Ateles*) in a curious admixture of form.

Immediately thereafter, Cartelle and Hartwig (1996) described *Caipora bambuiorum* from the caves of Toca da Boa Vista in Bahia, which they believed was related to the extant spider monkeys (*Ateles*) but much heavier, at approximately 20 kg. The holotype was part of a rich assemblage of mammalian fossils, comprised of several extant and extinct genera, including a massive sabre-toothed cat (*Smilodon populator*) and a giant ground sloth (*Nothrotherium maquinense*). Heymann (1998) questioned whether such large primates could have been fully arboreal, and suggested they may have been partly terrestrial; but regardless of their mode, it seems clear that by the Pleistocene, at least some species of platyrrhines had diversified into forms much larger than found today. Unlike the recent lemur extinctions in Madagascar, there is no compelling evidence that humans were complicit, and – owing to the notoriously poor taphonomic conditions throughout Amazonia – there is no evidence that these forms ranged beyond southeastern Brazil.

The name *Caipora* was chosen as homage both to Peter Lund, who first described *Protopithecus*, as well as to a name from Brazilian folklore, the *caipora*, which Lund (1836) described as "a very large ape, to which the Indians have given the name Caypore, which signifies the dweller in the wood." It is tempting to imagine that a last remnant of the Pleistocene megafauna still survived until Lund's time, but more likely the creature only survived in local memory – perhaps hunters' stories that became legends.[38] Similar legends have survived elsewhere in Brazil; Oren (1993) suggested that the widespread stories of the *mapinguari*, a fearsome beast with a hideous odor, might actually be a giant ground sloth, and Oren (2001) reported conversations with dozens of hunters who claimed to have encountered one. There is no direct evidence to support these claims, and these may only be tall tales handed down by local hunters; but

---

[38] The word *caipora* has a much broader meaning in Brazilian Portuguese today; it is attributed to the Tupi-Guarani *kaá porá*, "forest dweller," and applies to a number of fantastical creatures (a woman with one leg, a trickster spirit with backwards feet, etc.) as well as to the *fogo-fátuo* or will-o'-the-wisp. It can also mean, less commonly, any unfortunate or unlucky person, or someone who can never do things right (Dicionário Michaelis, 1998). One of these incarnations, the trickster spirit who enchants greedy hunters, is known in the Amazon as *curupira* (Oren, 2001).

Oren (2001) notes the recent discoveries of other large mammals, such as the Chacoan peccary, the Javan rhino and the saola (*Pseudoryx nghetinhensis*) of mountainous Vietnam, and suggests that in the expanse of the southern Amazon – still vast, and in some areas virtually unexplored – similar relict species might yet survive.

Whether or not the native Amazonians drove unknown species to extinction, they would certainly have had an impact on the primates which are still heavily hunted today – the spider monkeys, woolly monkeys and howlers. This raises the unsettling possibility that these and other primate populations may have experienced a resurgence in the years after 1500, when the indigenous societies collapsed following disease, genocide and forced relocation. Pedro Álvares Cabral, the sea captain whose small fleet anchored off Bahia in April 1500, had not expected to find a continent where he did, but he was nonetheless prepared: onboard he carried a small complement of convicts, or *degredados*, who were a long-term insurance policy of the Portuguese (Greenlee, 1938). When he weighed anchor two weeks later, he left two of them behind, with the mission of teaching Portuguese to the natives and converting them to Christianity – and (not stated in so many words) of spreading Lusitanian genes into the native population. This, it was believed, would facilitate the process of native assimilation, and prepare the way for later colonists.[39]

Unlike the Spanish, who threw themselves into mad quests for gold and immortality, the Portuguese – tempered by a century of experience up and down both

---

[39] One of these condemned convicts, Diogo Álvares, took well to the new land, fathering many children and eventually becoming an intermediary between the native Tupinambis and the Portuguese king (Levine, 1999).

coasts of Africa – were more interested in establishing trading posts in the New World, to enhance their network of commerce. Their focus remained for long on the East; Cabral's original mission had been to make trading contacts with India, which he accomplished after detours in Brazil and Madagascar.[40] But the Portuguese colonists made inexorable inroads into their new land, and although the bulk of their settlement remained along the Atlantic coast of eastern Brazil, traders and adventurers brought flag and fever far into the interior.

Cabral's discovery of Brazil had been unexpected, and the territory – initially thought to be a large island – was grudgingly ceded to the Portuguese under the terms of the Treaty of Tordesillas of 1494, which had been a Vatican-brokered peace agreement intended to divide the trading world between the Portuguese East and the newly discovered Spanish West. The exact line of demarcation was never precisely agreed on (having been thought, in 1494, to run through empty ocean) but if honored, it would have restricted the Portuguese to the east of the 46th meridian, extending roughly from modern São Paulo to the city of Belém on the southern mouth of the Amazon. Under the original terms, the Spanish had full claim to everything from Buenos Aires north to the Guianas and west to the Pacific – including the entire Amazon basin, from its mouths at Marajó to its headwaters in Peru.

The terms were not honored. Initially neither empire had much interest in the Amazon; there seemed to be no easy gold (the Spaniards' concern) nor advantageous

---

[40] Cabral is also credited with the first European discovery of Madagascar. With his subsequent landfalls in Mozambique and India, Cabral and his crew likely became the first men to have visited all four primate bioregions.

trade (the Portuguese'), and both nations were heavily preoccupied elsewhere. But the Portuguese slowly encroached, and the Spanish chose not to pursue the issue; the Andes were a barrier they could not easily pass, based as they were on the Pacific coast, and they allowed the Portuguese to roam freely. Other nascent colonial powers put up more of a fight; the French made inroads into the Amazon in the late 1500s, and the Dutch temporarily occupied northeastern Brazil in the 1630s and 1640s; but a stubborn guerilla resistance contained and then expelled the latter, and the French were defeated even earlier, in 1615. Immediately afterwards the Portuguese founded a settlement on the southern mouth of the Amazon – eventually to become Belém – and began exploring the Amazon proper, or rather scouring it for slaves.

During the 1600s, the principal explorers (for want of a better term) of the interior of Brazil were the *bandeirantes*, armed bands of hundreds of men who set out on protracted slave-hunting expeditions, marching for months or years at a time.[41] Establishing camps and even sowing crops as they went, the *bandeirantes* – often a racial blend of Portuguese colonist and native Indian – were the chief agents in extending Portugal's knowledge and control ever deeper into the continent's interior. The archetypal *bandeirante*, Pedro Teixeira, pushed far up the Río Napo in 1639 and founded Tabatinga as the new point of demarcation between the Spanish and Portuguese spheres – where the cultural dividing line essentially remains today. Most *bandeirantes*

---

[41] The name comes from the Portuguese *bandeira*, which literally means a flag, pennant or banner; this appears in the modern Portuguese name for the giant anteater, *tamanduá-bandeira*, referring to its extravagant flag-like tail. But in the military usage of medieval Portugal, a *bandeira* was a small unit which separated from a larger company for temporary scouting and raiding. In Brazil, by the time of Pedro Teixeira, the word had come to signify a group of backwoods militiamen (Bakewell, 1997), and so to the *bandeirantes* themselves, their appellation must have suggested a rough-and-ready scouting force with the right to take what they pleased.

were less ambitious, preferring to raid the forests for easy wealth, most often in the form of native slaves; once those populations had been depleted, by roughly mid-century, the *bandeirantes* began to focus more on uncovering precious minerals. Crusaders without a cross, terrestrial pirates following no compass but the unknown rivers, the *bandeirantes* penetrated the interior with pillage aforethought, and by the scars of their passage made future settlements possible.[42]

By the time Wallace and Bates arrived in Pará, more than two centuries after its founding, Brazilian influence had permeated the Amazon, and a working knowledge of Portuguese allowed them to operate throughout the region.[43] Settlements were small and often scattered, but numerous and growing. The city of Barra do Rio Negro, near present-day Manaus, had been founded in 1669 as the fortress São José do Rio Negro; by the time Wallace reached it the population was "five or six thousand" by his estimate, virtually all of mixed descent. He gave the population of the city of Pará (modern Belém) as about 15,000, and noted it was the largest city in the known Amazon. Bates, writing ten years later, estimated the total population of the provinces of Amazonas and

---

[42] Nation-building being what it is, the *bandeirantes* are now honored with a sculpted monument to their contributions, erected in the heart of São Paulo, as well as many other memorials throughout Brazil; they are considered to have been bold and heroic explorers. In the 1990s, Toyota introduced a sporty SUV called the Bandeirante for the Brazilian market, and the Brazilian aircraft manufacturer Embraer built a model of light passenger turboprop by the same name. In São Paulo today, *bandeirante* also refers to the local equivalent of junior Girl Scouts (Dicionário Michaelis, 1998).

[43] Portuguese was spoken by the Brazilian settlers and some native Indians, but the lingua franca for the native population was "Lingoa Geral," a Tupí dialect which the Jesuits had adapted for their own use and helped to spread some two centuries before. A far-flung and useful trade language, Bates noted that "printed grammars of it are always on sale at the shops of the Pará booksellers." Wallace, for his part, found it "very difficult to get hold of," and for the most part relied on young Indians who spoke both languages. By the time he had reached the Rio Uaupés, on the upper Rio Negro, even Lingoa Geral was very little known by the local people.

Pará (essentially the drainage of the main-channel Amazon) as approximately 230,000, which he calculated was one person for every four square miles.

A population roughly equivalent to the modern city of Plano, spread across a region four times the size of Texas, might not be expected to have a severe impact on primates except in the vicinity of settlements, and both Wallace and Bates noted this effect in Pará. Despite having a semi-permanent residence in Pará for over a year, Bates had little success in finding primates nearby:

> I have already mentioned that monkeys were rare in the immediate vicinity of Pará. I met with three species only in the forest near the city; they are shy animals, and avoid the neighbourhood of towns, where they are subject to much persecution by the inhabitants, who kill them for food.

Wallace, perhaps more attuned to life in the canopy, remembered it differently:

> Monkeys are plentiful enough in the neighbourhood of Pará; but they require looking for, and a certain amount of acquaintance with them is necessary in order to discover their haunts, and some practice is required to see them in the thick forest, even when you hear them close by you.

Both of them, however, were naturalists and collectors at heart, and when Wallace encountered his first troop of monkeys, his immediate reaction was to lay in wait with a companion, guns at the ready for an unwary target. His companion managed to wound one, dropping it from a tree, and Wallace moved in to observe it up close:

> The poor little animal was not quite dead, and its cries, its innocent-looking countenance, and delicate little hands were quite childlike. Having often heard how good monkey was, I took it home, and had it cut up and fried for breakfast...

Wallace's meal was likely a capuchin (*Cebus*) or squirrel monkey (*Saimiri*), then as now probably the smallest species most hunters would trouble to spend a bullet on.[44] Marmosets, for their part, were not much persecuted; Bates noted that the only monkey he saw frequently in Pará was "the little *Midas ursulus*," which "seems to be less afraid of the neighbourhood of man than any other monkey."[45] As mentioned in Chapter IV, Wallace evidently found *Saguinus bicolor* to be common around the small city of Barra do Rio Negro, using it as one of his examples of a primate contained by major rivers.

Wallace observed three species of tamarins during his sojourn: "*Jacchus bicolor*" (= *Saguinus bicolor*), "Jacchus tamarin" (probably *S. niger*) and a new species encountered on the upper Rio Negro (which Hershkovitz (1977) identified as *S. inustus*). Bates, with the benefit of more years' experience in the field, reported several other species: *Midas leoninus* (= *Cebuella pygmaea*), *Midas rufoniger* and *Midas rufiventer* (*Saguinus fuscicollis avilapiresi* and *Saguinus labiatus thomasi*, according to Hershkovitz).

Bates also commented on another, closely related species:

> The little *Midas argentatus* is one of the rarest of the American monkeys; indeed, I have not heard of its being found anywhere except near Cametá...

This is *Callithrix argentata*, the silvery marmoset, and the city of Cametá – its type locality – lies at its easternmost limits. Its perceived rarity, at least to Bates, was more likely due to its relatively restricted range. One of the individuals which Bates observed close up was a treasured pet, and clearly there was no thought of eating it:

---

[44] For food, anyway. According to de la Torre and Yépez (2003), the pygmy marmoset (*Cebuella pygmaea*) is sometimes used simply for target practice.

[45] This was probably *Saguinus niger*, the only callitrichid which naturally occurs in the region.

> The woman who owned it carried it constantly in her bosom, and no money would induce her to part with her pet. She called it Mico. It fed from her mouth and allowed her to fondle it freely, but the nervous little creature would not permit strangers to touch it.

Other primates were eagerly hunted, however, and Bates commented in particular on the *coaitá*, "called by zoologists spider-monkeys," and on average the largest platyrrhines in Amazonia.[46] On a visit to Obidos, a town on the northern bank of the central Amazon, Bates noted that "the flesh of this monkey is much esteemed by the natives in this part of the country," and the military commandant of the town, sharing their taste, "every week sent a negro hunter to shoot one for his table."

The use of firearms was an essential difference between the Brazilian settlers and the hunters of previous societies, and is a primary reason why hunting by "traditional" peoples today is often no longer sustainable. When Wallace and Bates were exploring, many native Indians still used arrows and blowguns for their hunting. Firearms were widely available, but of poor quality; Bates noted that hunters could be more effective with traditional weapons, "for the report of a firearm alarms the whole flock of birds or monkeys feeding in a tree, whilst the silent poisoned dart brings the animals down one by one, until the sportsman has a heap of slain by his side." Those skills are still retained, but in the intervening century, firearms have become the hunters' weapon of choice, and only under exceptional circumstances are more traditional weapons still used (e.g. the firearms prohibition in Manu National Park; see Silva *et al.*, 2005).

---

[46] *Ateles paniscus* averages 7.5 – 12.5 kg (Shepard *et al.*, 2005), exceeded only by the muriquis of southeastern Brazil (*Brachyteles* sp.), which may reach 15 kg. Virtually all muriquis are restricted to tiny scraps of forest in Minas Gerais, and the species has never been recorded outside of the Atlantic Forest along the eastern coast of Brazil. The muriquis themselves were utterly decimated by hunters in the first part of the twentieth century.

That century has seen tremendous changes in raw population and land use, in Amazonia and throughout the world. The states of Amazonas and Pará now have a combined population of over ten million inhabitants; Belém has at least 1.4 million citizens and Manaus, sprawling successor to Barra do Rio Negro, is estimated at 1.7 million. This exceptional pulse of urban growth has fed and sustained an array of impacts to primates throughout Amazonia. Some of these impacts are direct – in particular intensive overhunting and massive habitat destruction – and others are from sources Wallace and Bates could scarcely have imagined: altered rainfall regimes from regional and global climate change, or mass harvesting for biomedical use.

This last had a particular impact on the primates of South America, and its effects had been noted from at least the 1960s, when the harvesting began to accelerate. This intensive collection, combined with accelerating habitat destruction, coincided with another trend of the mid-twentieth century: the increasing interest in field studies of primates by a new generation of biologists, whose appreciation for these creatures in the wild was matched by a new awareness of their changing environment. Some in the biomedical community had also begun to question where exactly their study animals were coming from, and what effects their capture might have on the populations left behind; and in 1972 a group of medical researchers and conservationists convened a symposium to share what little was known of the status of platyrrhines in the wild.

Reporting on that symposium, Thorington and Heltne (1976) noted several species in particular which were extensively used – the squirrel monkey (*Saimiri sciureus*) outstandingly so. Between 1968 and 1972, over 173,000 squirrel monkeys were imported into the United States alone, many more than the heavily exploited rhesus macaques (*Macaca mulatta*) imported during the same four years (Mack and Eudey, 1984).[47] Although some of the squirrel monkeys were destined for the pet trade, the majority of the imports were used in biomedical research. Other platyrrhines in great demand included the night monkey or dourocouli (*Aotus*), which was used in antimalarial studies, and several species of tamarins, in particular the cotton-topped tamarin (*Saguinus oedipus*), for research on hepatitis (Thorington and Heltne, 1976). Hernández-Camacho and Cooper (1976) estimated that 30,000-40,000 cotton-topped tamarins had been trapped in the previous decade, for both the pet trade and biomedical research. USFWS data suggest that more than 13,000 were imported between 1968 and 1972 (Mack and Eudey, 1984). The offtake for research within habitat countries could also be severe; the Museu Nacional in Rio de Janeiro houses over 800 skulls of *Callithrix kuhlii*, one of the eastern Brazilian marmosets, which were used in research on yellow fever; the preserved skulls must have represented only a small fraction of the total consumed.

Most of the presentations at that first symposium focused on research in Colombia and Central America, those being the main regions of expertise for the participants. Thorington and Heltne (1976) noted the "obvious gaps in coverage," in particular the complete absence of any contributions from Brazil. "To our knowledge," they wrote, "there are simply no data available on the status of Brazilian populations of

---

[47] The rhesus monkeys, however, had been ferociously overharvested for much of the twentieth century. Nearly 90,000 rhesus monkeys were brought into the United States during the 1930s alone; at the height of the harvest, almost 600,000 rhesus monkeys were imported in the four years between 1956 and 1960 (Mack and Eudey, 1984).

primates in the Amazon." At the time, most of the attention to primate conservation in Brazil was focused on the lion tamarins (*Leontopithecus*) of Rio de Janeiro and adjacent regions, and much of this attention was due to the vocal efforts of one of Brazil's first primatologists, Adelmar Coimbra-Filho. Growing up in the southeast of Brazil in the early twentieth century, he witnessed firsthand the surge of mass deforestation in the 1950s and 1960s, as well as the explosive urbanization that saw forest streams paved over and captured in culverts. In a landmark article, Coimbra-Filho (1969) summarized the effects of massive habitat loss on the golden lion tamarins (then considered a single species, *Leontideus rosalia*) and during the 1970s he became a tireless advocate for their conservation.

The efforts devoted to the conservation of lion tamarins helped spread an understanding of their circumstances to an ever-growing audience, and thirty years later the program is considered a model of international conservation, involving both captive breeding and *in situ* habitat protection; the full story is provided by Kleiman and Rylands (2002). Together with long-term field studies on other endangered primates in the heavily impacted southeast of Brazil – in particular, the research by Karen Strier on muriquis (*Brachyteles* spp.) and Stephen Ferrari on the buffy-eared marmoset (*Callithrix aurita*) – the attention of conservationists was strongly focused on the primate fauna of the Atlantic Forest remnants (e.g. Rylands *et al.*, 1996).

Owing in part to limited resources, but especially to the vast and still-remote territories involved, knowledge of the conservation status of Amazonian species remained much less detailed. The one Amazonian marmoset whose status could be estimated was not encouraging: the pygmy marmoset, *Cebuella pygmaea*, which Moynihan (1976a) had reported on for that first symposium. Based on several visits to the Putomayo of Colombia, Moynihan saw a number of serious issues, including an ever-increasing human population, widespread deforestation, and "the beginning of a pollution problem, a by-product of the developing petroleum industry." (This last item has not been much emphasized for primates, but is surely more of a threat than is generally recognized.)

Moynihan (1976a) noted that *Cebuella* might have benefited in the short term from "the recent partial clearing of land by immigrant human settlers," by potentially providing new food sources and new secondary habitat. But he noted that the pygmy marmosets were both hunted intensely and collected for export and sale, "in large numbers with enormous mortality." This situation, extrapolated to the other Amazonian marmosets, suggested that despite the remoteness of their forests, they too might be facing a sharp decline.

Echoing these concerns, and the strong focus on *Leontopithecus* which had developed during the 1970s, Thorington (1978) highlighted *Cebuella* and *Leontopithecus* as the two most urgent conservation priorities within the Callitrichidae. At the time, immediately after the callitrichid reassessment of Hershkovitz (1977), each of these genera was considered monotypic, and Thorington noted that these two species (*sensu* Hershkovitz) accounted for 50% of the generic diversity of the family as it was then known.[48] Thorington did not discount the other marmosets and tamarins, but he viewed *Saguinus* and *Callithrix* as much less threatened on the generic level, although still possessing taxa of concern. In particular, he pointed out *C. aurita* and *C. flaviceps* (then considered only subspecies of *C. jacchus*) as critically endangered; recommended that *S. bicolor* receive far more attention than it had to date; argued for the equal conservation of both Panamanian and Colombian *S. oedipus*, whose resplitting into the Panamanian *S. geoffroyi* he accurately predicted; touched on the dangerous situation of *S. leucopus*, which Hernández-Camacho and Cooper (1976) had already summarized; and argued for the preservation of the widespread and fantastically diverse *S. fuscicollis*, considering its subspecies to be worthy of protection each in their own right.

Thorington's essay was remarkably prescient, and all of the issues he drew attention to have remained critical concerns today. Writing in the late 1970s, he could not help but present an alarmist view of deforestation for the time: "a treeless Amazon valley," predicted for "the misty future of 2000 A.D." That future has come and gone, and many more trees remain than some had thought; but the issues facing callitrichids are as severe as ever – although for many species reliable knowledge is still difficult to obtain. Thorington ended his essay with a call for precisely the same research that is still so desperately needed today: fundamental surveys of callitrichid distributions, the better to assess priorities for the establishment of Amazonian reserves.

New information trickled in during the following decade, as the next generation of primatologists began to compile information from their fieldwork. The first major

---

[48] At this time, *Callimico* was still considered to be in its own family, the Callimiconidae, and Hershkovitz (1977) had only recognized the single genus *Callithrix* for all the marmosets.

synthesis for callitrichids came with the 1993 volume by Rylands on *Marmosets and Tamarins*, which included a summary by Rylands *et al.* (1993) of conservation concerns for each recognized taxon of *Callithrix* and *Saguinus*, as well as a listing of what parks and reserves were in their presumed distribution. These distributions updated those presented by Hershkovitz (1977), but were themselves quickly superseded by the spate of new discoveries which were underway, in particular the seven new species of *Callithrix* described between 1992 and 2000.

As detailed in Chapters III and IV, these new species were typically described on the basis of a small handful of specimens, and often from a single locality; their distributions were presumed rather than assessed, and the full extent of many species remains uncertain at best. Several recent surveys have proven valuable in clarifying previous assumptions (e.g. Noronha *et al.*, 2008a,b), but for the majority of the Amazonian marmosets, their full distributions are little better understood than when Thorington first discussed them – and in some cases, especially the dwarf marmoset *Callibella*, the original assessment of Alfred Wallace still rings true.

This general lack of knowledge brings a severe challenge to any attempt to assess the conservation status of these species. Although most of the recent species descriptions mention conservation, and occasionally note pending threats to specific areas of forest, rarely if ever do they compare a species' estimated range with its potential occurrence in protected areas. The exception is Rylands *et al.* (1993), in which the authors made a meticulous catalogue of all protected areas within the range of each callitrichid taxon, as it was understood at the time. Half a dozen new species have been described since that time, however, and many new protected areas have been designated in the Brazilian Amazon during the past fifteen years. How well those parks and reserves may actually protect the various marmosets is another question entirely.

Assessing the conservation status of any species is a complex enterprise, and over the past thirty years a complex discipline has developed, a strange fusion of the academic and environmentalist cultures, in which multi-billion-dollar agendas are proposed and challenged by a variety of competing intellectual interests (e.g. Brooks *et al.*, 2006). Comparatively large amounts of money are often spent on a handful of species, which are considered to have either enhanced public appeal or a special rationale for exceptional protection – or, as in the case of the great apes, all this and more (e.g. Oates *et al.*, 2007).

For the Amazonian marmosets, the comfortable assumption – or necessary triage, as the case may be – has been that their remote location, and their general tolerance for secondary and disturbed habitat, confers a certain resilience on these particular species. Their ability to survive in proximity to humans is certainly an advantage, but this is only a factor when the forest matrix encircles and far outmatches the human habitation. Bates may have spied tamarins in the neighborhood gardens of old Pará, but they had the surrounding forest to retreat into; today those same forests have long since been destroyed, and the soil that nurtured those trees is now compacted beneath the narrow asphalt streets of downtown Belém.

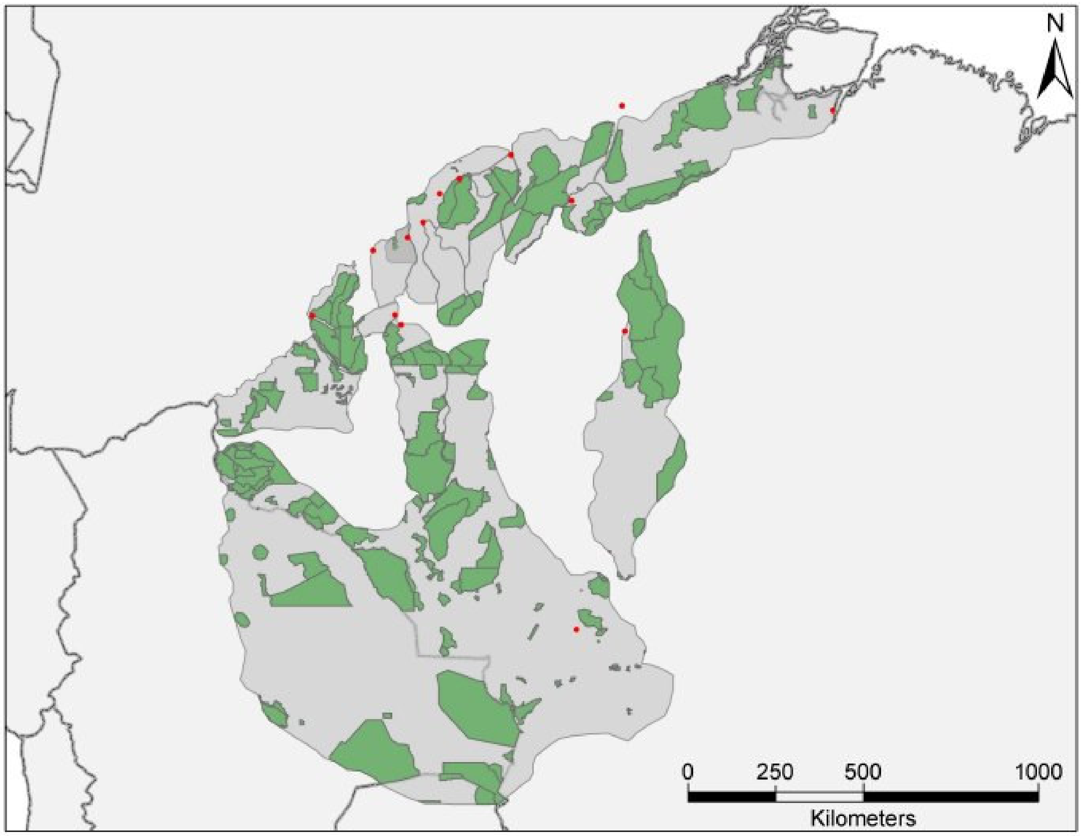

Figure 26. Protected area coverage of the Amazonian marmosets and *Callibella humilis*, using information made available by the World Database of Protected Areas (UNEP-WCMC, 2009) and current through February 2009. Red points indicate the type localities for all fifteen species considered (less the Rondônia marmoset, pending formal description), and indicate that in many cases the type localities – sometimes the only confirmed location for a particular species – are themselves not covered by protected areas. (Please note that the type locality for *Callithrix humeralifer*, as given by Hershkovitz (1977), appears to plot outside of this species' given range, but this is due to an evident error in the underlying shapefiles.)

Even a basic survey of ranges and protected areas demonstrates the difficulty in assessing the prospects of a species or a species group. In a preliminary analysis of protected area coverage, using the most recent World Database on Protected Areas (UNEP-WCMC, 2009), the distributions of most species of Amazonian marmosets seem to be reasonably well-represented in the current network of protected areas (Fig. 26). In this relatively simple approach, the estimated ranges for the Amazonian marmosets have been overlaid with the sum total of declared protected areas for the region.[49] At first glance there seems to be a thorough carpeting of large sections of forest by protected areas, many of them quite substantial. In the terms of the classic SLOSS debate – "single large or several small" – it seems the best possible solution to have several large reserves throughout a species' distribution, sprinkled liberally with many smaller ones. Several of the Amazonian marmosets have substantial portions of their range covered by protected areas, in some cases as much as 79 percent (Table 9).

But this sort of assessment can be easily misread, especially if the underlying assumptions of species distribution are not carefully considered beforehand. This is a particular concern for the Amazonian marmosets, with half the species group only recently described, and virtually none of them surveyed in full. For several of these species, including *Callithrix mauesi*, *C. saterei*, *C. acariensis* and *C. manicorensis*,

---

[49] This work was done in GIS by Krista Adamek of the Department of Wildlife and Fisheries Sciences, Texas A&M University, to whom all credit is due for the graphics and overlays. The shapefiles for the marmoset ranges are taken from the distribution data compiled by the Global Mammal Assessment of the IUCN, published in the 2008 IUCN Red List and Schipper *et al.* (2008). The shapefiles for protected areas were compiled and made publicly available by the World Database of Protected Areas, and are current through Feburary 2009.

Table 9. Protected area coverage for the Amazonian marmosets. *Callithrix* sp. nov., the Rondônia marmoset (Ferrari *et al.*, in press), has not yet been described and thus was not formally evaluated for the 2008 IUCN Red List of Threatened Species (IUCN, 2008).

species	**PA (km^2)**	**Range (km^2)**	**% Protected**	**Red List**
Callibella humilis	296.49	6375.24	4.7%	VU D2
Callithrix acariensis	6142.05	22442.06	27.4%	DD
Callithrix argentata	43883.32	137209.62	32.0%	LC
Callithrix chrysoleuca	4784.97	36452.64	13.1%	DD
Callithrix emiliae	62675.95	151987.22	41.2%	DD
Callithrix humeralifer	34120.07	63580.27	53.7%	DD
Callithrix intermedia	36005.67	62624.69	57.5%	LC
Callithrix leucippe	6894.39	14838.92	46.5%	VU A2c
Callithrix manicorensis	296.49	19881.52	1.5%	LC
Callithrix marcai	307.85	7000.64	4.4%	DD
Callithrix mauesi	11483.70	29586.31	38.8%	LC
Callithrix melanura	234103.84	850125.72	27.5%	LC
Callithrix nigriceps	25290.60	31646.92	79.9%	DD
Callithrix saterei	8208.62	19280.73	42.6%	LC
Callithrix sp. nov.	16615.01	70576.55	23.5%	–

virtually nothing is known of their distributions apart from their type localities, despite the shaded maps presented rather confidently in their original descriptions.

This by itself is hardly a sin, and the fact is that the Amazon is not much easier to survey today than it was in Bates' and Wallace's time, especially for the thinly populated, densely forested areas deep between the tributary rivers. Wallace himself dreamed of better ways to access the remote and tantalizing riches of the forest canopy:

> The whole glory of these forests could only be seen by sailing gently in a balloon over the undulating flowery surface above: such a treat is perhaps reserved for the traveller of a future age.

There have been a few limited attempts to survey the canopy from above, but for the most part, assessments must be done from below, which brings real limitations of finance and logistics. These factors, when acknowledged, certainly grant an understanding for the lack of available data. Even the muriquis of southeastern Brazil – the largest extant New World primates, surviving in the merest scraps and wisps of remnant forest – are still capable of surprises, and new populations are still being reported from intensively exploited landscapes (e.g. Talebi and Soares, 2005).

The problem arises through the strange alchemy of fact and supposition which can occur when assessments are conducted, and the results compiled and presented into crisp, polished maps with sophisticated overlays. The impeccably professional design can sometimes imply, through the gloss of its presentation, that the maps represent What Is Known, rather than what is only presumed or suspected. Although the Red List itself is careful to make this distinction (M. Hoffmann, pers. comm.), in practice it is all too easy for well-informed guesses to be taken as fully established facts – and when combined with an extensive array of parks and reserves, this can lead to all-too-human assumptions.

In the case of *Callithrix acariensis*, for instance, the southern quarter of its range is covered by an extensive set of protected areas which would seem to offer it a substantial degree of protection. There is, however, no evidence that the species occurs in these areas; the Acarí marmoset was described from a single captive female whose point of origin is unknown, and the type locality lies at the northernmost edge of its putative range. This situation recurs with several other species – such as *Callithrix leucippe*, which has not been reported from much of its presumed range, and *C. manicorensis*, most sightings of which have been along the west bank of the Rio Aripuanã.

Other species would seem to be well-covered by a variety of reserves throughout their range, such as *Callithrix humeralifer* (53.7%), *C. leucippe* (46.5%), *C. saterei* (42.6%) and *C. nigriceps* (79.9%). Some of the protected areas containing *C. melanura* are themselves larger than the entire known ranges of neighboring marmosets, and it seems likely that viable populations would flourish inside these reserves. A detailed assessment for each species would necessarily include some estimate of N_e, the effective population size, first outlined by Wright (1938) as the number of individuals required in a population to maintain its standing genetic diversity. This information, however, is almost completely lacking for marmosets in general; what research has been done is generally focused on the diversity of captive populations of lion tamarins.

A further question, however, is whether these reserves are adequate and effective at landscape protection – or whether, despite their extent on the map, the situation within their boundaries is no different from that without. The protected areas in this region are a pastiche of designations, not all of them designed specifically for biodiversity conservation. Much of the presumed range of *Callithrix nigriceps*, for instance, lies within a nominally protected area; but its range is crosscut by the Trans-Amazonian Highway, and cattle ranching is pervasive in the region – and again, the species has not been recorded from any protected area, which makes the presumed benefits circumstantial at best.

A full assessment of the conservation status of the Amazonian marmosets would require a detailed examination of each protected area within each species' range. Some basic analyses could be done remotely, in particular an overall estimate of habitat integrity within each protected area: the proportion of habitat lost to deforestation or other forms of conversion. The nature of each park and reserve also wants careful consideration – and, most importantly, the degree to which the park's regulations are enforced and outside encroachment is forestalled. In many cases, if not most, this will be virtually impossible, given the immensity of the landscape and the scarcity of personnel and other resources. The continued creation of new protected areas is certainly a net positive, but ultimately their effectiveness can only be determined by careful on-the-ground observation.

REFERENCES

Aguiar, J. M. and Lacher Jr., T. E. 2009. Cranial morphology of the dwarf marmoset *Callibella* in the context of callitrichid variability. In: *The Smallest Anthropoids: The Marmoset/Callimico Radiation*, S. M. Ford, L. C. Davis and L. M. Porter (eds.), pp.355–380. Springer, New York.

Aguiar, J. M., Amaral, A. T., Valladares-Pádua, C. B. and Prado, F. 2005. Black-Faced Lion Tamarin, *Leontopithecus caissara* Lorini and Persson, 1990. In: *Primates in Peril: The World's 25 Most Endangered Primates 2004-2006*, R. A. Mittermeier, C. Valladares-Pádua, A. B. Rylands, A. A. Eudey, T. M. Butynski, J. U. Ganzhorn, R. Kormos, J. M. Aguiar and S. Walker (eds.), p.22. Report to IUCN/SSC Primate Specialist Group (PSG), International Primatological Society (IPS) and Conservation International (CI), Washington, DC.

Aguiar, J. M. and Lacher Jr., T. E. 2005. Cranial morphology in callitrichid genera: Variability and diversification. Presented in the symposium "Advances in Marmoset and Goeldi's Monkey (*Callimico*) Research: Anatomy, Behavioral Ecology, Phylogeny, and Conservation" (S. M. Ford, L. M. Porter and L. C. Davis, organizers) at the 74th Annual Meeting of the American Association of Physical Anthropologists, Milwaukee, Wisconsin, USA, 6-9 April 2005.

Aguiar, J. M. and Lacher Jr., T. E. 2003. On the morphological distinctiveness of *Callithrix humilis* van Roosmalen *et al*., 1998. *Neotrop. Prim.* 11(1): 11–18.

Aguiar, J. M. and Lacher Jr., T. E. 2002. Patterns of morphological variation in the genus *Callithrix* in relation to landforms and protected areas. Presented at the XIXth Congress of the International Primatological Society, Beijing, China, August 2002.

Aguiar, J. M. 2001. *Callithrix humilis*. Unpublished report to the Margot Marsh Biodiversity Foundation, Great Falls, Virginia.

Aleixo, A. 2004. Historical diversification of a terra-firme forest bird superspecies: A phylogeographic perspective on the role of different hypotheses of Amazonian diversification. *Evolution* 58(6): 1303–1317.

Aleixo, A. 2002. Molecular systematics, phylogeography, and population genetics of *Xiphorhynchus* (Aves: Dendrocolaptidae) in the Amazon basin. Doctoral dissertation, Louisiana State University, Baton Rouge.

Allen, J. A. 1916. Mammals collected on the Roosevelt Brazilian Expedition, with field notes by Leo E. Miller. *Bull. Am. Mus. Nat. Hist.* 35(30): 559–610.

Alperin, R. 2002. Sobre a localidade tipo de *Mico marcai* (Alperin, 1993). *Neotrop. Prim.* 10(3): 126–128.

Alperin, R. 1993. *Callithrix argentata* (Linnaeus, 1771): Considerações taxonômicas e descrição de subespécie nova. *Bol. Mus. Para. Emílio Goeldi, Sér. Zool.* 9(2): 317–328.

Andriantompohavana, R., Lei, R., Zaonarivelo, J. R., Engberg, S. E., Nalanirina, G., McGuire, S. M., Shore, G. D., Andrianasolo, J., Herrington, K., Brenneman, R. A. and Louis Jr., E. E. 2007. Molecular phylogeny and taxonomic revision of the woolly lemurs, genus *Avahi* (Primates: Lemuriformes). *Texas Tech University Special Publications* 51: 1–59.

Andriantompohavana, R., Zaonarivelo, J. R., Engberg, S. E., Randriamampionona, R., McGuire, S. M., Shore, G. D., Rakotonomenjanahary, R., Brenneman, R. A. and Louis Jr., E. E. 2006. The mouse lemurs of northwestern Madagascar with a description of a new species at Lokobe Special Reserve. *Occ. Pap. Tex. Tech Univ. Mus.* (259): 1–23.

Anthony, N. M., Johnson-Bawe, M., Jeffery, K., Clifford, S. L., Abernethy, K. A., Tutin, C. E., Lahm, S. A., White, L. J. T., Utley, J. F., Wickings, E. J. and Bruford, M. W. 2007. The role of Pleistocene refugia and rivers in shaping gorilla genetic diversity in central Africa. *Proc. Natl. Acad. Sci. USA* 104(51): 20432–20436.

Ávila-Pires, F. D. de. 1986. On the validity of and geographical distribution of *Callithrix argentata emiliae* Thomas, 1920 (Primates, Callithricidae). In: *A Primatologia no Brasil – 2*, M. T. de Mello (ed.), pp.319–322. Sociedade Brasileira de Primatologia, Brasília.

Ávila-Pires, F. D. de. 1969. Taxonomia e zoogeografia do gênero '*Callithrix*' Erxleben, 1777 (Primates, Callithricidae). *Rev. Brasil Biol.* 29(1): 49–64.

Ayres, J. M. and Clutton-Brock, T. H. 1992. River boundaries and species range size in Amazonian primates. *Am. Nat.* 140(3): 531–537.

Ayres, J. M., Mittermeier, R. A. and Constable, I. D. 1982. Brazilian tamarins on the way to extinction? *Oryx* 16(4): 329–333.

Bakewell, P. J. 1997. *A History of Latin America: Empires and Sequels, 1450-1930.* Wiley-Blackwell, Oxford.

Barros, R. M. S., Pieczarka, J. C., Noronha, M. A., Silva Júnior, J. S. de, Moura, C. de S. and Nagamachi, C. Y. 1996. O cariótipo de *Callithrix* sp. n., nova espécie de primata. In: *Resumos. XXI Congresso Brasileiro de Zoologia*, p.219, Universidade Federal do Rio Grande do Sul, Porto Alegre, 5-9 February 1996.

Barroso, C. M. L., Schneider, H., Schneider, M. P. C., Sampaio, I., Harada, M. L., Czelusniak, J. and Goodman, M. 1997. Update on the phylogenetic systematics of New World monkeys: Further DNA evidence for placing the pygmy marmoset (*Cebuella*) within the genus *Callithrix*. *Int. J. Primatol.* 18(4): 651–674.

Bates, H. W. 1863. *The Naturalist on the River Amazons: A Record of Adventures, Habits of Animals, Sketches of Brazilian and Indian Life, and Aspects of Nature Under the Equator, During Eleven Years of Travel.* John Murray, London.

Bender, M. A. and Mettler, L. E. 1960. Chromosome studies of primates. II. *Callithrix*, *Leontocebus*, and *Callimico*. *Cytologia* (Tokyo) 25: 400–404.

Brooks, T. M., Mittermeier, R. A., Fonseca, G. A. B. da, Gerlach, J., Hoffmann, M., Lamoreux, J. F., Mittermeier, C. G., Pilgrim, J. D. and Rodrigues, A. S. L. 2006. Global biodiversity conservation priorities. *Science* 313(5783): 58–61.

Canavez, F. C., Moreira, M. A. M., Simon, F., Parham, P. and Seuánez, H. N. 1999. Phylogenetic relationships of the Callitrichinae (Platyrrhini, Primates) based on beta2-microglobulin DNA sequences. *Am. J. Primatol.* 48(3): 225–236.

Cartelle, C. and Hartwig, W. C. 1996. A new extinct primate among the Pleistocene megafauna of Bahia, Brazil. *Proc. Natl. Acad. Sci. USA* 93: 6405–6409.

Carvalho, C. T. de. 1959. Sobre a validez de *Callithrix leucippe* (Thos.) (Callithricidae, Primates). *Papeis Avulsos Dept. Zool. Sec. Agric. São Paulo* 13(27): 317–320.

Coimbra-Filho, A. F. 1997. Philip Hershkovitz. *Neotrop. Prim.* 5(2): 34–36.

Coimbra-Filho, A. F. 1969. Mico-leão, *Leontideus rosalia* (Linnaeus, 1766): Situação atual da espécie no Brasil (Callitrichidae, Primates). *Anais Acad. Brasil. Ciências* 41 (Suppl.): 29–52.

Cracraft, J. 1985. Historical biogeography and patterns of differentiation within the South American avifauna: Areas of endemism. *Amer. Ornithol. Union, Ornithol. Monogr.* 36: 49–84.

Cracraft, J. 1983. Species concepts and speciation analysis. In: *Current Ornithology*, Vol. 1, R. F. Johnston (ed.), pp.159–187. Plenum Press, New York.

Cruz Lima, E. da. 1945. *Mammals of Amazônia, Vol. 1. General Introduction and Primates*. Contribuições do Museu Paraense Emílio Goeldi de História Natural e Etnografia, Belém do Pará.

De Boer, L. E. M. 1974. Cytotaxonomy of the Platyrrhini (Primates). *Genen.*

*Phaenen.*17: 1–115.

de la Torre, S. and Yépez, P. 2003. Environmental education: A teaching tool for the conservation of pygmy marmosets (*Cebuella pygmaea*) in the Ecuadorian Amazon. *Neotrop. Prim.* 11(2): 73–75.

de la Torre, S., Snowdon, C. T. and Bejarano, M. 2000. Effects of human activities on pygmy marmosets in Ecuadorian Amazonia. *Biol. Conserv*. 94: 153–163.

Desmarest, A. G. 1827. Sagoin. *Dict. Sci. Nat.*, Paris 47: 9–24.

Digby, L. J. and Ferrari, S. F. 1994. Multiple breeding females in free-ranging groups of *Callithrix jacchus*. *Int. J. Primatol.* 15: 389–398.

Dollman, G. 1937. Exhibition and remarks upon a series of skins of marmosets and tamarins. *Proc. Zool. Soc. London, ser. C*, 107: 64–65.

Egler, S. G. 1992. Feeding ecology of *Saguinus bicolor bicolor* (Callitrichidae: Primates) in a relict forest in Manaus, Brazilian Amazon. *Folia Primatol.* 59: 61–76.

Egozcue, J., Perkins, J. E. M., Hagemenas, F. and Ford, D. M. 1969. The chromosomes of some Platyrrhini (*Callicebus*, *Ateles* and *Saimiri*). *Folia Primatol.* 11: 17–27.

Elliot, D. G. 1913. *A Review of the Primates. Monograph Series, Volume 1, Lemuroidea*: Daubentonia *to* Indris, *Anthropoidea*: Seniocebus *to* Saimiri. American Museum of Natural History, New York.

Emmons, L. H. and Feer, F. 1997. *Neotropical Rainforest Mammals: A Field Guide*. Second Edition. The University of Chicago Press, Chicago.

Encarnación, C. F. and Heymann, E. W. 1998. Body mass of wild *Callimico goeldii*. *Folia Primatol.* 69: 368–371.

Eriksson, J., Hohmann, G., Boesch, C. and Vigilant, L. 2004. Rivers influence the population genetic structure of bonobos (*Pan paniscus*). *Molec. Ecol*. 13: 3425–3435.

Erxleben, J. C. P. 1777. *Systema Regni Animalis per Classes, Ordines, Genera, Species, Varietates, cum Synonymia et Historia Animalium.* Weigand, Leipzig.

Faria, D. S. de. 1984a. Aspectos gerais do comportamento de *Callithrix jacchus penicillata* em mata ciliar do cerrado. In: *A Primatologia no Brasil*, M. T. de Mello (ed.), pp.55–65. Sociedade Brasileira de Primatologia, Brasília.

Faria, D. S. de. 1984b. Uso de árvores gomíferas do cerrado por *Callithrix jacchus penicillata*. In: *A Primatologia no Brasil*, M. T. de Mello (ed.), pp.83–96. Sociedade Brasileira de Primatologia, Brasília.

Ferrari, S. F., Sena, L., Schneider, M. P. C. and Silva Jr., J. S. In press. Rondon's marmoset, *Mico rondoni* sp. n., from southwestern Brazilian Amazonia. *Folia Primatologica*.

Ferrari, S. F. 2008. Gênero *Mico* Lesson 1840. In: *Primatas Brasileiros*, N. R. dos Reis, A. L. Peracchi and F. R. Andrade (eds.), pp.59–68. Universidade Estadual de Londrina and Technical Books Editora, Londrina, Paraná.

Ferrari, S. F., Iwanaga, S., Ravetta, A. L., Freitas, F. C., Sousa, R., Souza, L. L., Costa, C. G. and Coutinho, P. E. G. 2003. Dynamics of primate communities along the Santarém-Cuiaba highway in south-central Brazilian Amazonia. In: *Primates in Fragments: Ecology and Conservation*, L. K. Marsh (ed.), pp.123–157. Kluwer Academic / Plenum Publishers.

Ferrari, S. F., Sena, L. and Schneider, M. P. C. 1999. Definition of a new species of marmoset (Primates: Callithrichinae) from southwestern Amazonia based on molecular, ecological, and zoogeographic evidence. In: *Livro de Resumos do IX Congresso Brasileiro de Primatologia*, *Museu de Biologia Prof. Mello Leitão, Santa Teresa, Espírito Santo, Brazil, 25-30 July 1999*, S. L. Mendes (ed.), pp.80–81. Sociedade Brasileira de Primatologia.

Ferrari, S. F. 1993. Ecological differentiation in the Callitrichidae. In: *Marmosets and Tamarins: Systematics, Behaviour, and Ecology*, A. B. Rylands (ed.), pp.314–328. Oxford University Press, Oxford.

Ferrari, S. F. and Martins, E. S. 1992. Gummivory and gut morphology in two sympatric callitrichids (*Callithrix emiliae* and *Saguinus fuscicollis weddelli*) from western Brazilian Amazonia. *Am. J. Phys. Anth.* 88(1): 97–103.

Ferrari, S. F. and Lopes, M. A. 1992. A new species of marmoset, genus *Callithrix* Erxleben 1777 (Callitrichidae, Primates) from western Brazilian Amazonia. *Goeldiana Zoologia* (12): 1–13.

Fonseca, G. A. B. da and Lacher Jr., T. E. 1984. Exudate-feeding by *Callithrix jacchus penicillata* in semi-deciduous woodland (cerradão) in central Brazil. *Primates* 25: 441–450.

Ford, S. M. and Davis, L. C. 2009. Marmoset postcrania and the skeleton of the dwarf marmoset, *Callibella humilis*. In: *The Smallest Anthropoids: The Marmoset/Callimico*

Radiation, S. M. Ford, L. C. Davis and L. M. Porter (eds.), pp.411–448. Springer, New York.

Ford, S. M. and Davis, L. C. 2005. The skeleton of the dwarf marmoset, *Callibella humilis*: Functional and phylogenetic implications. Presented in the symposium "Advances in Marmoset and Goeldi's Monkey (*Callimico*) Research: Anatomy, Behavioral Ecology, Phylogeny, and Conservation" (S. M. Ford, L. M. Porter and L. C. Davis, organizers) at the 74th Annual Meeting of the American Association of Physical Anthropologists, Milwaukee, Wisconsin, USA, 6-9 April 2005.

Ford, S. M. 1980. Callithricids as phyletic dwarfs, and the place of the Callithricidae in the Platyrrhini. *Primates* 21: 31–43.

Garber, P. A. 1993. Feeding ecology and behaviour of the genus *Saguinus*. In: *Marmosets and Tamarins: Systematics, Behaviour, and Ecology*, A. B. Rylands (ed.), pp.273–295. Oxford University Press, Oxford.

Garber, P. A. and Teaford, M. F. 1986. Body weights in mixed species troops of *Saguinus mystax mystax* and *Saguinus fuscicollis nigrifrons* in Amazonian Peru. *Am. J. Phys. Anthropol*. 71: 331–336.

Garber, P. A. 1992. Vertical clinging, small body size, and the evolution of feeding adaptations in the Callitrichinae. *Am. J. Phys. Anth*. 88: 469–482.

Gascon, C., Malcolm, J. R., Patton, J. L., Silva, M. N. F. da, Bogart, J. P., Lougheed, S. C., Peres, C. A., Neckel, S. and Boag, P. T. 2000. Riverine barriers and the geographic distribution of Amazonian species. *Proc. Natl. Acad. Sci. USA* 97(25): 13672–13677.

Gascon, C., Lougheed, S. C. and Bogart, J. P. 1998. Patterns of genetic population differentiation in four species of Amazonian frogs: A test of the riverine barrier hypothesis. *Biotropica* 30(1): 104–119.

Gascon, C., Lougheed, S. C. and Bogart, J. P. 1996. Genetic and morphological variation in *Vanzolinius discodactylus*: A test of the river hypothesis of speciation. *Biotropica* 28(3): 376–387.

Geissmann, T. 2008. In search of China's last white-handed gibbons: A project report from the Nangunhe Nature Reserve in Yunnan Province. Gibbon Conservation Alliance, Jahresbericht Nr. 4, Zürich, Switzerland.

Gengozian, N., Batson, J. S. and Smith, T. A. 1978. Breeding of marmosets in a colony environment. *Prim. Med*. 10: 71–78.

Geoffroy Saint-Hilaire, I. 1827. Oustiti-*Jacchus*. *Dict. Class. Hist. Nat*. 12: 512–520.

Geoffroy Saint-Hilaire, I. 1851. *Catalogue méthodique de la collection de mammifères, de la collection des oiseaux et des collections annexes. Part. 1 – mammifères. Introduction et catalogue des Primates*. Museum Hist., Paris.

Gray, J. E. 1868. Notice of an interesting American monkey living in the Society's gardens. *Proc. Zool. Soc. Lond*. (1868): 256–257.

Gray, J. E. 1866. Notice of the new species of marmoset monkeys (*Hapale* and *Midas*). *Proc. Zool. Soc. Lond*. (1865): 733–735.

Gray, J. E. 1870. *Catalogue of Monkeys, Lemurs and Fruit-eating Bats in the Collections of the British Museum*. Trustees of the British Museum (Natural History), London.

Greenlee, W. B. 1938. *Voyage of Pedro Álvares Cabral to Brazil and India, from contemporary documents and narratives, translated with introd. and notes by William Brooks Greenlee*. Laurier Books Ltd.

Gregory, W. K. 1916. Studies on the evolution of primates. *Bull. Am. Mus. Nat. Hist*. 35: 239–255.

Groves, C. 2001. *Primate Taxonomy*. Smithsonian Institution Press, Washington, DC.

Haffer, J. 1969. Speciation in Amazonian forest birds. *Science* 165(3889): 131–137.

Hartwig, W. C. 1995. A giant New World monkey from the Pleistocene of Brazil. *J. Hum. Evol*. 28: 189–195.

Hartwig, W. C. and Cartelle, C. 1996. A complete skeleton of the giant South American primate *Protopithecus*. *Nature* 381: 307–311.

Hernández-Camacho, J. and Cooper, R. W. 1976. The nonhuman primates of Colombia. In: *Neotropical Primates: Field Studies and Conservation. Proceedings of a Symposium on the Distribution and Abundance of Neotropical Primates*, R. W. Thorington Jr. and P. G. Heltne (eds.), pp.35–69. National Academy of Sciences, Washington, DC.

Hershkovitz, P. 1977. *Living New World Monkeys (Platyrrhini) with an Introduction to Primates*, Vol. 1. The University Press of Chicago, Chicago.

Hershkovitz, P. 1975. Comments on the taxonomy of Brazilian marmosets (*Callithrix*, Callitrichidae). *Folia Primatol*. 24: 137–172.

Hershkovitz, P. 1970. Metachromism like it is. *Evolution* 24: 644–648.

Hershkovitz, P. 1969. The evolution of mammals on southern continents. VI. The recent mammals of the Neotropical region: A zoogeographic and ecological review. *Quarterly Review of Biology* 44(1): 1–70.

Hershkovitz, P. 1968. Metachromism or the principle of evolutionary change in mammalian tegumentary colors. *Evolution* 22: 556–575.

Hershkovitz, P. 1966a. On the identification of some marmosets Family Callithricidae (Primates). *Mammalia* 30(2): 327–332.

Hershkovitz, P. 1966b. Taxonomic notes on tamarins, genus *Saguinus* (Callithricidae, Primates), with descriptions of four new forms. *Folia Primatol.* 4: 381–395.

Heymann, E. W. 1998. Giant fossil New World primates: Arboreal or terrestrial? *J. Human. Evol.* 34(1): 99–101.

Hill, W. C. O. 1957. *Primates: Comparative Anatomy and Taxonomy, Vol. III. Hapalidae*. University Press of Edinburgh, Edinburgh.

Hill, W. C. O. 1959. The anatomy of *Callimico goeldii* (Thomas): A primitive American primate. *Trans. Amer. Phil. Soc., n.s.,* 49(5): 1–116.

Humboldt, F. H. A. von. 1812. *Recueil d'observations de zoologie et d'anatomie comparée, faites dans l'océan Atlantique, dans l'intérieur du nouveau continent et dans la mer du sud pendant les années 1799, 1800, 1801, 1802 et 1803. Premier volume. Deuxième partie. Observations de zoologie et d'anatomie comparée.* Schoell et Dufour & Co, Paris.

Illiger, C. 1811. *Prodromus Systematis Mammalium et Avium*. Salfeld, Berlin.

IUCN 2008. *2008 IUCN Red List of Threatened Species*. <http://www.iucnredlist.org>. Downloaded on 27 April 2009.

Jalil, M. F., Cable, J., Sinyor, J., Lackman-Ancrenaz, I., Ancrenaz, M., Bruford, M. W. and Goossens, B. 2008. Riverine effects on mitochondrial structure of Bornean orang-utans (*Pongo pygmaeus*) at two spatial scales. *Molec. Ecol.* 17: 2898–2909.

Jungers, W., Godfrey, L., Simons, E., Wunderlich, R., Richmond, B. and Chatrath, P. 2002. Ecomorphology and behavior of giant extinct lemurs from Madagascar. In: *Reconstructing Behavior in the Primate Fossil Record*, J. Plavcan, R. Kay, W. Jungers and C. P. van Schaik (eds.), pp.371–411. Kluwer Academic / Plenum Publishers, New York.

Kierulff, M. C. M., Raboy, B. E., de Oliveira, P. P., Miller, K., Passos, F. C. and Prado, F. 2002. Behavioral ecology of lion tamarins. In: *Lion Tamarins: Biology and Conservation*, D. G. Kleiman and A. B. Rylands (eds.), pp.157–187. Smithsonian Institution Press, Washington, DC.

Kingdon, J. 1997. *The Kingdon Field Guide to African Mammals*. Academic Press, London.

Kinzey, W. G. (Ed.). 1997. *New World Primates: Ecology, Evolution, and Behavior*. Aldine de Gruyter, New York.

Kleiman, D. G. and Rylands, A. B. (Eds.). 2002. *Lion Tamarins: Biology and Conservation*. Smithsonian Institution Press, Washington, DC.

Kuhl, H. 1820. *Beiträge zur Zoologie und vergleichenden Anatomie*. Verlag der Hermannschen Buchhandlung, Frankfurt am Main.

Lacher Jr., T. E., Fonseca, G. A. B. da, Alves Jr., C. and Magalhães Castro, B. 1981. Exudate-eating, scent-marking, and territoriality in wild populations of marmosets. *Anim. Behav*. 29: 306–307.

Lacher Jr., T. E., Fonseca, G. A. B. da, Alves Jr., C. and Magalhães Castro, B. 1984. Parasitism of trees by marmosets in a Central Brazilian gallery forest. *Biotropica* 16(3): 202–209.

Lawlor, T. E. 1969. The principle of metachromism: A critique. *Evolution* 23: 509–512.

Lehmann, J., Kern, D. C., Glaser, B. and Woods, W. I. (Eds.). 2004. *Amazonian Dark Earths: Origin, Properties, Management*. Springer, New York.

Lesson, R.-P. 1840. *Species des mammifères: Bimanes et quadrumanes; suivi d'un mémoire sur les Oryctéropes*. J. B. Baillière et Fils, Paris.

Leutenegger, W. 1979. Evolution of litter size in primates. *Am. Nat*. 114: 525–531.

Levine, R. M. 1999. *The History of Brazil*. Greenwood Press, Westport, Connecticut.

Linnaeus, C. 1771. *Mantissa Plantarum. Generum editionis VI et Specierum editionis*. Vol.3. L. Salvin, Stockholm.

Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Tenth Edition. L. Salvin, Stockholm.

Lorini, M. L. and Persson, V. G. 1990. Uma nova espécie de *Leontopithecus* Lesson, 1840, do sul do Brasil (Primates, Callitrichidae). *Boletim do Museu Nacional, Rio de Janeiro, nova sér., Zoologia* 338: 1–14.

Lougheed, S. C., Gascon, C., Jones, D. A., Bogart, J. P. and Boag, P. T. 1999. Ridges and rivers: A test of competing hypotheses of Amazonian diversification using a dart-poison frog (*Epipedobates femoralis*). *Proc. R. Soc. Lond., Ser. B Biol. Sci*. 266: 1829–1835.

Louis Jr., E. E., Engberg, S. E., McGuire, S. M., McCormick, M. J., Randriamampionona, R., Ranaivoarisoa, J. F., Bailey, C. A., Mittermeier, R. A. and Lei, R. 2008. Revision of the mouse lemurs, *Microcebus* (Primates, Lemuriformes), of Northern and Northwestern Madagascar with descriptions of two new species at Montagne d'Ambre National Park and Antafondro Classified Forest. *Primate Conservation* (23): 19–38.

Louis Jr., E. E., Engberg, S. E., Lei, R., Geng, H., Sommer, J. A., Randriamampionona, R., Randriamanana, J. C., Zaonarivelo, J. R., Andriantompohavana, R., Randria, G., Prosper, Ramaromilanto, B., Rakotoarisoa, G., Rooney, A. and Brenneman, R. A. 2006. Molecular and morphological analyses of the sportive lemurs (Family Megaladapidae: Genus *Lepilemur*) reveals 11 previously unrecognized species. *Texas Tech University Special Publications* 49: 1–49.

Mack, D. and Eudey, A. 1984. A review of the U.S. primate trade. In: *The International Primate Trade, Vol. 1: Legislation, Trade and Captive Breeding*, D. Mack and R. A. Mittermeier (eds.), pp.91–136. TRAFFIC U.S.A, Washington, DC.

Mann, C. C. 2002. The real dirt on rainforest fertility. *Science* 297(5583): 920–922.

Marroig, G. and Cheverud, J. M. 2009. Size and shape in callimico and marmoset skulls: Allometry and heterochrony in the morphological evolution of small anthropoids. In: *The Smallest Anthropoids: The Marmoset/Callimico Radiation*, S. M. Ford, L. C. Davis and L. M. Porter (eds.), pp.331–353. Springer, New York.

Marroig, G. and Cheverud, J. M. 2005. Size as a line of least evolutionary resistance: Diet and adaptive morphological radiation in New World monkeys. *Evolution* 59: 1128–1142.

Marroig, G., Cropp, S. and Cheverud, J. M. 2004. Systematics and evolution of the jacchus group of marmosets (Platyrrhini). *Am. J. Phys. Anthropol*. 123: 11–12.

Marsh, L. K. (Ed.). 2003. *Primates in Fragments*. Kluwer Academic / Plenum Publishers, New York.

Matschie, P. 1893. Zwei neue Affen (*Cercopithecus stuhlmanni* und *Hapale santaremensis*). *Sber. Ges. Naturf. Freunde, Berlin*: 255–258.

Meireles, C. M. M., Sampaio, N. I. C., Schneider, H. and Schneider, M. P. C. 1992. Protein variation, taxonomy and differentiation in five species of marmosets (genus *Callithrix* Erxleben, 1777). *Primates* 33(2): 227–238.

Miranda-Ribeiro, A. de. 1912. Zwei neue Affen unserer Fauna. *Brasilianische Rundschau* 2(1): 21–23.

Miranda-Ribeiro, A. de. 1940. Commentaries on South American primates. *Mem. Inst. Oswaldo Cruz, Rio de Janeiro* 35(4): 779–851.

Mittermeier, R. A., Louis, E. E., Richardson, M., Roos, C., Hawkins, F., Langrand, O., Konstant, W., Rasoloarison, R., Schwitzer, C., Rajaobelina, S., Ratsimbazafy, J. and Hoffmann, M. In prep. *Lemurs of Madagascar*. Third Edition. Conservation International Tropical Field Guide Series. Conservation International, Arlington, Virginia.

Mittermeier, R. A., Louis, E., Richardson, M., Konstant, W. R., Langrand, O., Hawkins, F., Ratsimbazafy, J., Rasoloarison, R., Ganzhorn, J., Rajaobelina, S. and Schwitzer, C. 2009a. *Lemurs of Madagascar Pocket Identification Guide: Diurnal and Cathemeral Lemurs*. Conservation International Tropical Pocket Guide Series #7. Conservation International, Arlington, Virginia.

Mittermeier, R. A., Louis, E., Richardson, M., Konstant, W. R., Langrand, O., Hawkins, F., Ratsimbazafy, J., Rasoloarison, R., Ganzhorn, J., Rajaobelina, S. and Schwitzer, C. 2009b. *Lemurs of Madagascar Pocket Identification Guide: Nocturnal Lemurs*. Conservation International Tropical Pocket Guide Series #8. Conservation International, Arlington, Virginia.

Mittermeier, R. A., Konstant, W. R., Hawkins, F., Louis Jr., E. E., Langrand, O., Ratsimbafazy, J., Rasoloarison, R., Ganzhorn, J. U., Rajaobelina, S., Tattersall, I. and Meyers, D. M. 2006. *Lemurs of Madagascar*. Second Edition. Conservation International, Washington, DC.

Mittermeier, R. A. 2002. Foreword. In: *Lion Tamarins: Biology and Conservation*, D. G. Kleiman and A. B. Rylands (eds.), pp.xv-xviii. Smithsonian Institution Press, Washington, DC.

Mittermeier, R. A., Rylands, A. B. and Konstant, W. R. 1999. Primates of the world: An introduction. In: *Walker's Primates of the World*, R. M. Nowak (ed.), pp.1–51. The Johns Hopkins University Press, Baltimore.

Mittermeier, R. A., Tattersall, I., Konstant, W. R., Meyers, D. and Mast, R. 1994. *Lemurs of Madagascar*. Conservation International, Washington, DC.

Mittermeier, R. A., Schwarz, M. and Ayres, J. M. 1992. A new species of marmoset, genus *Callithrix* Erxleben 1777 (Callitrichidae, Primates), from the Rio Maués region, state of Amazonas, Central Brazilian Amazonia. *Goeldiana Zoologia* (14): 1–17.

Mittermeier, R. A., Rylands, A. B. and Coimbra-Filho, A. F. 1988. Systematics: Species and subspecies — An update. In: *Ecology and Behavior of Neotropical Primates*, Vol. 2, R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho and G. A. B. da Fonseca (eds.), pp.13–75. World Wildlife Fund, Washington, DC.

Mittermeier, R. A. and Coimbra-Filho, A. F. 1981. Systematics: Species and subspecies. In: *Ecology and Behavior of Neotropical Primates*, Vol. 1, A. F. Coimbra-Filho and R. A. Mittermeier (eds.), pp.29–109. Academia Brasileira de Ciências, Rio de Janeiro.

Moynihan, M. 1976a. Notes on the ecology and behavior of the pygmy marmoset (*Cebuella pygmaea*) in Amazonian Colombia. In: *Neotropical Primates: Field Studies and Conservation. Proceedings of a Symposium on the Distribution and Abundance of Neotropical Primates*, R. W. Thorington Jr. and P. G. Heltne (eds.), pp.79–84. National Academy of Sciences, Washington, DC.

Moynihan, M. 1976b. *The New World Primates: Adaptive Radiation and the Evolution of Social Behavior, Languages and Intelligence*. Princeton University Press, Princeton.

Nagamachi, C. Y., Pieczarka, J. C., Muniz, J. A. P. C., Barros, R. M. S. and Mattevi, M. S. 1999. Proposed chromosomal phylogeny for the South American primates of the Callitrichidae family (Platyrrhini). *Am. J. Primatol.* 49: 133–152.

Natori, M. 1994. Craniometrical variations among eastern Brazilian marmosets and their systematic relationships. *Primates* 35(2): 167–176.

Neusser, M., Stanyon, R., Bigoni, F., Wienberg, J. and Mueller, S. 2001. Molecular cytotaxonomy of New World monkeys (Platyrrhini) – comparative analysis of five species by multi-color chromosome painting gives evidence for a classification of *Callimico goeldii* with the family of Callitrichidae. *Cytogenet. Cell Genet.* 94(3–4): 206–215.

Noronha, M. de A., Silva Júnior, J. de S., Spironello, W. R. and Ferreira, D. C. 2008. New occurrence records of Maués marmoset, *Mico mauesi* (Primates, Callitrichidae). *Neotrop. Prim.* 15(1): 24–26.

Noronha, M. de A., Spironello, W. R. and Ferreira, D. C. 2008. New occurrence records for *Mico melanurus* (Primates, Callitrichidae). *Neotrop. Prim.* 15(1): 26–28.

Nowak, R. M. 1999. *Walker's Primates of the World.* The Johns Hopkins University Press, Baltimore.

Oates, J., Sunderland-Groves, J., Bergl, R., Dunn, A., Nicholas, A., Takang, E., Omeni, F., Imong, I., Fotso, R., Nkembi, L. and Williamson, L. 2007. *Regional Action Plan for the Conservation of the Cross River Gorilla* (Gorilla gorilla diehli). IUCN/SSC Primate Specialist Group and Conservation International, Arlington, Virginia.

Oren, D. C. 1993. Did ground sloths survive to recent times in the Amazon region? *Goeldiana Zoologia* (19): 1–11.

Pelzeln, A. von. 1883. Brasilische Säugethiere: Resultate von Johann Natterer's Reisen in der Jahren 1817 bis 1835. *Verh. K. K. Zool.-Bot. Gesellsch., Beih.* 33: 1–140.

Peres, C. A., Patton, J. L. and da Silva, M. N. F. 1996. Riverine barriers and gene flow in Amazonian saddle-back tamarins. *Folia Primatologica* 67: 113–124.

Peres, C. A. 1989. Exudate-feeding by wild golden lion tamarins, *Leontopithecus rosalia*. *Biotropica* 21: 287–288.

Petter, J.-J., Albignac, R. and Rumpler, Y. 1977. *Faune de Madagascar. No. 44. Mammifères Lémuriens (Primates Prosimiens).* ORSTOM/CNRS, Paris.

Porter, C. A., Czelusniak, J., Schneider, H., Schneider, M. P. C., Sampaio, I. and Goodman, M. 1997. Sequences of the primate epsilon-globin gene: Implications for systematics of the marmosets and other New World primates. *Gene* 205(1-2): 59–71.

Porter, L. M. 2007. *The Behavioral Ecology of Callimicos and Tamarins in Northwestern Bolivia*. Pearson Prentice Hall, New Jersey.

Quammen, D. 1997. You looking for me? *Sports Illustrated*, 3 Feb. 1997, pp.66–76.

Radespiel, U., Olivieri, G., Rasolofoson, D. W., Rakotondratsimba, G., Rakotonirainy, O., Rasoloharijoana, S., Randrianambinina, B., Ratsimbazafy, J. H., Ratelolahay, F., Randriamboavonjy, T., Rasolofoharivelo, T., Craul, M., Rakotozafy, L. and Randrianarison, R. M. 2008. Exceptional diversity of mouse lemurs (*Microcebus* spp.) in the Makira region with the description of one new species. *Am. J. Primatol.* 70: 1033–1046.

Redford, K. H. and Stearman, A. M. 1993. Forest-dwelling native Amazonians and the conservation of biodiversity: Interests in common or in collision? *Conserv. Biol.* 7(2): 248–255.

Redford, K. H. 1991. The ecologically noble savage. *Orion* 9: 24–29.

Reichenbach, H. G. L. 1862. *Die vollständigste Naturgeschichte der Affen*. Dresden and Leipzig.

dos Reis, N. R., Peracchi, A. L. and Andrade, F. R. (Eds.). 2008. *Primatas Brasileiros*. Universidade Estadual de Londrina and Technical Books Editora, Londrina, Paraná.

dos Reis, N. R., Peracchi, A. L., Pedro, W. A. and Lima, I. P. de. (Eds.). 2006. *Mamíferos do Brasil*. Secretaria de Estado do Meio Ambiente e Recursos Hídricos e vários colaboradores. Londrina, Paraná.

Roda, S. A. and Pontes, A. R. M. 1998. Polygyny and infanticide in common marmosets in a fragment of the Atlantic Forest of Brazil. *Folia Primatol.* 69: 372–376.

Rosenberger, A. L. and Coimbra-Filho, A. F. 1984. Morphology, taxonomic status and affinities of the lion tamarins, *Leontopithecus* (Callitrichinae, Cebidae). *Folia Primatol.* 42: 149–179.

Rosenberger, A. L. 1981. Systematics: The higher taxa. In: *Ecology and Behavior of Neotropical Primates*, Vol. 1, A. F. Coimbra-Filho and R. A. Mittermeier (eds.), pp.9–27. Academia Brasileira de Ciências, Rio de Janeiro.

Rylands, A. B. In litt. Primate taxonomic listing. Unpublished report for the IUCN/SSC Primate Specialist Group, Conservation International, Arlington, Virginia.

Rylands, A. B., Mittermeier, R. A. and Coimbra-Filho, A. F. 2009. The systematics and distributions of the marmosets (*Callithrix*, *Callibella*, *Cebuella* and *Mico*) and callimico (*Callimico*)(Callitrichidae, Primates). In: *The Smallest Anthropoids: The Marmoset/Callimico Radiation*, S. M. Ford, L. C. Davis and L. M. Porter (eds.), pp.25–61. Springer, New York.

Rylands, A. B. and Mittermeier, R. A. 2009. The diversity of the New World primates (Platyrrhini): An annotated taxonomy. In: *South American Primates: Comparative Perspectives in the Study of Behavior, Ecology, and Conservation*, P. A. Garber, A. Estrada, J. C. Bicca-Marques, E. W. Heymann and K. B. Strier (eds.), pp.23–54. Springer, New York.

Rylands, A. B., Mittermeier, R. A., Coimbra-Filho, A. F., Heymann, E. W., de la Torre, S., Silva Jr., J. de S., Kierulff, M. C. M., Noronha, M. de A. and Röhe, F. 2008.

Marmosets and Tamarins Pocket Identification Guide. Conservation International Tropical Pocket Guide Series #5. Conservation International, Arlington, Virginia.

Rylands, A. B. and Chiarello, A. G. 2003. Official List of Brazilian Fauna Threatened with Extinction – 2003. *Neotrop. Prim.* 11(1): 43–49.

Rylands, A. B., Schneider, H., Langguth, A., Mittermeier, R. A., Groves, C. P. and Rodríguez-Luna, E. 2000. An assessment of the diversity of New World primates. *Neotrop. Primates* 8(2): 61–93.

Rylands, A. B., Fonseca, G. A. B. da, Leite, Y. L. R. and Mittermeier, R. A. 1996. Primates of the Atlantic Forest: Origin, distributions, endemism, and communities. In: *Adaptive Radiations of Neotropical Primates*, M. A. Norconk, A. L. Rosenberger and P. A. Garber (eds.), pp.21–51. Plenum Press, New York.

Rylands, A. B., Mittermeier, R. A. and Rodríguez-Luna, E. 1995. A species list for the New World primates (Platyrrhini): Distribution by country, endemism, and conservation status according to the Mace-Lande system. *Neotrop. Primates* 3(Suppl.): 113–160.

Rylands, A. B., Coimbra-Filho, A. F. and Mittermeier, R. A. 1993. Systematics, geographic distribution, and some notes on the conservation status of the Callitrichidae. In: *Marmosets and Tamarins: Systematics, Behaviour, and Ecology*, A. B. Rylands (ed.), pp.11–77. Oxford University Press, Oxford.

Rylands, A. B. and de Faria, D. S. 1993. Habitats, feeding ecology, and home range size in the genus *Callithrix*. In: *Marmosets and Tamarins: Systematics, Behaviour, and Ecology*, A. B. Rylands (ed.), pp. 262–272. Oxford University Press, Oxford.

Rylands, A. B. (Ed.). 1993. *Marmosets and Tamarins: Systematics, Behaviour, and Ecology*. Oxford University Press, Oxford.

Rylands, A. B. and de Faria, D. S. 1987. Habitats and feeding ecology of the genus *Callithrix. Int. J. Primatol.* 8: 438.

Rylands, A. B. 1984. Exudate-eating and tree-gouging by marmosets (Callitrichidae, Primates). In: *Tropical Rain Forest: The Leeds Symposium*, A. C. Chadwick and S. L. Sutton (eds.), pp.155–168. Leeds Philosophical and Literary Society, Leeds.

Rylands, A. B. 1982. The behaviour and ecology of three species of marmosets and tamarins (Callitrichidae, Primates) in Brazil. Doctoral dissertation, University of Cambridge, Cambridge.

Schipper, J., Chanson, J. S., Chiozza, F., Cox, N. A., Hoffmann, M., Katariya, V., Lamoreux, J. F., Rodrigues, A. S. L., Stuart, S. N., Temple, H. J., Baillie, J., Boitani, L., Lacher Jr., T. E., Mittermeier, R. A., Smith, A. T., Absolon, D., Aguiar, J. M., Amori, G., Bakkour, N., Baldi, R., Berridge, R. J., Bielby, J., Black, P. A., Blanc, J., Brooks, T. M., Burton, J. A., Butynski, T. M., Catullo, G., Chapman, R., Cokeliss, Z., Collen, B., Conroy, J., Cooke, J. G., Fonseca, G. A. B. da, Derocher, A. E., Dublin, H. T., Duckworth, J. W., Emmons, L., Emslie, R. H., Festa-Bianchet, M., Foster, M., Foster, S., Garshelis, D. L., Gates, C., Giménez-Dixon, M., Gonzalez, S., Gonzalez-Maya, J. F., Good, T. C., Hammerson, G., Hammond, P. S., Happold, D., Happold, M., Hare, J., Harris, R. B., Hawkins, C. E., Haywood, M., Heaney, L. R., Hedges, S., Helgen, K. M., Hilton-Taylor, C., Hussain, S. A., Ishii, N., Jefferson, T. A., Jenkins, R. K. B., Johnston, C. H., Keith, M., Kingdon, J., Knox, D. H., Kovacs, K. M., Langhammer, P., Leus, K., Lewison, R., Lichtenstein, G., Lowry, L. F., Macavoy, Z., Mace, G. M., Mallon, D. P., Masi, M., McKnight, M. W., Medellín, R. A., Medici, P., Mills, G., Moehlman, P. D., Molur, S., Mora, A., Nowell, K., Oates, J. F., Olech, W., Oliver, W. R. L., Oprea, M., Patterson, B. D., Perrin, W. F., Polidoro, B. A., Pollock, C., Powel, A., Protas, Y., Racey, P., Ragle, J., Ramani, P., Rathbun, G., Reeves, R. R., Reilly, S. B., Reynolds III, J. E., Rondinini, C., Rosell-Ambal, R. G., Rulli, M., Rylands, A. B., Savini, S., Schank, C. J., Sechrest, W., Self-Sullivan, C., Shoemaker, A., Sillero-Zubiri, C., Silva, N. De, Smith, D. E., Srinivasulu, C., Stephenson, P. J., Strien, N. van, Talukdar, B. K., Taylor, B. L., Timmins, R., Tirira, D. G., Tognelli, M. F., Tsytsulina, K., Veiga, L. M., Vié, J.-C., Williamson, E. A., Wyatt, S. A., Xie, Y. and Young, B. E. 2008. The status of the world's land and marine mammals: Diversity, threat, and knowledge. *Science* 322(5899): 225–230.

Schlegel, H. 1876. *Muséum d'Histoire Naturelle des Pays Bas. Revue Méthodique et critique des collections déposées dans cet établissement. Tome 7. Monographie 40: Simiae*. Brill, Leiden.

Schneider, H. 2000. The current status of the New World monkey phylogeny. *Anais da Academia Brasileira de Ciências* 72: 165–172.

Schneider, H., Sampaio, I., Harada, M. L., Barroso, C. M. L., Schneider, M. P. C., Czelusniak, J. and Goodman, M. 1996. Molecular phylogeny of the New World monkeys (Platyrrhini, Primates) based on two unlinked nuclear genes: IRBP Intron 1 and ε-globin sequences. *Am. J. Phys. Anthropol.* 100: 153–179.

Schröpel, M. 2003. Weight development of hand-reared callitrichids. *Neotrop. Prim.* 11(2): 110–114.

Schwartzman, S., Moreira, A. and Nepstad, D. 2000. Rethinking tropical forest conservation: Perils in parks. *Conserv. Biol.* 14(5): 1351–1357.

Sclater, P. L. 1871. Notes on rare or little-known animals now or lately living in the Society's Gardens. *Proc. Zool. Soc. London* (1871): 221–240.

Sclater, P. L. 1869. Remarks on two species of mammals described from specimens recently living in the Society's Gardens. *Proc. Zool. Soc. London* (1869): 592–596.

Sena, L., Vallinoto, M., Sampaio, I., Schneider, H., Ferrari, S. and Schneider, M. P. C. 2002. Mitochondrial COII gene sequences provide new insights into the phylogeny of marmoset species groups (Callitrichidae, Primates). *Folia Primatologica* 73(5): 240–251.

Sena, L. dos S. 1998. Filogenia do gênero *Callithrix* Erxleben 1777 (Callitrichinae, Platyrrhini) baseada em seqüências do gene mitocondrial da citocromo oxidase II (COII). Master's thesis, Universidade Federal do Pará, Belém.

Silva, M. N. F. da, Shepard Jr., G. H. and Yu, D. W. 2005. Conservation implications of primate hunting practices among the Matsigenka of Manu National Park. *Neotrop. Prim.* 13(2): 31–36.

Silva Jr., J. S. and Noronha, M. de A. 1998. On a new species of bare-eared marmoset, genus *Callithrix* Erxleben, 1777, from central Amazonia, Brazil (Primates: Callitrichidae). *Goeldiana Zoologia* (21): 1–28.

Simões, P. I., Lima, A. P. and Magnusson, W. E. 2008. Acoustic and morphological differentiation in the frog *Allobates femoralis*: Relationships with the upper Madeira River and other potential geological barriers. *Biotropica* 40(5): 607–614.

Simpson, G. G. 1980. *Splendid Isolation: The Curious History of South American Mammals*. Yale University Press, New Haven.

Snowdon, C. T. and Soini, P. 1988. The tamarins, genus *Saguinus*. In: *Ecology and Behavior of Neotropical Primates*, Vol. 2, R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho and G. A. B. da Fonseca (eds.), pp.223–298. World Wildlife Fund, Washington, DC.

Soini, P. 1988. The pygmy marmoset, genus *Cebuella*. In: *Ecology and Behavior of Neotropical Primates*, Vol. 2, R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho and G. A. B. da Fonseca, (eds.), pp.79–130. World Wildlife Fund, Washington, DC.

Soini, P. 1982. Ecology and population dynamics of the pygmy marmoset, *Cebuella pygmaea*. *Folia Primatol.* 39: 1–21.

Solomon, S. E., Bacci Jr., M., Martins Jr., J., Vinha, G. G. and Mueller, U. G. 2008. Paleodistributions and comparative molecular phylogeography of leafcutter ants (*Atta* spp.) provide new insight into the origins of Amazonian diversity. *PLoS ONE* 3(7): e2738. doi:10.1371/journal.pone.0002738.

Solomon, S. E. 2007. Biogeography and evolution of widespread leafcutting ants, *Atta* spp. (Formicidae, Attini). Doctoral dissertation, University of Texas at Austin, Austin.

Spix, J. de. 1823. *Simiarum et Vespertilionum Brasiliensium species novae; ou, Histoire Naturelle des Espèces Nouvelles de Singes et de Chauves-souris observées et recueillies pendant le voyage dans l'intérieur du Brésil*. Typis Francisci Seraphici Hubschmanni, Monachii.

SPSS, Inc. 2003. SPSS 13.0. Chicago, Illinois.

Stevenson, M. F. and Rylands, A. B. 1988. The marmosets, genus *Callithrix*. In: *Ecology and Behavior of Neotropical Primates*, Vol. 2, R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho and G. A. B. da Fonseca (eds.), pp.131–222. World Wildlife Fund, Washington, DC.

Stevenson, M. F. 1977. The common marmoset (*Callithrix jacchus jacchus*) as a model for ethological research. *Lab. Anim. Sci*. 27: 895–900.

Tagliaro, C. H., Schneider, H., Sampaio, I., Schneider, M. P. C., Vallinoto, M. and Stanhope, M. 2005. Molecular phylogeny of the genus *Saguinus* (Platyrrhini, Primates) based on the ND1 mitochondrial gene and implications for conservation. *Genet. Molec. Biol.* 28(1): 46–53.

Tagliaro, C. H., Schneider, M. P. C., Schneider, H., Sampaio, I. C. and Stanhope, M. J. 1997. Marmoset phylogenetics, conservation perspectives, and evolution of the mtDNA control region. *Molec. Biol. Evol.* 14(6): 674–684.

Talebi, M. and Soares, P. 2005. Conservation research on the southern muriqui (*Brachyteles arachnoides*) in São Paulo State, Brazil. *Neotrop. Prim.* 13(Suppl.): 53–59.

Tattersall, I. 1982. *The Primates of Madagascar*. Columbia University Press, New York.

Taylor, A. B., Eng, E. M., Anapol, F. C. and Vinyard, C. J. 2009. The functional significance of jaw-muscle fiber architecture in tree-gouging marmosets. In: *The Smallest Anthropoids: The Marmoset/Callimico Radiation*, S. M. Ford, L. C. Davis and L. M. Porter (eds.), pp.381-394. Springer, New York.

Telfer, P. T., Souquière, S., Clifford, S. L., Abernethy, K. A., Bruford, M. W., Disotell, T. R., Sterner, K. N., Roques, P., Marx, P. A. and Wickings, E. J. 2003. Molecular evidence for deep phylogenetic divergence in *Mandrillus sphinx*. *Molec. Ecol.* 12: 2019–2024.

Thomas, O. 1903. Notes on South American monkeys, bats, carnivores, and rodents, with descriptions of new species. *Ann. Mag. Nat. Hist., Ser. 7,* 12: 455–464.

Thomas, O. 1904. New *Callithrix*, *Midas*, *Felis*, *Rhipidomys*, and *Proechimys* from Brazil and Ecuador. *Ann. Mag. Nat. Hist.*, *Ser. 7*, 14: 188–196.

Thomas, O. 1912. On small mammals from the lower Amazon. *Ann. Mag. Nat. Hist., Ser. 8*, 9: 84–90.

Thomas, O. 1913. On some rare Amazonian mammals from the collection of the Para Museum, *Ann. Mag. Nat. Hist., Ser. 8*, 11: 130–136.

Thomas, O. 1920. On mammals from the lower Rio Amazonas in the Goeldi Museum, Pará. *Ann. Mag. Nat. Hist.*, S*er. 9*, 6: 266–283.

Thomas, O. 1922. On the systematic arrangement of the marmosets. *Ann. Mag. Nat. Hist., Ser.* 9, 9: 196–199.

Thomas, O. 1928. The Godman-Thomas expedition to Peru. VIII. On mammals obtained by Mr. Hendee at Pebas and Iquitos, upper Amazons. *Ann. Mag. Nat. Hist*., *Ser. 10*, 2: 285–294.

Thorington Jr., R. W. 1988. Taxonomic status of *Saguinus tripartitus* (Milne-Edwards, 1878). *Am. J. Primatol.* 15: 367–371.

Thorington Jr., R. W. 1978. Some problems relevant to the conservation of the Callitrichidae. *Primates in Medicine* 10: 1–11.

Thorington Jr., R. W. and Heltne, P. G. (Eds.). 1976. *Neotropical Primates: Field Studies and Conservation. Proceedings of a Symposium on the Distribution and Abundance of Neotropical Primates*. National Academy of Sciences, Washington, DC.

Trouessart, E. L. 1904. *Catalogus Mammalium tam viventium quam fossilium. Quinquennale Suplementum.* R. Friedlander and Sohn, Berolini.

UNEP-WCMC. 2009. World Database on Protected Areas. <http://www.unep-wcmc.org/wdpa.> Accessed April 21, 2009.

Vallinoto, M., Araripe, J., Rego, P. S. do, Tagliaro, C. H., Sampaio, I. and Schneider, H. 2006. Tocantins river as an effective barrier to gene flow in *Saguinus niger* populations. *Genet. Molec. Biol*. 29(2): 215–219.

Van Roosmalen, M. G. M. and Van Roosmalen, T. 2003. The description of a new marmoset genus, *Callibella* (Callitrichinae, Primates), including its molecular phylogenetic status. *Neotrop. Prim.* 11(1): 1–10.

Van Roosmalen, M. G. M., Van Roosmalen, T. and 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*, from Brazilian Amazonia. *Neotrop. Prim.* 10(Suppl.): 1–52.

Van Roosmalen, M. G. M. 2002. Conservation status of primates in the Brazilian Amazon. Presented at the XIXth Congress of the International Primatological Society, August 2002, Beijing, China.

Van Roosmalen, M. G. M., Van Roosmalen, T., Mittermeier, R. A. and Rylands, A. B. 2000. Two new species of marmoset, genus *Callithrix* Erxleben, 1777 (Callitrichidae, Primates), from the Tapajós/Madeira interfluvium, south central Amazonia, Brazil. *Neotrop. Prim.* 8(1): 2–18.

Van Roosmalen, M. G. M., Van Roosmalen, T., Mittermeier, R. A. and 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.

Veracini, C. 2009. Habitat use and ranging behavior of the silvery marmoset (*Mico argentatus*) at Caxiuanã National Forest (eastern Brazilian Amazonia). In: *The Smallest Anthropoids: The Marmoset/Callimico Radiation*, S. M. Ford, L. C. Davis and L. M. Porter (eds.), pp.221–240. Springer, New York.

Vinyard, C. J., Wall, C. E., Williams, S. H., Mork, A. L., Garner, B. A., Oliveiro Melo, L. C. de, Valença-Montenegro, M. M., Valle, Y. B. M., Monteiro da Cruz, M. A. O., Lucas, P. W., Schmitt, D., Taylor, A. B. and Hylander, W. L. 2009. The evolutionary morphology of tree gouging in marmosets. In: *The Smallest Anthropoids: The Marmoset/Callimico Radiation*, S. M. Ford, L. C. Davis and L. M. Porter (eds.), pp.395–409. Springer, New York.

Vivo, M. de. 1991. *Taxonomia de* Callithrix *Erxleben, 1777 (Callitrichidae, Primates).* Fundação Biodiversitas, Belo Horizonte.

Vivo, M. de. 1988. Sistemática de *Callithrix* Erxleben, 1777 (Callitrichidae, Primates). Doctoral dissertation, Universidade de São Paulo, São Paulo.

Vivo, M. de. 1985. On some monkeys from Rondônia, Brasil (Primates: Callitrichidae, Cebidae). *Pap. Avulsos Zool., São Paulo* 36(11): 103–110.

Wagner, J. A. 1840. *Die Säugethiere in Abbildungen nach des Natur mit Beschreibungen von Dr. Johann Christian Daniel von Schreber*. Suppl., vol. 1. Erlangen.

Wagner, J. A. 1842. Diagnosen neuer Arten brasilischer Saugtheire. *Wiegmann's Archiv für Naturgeschichte, Achter Jargang, Erster Band*: 356–362.

Wallace, A. R. 1876. *The Geographical Distribution of Animals, With A Study of the Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth's Surface*, Vol. 2. Harper & Brothers, New York.

Wallace, A. R. 1853. *A Narrative of Travels on the Amazon and Rio Negro, with an Account of the Native Tribes, and Observations on the Climate, Geology, and Natural History of the Amazon Valley*. London.

Wallace, A. R. 1852. On the monkeys of the Amazon. *Proc. Zool. Soc. London* 20: 107–110.

Wilson, D. E. and Reeder, D. M. (Eds.). 2005. *Mammal Species of the World: A Taxonomic and Geographic Reference*. Third Edition, Vol. 1. The Johns Hopkins University Press, Baltimore.

Wright, S. 1938. Size of population and breeding structure in relation to evolution. *Science* 87: 430–431.

Yamamoto, M. E., de Fátima Arruda, M., Alencar, A. I., de Sousa, M. B. C. and Araújo, A. 2009. Mating systems and female-female competition in the common marmosets, *Callithrix jacchus*. In: *The Smallest Anthropoids: The Marmoset/Callimico Radiation*, S. M. Ford, L. C. Davis and L. M. Porter (eds.), pp.119–133. Springer, New York.

Yépez, P., de la Torre, S., Pallares, M. and Snowdon, C. T. 2002. Área de vida y preferencias alimenticias del leoncillo *Callithrix (Cebuella) pygmaea* en el nororiente ecuatoriano. In: *CD Memorias del I Congreso de Ecología y Ambiente – Ecuador, País Megadiverso*, S. de la Torre and G. Reck (eds.). Universidad San Francisco de Quito, Ecuador.

Youlatos, D. 2009. Locomotion, postures, and habitat use by pygmy marmosets (*Cebuella pygmaea*). In: *The Smallest Anthropoids: The Marmoset/Callimico Radiation*, S. M. Ford, L. C. Davis and L. M. Porter (eds.), pp.279–297. Springer, New York.

APPENDIX A

Output Tables for River-Barrier Analyses
All-species MANOVA

Table 3

Levene's Test of Equality of Error Variances(a)

	F	df1	df2	Sig.
lnCL	.827	7	293	.566
lnOCP	1.336	7	293	.233
lnSKW	.796	7	293	.591
lnOWC	.931	7	293	.483
lnBL	2.060	7	293	.048
lnCONW	1.620	7	293	.129
lnBN	1.704	7	293	.108
lnPBG	1.264	7	293	.268
lnNP	1.814	7	293	.084
lnNL	.927	7	293	.486
lnPL	.680	7	293	.689
lnSGLL	.520	7	293	.819
lnSGLR	.954	7	293	.465
lnCJBL	.584	7	293	.769
lnCJBR	1.226	7	293	.288
lnSCNL	1.145	7	293	.335
lnSCNR	1.032	7	293	.409
lnJWCY	1.643	7	293	.123

Tests the null hypothesis that the error variance of the dependent variable is equal across groups.
a Design: Intercept+species

Table 4

lnOCP

	species	N	Subset		
			2	3	1
Tukey HSD(a,b)	14	113	3.5961		
	2	11	3.6036	3.6036	
	12	23	3.6056	3.6056	3.6056
	11	68	3.6099	3.6099	3.6099
	1	31	3.6247	3.6247	3.6247
	3	5	3.6289	3.6289	3.6289
	9	4		3.6304	3.6304
	7	46			3.6380
	Sig.		.059	.219	.065

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 12.086.
b Alpha = .05.

lnOWC

	species	N	Subset			
			2	3	4	1
Tukey HSD(a,b)	14	113	3.2518			
	12	23	3.2654	3.2654		
	2	11	3.2684	3.2684	3.2684	
	1	31	3.2702	3.2702	3.2702	
	11	68	3.2724	3.2724	3.2724	
	3	5		3.2968	3.2968	3.2968
	7	46			3.3027	3.3027
	9	4				3.3154
	Sig.		.610	.108	.054	.725

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 12.086.
b Alpha = .05.

lnBL

	species	N	Subset	
			2	1
Tukey HSD(a,b)	14	113	2.9851	
	11	68	3.0017	3.0017
	7	46	3.0238	3.0238
	2	11	3.0256	3.0256
	9	4	3.0300	3.0300
	1	31	3.0472	3.0472
	12	23	3.0504	3.0504
	3	5		3.0652
	Sig.		.136	.161

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .004.
a Uses Harmonic Mean Sample Size = 12.086.
b Alpha = .05.

lnNP

	species	N	Subset	
			2	1
Tukey HSD(a,b)	1	31	2.6612	
	3	5	2.6653	2.6653
	14	113	2.6669	2.6669
	2	11	2.6743	2.6743
	12	23	2.6805	2.6805
	11	68	2.6843	2.6843
	7	46	2.7058	2.7058
	9	4		2.7244
	Sig.		.299	.051

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .002.
a Uses Harmonic Mean Sample Size = 12.086.
b Alpha = .05.

lnPL

	species	N	Subset	
			2	1
Tukey HSD(a,b)	14	113	3.8152	
	2	11	3.8223	3.8223
	12	23	3.8294	3.8294
	11	68	3.8319	3.8319
	3	5	3.8322	3.8322
	1	31	3.8350	3.8350
	7	46		3.8433
	9	4		3.8440
	Sig.		.258	.157

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .000.
a Uses Harmonic Mean Sample Size = 12.086.
b Alpha = .05.

lnSGLL

	species	N	Subset		
			2	3	1
Tukey HSD(a,b)	14	113	3.3659		
	12	23	3.3825	3.3825	
	2	11	3.3908	3.3908	3.3908
	11	68	3.3934	3.3934	3.3934
	1	31	3.3945	3.3945	3.3945
	3	5	3.4155	3.4155	3.4155
	9	4		3.4231	3.4231
	7	46			3.4388
	Sig.		.062	.228	.079

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .002.
a Uses Harmonic Mean Sample Size = 12.086.
b Alpha = .05.

lnSGLR

	species	N	Subset		
			2	3	1
Tukey HSD(a,b)	14	113	3.3706		
	12	23	3.3905	3.3905	
	2	11	3.3916	3.3916	
	11	68	3.3943	3.3943	3.3943
	1	31	3.4027	3.4027	3.4027
	3	5		3.4217	3.4217
	9	4		3.4294	3.4294
	7	46			3.4404
	Sig.		.406	.175	.053

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 12.086.
b Alpha = .05.

lnCJBL

	species	N	Subset	
			2	1
Tukey HSD(a,b)	11	68	2.6501	
	14	113	2.6525	
	12	23	2.6755	2.6755
	3	5	2.6790	2.6790
	2	11	2.6859	2.6859
	1	31	2.6898	2.6898
	7	46	2.7122	2.7122
	9	4		2.7218
	Sig.		.074	.374

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .003.
a Uses Harmonic Mean Sample Size = 12.086.
b Alpha = .05.

lnCJBR

	species	N	Subset	
			2	1
Tukey HSD(a,b)	11	68	2.6531	
	14	113	2.6590	2.6590
	12	23	2.6765	2.6765
	2	11	2.6804	2.6804
	1	31	2.6898	2.6898
	3	5	2.6926	2.6926
	7	46	2.7128	2.7128
	9	4		2.7238
	Sig.		.106	.056

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .003.
a Uses Harmonic Mean Sample Size = 12.086.
b Alpha = .05.

lnSCNL

	species	N	Subset	
			2	1
Tukey HSD(a,b)	14	113	3.3957	
	1	31	3.4015	
	2	11	3.4093	
	11	68	3.4104	
	12	23	3.4206	3.4206
	3	5	3.4324	3.4324
	7	46		3.4526
	9	4		3.4527
	Sig.		.081	.195

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 12.086.
b Alpha = .05.

lnSCNR

	species	N	Subset		
			2	3	1
Tukey HSD(a,b)	14	113	3.3983		
	1	31	3.4053		
	11	68	3.4095	3.4095	
	2	11	3.4148	3.4148	3.4148
	12	23	3.4184	3.4184	3.4184
	3	5	3.4332	3.4332	3.4332
	9	4		3.4453	3.4453
	7	46			3.4520
	Sig.		.114	.096	.073

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 12.086.
b Alpha = .05.

lnJWCY

	species	N	Subset		
			2	3	1
Tukey HSD(a,b)	14	113	3.2280		
	1	31	3.2345		
	11	68	3.2432		
	12	23	3.2453	3.2453	
	3	5	3.2641	3.2641	3.2641
	2	11	3.2642	3.2642	3.2642
	7	46		3.2850	3.2850
	9	4			3.2859
	Sig.		.116	.059	.721

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 12.086.
b Alpha = .05.

All-Species Discriminant Analysis

Table 5

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	1.221(a)	46.6	46.6	.741
2	.713(a)	27.2	73.8	.645
3	.332(a)	12.7	86.4	.499
4	.196(a)	7.5	93.9	.405
5	.100(a)	3.8	97.7	.301
6	.032(a)	1.2	98.9	.176
7	.028(a)	1.1	100.0	.166

a First 7 canonical discriminant functions were used in the analysis.

Table 6

Wilks' Lambda

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 7	.141	561.287	126	.000
2 through 7	.314	332.260	102	.000
3 through 7	.538	177.829	80	.000
4 through 7	.717	95.622	60	.002
5 through 7	.857	44.282	42	.376
6 through 7	.942	17.053	26	.907
7	.972	8.047	12	.781

Table 7

Standardized Canonical Discriminant Function Coefficients

	Function						
	1	2	3	4	5	6	7
lnCL	-.940	-.484	-.745	-.503	-3.441	.213	2.673
lnOCP	-.132	-.297	.068	-.763	1.137	-.598	.004
lnSKW	.209	.005	.224	.522	-.225	-.133	.020
lnOWC	-.606	.181	-.066	-.057	.051	-.667	-.620
lnBL	.133	.226	.242	.546	.479	-.626	.276
lnCONW	.058	-.356	.265	.241	.229	.251	.269
lnBN	.663	.378	.264	.514	1.395	.525	.751
lnPBG	-.008	.194	-.345	-.664	-.690	-.972	-.974
lnNP	.417	.037	.101	.025	.090	.753	-.049
lnNL	.429	-1.030	.414	-.848	-1.146	.111	-.711
lnPL	-.099	.469	-.281	1.933	3.474	.676	-2.179
lnSGLL	-.197	-.332	-1.160	-.431	-.452	.480	.819
lnSGLR	-.463	-.701	.523	-.179	.776	-.289	-.484
lnCJBL	.216	-.217	.250	-.200	-.552	.812	-.461
lnCJBR	-.051	-.010	.152	.172	.358	-.581	.032
lnSCNL	.256	.895	.695	1.797	.204	.392	-.615
lnSCNR	.624	.929	.410	-1.115	-.376	-.103	1.243
lnJWCY	-.444	.322	.098	-.630	-.188	-.020	.010

Table 8

Functions at Group Centroids

	Function						
species	1	2	3	4	5	6	7
1	-.561	-2.364	.241	.010	.095	.034	-.046
2	-.078	-.102	.303	-.981	-1.419	-.057	.059
3	-1.356	.169	.657	.028	.305	-1.277	.275
7	-1.547	.699	.597	-.302	.207	.134	.078
9	-1.173	1.200	.848	.154	-.108	-.230	-1.360
11	-.769	.184	-.915	.216	-.064	-.003	-.001
12	.517	.309	.835	1.249	-.316	.054	.085
14	1.251	.150	-.017	-.175	.121	-.003	-.006

Unstandardized canonical discriminant functions evaluated at group means

Table 9

Classification Results(a)

		species	Predicted Group Membership								Total
			1	2	3	7	9	11	12	14	1
Original	Count	1	28	1	1	0	0	1	0	0	31
		2	0	7	1	0	0	1	1	1	11
		3	1	0	3	0	0	0	0	1	5
		7	0	4	6	25	8	3	0	0	46
		9	0	0	0	0	4	0	0	0	4
		11	5	5	6	3	5	32	3	9	68
		12	0	1	0	1	0	1	17	3	23
		14	6	5	2	1	4	7	12	76	113
	%	1	90.3	3.2	3.2	.0	.0	3.2	.0	.0	100.0
		2	.0	63.6	9.1	.0	.0	9.1	9.1	9.1	100.0
		3	20.0	.0	60.0	.0	.0	.0	.0	20.0	100.0
		7	.0	8.7	13.0	54.3	17.4	6.5	.0	.0	100.0
		9	.0	.0	.0	.0	100.0	.0	.0	.0	100.0
		11	7.4	7.4	8.8	4.4	7.4	47.1	4.4	13.2	100.0
		12	.0	4.3	.0	4.3	.0	4.3	73.9	13.0	100.0
		14	5.3	4.4	1.8	.9	3.5	6.2	10.6	67.3	100.0

a 63.8% of original grouped cases correctly classified.

Four-Species Basin Proxy MANOVA

Table 10

Levene's Test of Equality of Error Variances(a)

	F	df1	df2	Sig.
lnCL	1.064	3	219	.365
lnOCP	1.853	3	219	.139
lnSKW	1.534	3	219	.207
lnOWC	.147	3	219	.932
lnBL	1.467	3	219	.224
lnCONW	2.794	3	219	.041
lnBN	1.535	3	219	.206
lnPBG	1.228	3	219	.300
lnNP	2.358	3	219	.073
lnNL	.861	3	219	.462
lnPL	.706	3	219	.550
lnSGLL	.642	3	219	.589
lnSGLR	1.844	3	219	.140
lnCJBL	.166	3	219	.919
lnCJBR	1.305	3	219	.274
lnSCNL	.860	3	219	.463
lnSCNR	1.475	3	219	.222
lnJWCY	1.856	3	219	.138

Tests the null hypothesis that the error variance of the dependent variable is equal across groups.
a Design: Intercept+species

Table 11

lnCL

			Subset	
	species	N	2	1
Tukey HSD(a,b)	14	113	3.8150	
	2	11	3.8246	3.8246
	11	68		3.8323
	1	31		3.8350
	Sig.		.346	.267

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .000.
a Uses Harmonic Mean Sample Size = 27.262.
b Alpha = .05.

lnOCP

	species	N	Subset	
			2	1
Tukey HSD(a,b)	14	113	3.5961	
	2	11	3.6036	
	11	68	3.6099	3.6099
	1	31		3.6247
	Sig.		.246	.191

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 27.262.
b Alpha = .05.

lnOWC

	species	N	Subset	
			2	1
Tukey HSD(a,b)	14	113	3.2518	
	2	11	3.2684	3.2684
	1	31	3.2702	3.2702
	11	68		3.2724
	Sig.		.094	.956

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 27.262.
b Alpha = .05.

lnBL

	species	N	Subset	
			2	1
Tukey HSD(a,b)	14	113	2.9851	
	11	68	3.0017	
	2	11	3.0256	3.0256
	1	31		3.0472
	Sig.		.091	.593

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .004.
a Uses Harmonic Mean Sample Size = 27.262.
b Alpha = .05.

lnCONW

	species	N	Subset	
			2	1
Tukey HSD(a,b)	11	68	2.3465	
	2	11	2.3476	
	14	113	2.3492	
	1	31		2.3871
	Sig.		.995	1.000

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .002.
a Uses Harmonic Mean Sample Size = 27.262.
b Alpha = .05.

lnBN

	species	N	Subset	
			2	1
Tukey HSD(a,b)	1	31	3.1596	
	2	11	3.1667	
	11	68	3.1682	
	14	113		3.2044
	Sig.		.904	1.000

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .002.
a Uses Harmonic Mean Sample Size = 27.262.
b Alpha = .05.

lnPBG

	species	N	Subset	
			2	1
Tukey HSD(a,b)	1	31	3.5511	
	2	11	3.5647	3.5647
	11	68		3.5733
	14	113		3.5772
	Sig.		.360	.426

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 27.262.
b Alpha = .05.

lnNL

	species	N	Subset	
			2	1
Tukey HSD(a,b)	11	68	3.6713	
	14	113	3.6726	
	2	11	3.6830	3.6830
	1	31		3.6960
	Sig.		.231	.147

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 27.262.
b Alpha = .05.

lnPL

	species	N	Subset	
			2	1
Tukey HSD(a,b)	14	113	3.8152	
	2	11	3.8223	3.8223
	11	68		3.8319
	1	31		3.8350
	Sig.		.591	.110

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .000.
a Uses Harmonic Mean Sample Size = 27.262.
b Alpha = .05.

lnSGLL

	species	N	Subset	
			2	1
Tukey HSD(a,b)	14	113	3.3659	
	2	11	3.3908	3.3908
	11	68	3.3934	3.3934
	1	31		3.3945
	Sig.		.055	.985

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .002.
a Uses Harmonic Mean Sample Size = 27.262.
b Alpha = .05.

lnSGLR

	species	N	Subset	
			2	1
Tukey HSD(a,b)	14	113	3.3706	
	2	11	3.3916	3.3916
	11	68	3.3943	3.3943
	1	31		3.4027
	Sig.		.097	.699

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 27.262.
b Alpha = .05.

lnCJBL

	species	N	Subset	
			2	1
Tukey HSD(a,b)	11	68	2.6501	
	14	113	2.6525	2.6525
	2	11	2.6859	2.6859
	1	31		2.6898
	Sig.		.066	.052

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .003.
a Uses Harmonic Mean Sample Size = 27.262.
b Alpha = .05.

lnJWCY

	species	N	Subset	
			2	1
Tukey HSD(a,b)	14	113	3.2280	
	1	31	3.2345	
	11	68	3.2432	3.2432
	2	11		3.2642
	Sig.		.347	.100

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 27.262.
b Alpha = .05.

Four-Species Basin Proxy Discriminant Analysis

Table 12

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	1.170(a)	56.0	56.0	.734
2	.738(a)	35.3	91.3	.652
3	.181(a)	8.7	100.0	.391

a First 3 canonical discriminant functions were used in the analysis.

Table 13

Wilks' Lambda

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 3	.225	315.110	54	.000
2 through 3	.487	151.677	34	.000
3	.847	35.087	16	.004

Table 14

Standardized Canonical Discriminant Function Coefficients

	Function		
	1	2	3
lnCL	-1.322	.031	-2.810
lnOCP	-.120	.276	.536
lnSKW	.062	.090	.066
lnOWC	-.334	-.352	-.155
lnBL	.136	-.179	.548
lnCONW	-.185	.441	.248
lnBN	.662	.218	1.424
lnPBG	.173	-.507	-.851
lnNP	.360	.299	.180
lnNL	.069	1.281	-1.191
lnPL	.099	-1.124	3.726
lnSGLL	-.581	-.290	-.601
lnSGLR	-.666	.636	.735
lnCJBL	.372	.452	-.488
lnCJBR	-.262	.028	.229
lnSCNL	.613	-.442	1.234
lnSCNR	1.225	-.111	-1.465
lnJWCY	-.142	-.281	-.587

Table 15

Functions at Group Centroids

species	Function		
	1	2	3
1	-1.784	1.546	.149
2	-.071	.204	-1.847
11	-.824	-1.097	.071
14	.992	.216	.096

Unstandardized canonical discriminant functions evaluated at group means

Table 16

Classification Results(a)

			Predicted Group Membership				Total
		species	1	2	11	14	
Original	Count	1	28	2	1	0	31
		2	0	8	1	2	11
		11	6	7	44	11	68
		14	4	6	11	92	113
	%	1	90.3	6.5	3.2	.0	100.0
		2	.0	72.7	9.1	18.2	100.0
		11	8.8	10.3	64.7	16.2	100.0
		14	3.5	5.3	9.7	81.4	100.0

a 77.1% of original grouped cases correctly classified.

Four-Species Basin Merge MANOVA
Table 17

Levene's Test of Equality of Error Variances(a)

	F	df1	df2	Sig.
lnCL	.789	3	301	.501
lnOCP	2.412	3	301	.067
lnSKW	1.480	3	301	.220
lnOWC	1.154	3	301	.328
lnBL	2.229	3	301	.085
lnCONW	1.576	3	301	.195
lnBN	2.928	3	301	.034
lnPBG	1.128	3	301	.338
lnNP	1.749	3	301	.157
lnNL	.719	3	301	.541
lnPL	.448	3	301	.719
lnSGLL	.511	3	301	.675
lnSGLR	2.157	3	301	.093
lnCJBL	2.415	3	301	.067
lnCJBR	6.159	3	301	.000
lnSCNL	.462	3	301	.709
lnSCNR	1.276	3	301	.283
lnJWCY	2.537	3	301	.057

Tests the null hypothesis that the error variance of the dependent variable is equal across groups.
a Design: Intercept+basin

Table 18

lnCL

			Subset	
	basin	N	2	1
Tukey HSD(a,b)	3	136	3.8174	
	1	17	3.8295	3.8295
	4	31		3.8350
	2	121		3.8381
	Sig.		.076	.310

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .000.
a Uses Harmonic Mean Sample Size = 37.489.
b Alpha = .05.

lnOCP

	basin	N	Subset	
			2	1
Tukey HSD(a,b)	3	136	3.5977	
	1	17	3.6131	3.6131
	2	121		3.6222
	4	31		3.6247
	Sig.		.090	.286

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 37.489.
b Alpha = .05.

lnOWC

	basin	N	Subset	
			2	1
Tukey HSD(a,b)	3	136	3.2541	
	4	31	3.2702	3.2702
	1	17		3.2789
	2	121		3.2859
	Sig.		.091	.100

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 37.489.
b Alpha = .05.

lnBL

	basin	N	Subset	
			2	1
Tukey HSD(a,b)	3	136	2.9961	
	2	121	3.0117	3.0117
	1	17		3.0414
	4	31		3.0472
	Sig.		.702	.066

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .004.
a Uses Harmonic Mean Sample Size = 37.489.
b Alpha = .05.

lnCONW

	basin	N	Subset 2	Subset 1
Tukey HSD(a,b)	1	17	2.3511	
	3	136	2.3515	
	2	121	2.3555	
	4	31		2.3871
	Sig.		.966	1.000

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .002.
a Uses Harmonic Mean Sample Size = 37.489.
b Alpha = .05.

lnBN

	basin	N	Subset 2	Subset 1
Tukey HSD(a,b)	4	31	3.1596	
	1	17	3.1604	
	2	121	3.1663	
	3	136		3.1989
	Sig.		.918	1.000

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .002.
a Uses Harmonic Mean Sample Size = 37.489.
b Alpha = .05.

lnPBG

	basin	N	Subset 2	Subset 1
Tukey HSD(a,b)	4	31	3.5511	
	1	17	3.5633	3.5633
	2	121		3.5743
	3	136		3.5753
	Sig.		.287	.297

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 37.489.
b Alpha = .05.

lnNP

	basin	N	Subset	
			2	1
Tukey HSD(a,b)	4	31	2.6612	
	3	136	2.6692	2.6692
	1	17	2.6784	2.6784
	2	121		2.6955
	Sig.		.420	.092

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .002.
a Uses Harmonic Mean Sample Size = 37.489.
b Alpha = .05.

lnNL

	basin	N	Subset	
			2	1
Tukey HSD(a,b)	3	136	3.6743	
	2	121	3.6771	
	1	17	3.6842	3.6842
	4	31		3.6960
	Sig.		.223	.101

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .000.
a Uses Harmonic Mean Sample Size = 37.489.
b Alpha = .05.

lnPL

	basin	N	Subset	
			2	1
Tukey HSD(a,b)	3	136	3.8176	
	1	17	3.8280	3.8280
	4	31		3.8350
	2	121		3.8375
	Sig.		.152	.211

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .000.
a Uses Harmonic Mean Sample Size = 37.489.
b Alpha = .05.

lnSGLL

	basin	N	Subset	
			2	1
Tukey HSD(a,b)	3	136	3.3687	
	4	31		3.3945
	1	17		3.3994
	2	121		3.4128
	Sig.		1.000	.257

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .002.
a Uses Harmonic Mean Sample Size = 37.489.
b Alpha = .05.

lnSGLR

	basin	N	Subset	
			2	1
Tukey HSD(a,b)	3	136	3.3739	
	1	17		3.4015
	4	31		3.4027
	2	121		3.4144
	Sig.		1.000	.507

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .002.
a Uses Harmonic Mean Sample Size = 37.489.
b Alpha = .05.

lnCJBL

	basin	N	Subset	
			2	1
Tukey HSD(a,b)	3	136	2.6564	
	2	121	2.6767	2.6767
	1	17	2.6831	2.6831
	4	31		2.6898
	Sig.		.166	.739

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .003.
a Uses Harmonic Mean Sample Size = 37.489.
b Alpha = .05.

lnSCNL

			Subset	
	basin	N	2	1
Tukey HSD(a,b)	3	136	3.3999	
	4	31	3.4015	
	1	17	3.4185	3.4185
	2	121		3.4291
	Sig.		.093	.546

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 37.489.
b Alpha = .05.

lnSCNR

			Subset	
	basin	N	2	1
Tukey HSD(a,b)	3	136	3.4017	
	4	31	3.4053	
	1	17	3.4221	3.4221
	2	121		3.4280
	Sig.		.050	.875

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 37.489.
b Alpha = .05.

lnJWCY

			Subset	
	basin	N	2	1
Tukey HSD(a,b)	3	136	3.2309	
	4	31	3.2345	
	2	121		3.2617
	1	17		3.2653
	Sig.		.970	.969

Means for groups in homogeneous subsets are displayed.
Based on Type III Sum of Squares
The error term is Mean Square(Error) = .001.
a Uses Harmonic Mean Sample Size = 37.489.
b Alpha = .05.

Four-Basin Merge Discriminant Analysis

Table 19

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	1.100(a)	59.0	59.0	.724
2	.685(a)	36.7	95.7	.637
3	.080(a)	4.3	100.0	.272

a First 3 canonical discriminant functions were used in the analysis.

Table 20

Wilks' Lambda

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 3	.262	392.740	54	.000
2 through 3	.550	175.355	34	.000
3	.926	22.552	16	.126

Table 21

Standardized Canonical Discriminant Function Coefficients

	Function		
	1	2	3
lnCL	-1.272	-.096	-1.937
lnOCP	-.160	-.343	.231
lnSKW	.277	-.036	.083
lnOWC	-.609	.210	-.236
lnBL	.289	.164	.214
lnCONW	.115	-.415	.253
lnBN	.854	.269	1.362
lnPBG	-.163	.256	-1.033
lnNP	.430	-.011	.270
lnNL	.265	-1.124	-1.323
lnPL	.137	.362	3.296
lnSGLL	-.537	-.058	-.065
lnSGLR	-.439	-.849	.486
lnCJBL	.179	-.275	-.081
lnCJBR	.019	-.061	-.023
lnSCNL	.679	.784	1.043
lnSCNR	.805	.897	-1.367
lnJWCY	-.462	.348	-.527

Table 22

Functions at Group Centroids

basin	Function 1	Function 2	Function 3
1	-.477	-.010	-1.149
2	-1.042	.517	.100
3	1.150	.080	.034
4	-.718	-2.362	.093

Unstandardized canonical discriminant functions evaluated at group means

Table 23

Classification Results(a)

			Predicted Group Membership				
		basin	1	2	3	4	Total
Original	Count	1	9	4	3	1	17
		2	23	77	14	7	121
		3	13	14	102	7	136
		4	1	1	0	29	31
	%	1	52.9	23.5	17.6	5.9	100.0
		2	19.0	63.6	11.6	5.8	100.0
		3	9.6	10.3	75.0	5.1	100.0
		4	3.2	3.2	.0	93.5	100.0

a 71.1% of original grouped cases correctly classified.

APPENDIX B

Specimens Examined

Callibella humilis: INPA 4090, 4091; MPEG 24769; *Callithrix acariensis*: INPA 3931; *Callithrix argentata*: AMNH 94935, 94941, 95930, 94934, 94933, 37460, 95931, 95929, 94938, 94939, 94940, 94942, 95919, 95921, 94944, 94945, 94946, 94947, 94948, 94936, 94937, 37461, 96472, 96473, 96474, 96475, 96476, 96477, 96478, 96479, 94943, 96480, 95920, 95914, 95915, 95917, 95918, 95920, 95922, 95923, 95924, 95925, 95926, 95927, 95928, 94981, 95127, CMNH 12187, FMNH 19499, 19533, 50839, 50840, 50841, 92177, 92178, 92179, 92180, HMCZ 30578, 30579, 30580, 30582, 30583, 30585, 30576, 30577, 30603, 30604, 30605, 30606, 32163, 32164, 32165, HMNK 71447, LACM 27299, MNRJ 2845, 5953, 5946, 23826, MZUSP 4865, 4900, 4901, 4904, 4907, 4908, 4909, 4911, 4913, 4940, 4959, 4964, 4965, 4966, 4969, 4970, 4972, 4973, 4974, 4975, 5007, 11407, 3588, 3589, 3590, 3591, 3593, 3594, 3596, 4313, 11272, 11307, 11308, 4833, 4916, 4968, 4840, 4899, 4905, 4910, 4914, 4918, NMNH 239458, 239459, 239461, 239462, 239463, 239460, 239457, 461725, SMNH A610458, A610511, A620512, A620418, A621037, A621011, A621038, A621029, A617394, A620370, A617493, A617494; *Callithrix chrysoleuca*: AMNH 91833, 91834, 91835, 91836, 91837, 91838, 91839, 92296, FMNH 50821, 50822, 50823, 50824, 50825, 50826, 50827, 50828, 50829, 50830, 50831, 50832, 50833, 50834, MNRJ 5944, 5947, 5948, 5949, 5950, 5951, 5952, MPEG 23064, MZUSP 4886, 4887, 4888, 4892, 4893, 4894, 4896, 4976, 5008, 5018, 5022, 5028, 5030, 11410, 13466, 13467, SMNH A611482, A611481, A611502, A611517, A621493, A611479, A611503, A611497, A611520, A611579, A611609; *Callithrix emiliae*: BMNH 20.7.14.12; *Callithrix humeralifer*: AMNH 93540, 93542, 93543, 93544, 93545, 94921, 94924, 94084, 94086, 37467, 94925, 94926, 94927, 94928, 94929, 94930, 94931, 94932, 94925, 94926, FMNH 19508, 92165, 92166, 92167, 92168, 92169, 92170, 92171, 92172, 92173, HMCZ 30586, 30587, MNRJ 2838, 2839, MZUSP 11254, 11264, 11265, 11270, 11302, 11303, 11304, 11332, 11333, 11298, 11299, 11300, 11301, 11306, 11309, 11312, 10098, 10099, 11250, 11253, 11255, 11256, 11257, 11258, 11260, 11261, 11263, 11357, 11397, 11398, 11401, 3577, 3578, 3580, 3581, 3583, 3585, 3586, NMNH 461726, 461727, 461728, 461729, SMNH A610610, A610609, A610604, A610615, A620605, A620612, A620614; *Callithrix intermedius*: MPEG 8156, 23065; *Callithrix leucippe*: AMNH 133708, 133709, 133712, 37459, 133866, BMNH 9.3.9.2, FMNH 92174, 92175, 92176, HMCZ 37826, MNRJ 4115, 4508, 5116, MZUSP 3598, 3600, 3602, 11281, 11291, 11296, 11305, 11311, 11361, 11402; *Callithrix manicorensis*: INPA 2512, 3930; *Callithrix marcai*: MNRJ 2851, 2856, 2857; *Callithrix mauesi*: INPA 4082, 4109, MPEG 22177, 23962, 23963, 23964; *Callithrix melanura*: AMNH 37059, 37060, 37061, BMNH 3.7.7.15, 3.7.7.16, 76.2.12.9, CMNH 5011, 5012, 5013, 5016, 1963, 1964, 1965, 1966, 4985, FMNH 51888, 44859, 26730, HMCZ 34573, DMNH 2557, 2558, 2559, 2560, MNRJ 2854, 2855, 5845, MPEG 13289, 13290, 13296, 15266, 15267, 21395, 21396, MZUSP 3367, 3368, 3369, 3370, 3376, 3377, 7910, 7911, 4263, 4264, 4265, 4266, 6328, 6330, 11415, 6329, 6332, NMNH 555657; *Callithrix nigriceps*: MPEG 21996, 21997, 21998, 21999, 22955, 22960, 22962; *Callithrix rondoni*: MNRJ 28486, MPEG 21366, 21367, 21646, 21647, 21649, 21653, 21659, 21885, 21886, 21887, 21890, 21893, 21894, 21896, 21897, 24608, 24609, 21885A, MZUSP 18957, 18959, 18960, 18961, 20060, 20069, 20070, 20142; *Callithrix saterei*: MPEG 23955, 23956, 23957, INPA 4102, 4104; *Cebuella pygmaea*: AMNH: 74056, 74369, 75280, 76327, 76328, 182943, 182944; MPEG: 382, 26367; *Leontopithecus caissara*: MNRJ: 28861; *Leontopithecus chrysomelas*: MNRJ: 24573; *Leontopithecus chrysopygus*: HMNK: 304; *Leontopithecus rosalia*: NMNH: 337334; *Saguinus midas midas*: MPEG: 15269; RMNH: 20566, 20568, 20569, 20582, 20571, 20574, 20575, 20577, 20578, 20580, 22562, 22572, 24089, 22546.

VITA

John Marshall Aguiar received a B.A. in Biology and a B.A. in English from the University of Richmond, Virginia in 1992. He received an M.A. in Biology from Old Dominion University in Norfolk, Virginia in 1997. He may be contacted at the Department of Wildlife and Fisheries Sciences, Texas A&M University, 210 Nagle Hall, College Station, Texas 77843-2258.