MARMOSET MISCONCEPTIONS

Paul A. Garber,[1] Alfred L. Rosenberger,[2] and Marilyn A. Norconk[3]

[1]Department of Anthropology
University of Illinois
Urbana, Illinois 61801
[2]National Zoological Park, Department of Zoological Research
Smithsonian Institution
Washington, DC 20008
and Department of Anthropology
University of Illinois at Chicago
Chicago, Illinois 60680
[3]Department of Anthropology
Kent State Univerity
Kent, Ohio 44242

INTRODUCTION

Beginning with the early 16th century reports by Western scientists of tiny, primitive, clawed, squirrel-like monkeys inhabiting the forests of South America, misconceptions and bias regarding tamarin and marmoset phylogeny, classification, ecology, behavior, and anatomy have continued. For example, as recently as 1992, Martin tenaciously guarded the notion that callitrichines should be specially treated and proposed a scheme of classification that by his own admission was unlikely to represent the evolutionary history of this group. He advocated dividing New World monkeys into two major clades, the 'true' New World monkeys and the 'clawed' New World monkeys for systematic purposes. Tamarins, marmosets, and Goeldi's monkeys were assigned to the latter group, although Martin (1990) followed the tradition of Simpson (1945), Simons (1972) and others in aligning *Callimico* with noncallitrichine ceboids ("...because it lacks some of the defining features of marmosets and tamarins, such as reduction in the number of molar teeth and twinning; "pg. 714).

As we discuss below - and as Martin apparently agrees despite his systematic arrangement - not only do the genera *Callimico*, *Saguinus*, *Leontopithecus*, *Callithrix*, and *Cebuella* represent a monophyletic group (subfamily Callitrichinae) (Rosenberger, 1981, 1992), but recent immunological (Sarich & Cronin, 1980), biochemical (Seuanez et al., 1989), and molecular data (Schneider et al, 1993) tentatively place Goeldi's monkey as a sister group to the *Callithrix*/*Cebuella* clade. We doubt this later linkage will stand against the scrutiny of further research, but nevertheless it represents strong evidence against a classification scheme that would place *Callimico* anywhere but within the Callitrichinae.

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Given the recent data available on callitrichine behavior, ecology, and anatomy, we use this paper to highlight and dispel several commonly held misconceptions about tamarins and marmosets. We occasionally exercise all too much license in stating points of view that are perhaps more prevalent as intellectual currents than published ideas. Our apologies. We assume there is a large, multidisciplinary audience interested in callitrichines and our intention is to move the field forward by crossing off overly simplistic ideas and ill-founded notions, even if this means stating the obvious or the unlikely as a way of making a point.

Misconception #1. Tamarins, Marmosets, and Goeldi's Monkeys Are a Systematic Enigma, Difficult to Classify

Despite unambiguous morphological evidence of the dentition, cranium, and postcranial skeleton supporting monophyly for tamarins, marmosets and Goeldi's monkeys (Rosenberger, 1981; Ford 1986; Kay, 1990), several researchers still embrace the archaic taxonomic placement of *Callimico* outside the tamarin and marmoset clade. The dual effect of this is to endorse a platyrrhine classification scheme that overrepresents biodiversity by setting up a single-species family, *Callimico*nidae, and to openly accept taxonomic groups of mixed ancestry, as in Martin's decision to include *Callimico* in the Cebidae. We strongly advocate accepting a classification scheme that places the genera *Saguinus*, *Leontopithecus*, *Callimico*, *Cebuella*, and *Callithrix* in the Subfamily Callitrichinae.

Misconception #2. *Callimico* Is an Intermediate between Marmosets and Tamarins and Other Platyrrhines

The molecular and morphological evidence linking *Callimico* with tamarins and marmosets dispels the notion of 'intermediacy' an idea that must be applied cautiously. In a cladistic model, phylogenetic relationships are linked through ancestral- descendent affinities with one taxon or a collection of taxa. There is no intermediacy, no measure of shared/equal affinities with more than one group. Thus an intermediate set of characters has no bearing on classification. The concept of 'intermediacy' does have value in realizing a continuity of form or behavior between taxa, and this recognition of continuity is key to understanding or rationalizing how apparently disparate taxa may in fact be closely related via ancestry. *Callimico* is a case in point. Few researchers currently doubt its close taxonomic affinity with other callitrichines. Yet the 'extra' molar and the 'absence' of a twin offspring are reminders that we should be able to reconcile the root or origin of the callitrichine stock elsewhere among the platyrrhines, where three molars and singleton births are the norm. By the same token, we might expect to find a comparable 'intermediate' among non-callitrichine platyrrhines as a conceptual and phylogenetic bridge toward callitrichines. *Saimiri* may be this link.

Misconception #3. Callitrichines Are an Isolated Stock of New World Monkeys

Irrespective of *Callimico*'s place in the tamarin and marmoset clade, there is another entrenched view which holds that callitrichines are a lone radiation without ties to other platyrrhines. This view is wrong. The idea has been furthered for decades by reading too much into classification, and by a philosophy that emphasizes static gaps as opposed to phylogenetic and adaptive continuities. This is one reason why we prefer to move from a family-level allocation of marmosets, tamarins and *Callimicos*, to a subfamily rank. The subfamily distinction offers a framework in which each of the 4 or 5 major platyrrhine radiations can be defined (i.e. Atelinae, Pitheciinae, Callitrichinae, Cebinae, and possibly Aotinae), and then re-aligned with related subfamilies into the same family (i.e. include Cebinae and Callitrhichinae in the Cebidae).

It appears that virtually all systematists now recognize that as a group, callitrichines are closely related to another known lineage of living platyrrhines. There is a healthy debate about which non-callitrichines are actually their nearest relatives (Schneider & Rosenberger, this volume). Evidence is mounting from morphological and molecular studies that *Saimiri* and *Cebus* are callitrichine sister-taxa. Although the histories of each of these genera are not well known and are likely complex, this linkage should offer a phylogenetic perspective on the most important adaptive features of the callitrichine radiation. For example, we expect researchers may begin to recognize more continuity in form, function and behavior. How large is the gap in foraging adaptations between squirrel monkeys and the typically insectivorous-frugivorous callitrichines? Why should we assume the high-pitched vocalizations of cebus monkeys, squirrels and callitrichines are parallelisms rather than shared-derived traits? Another view is that callitrichine and cebines are monophyletically related, part of a broader adaptive sub-radiation of platyrrhines (Rosenberger, 1980, 1992). Knowing that callitrichines are part of a larger group also justifies classifying them at a level below the family.

Misconception #4. Callitrichines Are either Primitive or Derived

Here we overstate the case in our effort to make a point. While this debate has basically polarized views on callitrichines for a century, in modern terms such expressions only serve as shorthand caricatures. Characters are primitive or derived, not lineages or taxa. Taxa are always a mixture of ancestral and derived traits, and some lineages may be relatively more conservative than others. Therefore, whereas we are convinced that many well known callitrichine features are not primitive primate or platyrrhine features (e.g., claws, twining, tricuspid teeth; see Hershkovitz, 1977; Rosenberger, 1977; Ford, 1980; Garber, 1980), we must continue to reevaluate our interpretations of the derived or primitive nature of traits and trait complexes as new fossil and comparative data become available. Overall, we maintain that callitrichines have not retained the ancestral platyrrhine morphology and behavior, and in this respect, the radiation is best considered as derived. The *Callimico* lineage, bearing single infants instead of twins and having three molars rather than two, is the least derived branch (in terms of these characters). *Callithrix* and *Cebuella*, using the yardsticks of skulls, teeth, postcrania, and genetic evidence, are the most derived forms. By the same token, *Leontopithecus* and *Saguinus* each present their own unique features and evolutionary trajectories.

We include another example where caution must be used in assessing the primitive or derived nature of callitrichine biology, namely adult body size. Although we believe that many tamarins and marmosets are secondarily reduced in body size, this does not conflict with the possibility that early platyrrhines were small. Those early forms would have been part of an initial radiation, one that may not be directly ancestral to all living platyrrhines. That is, in general terms, we would not expect them to be monophyletically related to cebids. Takai & Anaya (1996) have recently described extremely small platyrrhine teeth from the oldest primate site in South America. Early Old World anthropoids were also small. As discussed below, platyrrhine groups have experienced increases and decreases in body size several times in parallel. The challenge to paleoanthropologists is to identify which size-shifts (and features among the taxa) are homologous.

Misconception #5. Callitrichines Are a Recent, Derived Group

There is no direct linkage between time of origin and preponderance of derived traits. Based on cladistic evidence and related fossils 18–20 million years old, Rosenberger (1979) inferred that callitrichines were an ancient group in spite of their derived morphology. He also argued that *Mohanamico* was definitively callitrichine, possibly part of the *Callimico* lineage (Rosenberger, 1992). Interesting fossils recovered from La Salla, Bolivia, about 25 million years ago, also are very callitrichine-like (Takai & Anaya, 1996). Thus, although there it may have been a suggestion some years ago to link the derived aspect of callitrichine anatomy with a recent origin, perhaps in connection with Pleistocene refugia, this now is an unlikely scenario.

Misconception #6. Marmosets and Tamarins Represent Two Natural and Ecologically Distinct Adaptive Radiations

Critical to this idea are two assumptions: one, that these are natural, phylogenetic groups, and two, that based on their dentitions there is a clear ecological division between marmoset gum-eaters and tamarin fruit- insect eaters. These dichotomies are not supported by the evidence (Garber, 1992; Ferrari, 1993). There is universal agreement that marmosets (*Callithrix* and *Cebuella*) are a monophyletic group, but there is no evidence that *Saguinus* and *Leontopithecus* similarly represent a monophyletic group. The relatively large canines and small incisors that these two 'tamarin' genera share are ancestral callitrichine features and do not prove they are closely related. Although there is a continuing debate as to which one of these two genera is closer to *Callithrix/Cebuella* (Schneider & Rosenberger, this volume), there are no acceptable arguments supporting a close cladistic linkage between *Saguinus* and *Leontopithecus*.

Initial studies of callitrichine diet and dental morphology presented a simple ecological dichotomy with marmosets as gum- eaters and tamarins as fruit-eaters (Coimbra-Filho & Mittermeier, 1977). *Callithrix/Cebuella* have tall lower incisors combined with a set of incisor-like canines which form a dental scraper. The other callitrichines all have the primitive condition of low-crowned incisors and tall canine tusks. Clearly, *Saguinus* and *Leontopithecus* lack the scraping specialization and are more prone to eat prey, fruits and gums that do not require extensive chiseling with their front teeth. However, we are not at all certain that gum-eating alone, and not extractive foraging of insects under bark, or the two combined, has shaped the anatomy of ancestral marmosets via natural selection. Marmoset species show a range of dental and digestive morphologies, occupy a diversity of habitats, and most are larger in body size than *Callithrix jacchus* and certainly larger than *Cebuella*, which are reported to be the most dependent on gums as a dietary staple. It is possible that intense specialization on plant gums evolved locally in some forms of *Callithrix* and *Cebuella*.

Misconception #7. Callitrichines Are Dwarfs

We hope to redirect the discourse on this highly interesting issue. New World primates are unique in their extreme variation in body size. Given the constraints that smaller and larger body size place on positional behavior, feeding ecology, reproductive output, and susceptibility to predators, evolutionary changes in rates and patterns of growth and development likely represent fundamental changes in the manner in which a species exploits it environment. Among free-ranging living platyrrhines, adult body weight ranges from 120 grams in the pygmy marmoset (*Cebuella pygmaea*) to over 12,000 grams in the woolly spider monkey (*Brachyteles arachnoides*) (Ford & Davis, 1992; Rosenberger, 1992). This represents over two orders of magnitude and far exceeds the range found in extant cercopithecoids and pongids, groups that are distributed across much more landmass and many more ecozones.

Based on our current understanding of platyrrhine phylogeny, major increases and decreases in body size have occurred independently in several different lineages. These include *Cebus*, *Saimiri*, callitrichines, and atelines (Kay 1990, 1994; Rosenberger & Strier, 1990; Ford & Davis, 1992; Rosenberger, 1992; Cartelle & Hartwig, 1996). For example, Ford & Davis (1992:438–439) surmise that over the course of platyrrhine evolution capuchin monkeys have "nearly tripled in body size...independent of all other New World monkey lineages." *Saimiri*, in contrast, has probably undergone a significant body size reduction in comparison to its nearest early Miocene fossil relative *Dolichocebus* (Rosenberger, 1990). Relatives of spider and howler monkeys were, in the recent past, twice as large as any remaining alive today (Cartelle & Hartwig, 1996; Hartwig & Cartelle, 1996). Although it is unclear how frequently increases and especially decreases in body size have occurred in platyrrhine evolution, these events appear to have played a major role in shaping the reproductive, mating, and social systems of New World primates (Ford & Davis, 1992; Martin, 1992; Garber, 1994).

The picture of body size evolution among callitrichines is more complex and interesting than one might gather from the historical focus on the relatively narrow paradigm of the dwarfism hypothesis. For example, in addition to selection for size reduction connected with the origins of the group, among callitrichines there is evidence of several independent size-reduced lineages, perhaps going from a *Saguinus*-sized creature (400–600 gms) to a *Callithrix*-sized creature (400–250 gm) and, from a *Callithrix*-sized animal to *Cebuella* (125 gms). Related to the latter case, consider that Rosenberger & Coimbra-Filho (1984) and Rosenberger (1992) have also argued that *Leontopithecus*, possibly the sister-group of *Callithrix*/*Cebuella*, has undergone a body size increase since splitting from this clade. Thus, whether or not callitrichines arose as miniatures relative to the last common ancestor, they shared with other platyrrhines the body sizes of subsequent independent lineages continues to be an object of selection.

The notion of dwarfing also remains ill-defined and thus easily abused. Adult female squirrel monkeys (680 gm) are barely distinguishable in body weight from adult female golden lion tamarins (575–622 gm; Dietz et al, 1994) and adult female moustached tamarins (550–620; Garber et al., 1993). Thus there is nothing remarkable about callitrichine body size *per se*. Historically, the semantic implications of the dwarfism hypothesis became accepted despite limited biometric data of any kind, the strong influence of typology and orthogenesis in systematic thinking, and the lack of a sound cladistic framework for interpreting platyrrhine evolution. The impetus for a dwarfing theory as an evolutionary explanation was promoted by W.K. Gregory and R.I. Pocock in the 1920s, who thought callitrichine morphology was generally not primitive. One can imagine Gregory, a paleontologist, being enthusiastic about the idea as a counter example to Cope's Law of evolutionary size increase.

Given the present data, it cannot be stated with certainty that *Leontopithecus*, *Callimico*, and most species of *Saguinus* are smaller in body size than ancestral callitrichines; or that the extant forms as a group represent radically small, phylogenetic dwarfs. What we can do profitably is clarify the boundaries of the discussion. We suggest the term dwarf is best restricted to a special case of hypomorphosis (evolutionary size reduction) that results in maintenance of the same shape and form as a lineage evolves from a larger-bodied ancestor to a smaller descendant (proportioned dwarfism). Size reduction in an evolving lineage that produces shape changes relative to the ancestral condition results in hypomorphs, not dwarfs. Data presented by Garber & Leigh (in press) indicate that differences in adult body weight among extant callitrichines can be explained by ontogenetic changes in growth rates rather than by any significant decrease in the age at maturation. Differences in growth rates during particular developmental periods may result in significant size and shape differences among taxa. In addition, there is evidence of significant differences in limb proportions (Jungers, 1985; Garber, 1991), and hand size and shape among callitrichine species (Bicca-Marques, in prep), as well as reports of overscaling in the cheekteeth (Plavcan & Gomez, 1990) and the size of the eye (Martin, 1992). Together, these data do not support the contention that callitrichines are proportioned dwarfs.

Misconception #8. Claw-Like Nails in Callitrichines Are an Adaptation to Gum Feeding

All species of callitrichines have laterally compressed and elongated claw-like nails on all digits except the big toe, which bears a flattened nail. These claw-like nails are termed tegulae to distinguish them from the true claws of many nonprimate mammals (faculae) and nails shaped like ours and other catarrhines (ungulae). Histologically, the claw-like tegulae of tamarins, marmosets, and Goeldi's monkey are thought to be the same as the nails of other New World monkeys, many of which (e.g., *Saimiri*, *Aotus*, *Pithecia*) exhibit the compressed and pointed shape, but are not hooked like claws. Since many species of tamarins and marmosets are known to cling to large vertical trunks while feeding on plant gums (Garber, 1992), it has often been assumed that the evolution of claw-like nails is directly related to the evolution of a gum feeding habit.

There are several problems with this inference. One is theoretical: during gum feeding, all callitrichines embed their claw-like nails into the tree trunk to maintain support. Although gum feeding—vertical clinging—clawed digits are associated as a trait complex, this by itself does not establish causality. The other main problem is that there is considerable variability in the degree to which plant gums are exploited by different callitrichine taxa. Plant gums are critically important in the diet of most marmoset species (although as mentioned differences in anterior dental morphology and digestive physiology exist among and between marmosets of the *Callithrix*-jacchus group and marmosets of the *Callithrix*-argentata group suggesting differing degrees of gum feeding specializations). In contrast, Goeldi's monkey has not been observed to feed on plant gums, and for many *Saguinus* and *Leontopithecus* species, gum feeding may comprise only 1–8% of the annual diet. Overall, the feeding ecology of callitrichines is distinguished from other platyrrhines by the ability of these primates to exploit a range of resources that are associated with tree trunks in the forest understory. This includes plant gums, bark refuging insects, small vertebrates concealed in knotholes, prey hidden in bromeliads that grow along the main axis of the tree, as well as use of vertical trunks to scan for insects and small vertebrates located on the ground. Given the highly faunivorous diet of all callitrichines, the evolution of claw-like nails is best understood as a foraging adaptation enabling these small primates to exploit high protein and carbohydrate resources restricted to particular microhabitats in the forest understory. In the absence of claw-like nails, access to large vertical trunks would be highly limited. Gum feeding and tree gouging in extant marmosets (*Ce-*

buella and *Callithrix*) represent a derived behavioral pattern related to an expansion of the original trunk foraging adaptation.

Misconception #9. Callitrichines Have Simple Social and Mating Systems

Initial reports of callitrichine social and mating systems were based first on lab studies and later on short-term field research on a few species. This work continued to build on the premise that tamarins and marmosets lived in small, monogamous social groups characterized by a pair bond between a single adult male and a single adult female. This characterization drew largely from captive studies in which (1) large groups were often found to be unstable, (2) only a single female in each group gave birth, (3) adult males and other group members helped care for the young, as well as the assumptions that (4) tamarins and marmosets were primitive platyrrhines and (5) the ancestral mating system for New World monkeys is monogamy. It is now apparent that among platyrrhines a monogamous pair bonded social system is found only in *Aotus* and *Callicebus*, and that monogamy in night and titi monkeys is best understood as a derived behavioral/social pattern (Garber,1994; Garber & Leigh, in press). In contrast, tamarins and marmosets live in multimale, multifemale groups of 5–15 animals. In all species for which data are available there is evidence of a extremely broad range of mating and grouping patterns including polyandry, polygyny, and less often monogyny. There is no evidence from the wild that a single male and a single female maintain an exclusive mating relationship over an extended period of time. Although only a single female in each group typically gives birth, groups with two breeding females have been reported in a few species (*Saguinus fuscicollis*, *Callithrix jacchus*, *Leontopithecus rosalia*).

Less is known regarding the social and mating system of *Callimico*. These callitrichines are reported to live in multimale, multifemale groups of at least 5–8 individuals. Observations in the wild indicate that more than a single female in a group may breed. Although *Callimico* is the only callitrichine that gives birth to single infants rather than twins, all species in the subfamily are characterized by an extremely high reproductive rate. Early age at maturation (approximately 2 years) coupled with the potential of female tamarins and marmosets to produce 2 litters of two offspring each year, and the potential of female Goeldi's monkeys to produce 2 litters per year each containing one offspring, results in intrinsic rates of population increase that are greater than those found in any other group of higher primates (Martin, 1992; Garber, 1994). The ability of individual callitrichines to achieve their reproductive potential is directly related to a range of proximate environmental, social and demographic factors. These include group size and composition, availability of helpers to care for young, age, kinship, opportunity to migrate with one or more peers, the presence of breeding vacancies in nearby groups, and the availability of suitable habitats within their range.

Callitrichine social groups are based on high levels of both competition and cooperation. Within each group, males and females compete for extremely limited reproductive opportunities. Intragroup aggression is rare, and competition appears to be mediated through olfactory cues, age-related dominance, and cooperation. Individuals may need to cooperate to insure infant survivorship, maintain range integrity and access to productive feeding sites, detect predators, and form social bonds that aid in paired migration or group fissioning. Behavioral options and behavioral tactics in callitrichine social groups appear to be extremely complex and dynamic, and any notion that tamarins, marmosets, or Goeldi's monkeys live in simple social or mating systems is completely in error.

In closing, we wish to highlight the social and ecological complexity of the callitrichine radiation, and underscore the importance of dispelling tamarin and marmoset misconceptions as a necessary step in understanding platyrrhine systematics and evolution. We hope this Introduction has indicated new directions of inquiry and debate.

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