CRITICAL ISSUES IN CEBINE EVOLUTION AND BEHAVIOR

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Cebus and *Saimiri*, together with *Callicebus* and *Aotus*, represent four genera of New World monkeys whose unresolved taxonomic position has served to muddle platyrrhine cladistics. Their affinities remain somewhat problematic (Schneider and Rosenberger, this volume), although we argue that in the past 20 years, new molecular, genetic, morphological and behavioral analyses have narrowed the range of possible explanations regarding *Cebus* and *Saimiri*, in particular. Here, we attempt to clarify cebine evolutionary relationships and outline some interesting and relevant directions for future studies in behavior and ecology.

PART I: SYSTEMATICS AND MORPHOLOGICAL EVOLUTION (A.L. Rosenberger, M.A. Norconk, and P.A. Garber)

As is usually the case in systematics, without the proper frame of reference it is often easier to understand what a taxon is not, phylogenetically, rather than what it is. For example, *Cebus* has a grasping tail, but it is not an ateline. *Cebus* is said to have a partially

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Table 1. Genus level classification of cebines

Family Cebidae
  Subfamily Cebinae
    Tribe Cebini
      Cebus - Cebus monkey
    Tribe Saimiriini
      (*)*Saimiri* - Squirrel monkey; Middle Miocene, Colombia
      **Laventiana* - Middle Miocene, Colombia
      **Dolichocebus* - Early Miocene, Argentina
  Other cebines
      **Chilecebus* - Early Miocene, Chile
      **Antillothrix* - Pleistocene/Recent, Dominican Republic

*Extinct genus. (*) Living genus which includes *Neosaimiri* as a subgenus. See Schneider and Rosenberger (this volume) and Rosenberger (1992) for references and discussion. "Other cebines" include fossils whose relationships *within* Cebinae are uncertain.

opposable thumb, but it is not a catarrhine. Nor is it likely that the relatively large capuchin brain will conjure up fantasies of a special evolutionary relationship with hominids.

The same would hold for *Saimiri*. With a round head, short face, agouti coloration, long tail and insectivorous diet, one might mistake it for a talapoin, which it is not. Like *Cebus*, *Saimiri* has a relatively large brain, highly sexually dimorphic canines, and shares a long, novel sequence of the IRBP and epsilon globin genes, with *Cebus*, to the exclusion of other platyrrhines. What are we to make of these similarities? The null hypothesis should be that *Cebus* and *Saimiri* are closely related.

As Schneider and Rosenberger (this volume) relate, there are dichotomous views on the relationships of *Cebus*. One view nests capuchins within a group that also includes callitrichines and *Saimiri* - all cebids (Table 1). The other view places *Cebus* quite outside the radiation of most modern forms, albeit with *Saimiri* again appearing as a potential sister-taxon. This latter view can be termed the "outlier" hypothesis, and argues that capuchins represent an ancient platyrrhine radiation isolated from all other genera for perhaps 20 million years. The fossil record is of little help here, and the crucial single step to resolving this conflict rests with understanding the linkage between *Cebus* and *Saimiri*. To us, capuchins and squirrel monkeys represent a pair of closely related genera and this makes the outlier hypothesis patently untenable. The hypothesis that *Cebus* and *Saimiri* are sister taxa has been tested often, at least implicitly, and it has been rarely if at all refuted.

Every point of similarity (either primitive or derived) found between *Cebus* and *Saimiri* is a corroboration of the null hypothesis. Every potential point of derived similarity found between either *Cebus* or *Saimiri* and a taxon outside this pair must be demonstrated to be homologous if it is to weaken the null hypothesis. In general, the modern radiation of extant capuchins is characterized by relatively large brain size, enhanced manual dexterity and tool use, elaborate visual system, semi-prehensile tail, complex system of social communication and group coordination, thickly enameled teeth, premolar dominance, hyper-short face, and narrow inter-orbital distance. Although it is possible that each of these traits could be interpreted as autapomorphic, unique add-ons that accumulated since the genus split from the stem of the platyrrhine radiation, we feel that this is highly unlikely. Moreover, if capuchins do represent an old, isolated lineage, then it is necessary to posit that *Cebus* and *Saimiri* have convergently evolved short faces, broad premolars, minuscule third molars, narrow nasal bones, rounded braincases containing relatively large brains, and highly dimorphic canines honing on a *Cebus*-like premolar anvil. Given that these traits are distributed across the face, cranium, and dentition supporting a prey-based foraging strategy, arguments for evolutionary convergences in each of these traits are difficult to reconcile.

What is the genesis of the "outlier hypothesis" This result appeared in three numerical cladistic studies (Dunlap et al., 1985; Ford, 1986 et seq.; Kay, 1990), all of which shared the same set of built-in constraints. In each of these studies, catarrhines were used as the principle source of cladistic information (the out-group). No *a priori* study was undertaken to specify homologies shared by platyrrhines and catarrhines. Reconstructing the ancestral platyrrhine pattern was left to the algorithms. We suggest their approach biased the analyses to search for platyrrhines with the highest frequency of catarrhine-like features, based on the available sample. *Cebus* molars were anatomically likened to those of *Apidium*; *Cebus* ankle joints were said to resemble early Fayum parapithecid anthropoids; and *Cebus* forearm muscles were compared favorably with extant Old World monkeys. Thus, the outlier hypothesis was driven by the limits of a methodology.

The null hypothesis regarding the systematic position of *Cebus*, as a member of a lineage linked with *Saimiri*, remains the most compelling (Schneider and Rosenberger, this volume). It will be strengthened as we continue to explore differences in cebine ontogeny (Hartwig, 1995 ; Armstrong and Shea, in press) and how that influences patterns of behavior and ecology. We argue that *Cebus* and *Saimiri* are closely related genera, separated for millions of years but still bound to the pre-catching guild of cebids (Table 1). It is not surprising that over time they would accumilate morphological differences that might lead to questions of ancestry. However, it is a set of unique similarities that unite these lineages phylogenetically.

PART II. BEHAVIOR AND ECOLOGY ISSUES IN *Cebus* AND *Saimiri* (L.M. Fedigan and S. Boinski)

To most casual observers *Saimiri* and *Cebus* are strikingly similar in their general appearance and demeanor. Whether in cages or a neotropical forest, these beasts are usually recalled as busily moving about, poking, prying, peeling, and scraping substrates looking for tasty bits, and bustling about fruit sources, bumping and jostling each other like a litter of puppies at a food bowl. Although questions exist regarding their precise taxonomic affinities (but see new molecular data in Schneider and Rosenberger, this volume), *Saimiri* and *Cebus* are readily pooled into an ecological 'clade' of insectivorous primates. Despite these similarities, many of issues relevant to the behavioral ecology of *Cebus* and *Saimiri* are most obvious when their many differences are noted.

First, the systematics and genetic structure of these genera are dramatically different. *Cebus* has four well-defined species. *C. albifrons*, *C. olivaceous*, and *C. capucinus* replace each other geographically and together form a tidy clade which is clearly morphologically and behaviorally different from *C. apella* (Mittermeier and Coimbra-Filho,1981; Groves, 1987). In contrast, *Saimiri* presents systematists with a messy pattern of parapatric and allopatric populations and with evidence of species distinctions. The meticulous and herculean efforts of Hershkovitz (1984) and Thorington (1985) in sorting out *Saimiri* taxonomy, based largely on pelage, osteological, and chromosomal characters, are now in the process of being refined to include more recent behavioral and molecular data (i.e., Costello et al., 1993; Silva et al., 1993; Garcia et al., 1995). Consensus on the species- and subspecies-level taxonomy of *Saimiri*, however, is unlikely to be achieved even within the next decade.

Second, adult capuchins can easily weigh four to six times more than an adult squirrel monkey. Although body proportions are not markedly dissimilar, the consequences from the size differences reverberate throughout the biology of both genera. First, all else being equal, *Saimiri* are much more vulnerable to predation than *Cebus*. A much broader range of potential predators can capture a *Saimiri* than a *Cebus*. For example, 50% of infant *S. oerstedi* are lost to confirmed or probable predation by avian predators by six months of age (Boinski, 1987). One probable consequence of their enhanced vulnerability to predation, is that *Saimiri* troop sizes can easily be three to six or seven times larger than a *Cebus* troop. Extremely large troop sizes appear to be an anti-predator adaptation in *Saimiri* (Boinski, 1988a), as do numerous peculiarities in *Saimiri* reproduction, including their remarkably synchronous seasonal birth peaks and the extended, unusually variable duration of gestation (Boinski, 1987; Hartwig, 1995).

Third, both genera are highly vocal in the wild, and individual troop members may produce more than a 1000 vocalizations each day in the course of normal activities (Boinski, 1991; 1993; Boinski and Mitchell 1992, 1995; Boinski and Campbell 1995, In press). In *Saimiri*, however, a much larger proportion of calls can be described as 'contact' calls with the function of exchanging positional information among visually isolated troop members. In *Saimiri*, the enhanced susceptibility to predation due to their smaller body size appears responsible for the greater emphasis of contact calls. The number of contact calls produced by a squirrel monkey is positively related to the extent of spatial separation between the squirrel monkey and its nearest neighbor. Only in infant capuchins are such 'security-blanket' vocalizations found.

Another repercussion of the body size difference is that *Cebus* have greater bite force and manual strength than do *Saimiri* (Janson and Boinski,1992). *Saimiri* are foliage gleaners, extracting arthropods and small vertebrates off leaf and bark surfaces or from within leaf curls. *Cebus* can twist, rip, bite, and crunch open hard substances to extract grubs, and other social insects unavailable to *Saimiri*. Even when foraging in mixed-species groups, the two genera overlap little in the sites in which they forage for arthropods. *Cebus* can also harvest high-quality fruit sources, such as dense clusters of hard-husked palm fruits, which are completely inaccessible to sympatric *Saimiri* because the latter cannot penetrate the husks.

Fifth, although both species have anomalously large brains relative to body size compared to other primates, the concomitant developmental trajectories that produce the large brains are markedly different and appear to reflect very different selective regimes (Hartwig, 1995, 1996). *Cebus* has more postnatal brain growth and slower motor skill development than other New World primates. Neonates are highly precocial in *Saimiri* in terms of both brain growth and motor skill development. Another developmental difference is that *Saimiri* evidences much more marked geographic variation in development than has yet been reported in *Cebus*. Infants are in great part weaned by 4.5 months in *S. oerstedi* in Costa Rica and are rarely in close vicinity to their mothers by 8 months of age (Boinski and Fragaszy, 1989). In contrast, *S. sciureus* in Peru are weaned by about 19 months of age (Mitchell, 1990; Boinski and Mitchell, 1995).

Finally, in regard to the extent and breadth of field studies the positions of the two genera are reversed. *Cebus* has been the subject of detailed long-term behavioral and ecological field studies since Oppenheimer's field work on Barro Colorado Island in the mid 1960's (see Freese and Oppenheimer (1981) for historical review). The number of field observational and experimental studies shows no signs of diminishing (see below). The long-term field legacy for *Saimiri* is far different. Squirrel monkeys were one of the five monkey species studied in Terborgh's (1983) and his associates year-long ecological study of the primate community at Manu, Peru. Fortuitous field conditions facilitated Boinski's (1986) studies of squirrel monkeys in Costa Rica, the first with detailed social observations of individually recognized troop members. Mitchell (1990) quickly followed with her superb investigation of the ecology and complex social behavior of *Saimiri* in Manu. The third, and only other population of squirrel monkeys studied for an extended period (although the results remain largely unpublished) is of an artificially stocked population on Isla de Santa Sofia, a 400-ha island in Amazonas, Colombia (Bailey et al., 1974; Sponsel et al., 1974). To our knowledge, no other researchers have undertaken long-term behavioral field studies of *Saimiri*. Quite a few workers, however, mention *Saimiri* in reports on other neotropical primates (e.g. Peres, 1994).

Clearly, the main challenge awaiting further insights into *Saimiri* are additional long-term field studies of behavior and ecology at new sites. Squirrel monkeys have the most geographically variable social organization of any group of closely related primate populations (Mitchell et al., 1991; Boinski, In press). *S. oerstedi* arguably exhibits the most egalitarian, least aggressive social organization of primates with large multi-female, multi-male social organizations (Boinski, 1988a, 1994; Boinski and Mitchell, 1994). Moreover, *S. oerstedi* is one of the minority of primate taxa in which female dispersal is the rule and negligible female-female bonds are evident. In contrast, Peruvian females are dominant to males and female-female social bonds are strong (Mitchell, 1990,1994). Colombian *Saimiri* are reminiscent of those in Peru, with male transfer and female-female bonds, but during the four month-long dry season, food becomes extremely scarce and troops fission into small subgroups (R. C. Bailey, pers. comm). In Suriname, a fourth type of social organization occurs. Males are fully integrated into the social group, most males are dominant to most females and much time is allocated to dyadic dominance displays in the wild (Boinski, unpublished data). The Peru-Costa Rica contrast has been explained by differing levels of within-group food competition. Studies begun by Boinski in Suriname aim to extend and test this model on a squirrel monkey population that exhibits a very different social organization.

Unlike *Saimiri* studies, recent studies of *Cebus* have been spurred by a surge of interest in primate cognition. The investigation of cognitive abilities is a hot topic throughout primatology, and fundamental to this issue is the study of social and ecological pressures that were likely to have selected for intelligence. Both social and foraging intelligence are now being investigated in captive and field studies. Among the topics under investigation are formation of coalitions (Perry, 1995a, 1996b), reconciliation (Perry, 1995b), cognitive capacities under captive, experimental conditions (Visalberghi, 1988, 1990; Anderson and Roeder, 1989; Fragaszy and Visalberghi, 1990; Visalberghi and Fragaszy, 1990; Fragaszy et al., 1994; Marchal and Anderson, 1993), spatial memory and rule-based foraging (Garber and Paciulli, 1996; Janson, this volume), social interactions and vocal behavior leading to troop travel decisions (Boinski 1993, this volume; Boinski and Campbell, 1995), alarm calls (Norris, 1990), choice of plants used for medicinal purposes (Baker, 1996), hunting (Fedigan, 1990, Rose, 1994a,1996; Perry and Rose, 1994), ontogeny of foraging skills (MacKinnon, 1995), food sharing (de Waal et al., 1993), tool making (in captivity: Anderson, 1990; Westergaard and Suomi, 1994a,b; in the wild: Boinski, 1988b, Chevalier-Skolnikoff, 1990, Fernandes, 1991).

We are also just starting to piece together the picture of social dynamics in capuchins. We know that males disperse and that females are usually philopatric. Does this mean that females form matrilines and that female relatedness underlies much of the affinitive interaction patterns? Capuchins readily form coalitions, they often allonurse and alloparent each others' young, and they engage in frequent triadic interactions (O'Brien

1988, 1991, 1993; O'Brien and Robinson, 1991; Perry, 1996b; Robinson, 1993). Are these patterns based on kinship, rank, friendship, or some other factor? Years ago, Bernstein (1966) conducted experiments in captivity to show that capuchins, unlike macaques, do not form linear dominance hierarchies, and capuchin field workers experience some difficulties in determining rank other than that of alpha individuals. How is dominance rank acquired and is it linear? All four capuchin species exhibit a pattern of prominent alpha males, but in *C. albifrons* and *C. capucinus*, adult males within the same group associate strongly with each other, they cooperate actively in group defense, they look for and retrieve lost males, and they sometimes transfer groups together (Fedigan, 1993, Fedigan et al., this volume; Perry, 1996a; Rose, 1994b). How far and how often males disperse is unknown, but in the white-faced capuchins that have been under observation for 13 years in Santa Rosa National Park, Costa Rica, small parties of adult males invade groups every few years, fighting with the resident males, and injuring females and infants in the process. At other times, single males join groups quietly and inconspicuously over an extended period of time. Resident males of a group sometimes exhibit extensive male care, protecting, carrying, and retrieving infants, and even allowing them to suckle. What factors underlay these highly variable patterns of male social behavior are as yet unknown, but field studies focused on males are underway. Field studies have also investigated female social behavior, particularly the feeding and traveling costs of female *Cebus olivaceus* in groups of different sizes (Miller, 1992, this volume).

As with *Saimiri*, we still have much to learn about *Cebus* mating systems. Some capuchin species mate cryptically (e.g., *C. capucinus*, see Parish et al., 1996), whereas in others the females clearly and overtly choose the alpha male for mating (e.g., *C. apella*, see Janson,1984; Phillips et al., 1994). Two of the four *Cebus* species (*C. albifrons* and *C. capucinus*) live in groups that are decidedly multi-male. The other two species (*C. olivaceus* and *C. apella*) live in what might best characterized as "age-graded male" (or functionally speaking, unimale) systems. In these cases, the top-ranking male is the only reproductively active male, and is highly conspicuous socially (Izawa, 1980; Janson, 1984; Robinson, 1988; O'Brien, 1991). Male capuchins in at least two of the *Cebus* species exhibit strong male-male bonds, and female kinship and dominance systems do not seem as clear cut as in cercopithecines.

Capuchins in captivity live very long lives, up to 47 years, which is much longer than expected for a primate of their body size, but less surprising in terms of their brain-to-body weight ratio. Are members of this genus similarly long-lived in the wild? The entire pace of life seems slower than expected in capuchins - weaning age, age at first birth, interbirth intervals, estrous cycle length (Fedigan and Rose, 1995). Is this "slow" life history pattern related only to their large brains, or are there other factors involved? We need more long-term life history and ecological data from field studies on both this genus and other primates exhibiting large brain to body ratios, such as squirrel monkeys. Birth rates are highly variable from year to year, however, we have yet to document the factors that might affect annual variation in reproduction. Capuchins have long been thought to be nonseasonal breeders, but at least one study found significantly more infants born in the dry than the wet season (Fedigan et al., this volume). Is it possible, as Susan Perry has suggested, that females of the same group exhibit some loose form of breeding synchrony, resulting in clusters of births within a troop over a several month-long period, but not strict seasonality? Capuchins appear to rely on pheromones and olfactory communication. This seems to be indicated by their neurophysiology and by their frequent use of behaviors with an olfactory component, such as urine-washing (Robinson, 1979), fur-rubbing with odoriferous substances (Ludes and Anderson, 1995; Baker, 1996), and mutual handsniffing (Perry, 1996b). Plausibly, olfactory communication might underlie the phenomenon of birth clusters within a troop.

A number of factors about the capuchins' relationship to their environment are also distinctive. As mentioned above, these monkeys are famous as extractive, manipulative foragers. Capuchins seem to specialize in food that "fights back", that is, flora and fauna with highly evolved defense mechanisms. What ecological factors might have selected for this pattern and what are the repercussions for the capuchins' ability to adapt and survive under rapidly changing ecological conditions? For example, how do these opportunistic, omnivorous feeders fare under the all too prevalent conditions in Central and South America of forest destruction and fragmentation? And how do they fare under the less common conditions of forest regeneration? In many parts of their range, capuchins are reported to prey on small vertebrates (e.g. birds, lizards, small mammals, see Newcomer and DeFarcy, 1985; Fedigan, 1990; Perry and Rose, 1994). Is this a recent adaptation or do they exhibit behaviors indicating that they have long been effective at vertebrate predation? They are also renowned for their ability to mount an impressive, effective, and cooperative anti-predator display by vocalizing, mobbing, and breaking branches on the source of the disturbance (e.g., Boinski, 1988b), and thus driving off creatures many times their size (cats, coyotes, boa constrictors, ecotourists). Finally, capuchins exhibit considerable variability from group to group and species to species in their diet and the way they manipulate and extract food — is this variation due to food availability or local traditions (Chapman and Fedigan, 1991)?

This brief review of issues in the behavioral ecology of *Cebus* and *Saimiri* make it clear that we need more long-term intensive studies of known individuals, groups and populations before we can fully understand the mechanisms that underpin many of the patterns discussed here. The last decade has seen a great increase in our knowledge of cebine behavioral ecology. With the increasing attention paid to the neotropical primates and the availability of new non-invasive techniques for biological sampling in the field, the next decade should prove to be an even greater leap forward in our understanding of these animals.

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