

NEW PERSPECTIVES ON THE PITHECIINES

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If the callitrichines were the first major group of platyrrhines to benefit scientifically from the explosion of interest in platyrrhine biology in the last two decades, the sakis and uakaris are the surprise discovery. They are the evolutionary secret of the New World monkey radiation, hidden until now by the lack of a sound framework for platyrrhine systematics, the absence of any glimmerings of a fossil record and sheer ignorance of their behavior and ecology. Much the same situation existed for callitrichines. For nearly a hundred years, scientists have debated one way or the other - Are the callitrichines primitive or are they derived? No such uncertainties were ever associated with "pitheciines". Classifications dating to J.E. Gray and St. George Mivart in the middle 1800s show that taxonomists even then treated the three modern genera, *Pithecia*, *Chiropotes*, and *Cacajao* as a divergent, natural group. In modern terms, this implies they are monophyletic, related more closely to one another than any are to living non-pitheciine platyrrhines. Until recently, this legacy was the upshot of "pitheciine" biology: sakis and uakaris are behaviorally enigmatic and structurally bizarre, but they are an evolutionary cohesive group.

Although none would contest the notion that characteristic features of sakis and uakaris are derived, this observation addresses only one issue - monophyly. United by specialized craniodental anatomy that is quite divergent relative to other platyrrhines, we do not view these animals as marginal outliers, but as the survivors of a once diverse radiation whose origins can be traced through extant forms such as *Callicebus* and *Aotus* (Table 1). Obviously, our view hinges in part on a question of definition: What is a pitheciine? Here we break with tradition by including five living genera, not three - *Pithecia*, *Chiropotes*, *Cacajao* and *Callicebus* and *Aotus* (Table 1). This interpretation of the subfamily developed over the past two decades is based on studies of morphology (Kinzey, 1992; Rosenberger 1992), molecular genetics (Schneider, 1996; Schneider and Rosenberger, this

Table 1. Genus level classification of the Pitheciines

Family Atelidae
Subfamily Pitheciinae
Tribe Pitheciini
Subtribe Pitheciina
<i>Pithecia</i> - Sakis
<i>Chiropotes</i> - Bearded sakis
<i>Cacajao</i> - Uakaris
* <i>Cebupithecia</i> - Middle Miocene, Colombia
Subtribe Soriacebina
* <i>Soriacebus</i> - Early Miocene, Argentina
Tribe Homunculini
Subtribe Homunculina
* <i>Homunculus</i> - Early Miocene, Argentina
(* <i>Aotus</i> - Owl monkeys; Middle Miocene, Colombia)
* <i>Tremacchus</i> - Early Miocene, Argentina
<i>Callicebus</i> - Titi monkeys
Other pitheciines
* <i>Carlocebus</i> - Early Miocene, Argentina
* <i>Lagonimico</i> - Middle Miocene, Colombia
* <i>Xenothrix</i> - Pleistocene/Recent, Jamaica

Extinct genus. () Living genus which includes an extinct species. See Schneider and Rosenberger (this volume) and Rosenberger (1994) for references and discussion. "Other pitheciines" include fossils whose relationships within Pitheciinae are uncertain.

volume) and feeding ecology (e.g. Ayres, 1989; Kinzey and Norconk, 1990; van Roosmalen *et al.*, 1988). Schneider and Rosenberger (this volume) review the alternative phylogenetic interpretations. The point we wish to make here is that the Victorian-era pigeonhole of a three-genus subfamily - pitheciines - detracts from one's capacity to see the broader picture, such as the continuity linking the least derived "pitheciin" genus, *Pithecia*, with forms like *Callicebus* on the one hand, and *Chiropotes* and *Cacajao* on the other hand.

As Table 1 shows, there are more fossil genera classifiable as pitheciines by our criteria of monophyly than there are living pitheciines. Our tally of 12 genera, extinct and extant, means pitheciines are more abundant, generically, than any other platyrrhine subfamily. Moreover, they are morphologically diverse and geographically widespread. These points are profoundly important in considering the evolutionary history of pitheciines and their role within the platyrrhine radiation. The anatomical variety among these taxa provides not only the linkage that anchors sakis and uakaris to *Callicebus* and *Aotus*, but also the connection of this larger group to atelines (Schneider and Rosenberger, this volume).

The feeding ecology of the pitheciines is becoming well known. All of the long-term studies of the three larger pitheciins (saki-uakaris) have focused on feeding (Ayres, 1986, 1989; van Roosmalen *et al.*, 1988; Kinzey and Norconk, 1990, 1993; Peres, 1993; Setz, 1994) and they agree that pitheciins occupy a predispersal seed predator niche in the Neotropics. As such, they can ingest fruit at early stages of maturity and may escape seasonal reduction in food resources during the dry season (Norconk, this volume). There are subtle differences in the diets of *Pithecia*, *Chiropotes*, and *Cacajao*, but they are similar in showing a preference for seeds of large-seeded fruit of the families Lecythidaceae and Sapotaceae (Ayres 1981, 1986; van Roosmalen *et al.*, 1988; Kinzey and Norconk, 1990, 1993; Peres 1993). With evidence from long-term studies of feeding ecology, we are beginning

to appreciate the tremendous value of seeds as dietary resources. It is significant that the feeding pattern of *Pithecia* fits well into this picture, for its dental specializations are far less extreme than the system shared by *Chiropotes* and *Cacajao*. As Kinzey (1992) and Rosenberger (1992) have discussed, the dentitions of *Callicebus* and *Aotus* are also best interpreted as part of the hard-fruit and seed-adapted continuum. In fact, *Callicebus*, and less so *Aotus*, are at the pole opposite that occupied by *Chiropotes* and *Cacajao*, with *Pithecia* nestled in the middle but closer to the latter. Morphologically, some of the fossils listed in Table 1 are also avatars of hypothetical morphotypes, filling in the anatomical gaps between, say, *Pithecia* and *Callicebus* (cf. *Soriacebus*).

Aotus may be the most generalized of the pitheciines ecologically. Wright (this volume) describes a diet of fruit supplemented with few leaves and abundant in insects. Ingestion of seeds was not mentioned at all by Wright for *Aotus* and they lack the narrow-tip, procumbent incisors that is characteristic of the other pitheciines. *Callicebus* and *Pithecia* spp. all ingest some leaves, but *Chiropotes* and *Cacajao* rarely take any. Ingestion of insects does not appear to indicate significant differences among the species - they all ingest insects. However, *Aotus* appears to be very general, lacking most of the important derived postcanine dental and feeding specialties shared by the larger pitheciines (although it does have an unusual, enlarged anterior dentition which is related to food harvesting; see Rosenberger, 1992).

There are two viable interpretations to the relatively generalized dentition and feeding behavior of *Aotus*. Either owl monkeys retain a more insectivorous postcanine dentition in concert with new "pitheciine" harvesting specializations of the anterior teeth; or the molars are derived as an insectivorous-folivorous adaptation associated with the shift to nocturnality. We favor the latter view, in part. Some of the fossil pitheciines, such as *Soriacebus* and *Lagonimico*, have postcanine teeth that do not resemble the flat-crown, crushing molars of saki-uakaris. This, too, is evidence for adaptive diversity and phylogenetic continuity within this broadly defined group.

While awareness of the dental specializations foreshadowed the demonstration of saki-uakaris as seed predators based on field observations, we have made little headway toward understanding their social behavior. Wright's (1989) comparative field study of the two smallest members of this subfamily confirmed that both *Callicebus moloch* and *Aotus* not only live in small family groups, but also that the adult members of the group exhibit behaviors that appear to reinforce long-term sociosexual bonds. In contrast, we can construct only superficial outlines of the social systems of the three larger members of this subfamily. *Chiropotes* and *Cacajao* form groups of 15 or more individuals that are not "family" oriented, in the traditional sense of monogamy. Small group sizes reported for *Pithecia* has led to the conclusion that they are monogamous (Buchanan et al., 1981; Robinson et al., 1987). However, preliminary observations of white-faced saki social behavior make it apparent that sakis challenge the traditional criteria we apply to primate monogamy.

First, in support of the interpretation that *Pithecia pithecia* is monogamous:

1. Based on the evidence of a few vocal playback experiments at Lake Guri, Venezuela, white-faced sakis responded as if they defend territories in a very traditional way. Adult males and females were attracted to playbacks of loud calls recording during an inter-troop encounter, by approaching the speaker and giving the same kind of call in response (Norconk and Araya, unpub). This represents the first suggestion of territorial behavior in *Pithecia* spp. Previously, *Pithecia* was considered non-territorial and group sizes larger than a family unit

were interpreted as aggregates of mated pair units (Happel, 1982; Oliveira *et al.*, 1985; Soini, 1986).

2. Both males and females are forced to disperse from their natal group at about three years of age. We observed individuals of both sexes permanently segregated from, and interacting aggressively with, the core social group.

Second, confounding the view that *Pithecia pithecia* is monogamous:

1. More than one adult of each sex coexists in a social group. Our observations of adult males (Gleason and Norconk, 1995) suggest that sakis operate within a complex social context involving cooperation and competition among adult males and among adult females. Although our group of nine individuals may be unusually large due to the animals' inability to disperse from the island, similar observations of group size have been made in terra firme (Kinzey *et al.*, 1988 for *P. pithecia*; Soini, 1986 for *P. hirsuta*).
2. There is no evidence of paternal care, although there is some very interesting data suggesting allomaternal care by full-sized daughters or other adult females (Ryan, 1995 for *P. pithecia*, Soini, 1986 for *P. hirsuta*). The behavior is not very complex, but consists of mother foraging or feeding 50 to 100 m away from the infant and "caretaker", within earshot of the infant who often gives a separation call.
3. It appears that both males and females jostle for reproductive position within a social group. After seven years of monitoring this group, we have never observed more than one female to give birth in the same year although our hormonal work (Scheidtler and Norconk, unpubl.) shows that more than one female was reproductively active. We have also observed copulations by one male only, even when three adult males were resident.

In sum, *Pithecia pithecia* is not a "typical" monogamous primate. For the larger pitheciins, data on group size and social aggregates support a view that these sakis are organized on the "multiple male" theme: group sizes range from 15 to more than 30. Groups of *Chiropotes* and *Cacajao* divide up during feeding and coalesce during long distance travel although group fission may be more marked in *Cacajao calvus* than *Chiropotes satanas*. We are not yet sure of the relationship between the small feeding parties and social interactions. Ayres (1986) observed small groups of uakaris isolated for hours or days at a time, but as intriguing as it is, there is still little evidence to add support to the hypothesis that "large groups [of *Chiropotes*] might be relatively permanent aggregations of monogamous subunits" (Robinson *et al.*, 1987:49). Nevertheless, the temporary unions which form for feeding and possibly reproductive reasons, is yet another point of continuity between the larger and smaller pitheciins; the big groups of *Chiropotes* and *Cacajao*, the intermediate-sized groups of *P. pithecia* and the small, pair-bonded units of *Callicebus* and *Aotus*. It suggests that the social organization of ancestral pitheciins may have been structured about the preference to form small parties to mitigate/benefit feeding and foraging strategies.

The growing body of data from field work, systematics and paleontology, when synthesized in an evolutionary perspective which recognizes the mosaic nature of change, provides evidence that the pitheciins are indeed an *adaptive radiation*. The fossil record amplifies this point as do the studies on extant species. Pitheciins as a whole are not radical and uninterpretable, but saki-uakaris are the rule breakers within the larger group that challenge and enlarge evolutionary models. We are coming to realize that pitheciins are a

bizarre offshoot *within* a diversified ecological array pivoting on dental adaptations allowing hard-fruit harvesting.

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