Part I **Fossil History, Zoogeography and Taxonomy of the Pitheciids**

Chapter 2

The misbegotten: long lineages, long branches and the interrelationships of *Aotus*, *Callicebus* and the saki–uacaris*

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Introduction

An important shift in thinking has become cause for renewed scrutiny concerning the course of platyrrhine evolution and the shape of New World monkey (NWM) classification. For the first time in nearly 200 years, *Aotus* is being moved across a major taxonomic divide. It is being considered as a genus aligned with marmosets and tamarins rather than titi monkeys and saki–uacaris and, more generally, atelines. The emergence of this debate reflects the impact of molecular cladistics since the early 1990s. The conversation has turned from a prolonged controversy (e.g. Rosenberger 1981, 2002) over marmosets and tamarins, a dispute that was fundamental to modernizing our views of NWM evolution and appears to be resolved *for the moment*. Now, beginning with the successful molecular cladistic analysis of Schneider *et al.* (1993), the deliberation is over *Aotus*: is it a pitheciine, an atelid, a stem platyrrhine or a cebid? The prevailing opinions that warrant close examination are the last and the first – *Aotus* is either a cebid or a pitheciine. However, the crux of the matter is that the hypothesis of *Aotus* as a "cebid" is based almost entirely on genes; the idea that it is a pitheciine is based entirely on morphology.

While some morphologists align *Aotus* more closely with the molecular trees (e.g. Kay 1990; Horovitz 1999; see also Meldrum & Kay 1997; Kay *et al.* 1998a), we believe this assessment does not adequately account for anatomical evidence bearing on *Aotus*, *Callicebus*, *Pithecia*, *Chiropotes* and *Cacajao*, no less their fossil relatives (Rosenberger 2002). How is the *Aotus* matter different? *Aotus* has rested comfortably near *Callicebus* in morpho-space ever since higher level classifications of the platyrrhines were developed in the early 1800s (Rosenberger 1981). There was not a hint that *Aotus* could be related to anything but a pitheciine or ateline until the 1990s (see Tejedor 2001). As a consequence, morphologists challenged by the molecular evidence regarding *Aotus* have no fallback position from which our information can be reinterpreted. The molecules conflict with the morphology rather directly. The discord goes beyond that: the molecules clash with ecology and behavior. *Aotus* and *Callicebus* are bound together by a unique combination of attributes: social monogamy, biparental care with extensive input by males, no sibling care, long call advertising, territoriality, locomotion and feeding (e.g. Robinson *et al.* 1987; Wright 1996; Fernandez-Duque 2007; Norconk 2011). One is hard-pressed to find any two genera of modern NWM more alike than *Aotus* and *Callicebus*, except for the obvious dyads that split cladistically relatively recently, and only arguably into distinct genera – *Callithrix* and *Cebuella*, and *Cacajao* and *Chiropotes*.

Given the narrow scope of this chapter, a complete analysis of the problem is impossible. For one, it would require a full explication of the fossil record pertaining to *Aotus*, *Callicebus* and the saki–uacaris. Instead, to introduce these taxa in condensed form, and to clarify our use of taxonomic terms, we present a classification of pitheciines (Table 2.1), extending the scheme of Rosenberger *et al.* (1990). In an effort to summarize our assessment, we also advocate a stance rather than illuminate the conjectures and refutations: *Aotus* is a pitheciine, not a cebid. Overall, our aim is to present a synopsis of three aspects of the problem that must be accounted for in order to unravel the *Aotus* puzzle: (1) the morphological evidence linking *Aotus*, *Callicebus* and saki–uacaris cladistically; (2) a critical assessment of the molecular evidence; and (3) a synthesis of the evolution of pitheciine feeding adaptations which we further promote as heuristic evidence that *Aotus* is, in fact, pitheciine – phylogeny and adaptation are two sides of the same evolutionary coin, to paraphrase Fred Szalay.

Pithecia, *Chiropotes* and *Cacajao* – at the end of a morphocline

The craniodental morphology, our focus, leads to the following: *Aotus* is most closely related to *Callicebus*, and *Callicebus* (via the ancestral morphotype of *Aotus* and *Callicebus*) is linked with saki–uacaris. Dentally, *Pithecia*, *Chiropotes* and *Cacajao* have effectively defined pitheciines because the

Evolutionary Biology and Conservation of Titis, Sakis and Uacaris, eds. Adrian A. Barnett, Liza M. Veiga, Stephen F. Ferrari and Marilyn A. Norconk. Published by Cambridge University Press.

characters of saki-uacaris are striking structurally and adaptively while also being cladistically informative (Figure 2.1). *Pithecia* is the most primitive craniodentally on the whole, and thus the foundation for comparisons with other forms. *Chiropotes* and *Cacajao* present an exaggerated version of the pattern. But the greater challenge is to sort out how their anatomy evolved transformationally: how and why did platyrrhines arrive at a *Pithecia*-like pattern? Kinzey (1992), Rosenberger (1992) and Meldrum & Kay (1997) presented workable models of this transition, blending the moderns with information from the fossil record, which we extend here.

Table 2.1 A classification of living and fossil pitheciines, mostly to the genus level, based on Rosenberger *et al.* (1990) and Rosenberger (2002). Dagger symbols mark the fossils.

- Family Atelidae, Gray, 1849
  - Subfamily Pitheciinae Gray, 1849 (Mivart, 1865)
    - Tribe Pitheciini Gray, 1849 [pitheciins]
      - *Pithecia* Desmarest, 1820
      - *Chiropotes* Lesson, 1840
      - *Cacajao* Lesson, 1840
      - †*Cebupithecia* Stirton & Savage, 1951
      - †*Nuciruptor* Meldrum & Kay, 1997
      - †Proteropithecia Kay *et al.*, 1998
    - Tribe Soriacebina, Rosenberger *et al.*, 1990
      - †*Soriacebus* Fleagle *et al.*, 1987
    - Tribe Homunculini [homunculins]
      - *Callicebus* Thomas, 1903
      - †*Homunculus* Ameghino, 1891
      - †Miocallicebus Takai *et al.*, 2001
      - †*Aotus dindensis* Setoguchi & Rosenberger, 1987
      - †*Tremacebus* Hershkovitz, 1974
    - Tribe indet.
      - †*Xenothrix* Williams & Koopman, 1952
      - †*Lagonimico* Kay, 1994
      - †*Carlocebus* Fleagle, 1990

Pithecia (Figures 2.1, 2.2) has a procumbent, wedge-like lower incisor battery, piercing canines and rugose cheek teeth, a combination that has been explained cogently as mechanical adaptations to hard-fruit harvesting and seed-eating (see Rosenberger & Kinzey 1976; Kay 1990; Kinzey 1992; Rosenberger 1992; Martin *et al.* 2003; Norconk *et al.*, Chapter 6).

The most obvious morphological link between the saki–uacaris and *Callicebu*s and *Aotus* involve incisor and canine morphology (Figures 2.1 and 2.3). Although the gross anatomy of the canine and postcanine teeth of *Callicebus* bears little direct resemblance to pitheciines, the lower incisors demonstrate an uncanny likeness. They are tall, narrow and compressed together in an arch, but they do not jut out and are not shaped into the chisel-like apical edge of saki–uacaris. Upper central incisors of *Callicebus* and *Pithecia* also have an unusual lingual tubercle on the cingulum, which is not found in other platyrrhines. These features formed the beginnings of the cladistic link between *Callicebus* and pitheciines (Rosenberger 1977, 1981; Ford, 1986; Kinzey 1992; Meldrum & Kay 1997; Kay *et al.* 1998; but see Kay 1990 for a different view). The hypothesis was extended and confirmed by behavior and ecology (see Robinson *et al.* 1987; Kinzey 1992; Norconk 2011) and a host of molecular studies (see below).

For additional perspective on the functional significance of the incisor–canine complex of *Callicebus* as a cladistic link to pitheciins, the comments of Kinzey (1977, p. 140) concerning the feeding behavior of wild *Callicebus* are especially pertinent:

> Although most fruit appeared to be placed in the corner of the mouth where canine or premolars apparently tore off the husk or removed the edible pulp, a different method was used to obtain the edible portion of palm fruit [the second ranked food source]. The fruit was held between the two hands and the upper and lower incisors were used together to scrape the thin layer of hard pericarp from the pith. This behaviour very well may have accounted for the characteristic wear previously noted on *C. torquatus* incisors …

Figure 2.1 Anterior teeth of modern pitheciines and Ateles. Clockwise from bottom left: (a) *Cacajao melanocephalus*; (b) *Chiropotes satanas*; (c) *Pithecia pithecia*; (d) *Callicebus torquatus lugens*; (e) *Aotus grisimembra*; (f) *Ateles belzebuth hybridus*. Compared to *Ateles*, notice the reduction in the second upper incisor relative to the central incisor in *Aotus*, *Callicebus* and saki–uakaris, also the everted lower canines of *Aotus* (essentially vertical in *Ateles*), and the high-crowned upper central incisors, resembling pitheciins. The scoop-like, compressed lower incisor battery of all pitheciines, which is more proclivous in pitheciins than in homunculins, is produced by the "non-verticality" of the lateral lower incisor in this view. The face of *Pithecia* may be the most primitive form among saki–uacaris, in general (Kinzey, 1992).

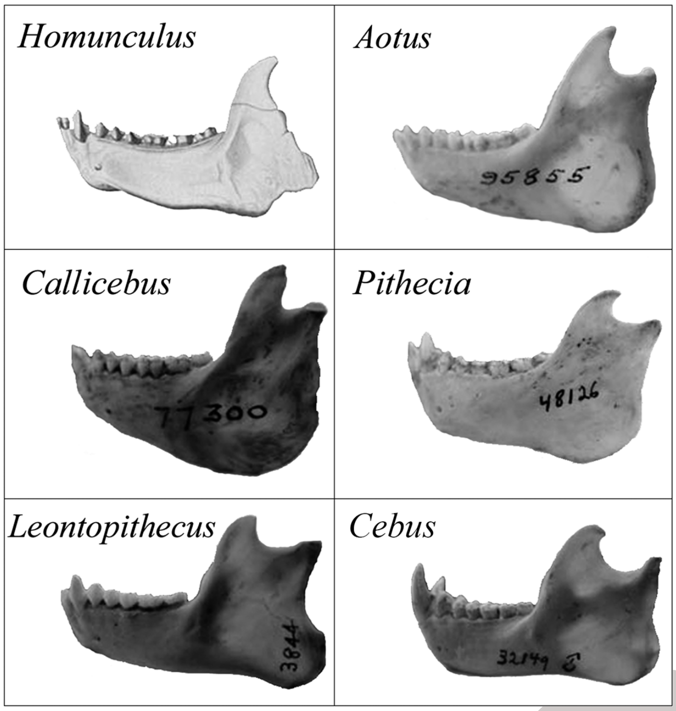

Figure 2.2 Lateral jaw profiles of selected platyrrhines brought to approximately the same length. Clockwise from top left: the Miocene fossil *Homunculus patagonicus* (from Bluntschli, 1931); *Aotus* sp., *Pithecia pithecia*, *Cebus capucinus*, *Leontopithecus rosalia*, *Callicebus* sp. Cebids typically have jaws that do not deepen much or at all, nor do they flare out posteriorly, as in pitheciines and atelines, which is the derived condition for platyrrhines. *Homunculus* and *Aotus* may represent the morphotype pitheciine condition, while the gonial inflation of *Callicebus* is derived (but see Figure 2.4) in one direction; the anteriorly deep and robust jaw of *Pithecia* (and other saki–uacaris) is derived in a different direction. The unusually elevated mandibular condyle in *Aotus* and *Callicebus* (likely in *Homunculus* also) is evident.

Kinzey implies here (and ALR, who worked with Kinzey in the field on the *Callicebus* project, confirms) that it was the hardness of the substrate beneath the pericarp that wore the incisors of *Callicebus* so heavily. Thus Kinzey's remarks (1977) anticipated the preadaptive, ecophylogenetic nature of *Callicebus* morphology and behavior as a prelude to the highly specialized, prying, gouging and stripping activities of pitheciins. While the incisors of *Aotus* are superficially different in some details, their battery is also well designed for gouging and stripping hard husks (Figure 2.3) in the same manner, as Kinzey (1974) pointed out. *Aotus* incisors are modestly high-crowned and somewhat inclined. The principle difference from *Callicebus* and pitheciins is that the incisors of some forms of *Aotus* are relatively wide at the apical edge, although this variation is not so impressive in all owl monkey taxa (Figure 2.3).

Callicebus and *Aotus* – novelties among the nondescript

Methodologically, there are two bodies of morphological evidence that speak directly to the narrow affinities of *Aotus*: studies employing parsimony algorithms and studies using non-algorithmic character analyses. The solutions of some of the older parsimony studies may (e.g. Ford 1986) or may not (e.g. Kay 1990) resemble the results from conventional character analysis, but the recent ones do not (e.g. Horovitz 1999; Horovitz *et al.* 1998). Some of the possible reasons for these discrepancies have been discussed elsewhere (Rosenberger 2002). Additional insight into the limitations of the parsimony method has highlighted the inherent potential for taxonomic sampling artifacts to bias results, whether the evidence is molecules or morphology (e.g. Rosenberger & Kearney 1995; Collins 2004; Sargis 2007; Silcox 2007; Matthews & Rosenberger 2008). In any event, the morphology-based parsimony studies that resemble molecular results offer only tepid support for the *Aotus*-cebid hypothesis.

Our character analysis relies on the morphology of the mandible, incisors, canine, face and auditory bulla. The lateral profile of mandible in NWM discriminates cebids from atelids (Figure 2.2; Rosenberger 1977, 1979). Cebids have a relatively horizontal body that does not expand inferiorly and posteriorly at the angle of the mandible. Widespread among early anthropoids and other primates, this condition is probably primitive among platyrrhines. The atelid state, a posteriorly deepening corpus with an inflated, rounded mandibular angle is very likely derived. The *Pithecia* mandible, while preserving the dilation posteriorly, is derived relative to the ancestral atelid state in being much deeper and thicker anteriorly in connection with their advanced incisor–canine morphology and its derived, U-shaped jaws.

Homunculus, an early Miocene pitheciine, closely resembles the typical pattern of *Aotus*. We take this pattern as the morphotypic condition of pitheciines and atelines, evidence that *Aotus* is related to atelids and not to cebids. However, a deeper set of resemblances is also shared by *Aotus* and *Callicebus*. Figure 2.4 shows individual mandibles belonging to three species of *Aotus* and *Callicebus*. It illustrates a variation in *Aotus* that overlaps a generic hallmark of *Callicebus*, enormous inflation of the mandibular angle.

Aotus and *Callicebus* also share a high temporomandibular joint, produced by a tall, anteroposteriorly short mandibular ramus that rises well above the tooth row. The combination of a high jaw joint and deep gonial region, where the superficial masseter muscle inserts, indicates a relatively vertical orientation of the muscle, long fibers and a relatively vertically oriented adductor force generated by them during jaw closing. Differences from cebids are evident (Figure 2.2). There the ramus tends to be low and long in the anteroposterior axis. The relatively squat ramus is especially typical of cebines. This pattern is more consistent with a temporalis-dominated feeding system applying forces in a relatively horizontal direction (Anapol & Lee 1994). Thus, the similarities of *Aotus* and *Callicebus* in form and function are themselves unique and distinguished from patterns found among cebids.

The morphology of the auditory bulla in *Aotus* and *Callicebus* is highly distinctive and unmatched by other

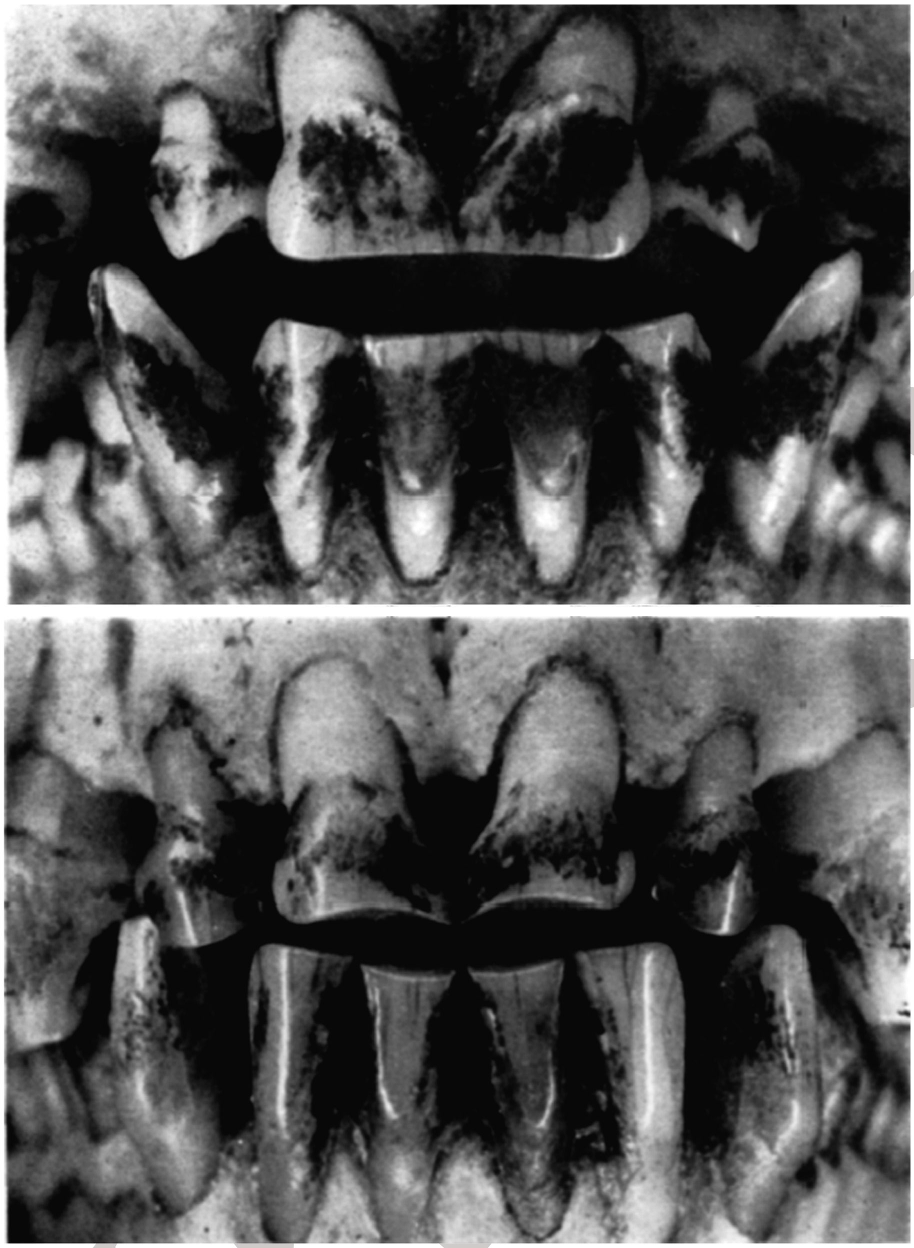

Figure 2.3 Close-ups of the anterior teeth of *Aotus trivirgatus* (top) and *Callicebus torquatus* (bottom), brought to same approximate bi-canine width. Note the relative narrowness of the lower incisor span of *Aotus* and *Callicebus* and the everted lower canines of *Aotus*, essentially absent in *Callicebus* due to extreme crown reduction. Compare the incisor proportions with the example of *Aotus* in Figure 2.1, and also the moderately everted canines of *Callicebus* in Figure 2.1.

platyrrhines (Figure 2.5). Their bullae are quite inflated and composed of a broadly distributed field of densely cancellous bone. There is an unusual, enlarged anterolateral compartment, a lobe-like extension in front of the acoustic meatus that encroaches on the temporomandibular joint. Unlike the teardrop outline of cebids, which is probably primitive for platyrrhines, the bullae of *Aotus* and *Callicebus*, like *Pithecia*, are also irregularly shaped and broad posteriorly. So, while pitheciines may be derived in overall bullar shape, the rare details found exclusively in *Aotus* and *Callicebus* are probably joint synapomorphies. Little is known about bullar functional morphology, but here the spongy bone may help dampen vibration, perhaps insulating the middle ear from bone conducted sound. An adaptive connection with the stentorian vocalizations of *Aotus* and *Callicebu*s, which are prodigious especially in relation to their small body size, may have been a selective factor.

In addition to basic phenetic similarities in the crania of *Aotus* and *Callicebus*, including many features probably primitive for platyrrhines, their joint canine and facial morphologies are distinctive and probably derived. Canines are moderate (*Aotus*) and very small (*Callicebus*) in size. In all cebid genera, male canines are large and projecting, and in callitrichines even female canines are large tusks. The cebid pattern may be derived among NWM, which is not consistent with a placement of *Aotus* within the clade. *Aotus* also shares no derived cebine features; no vaulted frontal bone, no narrow

Figure 2.4
A comparison of the "typical" jaw profile in genus *Callicebus* (top, *C. torquatus*) with individual variations found in *Aotus* (middle, *A. nigriceps*; bottom, *A. infulatus*), brought to the same approximate length. The middle image is cropped slightly at the base, where it was embedded in clay.

nasals from base to tip, no wide snout, no anteroposteriorly long mandibular ramus.

It is striking that *Aotus* and *Callicebus* have a combination of moderate-to-minuscule canines (see Kay *et al.* 1988), correspondingly reduced faces with abbreviated premaxillae, relatively tall incisors, compact incisor–canine batteries and parabolic jaws. This picture also differs from our interpretation of *Homunculus* (see Tejedor & Rosenberger 2008), which is in many respects primitive for pitheciines. It had more V-shaped jaws, a precanine diastema, staggered incisors and a large snout. The distribution of characters suggests that homunculins (e.g. *Aotus, Callicebus* and allies; Table 2.1) and pitheciins evolved from a pattern like this in two distinct directions.

The best explanation we have for the *Aotus*–*Callicebus* pattern is that it reflects a structural compromise between adaptations for feeding and mating (Rosenberger *et al.* 1990). The incisor battery is tuned to fruit harvesting while the canine complex has been selected for a low-crowned form of monomorphism that evolved in connection with a pair-bonded monogamous mating system, a source of selection that compromises, or constrains, the dietary imperative. Metrically, the canines of *Aotus* and *Callicebus* are the least dimorphic among modern platyrrhines in their body size class (Kay *et al.* 1988), and they are clearly distinguished from other modern species that have monomorphic canines by their anatomy and biological roles. Callitrichines, for example, have large, same-sized canines in males and females and use them in agonistic situations, manifesting an altogether different socio-sexual context. This makes it highly likely that the contrasting pattern shared by *Aotus* and *Callicebus* is homologously derived (Rosenberger *et al.* 1990).

The molecular evidence – the long lineage hypotheses meets long branch attraction

We are cognizant of the impressive number of molecular cladistic studies since the 1990s, which have favored a linkage between *Aotus* and cebids. Our reading of the molecular support for this hypothesis is that it presents several problematic outcomes and contingencies. (1) The precise location of *Aotus* within the cebid branching sequence is not often replicated, and polytomies involving its position are not unusual. (2) The *Aotus* linkage within the cebid clade occurs with quantifiably low levels of support. (3) Rooting *Aotus* with the cebids often coincides with a reduced level of support for more distal clades that are very strongly supported by morphology and molecules alike. (4) The tendency is for rooting *Aotus* within the cebids adjacent to taxa that share a particular evolutionary history that may make them prone to skewed molecular results – they are long-lived lineages (Rosenberger 1979, *et seq.*) susceptible to a methodological artifact known as long branch attraction. A speciation-level process, such as reticulation, is another source of low resolution in phylogeny reconstruction (e.g. Doolittle 1999) that may have to be considered here.

Figure 2.6 summarizes the quantitative evidence backing platyrrhine clades in an array of molecular studies. They do not produce symmetrical cladograms: relationships differ; polytomies appear in different combinations, at different nodes and in different proportions relative to dichotomies; and higher-level linkages often differ. The studies from which these data were generated also tend to provide several alternative results, concluding with or without a final, "preferred" cladogram. Thus, in the absence of across-the-board consensus within and among these reports, the chart is but one way to quantitatively assess how well the *Aotus*-cebid hypothesis fares relative to other platyrrhine groupings, while the qualitative points mentioned above suggest additional reasons why caution is called for.

The *Aotus*-cebid clade ranks lowest overall in node support by comparison with the other four groups (Figure 2.6). Callitrichines and pitheciines are the clades whose monophyly is most consistently supported. The atelines vary somewhat. But surprisingly, the cebines are not linked with high

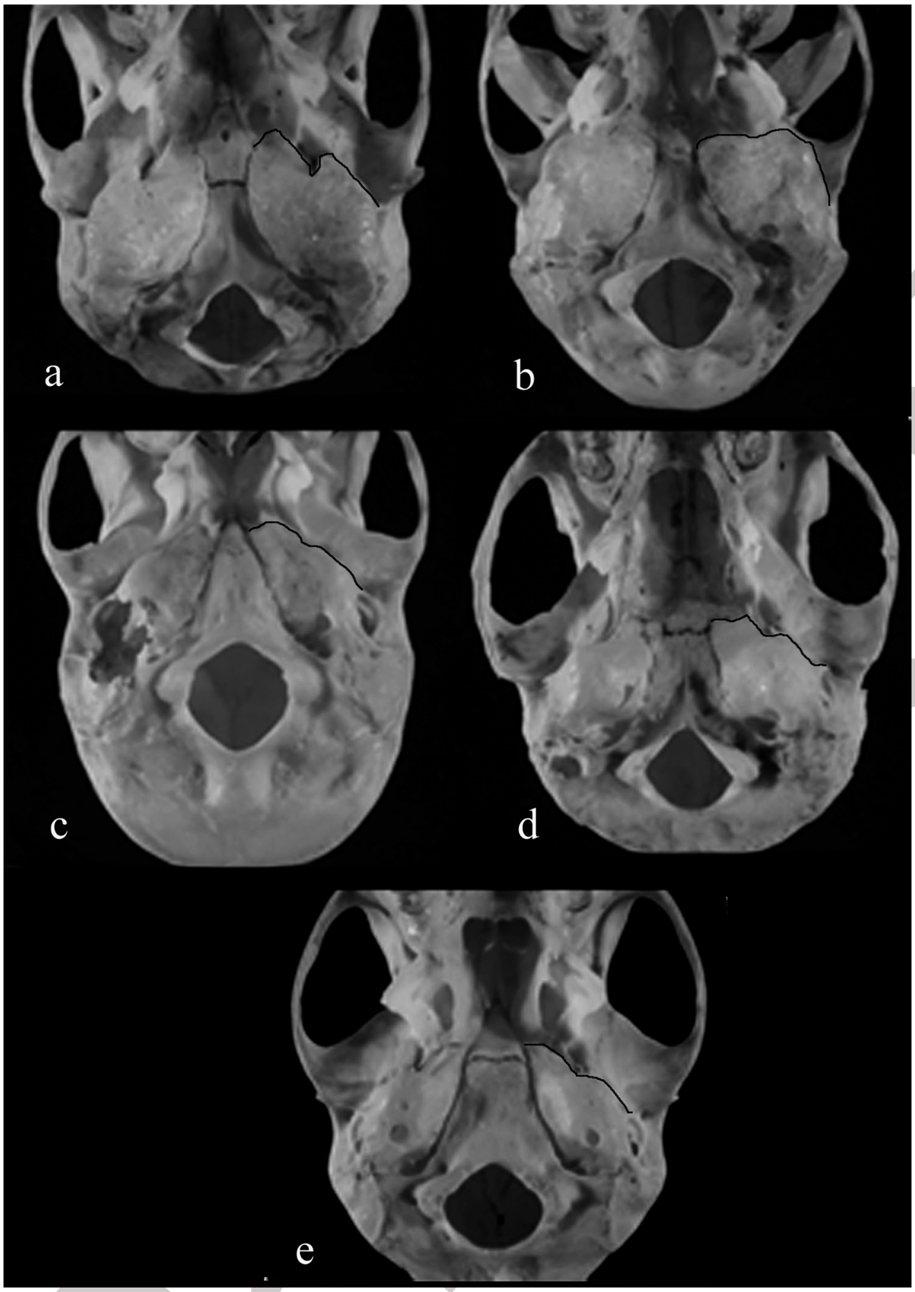

Figure 2.5 The auditory regions of selected platyrrhines, brought to approximately the same skull lengths. The anterolateral margin is outlined from the auditory meatus to the anteromedial pole. (a) *Aotus*, (b) *Callicebus*, (c) *Saimiri*, (d) *Pithecia*, (e) *Cebus*. The teardrop-shaped auditory bullae of cebids resembles archaic Old World anthropoids and is probably primitive for NWM. The irregular shape of the pitheciines, which is very wide posteriorly at the level of the eardrum, is a derived pattern.

reliability, although this is a very securely established node by morphology and molecules. Actually, the *Saimiri–Cebus* link is a triumph of modern phylogenetic reasoning, for these animals are dramatically different in so many ways. We suggest that their depressed level of support in the molecular studies is a local artifact, directly influenced by misclassification of *Aotus*.

An explanation for the persistence of a low-resolved solution for *Aotus* is that its position is simply an error that repeatedly affects a same combination of platyrrhine genera due to the long branch attraction phenomenon. Felsenstein (1978) showed that there is a high likelihood that the terminal taxa of relatively long branches will come to resemble one another due to convergence when the time interval separating their initial differentiation is relatively short (Figure 2.7). Under a random model of nucleotide evolution there is a high probability this can occur, as in theory there are only four possible character state changes, and fewer still in practise. The more time available for evolution following a limited amount of genetic separation at the origin, the more likely the character states of lineages will converge. And, as the chemistry is the same, there is no way of knowing, say, if two Gs in the same position are homologous. Bergsten (2005) showed empirically that long branch attraction is a real phenomenon, arguing that

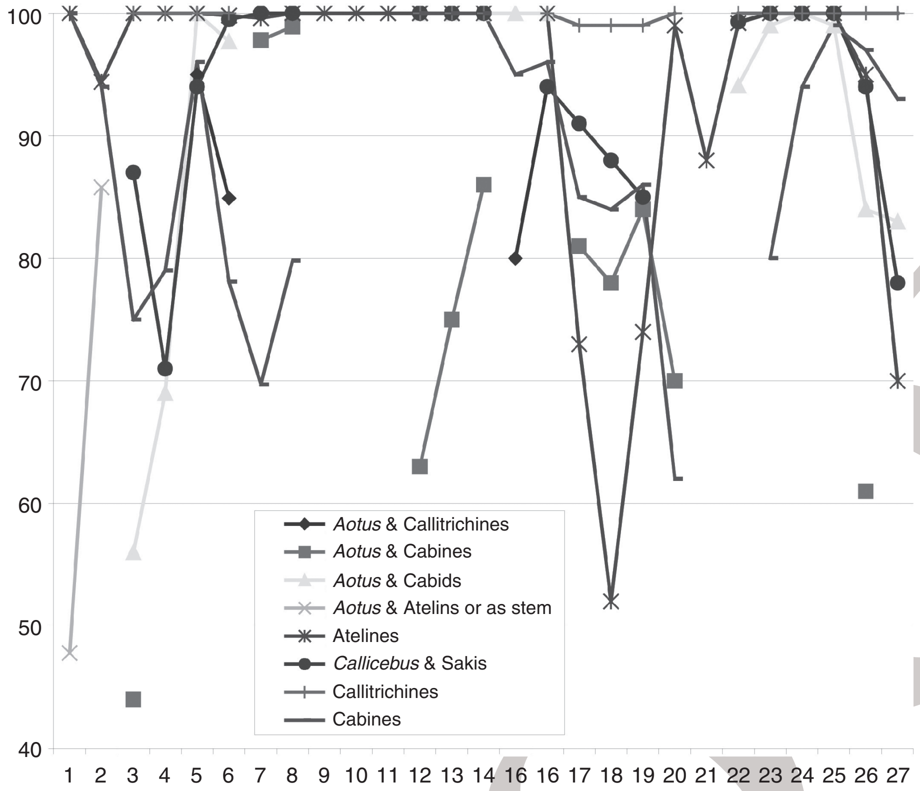

Figure 2.6 Line chart showing measures of bootstrap support for monophyletic groups returned in molecular studies of platyrrhine interrelationships based on parsimony analyses. See also text. The various "*Aotus* clades" are shown, defined in the inset legend, as in one placement that posits *Aotus* as the stem lineage of crown platyrrhines. The *Aotus* links have consistently lower and more variable support values across these studies. Sources: Canavez *et al.* (1999), Goodman *et al.* (1998), Harada *et al.* (1995), Opazo *et al.* (2006), Porter *et al.* (1997), Prychitko *et al.* (2005), Ruiz-Garcia & Alvarez (2003), Schneider *et al.* (1993, 1996, 2001), Steiper & Ruvolo (2003), and von Dornum & Ruvolo (1999).

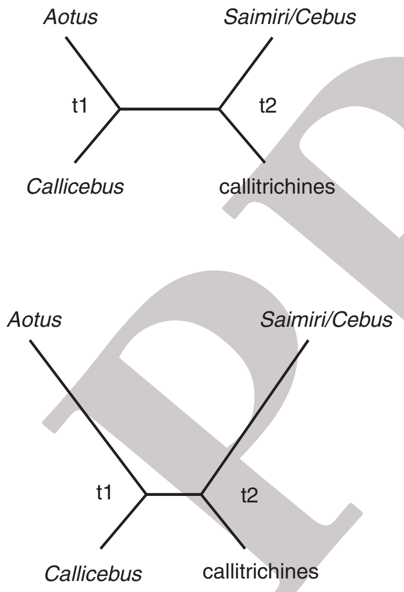

Figure 2.7 The long branch attraction artifact, modified from Felsenstein (1978). Two unrooted tree models of relationships are shown. If the temporal separation (t1–t2) between the splitting times of clades is relatively short while the descendant lineages in question have evolved for a long period of time, random selection of nucleotide substitutions will perforce result in proportionately large amounts of convergence because the pool of potential states changes remains small. Parsimony trees are therefore prone to mistake convergent similarities as homologous-derived features.

it is commonplace when the in-group also contains relatively short branches.

There are several long generic lineages, as demonstrated by the fossil record (e.g. Rosenberger 1979; Delson & Rosenberger 1984; Setoguchi & Rosenberger 1987; Rosenberger *et al.* 2009) and also the molecules (e.g. Opazo *et al.* 2006), as well as some that are very likely short (*Callithrix* and *Cebuella*; *Chiropotes* and *Cacajao*). The *Aotus* lineage, represented by a congeneric species in the middle Miocene La Venta fauna of Colombia and by *Tremacebus* in the early Miocene of Patagonia, is an established long lineage. The *Saimiri* lineage is represented by another La Ventan species and also appears to be represented in the early Miocene in Patagonia by *Dolichocebus*. In more general terms, the cebine lineage is certainly confirmed in the late–early Miocene by *Killikaike* (Tejedor *et al.* 2006). Thus the genera most closely aligned with *Aotus* in molecular studies are the most basal branches of the cebid clade and are each long-lived, thus increasing the potential for them to converge with the equally long-lived *Aotus* as an artifact: the algorithm is mistaking new analogies for derived homologies. Steiper & Ruvolo (2003), among others, have emphasized the possibility of a rapid differentiation of the early platyrrhine lineages. In other words, all the conditions Felsenstein (1978) predicted as potentially troublesome may align here. Long branch attraction may also explain the cladistic noise vexing Schneider *et al.* (2001) in their assessment of molecular studies, wherein they state: "… two major points regarding the branching pattern of the most ancient lineages remain to be clarified: (1) what is the exact branching pattern of *Aotus*, *Cebus*, *Saimiri* and the small callitrichines? (2) Which two of the three main lineages (pitheciines, atelines and cebids) are more closely related to one another?" *Aotus* may be the muddle in the middle.

Pitheciine evolution – an ecophylogenetic scenario

While the problem of *Aotus* cladistics deserves special attention as a decisive datum regarding the history of two large branches of the platyrrhines, the question of saki–uacari origins is also important. They are the only obligate seed-eaters among the living primates (Norconk *et al*., Chapter 6). How did seed-eating evolve here?

It seems clear that the anterior teeth came first, but not in the radical configuration of modern pitheciins (Rosenberger *et al*. 1990; Kinzey 1992; Rosenberger 1992). As Kinzey, Rosenberger and colleagues inferred some years ago, there are probably related seed-eaters awaiting discovery in the fossil record that exhibit primitive "stages" of the mosaic rather than the primary tier features, e.g. occlusal flattening of P4s and the adjacent molars, crenulation of the cheek teeth, eversion of the canines, etc. *Soriacebus* and *Homunculus* are two important examples that fit the prediction. Both have saki-like attributes in the lower incisors and, in addition, *Soriacebus* demonstrates robust canines and a wedge-shaped anterior lower premolar. A reinterpretation of *Homunculus* expands this argument with more anatomical detail on the anterior teeth and jaws (Tejedor & Rosenberger 2008). Discovery of *Proteropithecia* in Patagonia and *Nuciruptor* in Colombia (Meldrum & Kay 1997; Kay *et al*. 1998) also demonstrates later "stages", with more modern canine and postcanine teeth, but not the full-blown *Cebupithecia*- and saki-like low, corrugated crowns. This body of evidence represents one of the few cases among the primates where a model evolutionary sequence can be reconstructed from fossils towards the emergence of a new dietary adaptive zone.

What does this transformation mean in terms of feeding? Sclerocarpic foraging for hard, unripe fruits and for arils that coat large, hard seeds like a palm nut probably preceded obligate seed eating, perhaps as a way of minimizing competition with other sympatric platyrrhine frugivores that prefer juicy ripe fruit (Kinzey 1992; Rosenberger 1992; Norconk *et al*., Chapter 6; see also Kinzey & Norconk 1990). As reported by Kinzey (1974, 1977), *Callicebus* uses its incisor teeth (and canines) as a rasp to remove aril from large, hard palm nuts, which also results in heavy tooth wear. We may logically interpret this as an anatomical–behavioral pattern more primitive than the pitheciine pattern.

Thus one can imagine the breaching impetus of obligate seed predators evolving as a new "processing image", extending the propensity to gouge and scrape. It could have begun with a *Callicebus*-like species – *Homunculus* would be the paleontological example – a relatively generalized fruit-feeder that finds ecological advantage by focusing on tough fruits with a large seeds. At a medium-to-small body size, without exhibiting an acrobatic locomotor habit and a large home range socioecological strategy, they could perhaps have afforded (or been constrained) to eat – or were competitively advantaged by being able to eat – less ripe, less sugar-rich fruits than animals like *Ateles*. These pre-seed-eating pitheciines would have been cognitively disposed to finding and treating food objects with the anterior teeth, rather than seeking fruits of a smaller size and softer consistency that can be masticated by the postcanines without investing much energy in anterior-tooth processing. Eventually the lineage would evolve taller, more inclined incisors, better able to resist wear and to wedge leguminous pods apart with greater mechanical advantage. Adding modified canines and anterior premolars (and jaws, etc.), incorporating them as specialized puncturing and prising devices, would "complete" the transition to build a seed extraction platform.

Pitheciines may also have been preadapted to seed-eating because their digestive systems appear to be capable of processing low-quality foods, in a manner analogous to folivores (Norconk *et al*., Chapter 6). Rosenberger *et al*. (2009) suggested that in addition to morphology, the geographical distribution of modern pitheciines, the feeding habits of *Aotus* and *Callicebus*, and especially the occurrence of homunculins and pitheciins in the remote, early and middle Miocene of Patagonia, suggests that the earliest pitheciines may have been "junk food" feeders living in low-productivity habitats unlike the lowland rainforests of Amazonia. They would have been adapted to eating leaves for a protein supplement, but most of the dietary needs probably came from unripe fruit or hard-husked fruit. This scenario emphasizes a year-round selective regime different from the fruit- and insect-rich environment of Amazonia.

Postscript – where does this leave us?

Aotus was once thought to be utterly nocturnal, *Callicebus* was thought to be tedious and saki–uacaris were thought to be way out there – rare and bizarre. None of these suppositions are correct. *Aotus* can be cathemeral, *Callicebus* is exciting and saki–uacaris are the living remains of a large radiation at the centre of platyrrhine evolution. Neither morphology nor molecules per se are what made these animals intriguing and interpretable. The revelations came from ecology, behavior and palaeontology. Learning why some answers diverge may be more interesting than the question that initially exposed their asymmetries. The *Aotus* conundrum may lead there. Meanwhile, as morphologists, we say to those who know the animals best – if you are interested in knowing who, phylogenetically, *Aotus* and *Callicebus* are, follow what Darwin did and watch what they do.

Acknowledgments

Thanks to the editors of this volume for inviting us to participate. A special thanks to Marilyn Norconk. We owe the point about reticulation to one of the reviewers. We thank the staffs and Departments of Mammalogy and Vertebrate Palaeontology, American Museum of Natural History, for supporting our research. MFT gratefully acknowledges fellowship awards given by the Wenner-Gren

Foundation for Anthropological Research and the New York Consortium in Evolutionary Primatology (NYCEP, funded by NSF DGE 0333415). ALR was supported by PSC-CUNY grants and a Tow Research Fellowship from Brooklyn College. Thanks also to Teresa Quaranta for assistance with illustrations.

Endnote

* This chapter is dedicated to Warren G. Kinzey, who put pitheciines on the map.

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