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The Primate Fossil Record

Edited by

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TOURO UNIVERSITY

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10 | Platyrrhine paleontology and systematics: The paradigm shifts

ALFRED L. ROSENBERGER

Prologue

The risk I take in this essay is that of a critic. Ultimately, my intention is to shed more light on platyrrhine evolution and on problem areas where we may have gone astray because of method. Accomplishing this without being critical is difficult.

While debates about primate phylogeny are real, and scientifically healthy, a philosophical context veils the circumstances. First, the posture of our contemporary systematic literature is to advocate positions rather than elucidate hypotheses by conjecture and refutation. Debates about phylogeny are often entwined in a web of taxa and traits which *requires* an exegesis if it is to be properly understood. Second, with automated tree-building, and a limited capacity to objectively select the "truth" from among many potential tree-solutions, we are flooded with hypotheses that are methodologically immunized from rejection, so they are presented as viable models for the sake of consistency. Peer review and editorial direction can easily change the *status quo* and move us toward a more constructive dialogue.

My sense is that "knowing" the phylogeny of platyrrhines is within our grasp for several interconnected reasons. First, the empirical evidence reveals a surprising number of long-lived lineages (Rosenberger, 1979*b*; Delson & Rosenberger, 1984), which should make easier the job of reconstructing history. Second, from an analytical perspective, the living forms are known to comprise a number of high-level clades that are morphologically coherent, distinctive and derived in pattern, whose behavioral ecology is also fairly well known. To stereotype them: pitheciins are dentally bizarre seed-eaters; atelines are postcranially modified climbers; callitrichines are dentally specialized, small-bodied claw-clinging locomotors; cebines are large-headed, predaceous, frugivorous omnivores. Thus, we are dealing for the most part with what we might call a "shallow phylogeny", a radiation where solid knowledge of the living can be extended to the past in order to maximize our interpretive capacity.

A third reason why we should have confidence in the interpretation of fossil platyrrhines comes from the force of genetic evidence. Schneider & Rosenberger (1996) have stressed the satisfying congruence in the results of morphological and molecular studies of platyrrhine cladistics. While I would not go so far as Fleagle (2000) did in endorsing our position, the independent corroboration of many facets of the cebid–atelid cladistic model (Rosenberger, 1981*b*, 1984, 1992) more than confirms the branching sequence for the living forms. It validates many of the characters used to generate the tree, and these are eminently applicable to fossils.

Nearly the entire literature on platyrrhine higher phylogeny and systematics over the past 20 years is slanted toward cladistics. Rare is the paper that eschews PAUP (Phylogenetic Analysis Under Parsimony: Swofford, 1993), but some of the best analyses of fossils (e.g., Meldrum & Kay, 1997*a*, on *Nuciruptor*) prove not to need algorithms at all. I believe there are some systematic problems that can benefit from a judicious use of numerical cladistics. But these methods are not easily applied to the broad sweep of morphological characters we are used to dealing with in primate systematics. The promise that large data sets and parsimony algorithms would bring greater objectivity to systematics has not been realized, for that pivotal series of decisions upon which all else is based – character selection – is by definition a subjective, idiosyncratic process, often rooted in experience and training.

Cladistics in a strict sense narrowly defines "phylogeny" as a branching sequence, as recency of common ancestry, or a network of collateral relationships. Among fossil New World monkeys there is an excellent opportunity to find examples of true phyletic evolution, ancestral–descendant relationships. Their importance to the story of platyrrhine evolution is being misread if ancestors and descendants are simply labeled sister taxa without further inquiry. Several likely generic lineages have already been identified (Delson & Rosenberger, 1984; Setoguchi & Rosenberger, 1987; Rosenberger, 1979*b*). Indeed, the preponderance of long-lived lineages seems to be a high-level evolutionary pattern among platyrrhines. The fossils themselves beckon a broader set of questions, and methods suitable to a more inclusive phylogenetic enterprise. Neither cladistic analysis nor molecular systematics can help us retrieve the entire story. In my view, the non-automated approach to morphology and character analysis that pays particular attention to homology, polarity, character weighting, functional morphology, behavior, etc., is a superior methodology. It stands up well against parsimony routines based on any form of data. In fact, the broad confirmation emerging from the genetic evidence (simple characters for which I think parsimony algorithms work well) of the most important cladistic hypotheses emerging from morphology (e.g., Schneider & Rosenberger, 1996) should be viewed as a scientific triumph for both approaches.

A turning point

Philip Hershkovitz's *Living New World Monkeys (Platyrrhini)* (1977) is sometimes described as the most important reference work on platyrrhine systematics of the last 200 years. With more than 1000 pages and over 2500 references, the book is famous for its ultra-encyclopedic account of nomenclature and place-name geography. For a work of such extraordinary dimensions by a man of stunning ability, ambition and purpose, Hershkovitz's book (1977) was oddly self-limiting. It hardly dealt with fossils. By 1977, eight fossil genera were described, two recently named by Hershkovitz himself, *Stirtonia* in 1970 and *Tremacebus* in 1974. In his opening, Hershkovitz stated that there were then no known callitrichine fossils, and he may have set aside the non-callitrichine fossils for Volume 2, or even a third volume. But the short shrift he gave paleontology, in a book of this scope, symbolizes a turning-point. It marks the end of an era when platyrrhine systematics could confidently advance without being fully informed by the fossil record.

In even more dramatic fashion, Hershkovitz (1977) epitomized the last gasp of non-synthetic, gradistic thinking (Rosenberger, 1980, 1981*b*). The sheer volume of information he assembled on callitrichines and other platyrrhines precipitated a crisis in theory, because there was none. In his effort to touch upon all things platyrrhine, ranging from Hershkovitz's own morphological forte to reproductive physiology, ontogeny, behavior, disease, parasites, nutrition, feeding habits, locomotion, longevity, social organization, mating strategies, growth, cognition, and more, the book was virtually born an intellectual white elephant – gigantic, obvious, going nowhere and anxious to be spoken for. It was hardly likely that Hershkovitz's model of platyrrhine evolution, summarized in an opening paragraph, could *explain* patterns embedded in such a huge body of information.

An integrating idea and a robust method were needed to mold key pieces of the data into a testable evolutionary model. This occurred as other advances were taking place in the late 1960s and 1970s, and included major refinements in systematic methodology, growing knowledge of the form and function of modern and early primate morphology, exploding awareness of primate behavior and ecology, and evolutionary models that explained evolutionary differentiation and diversity. The intellectual mix revived a profound challenge to Hershkovitz's (1977) central organizing hypothesis, that callitrichines were primitive. The factual bases for this observation were all part of the book, but they were misinterpreted (apparently). So, it is a coincidence brought about by time rather than epiphany which has this masterwork punctuating the first major reformation in the scientific study of the New World monkeys.

A century-and-half of fossils

The history of platyrrhine paleontology was a quiet one until the late 1960s and 1970s. The early history of platyrrhine paleontology was dominated by one fossil species, *Homunculus patagonicus*, based on a small collection of craniodental and postcranial specimens (Ameghino, 1891*a*, 1891*b*). Although subfossils were already known from the Lagoa Santa caverns of Brazil for several decades (Lund, 1838), only two other significant discoveries were made in the entire continent of South America in the first half of the twentieth century. Both *Tremacebus harringtoni* and *Dolichocebus gaimanensis* were overinterpreted as congeners of *Homunculus* (Rusconi, 1933; Bordas, 1942) until they were recognized as generically distinct (Kraglievich, 1951; Hershkovitz, 1974). With so little known, non-specialists such as Simpson and Gregory, whose brilliance contributed much to contemporary thinking on primates, also saw platyrrhine evolution through the lens of *Homunculus*.

The breakthrough of the twentieth century was Ruben Arthur Stirton's discovery of many vertebrate fossils at the middle Miocene site of La Venta (Stirton, 1951; Stirton & Savage, 1951; Kay *et al.*, 1997*a*). Given the nature of this material, even the first analysis was hardly hampered by the *Homunculus* specter. Stirton and Donald Elvin Savage's major primate discoveries were of taxa remarkably similar to living forms, *Neosaimiri fieldsi* and *Cebupithecia sarmientoi*.

At about the same time, *Xenothrix mcgregori* was released from 30 years of anonymity in a scrap-drawer of unallocated bones and diagnosed a platyrrhine (Williams & Koopman, 1952). The extraordinary discovery of extinct New World monkeys from Jamaica opened up a new geographical dimension in the evolutionary history of primates, and a chapter that grows more and more interesting with new fossils (MacPhee, 1996; see MacPhee & Horovitz, this volume). By the 1950s, after over a century of platyrrhine paleontology, the few fossils still had no appreciable impact on platyrrhine classification, systematics, or historical reconstruction.

The modern era of platyrrhine paleontology and systematics arose in the years bracketed by the publication in 1969 of the Oligocene *Branisella boliviana*, by Robert Hoffstetter, a seasoned paleontologist who knew the big questions, and by the appearance of Hershkovitz's book, in 1977. *Branisella*, more than any fossil found before, hinted at something different, early South American primates that might bridge the morphological gap between platyrrhines and Fayum catarrhines, or early anthropoids, or even North American omomyids. *Branisella* seemed relevant to platyrrhine origins, and the new biogeography based on continental drift and plate tectonics.

The rate of discovery of fossils increased dramatically in the 1980s and 1990s, with increasing interest, more participants, new ideas and a wealth of related research. The symbolic importance here was that fossil platyrrhines had finally become a field of study in their own right (Fleagle & Rosenberger, 1990). The scientific importance was that the foundation data was being multiplied at an unprecedented rate. Something of a critical mass was achieved in the early 1990s, when the number of fossil genera eclipsed the tally of living genera.

The paradigms shift

The first critical insight after Hershkovitz (1977) was that callitrichines were a sister group to a living platyrrhine clade. That clade could be found by tracing back apomorphies that callitrichines shared at least one link up or down a platyrrhine cladogram. This notion complemented the finding that non-marmosets could not be held together as a monophyletic group, which freed up both cebine genera, *Cebus* and *Saimiri* – the non-marmosets most like callitrichines, with short faces, reduced rear teeth, shallow jaws and gracile zygomatic arches – as possible relatives. Together, these ideas clinched the need for a wholesale revision in thinking. The cebid–atelid model began to replace the cebid–callitrichid schema (Rosenberger, 1981*b*). New ingredients fomented this revolution in the form of character analyses.

Rosenberger (1979*b*, 1981*b*; see also Szalay & Delson, 1979) and Susan Marie Ford (1986*a*, 1986*b*) were the first to present explicit, modernistic studies of platyrrhine interrelationships based on the morphocline polarity of characters. Fossils provided critical temporal evidence in character analyses and, secondarily, as heuristic checks on the relationships between groups whose modern relatives were morphologically divergent, such as *Cebus* and *Saimiri*, and *Aotus* and *Callicebus*. A feeding–foraging model was also proposed to explain the diversity of platyrrhines (Rosenberger, 1980, 1992) as an array of lineages inhabiting different adaptive zones and further differentiating along different adaptive modalities.

To better evaluate the correspondence between these hypotheses I developed a simple method to calculate a correlation coefficient that reflects congruency of the summary cladograms. The approach was inspired by methods used to test the match between cladisitc hypotheses and stratigraphic evidence from the fossils record (see Benton, 1998). Nodes of the cladograms (Fig. 10.1) were systematically numbered to reflect their branching order, thus ascribing a numerical designation for each monophyletic group. Trichotomies were treated the same as a dichotomous branching. Pair-wise comparisons of each of the genera, which for the 16 living platyrrhines amount to 120 entries, then defined the last common ancestors they shared. For example, in the Rosenberger tree: *Cebuella*:*Callithrix* = 7, *Cebuella*:*Leontopithecus* = 6 ... *Cebuella*:*Cacajao* = 1 ... *Cebuella*:*Alouatta* = 1, etc. The resulting table is a summary of all the cladistic relationships depicted in the tree. Matrices were developed for six studies and correlation coefficients were computed to compare their correspondence.

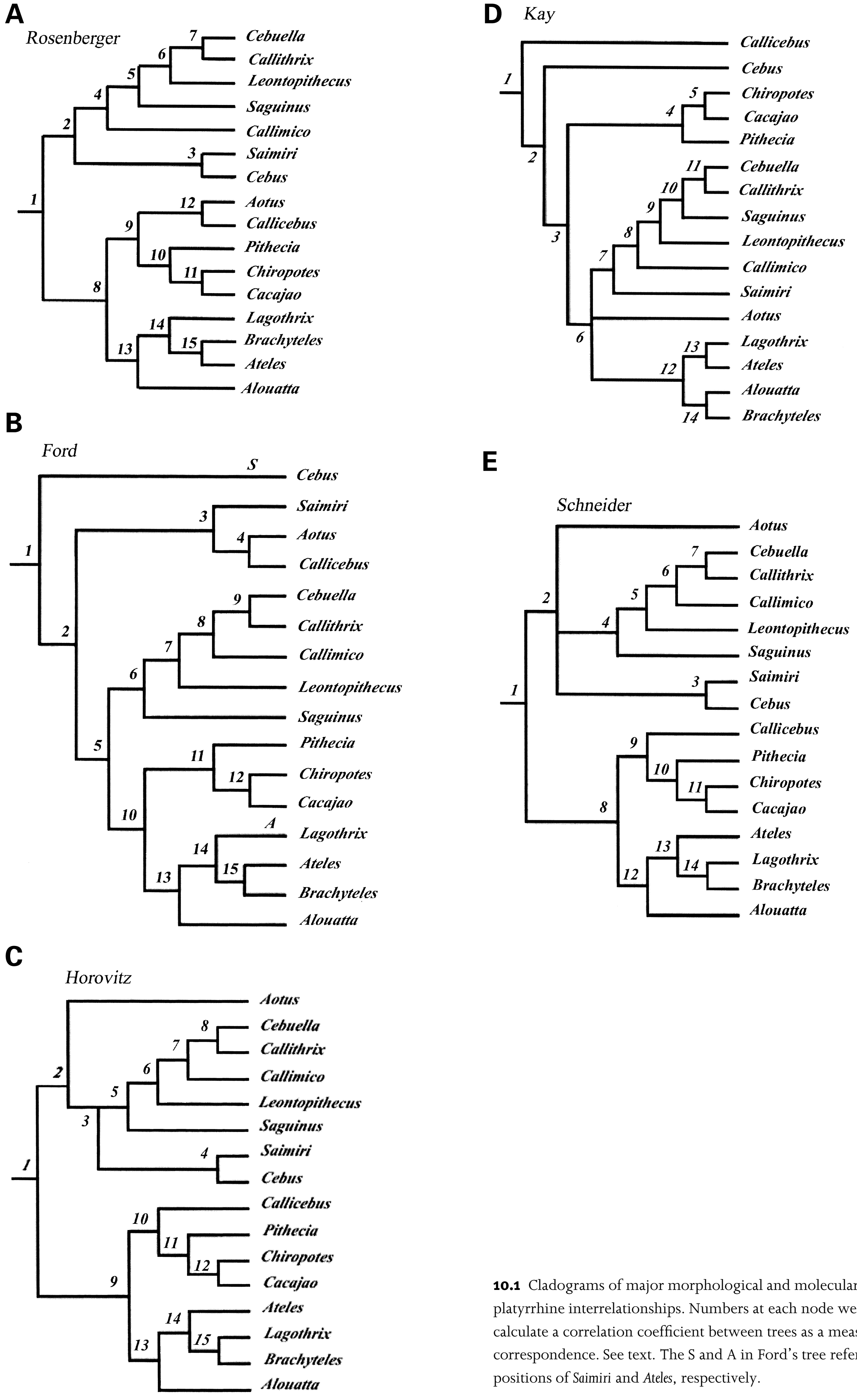
The results are instructive (Table 10.1). The Schneider (2000) and Horovitz (1999) cladograms are virtually identical, as expected, with a coefficient of 0.997. This is a welcome result, in part, because Horovitz used Schneider's data on four nuclear genes, to which she added mtDNA data and a large number of morphological characters analyzed simultaneously. (This part of the Horovitz study involved the 16 living genera only, not fossils; see below.) The close congruence between the two Ford studies (1986*b*), with a correlation coefficient of 0.842, compares two of the several possible permutations of her base tree, which presented two alternative cladistic positions for *Saimiri* and *Ateles*. This value is essentially the same as the correlations (0.849, 0.842) between Rosenberger's tree (1984, 1992), based on morphology, and the results of Schneider and of Horovitz. Yielding coefficients between 0.284 and 0.484, the least congruous of all the trees is Kay's (1990), which is radically different in both high-level branches and lower, genus-to-genus nodes.

I believe an important lesson that we can draw from this relates to characters. A common aspect of the projects of Ford (1986*b*), Horovitz (1999) and Rosenberger (1981*b*, 1992) is that they combined data from different systems. Kay's study (1990), on the other hand, used dental characters. An earlier project by Ford (1986*a*), which yielded different results from her synthetic studies, was also based on a several joint complexes of a single system, the postcranium. Both these efforts produced many characters, but the results of neither have been well replicated.

Lessons from a character tree

Differences of opinion regarding the phylogenetic relationships of several fossils relate to contrasting views on the valence of single-system characters. That is what underscores the debate between Kay (1990) and Rosenberger *et al.* (1990) over *Mohanamico* and *Aotus dindensis*. A bias toward dentition seems also to have influenced Horovitz's (1999) study of all the platyrrhine fossils, which turned into a "character tree" instead of a cladogeny (Fig. 10.2). She showed that the cladistic relationships of the extant genera can be retrieved reasonably well with molecular and morphological data when the latter is composed of craniodental characters. However, the same data set and algorithms did a rather poor job of allocating fossils to clades. The reason for this may be that the dental characters dominated the matrix and drove the results.

The anomalous cladistic linkages of *Neosaimiri*/*Tremacebus* and *Dolichocebus*/*Soriacebus ameghinorum* are instructive (Table



10.1 Cladograms of major morphological and molecular studies of platyrrhine interrelationships. Numbers at each node were used to calculate a correlation coefficient between trees as a measure of their correspondence. See text. The S and A in Ford's tree refer to alternative positions of *Saimiri* and *Ateles*, respectively.

Table 10.1. Correlation coefficients measuring the correspondence of cladograms

	Kay	Ford A	Ford B	Schneider	Horovitz
Rosenberger	0.279	0.662	0.634	0.849	0.842
Kay		0.484	0.406	0.288	0.284
Ford A			0.843	0.748	0.732
Ford B				0.757	0.744
Schneider					0.997

Table 10.2. Distribution of derived dental character states from Horovitz's (1999) matrix

	Incisors	Canines	Premolars	Molars
Neosaimiri	0	3	14	10
Tremacebus	0	0	1	2
Dolichocebus	0	3	4	5
Soriacebus ameghinorum	2	3	5	7
Total Study Group (n = 41)	7	9	20	21

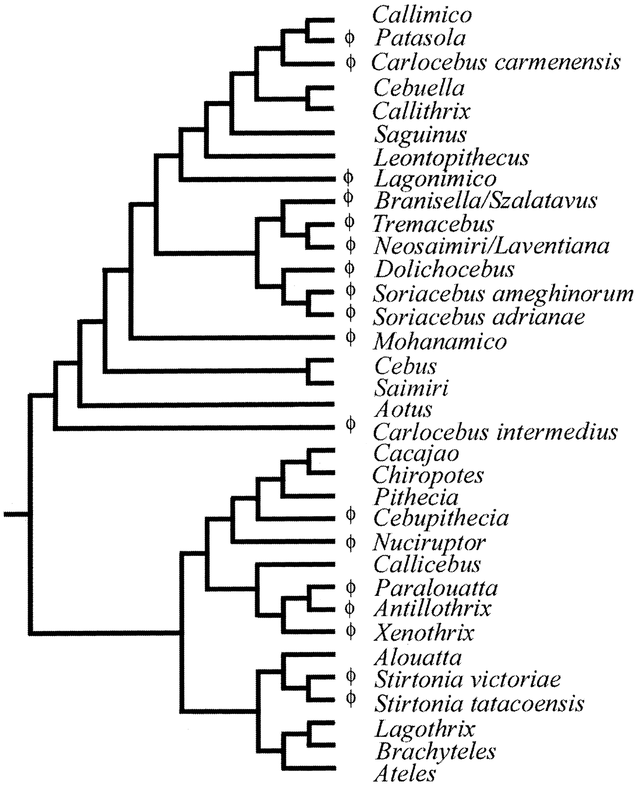


Fig. 10.2 Horovitz's (1999) cladogram of living and fossil (ϕ) platyrrhines, using her genus-level taxonomy.

10.2, Fig. 10.2). Fifty-five of the 86 characters (64%) used in Horovitz's (1999) analysis were dental features, so at the outset it would appear likely that teeth would weigh heavily in the analysis. For the *Neosaimiri/Tremacebus* link, it is evident that premolar characters would be dominating followed by the molars, because of the high frequency of these features in *Neosaimiri*, in contrast with only one premolar trait and two molar states that could be scored in *Tremacebus*. *Neosaimiri*, in fact, shows a disproportionately high frequency of derived premolar features in this study. For the *Dolichocebus/S. ameghinorum* pairing, there was much greater equality in the distribution of "informative" features. Here the question is more a matter of the believability of results rather than an expectation of inherent data bias (see below). But what is also interesting is that there is substantial fossil cranial material for one of the taxa in each of these sets that was thoroughly overshadowed by the quantity of dental evidence representing the other form.

Tremacebus is known from the type skull and a questionably allocated, damaged jaw from another locality, and there is no skull known for *Neosaimiri*. Since there was little anatomical overlap between these taxa in the input matrix (Table 10.2), there could not be much that would support this cladistic result *directly*. The orientation of the M_1 cristid obliqua proved to be the only derived feature sustaining this node. One obvious question is: Why should we have confidence in this result when the cranium of *Tremacebus* presents far more compelling data (e.g., Fleagle & Rosenberger, 1983)?

There are 29 potential cranial characters in the matrix that might drive the placement of *Dolichocebus* but none aligns it with *Tremacebus*, even as both supposedly belong to the same monophyletic group. *Dolichocebus* and *Tremacebus* present two of the best-known crania among the fossil platyrrhines, and cranial characters have been shown to be informative regarding New World monkey relationships. All have apparently been swamped by the dental data. Why? Perhaps it is the nature of the cranial traits selected. Three are listed as shared derived in *Dolichocebus*, the shape of the ectotympanic, cranial capacity and infraorbital foramen position. None could be scored for *Soriacebus*. Nor are any of the features proposed by Rosenberger (1979*b*) as shared derived features linking *Dolichocebus* with *Saimiri* and other cebines listed in the Horovitz data set.

I believe these results are methodological artifacts – a character tree not based on homology – rather than a reconstruction of relationships. This is not necessarily an objectionable result, so long at it corresponds with other evidence or presents a heuristically valuable perspective. Horovitz (1999) proposes a clade of: (((*Soriacebus*, *Dolichocebus*) ((*Neosaimiri*, *Tremacebus*) *Branisella*))). Nothing in the literature seems to support this. The single derived feature that holds this branch together is a P^4 hypocone. Putting this into other terms, it suggests that from a full range of craniodental features found distributed in this adaptive radiation of at least five genera, a premolar cusp is the only one that can explain differentiation. Nowhere among extant platyrrhines is a

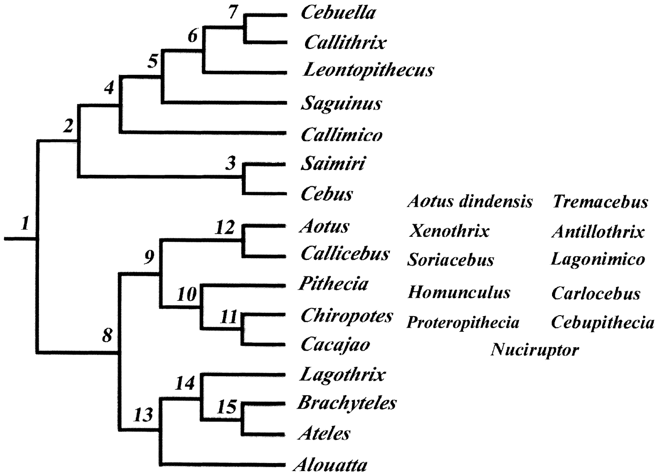


Fig. 10.3 Rosenberger's cladogram of living platyrrhine genera with a list of fossil taxa assigned to pitheciines. *Aotus dindensis* is an extinct species of *Aotus*.

clade of similar diversity supported by such a narrow anatomical basis.

Lessons from the pitheciines

Pitheciines are a major fraction of the platyrrhine radiation (Fig. 10.3). Kay and colleagues (Kay, 1990; Meldrum & Kay, 1997*a*; Kay *et al.*, 1998*a*) recognize three fossil genera, and I recognize eleven, plus five living – saki-uakaris, owl and titi monkeys. All of these fossils, in one way or another, share craniodental and mandibular characters that are typically found only in pitheciins or pitheciins and the *Callicebus–Aotus* clade among the living. The inclusion of *Callicebus* in this group seems to be accepted by all at this point, as suggested by the cladograms illustrated above (Fig. 10.1), but the implications of this for character analysis have yet to be broadly appreciated. The status of *Aotus* is also an interesting aspect of the pitheciine story.

The key to interpreting pitheciines comes from two directions. One is that the dental morphology of pitheciins is virtually self-polarizing, meaning it is so different from other platyrrhines that all workers agree the flat-basined cheek teeth, stylate incisors and pyramidal canines are homologous and derived among New World monkeys. The other clues come from molecules (e.g., Horovitz, 1999; von Dornum & Ruvolo, 1999; Schneider, 2000). They are unanimous in supporting saki-uakari monophyly and an immediate linkage of *Callicebus* as their sister taxon. By extension, the original morphological argument (Rosenberger, 1981*b*, 1984, 1992) which linked *Callicebus* and *Aotus* with saki-uakaris as pitheciines is confirmed. This was based on a dental and mandibular transformation series shared in step-wise fashion by the five genera, and cranial features also shared by *Callicebus* and *Aotus*.

Several numerical cladistic studies have confirmed the affiliation of *Callicebus* and saki-uakaris. Horovitz and colleagues used morphological as well as genetic evidence, in various combinations (e.g., Horovitz & Meyer, 1995; Horovitz *et al.*, 1998; Horovitz, 1999; Horovitz & MacPhee, 1999). Kay (1990), also using a subset of the Rosenberger (1979*b*) dental characters as well as his own, arrived at a very different conclusion regarding *Callicebus* (Fig. 10.1). Neither of these studies included features of the mandible which distinguish all pitheciines. I suspect that is part of the reason why *Aotus*, and for Kay *Callicebus*, failed to group with them. The clustering of *Aotus* with cebines and callitrichines by algorithms (e.g., Horovitz, 1999) based largely on dentition is not surprising, for there are numerous phenetic similarities shared by them in cheek tooth morphology (see also Rosenberger *et al.*, 1990).

The sheer anatomical oddness of saki-uakaris would seem to predict that some type of intermediacy in form and adaptive context would eventually be discovered, probably involving taxa that occupied a transitional adaptive zone and exercised characters preadaptive to the derived saki-uakari patterns. Kinzey (1992) and Rosenberger (1992) have argued from morphologic and behavioral evidence that *Callicebus* and *Aotus* fit this prediction, but there are fossils that fit this picture even better.

With the concept of pitheciines broadened, one is faced with another paleontological dilemma, to select an analytical approach that balances the wealth of data available for the living with the dearth of evidence presented by the fossils. Results so far do not support the implied contention that more anatomical data points can get around a lack of well-understood, taxon-defining features. Although Horovitz (1999) scored a great many dental traits, the mandibular and cranial data did not achieve parity.

Pitheciines show that character weighting is a powerful tool that should not be ignored. The recipes for polarity determination, e.g., parsimony, in-group – out-groups distribution, temporal precedence, ontogeny, function, etc., are valuable perspectives but there are many circumstances when a polarity hypothesis is robust even when ancestral conditions are moot. This is the case for pitheciines. It follows that homology decisions, which I believe are a fundamental precondition to investigating morphocline polarity, can be equally well guided by realizing the power of autapomorphous traits. Any of the stereotypical features of saki-uakaris that are shared with any platyrrhine genus is more likely than not to be homologous. The likelihood of homology increases as unique shared similarities span anatomical/adaptive systems to form a pattern, e.g., from molars, to incisors, to mandibles, to heads, to feet. Some of the present difficulties with parsimony studies of platyrrhine fossils is that this strong, coherent body of data is subdivided into minutia in order to extract individual character states which together form a long list rather than an integrated working unit, thus causing them to lose phylogenetic signal.

Lessons from the record: *Xenothrix*

Xenothrix, long known from a single mandible with only two molar teeth, has been an especially vexatious taxon (Williams & Koopman, 1952; Hershkovitz, 1970; Rosenbeger, 1977; Rosenberger *et al*., 1990; MacPhee & Fleagle, 1991; MacPhee, 1996; Horovitz, 1999; Horovitz & MacPhee, 1999). The first studies could not place it unambiguously (Williams & Koopman, 1952; Hershkovitz, 1970). As my ideas of platyrrhine phylogeny developed, I became more convinced that *Xenothrix* is a Jamaican pitheciine, possibly most closely related to *Callicebus* among the living. Recently, with new material in hand, Ross D. E. MacPhee and colleagues proposed that *Xenothrix* is part of a monophyletic Antillean clade, Xenotrichidae, whose sister taxon is *Callicebus* (Fig. 10.2). The proposed clade is comprised of *Xenothrix*, *Paralouatta* and *Antillothrix*.

After studying the new material I come to a different conclusion, briefly outlined here. I believe *Xenothrix* is a Jamaican owl monkey most closely related to *Aotus* and *Tremacebus*, which I believe are sister taxa to the *Callicebus* lineage. Among the new mandibles are a few important morphological details that confirm earlier studies and extend a set of derived similarities to include *Aotus*. For example, more is known of the gonial region, which was even more highly expanded (in at least some individuals) than could have been guessed from the type specimen, which was a young animal as MacPhee (1996) noted. In part, this is because the mandibular corpus is extraordinarily deep below the molar region – again, more than the type demonstrates. The ramus of the jaw is anteroposteriorly short, and probably had a significant coronoid process with a deep sigmoid notch. Alveoli in the several jaws also confirm a consistently small lower canine, unlikely to be gender-related.

These features are all consistent with the idea that *Xenothrix* is a pitheciine closely resembling *Callicebus* and *Aotus*. The small canines and deep jaws are probably synapomorphies shared with *Callicebus* and possibly with *Aotus* as well. Two high-weight, derived features link *Xenothrix* and *Aotus*, one dental and one cranial. Regarding the dentition, the first upper incisor alveolus is greatly enlarged in the fossil, relative to the I^2 socket. This is paralleled by a relatively large interalveolar distance separating right and left I^1s. I interpret the morphology as an indication of a greatly broadened I^1 crown, which is a novelty of *Aotus* (Rosenberger, 1992) among the extant platyrrhines.

Of even more importance, the orbit of *Xenothrix* is enlarged, like *Aotus* and *Tremacebus*. This is evident in two ways: (1) The lower anterior rim of the right orbit is preserved in a wide arc that indicates a large orbital diameter. (2) The posterior floor of the orbit preserves intact on both sides evidence of the inferior orbital fissure, an opening between the orbital and temporal fossae related to eyeball hypertrophy. This fissure is typically closed in *Callicebus*, where the orbit is tightly sealed from the temporal fossa. In all important respects, the morphology of this region, including the shape of the maxillary tuberosities, conforms with *Aotus*. One way that *Xenothrix* differs from *Aotus* in orbit-related features is the size of the maxillary sinus, which is secondarily reduced in living *Aotus* and in the fossil *A. dindensis* (Setoguchi & Rosenberger, 1987). The deep face of *Tremacebus*, however, probably reflects a large maxillary sinus, more like *Xenothrix* perhaps.

In the final analysis by Horovitz (1999: Table 2B), three synapomorphies linked *Xenothrix*, *Antillothrix* and *Paralouatta*: nasal fossa width, C_1/P_4 alveolus size, and the M_1 bulging protoconid. How much confidence should we attribute to them? For nasal fossa width, generally speaking, no data could be collected on half the taxa (20/41) in the matrix and the other half were deemed to have the primitive state. For the canine/premolar ratio, homoplastic derived states occur in *Tarsius* and *Carlocebus carmenensis*. This alone would not be a cause for alarm, even though one immediately wonders about homologies. However, *C. carmenensis* falls out as a callitrichine in this analysis (linked with *Callimico* and the fossil *Patasola*) and its congener, *Carlocebus intermedius*, is linked with *Soricacebus* and *Dolichocebus* (see above), leaving me to wonder even more about the signal potential of *Carlocebus* characters, which are all dental.

The features that I worked with in the past (Rosenberger,1977; Rosenberger *et al*., 1990) helped place *Xenothrix* within a clade for the first time. The analyses of Antillean primates by MacPhee (1995) and MacPhee *et al*. (1995) supported the linkage of *Xenothrix* with *Callicebus* based on small, probably non-projecting canines, occlusal anatomy and the expanded gonial region. With discovery of the face, I now prefer to weight more heavily a new set of characters crucial to the adaptive zone occupied by a taxon closely related to *Callicebus* (see Rosenberger, 1992). Enlarged orbits and eyeballs are *the* fundamental adaptive breakthrough of owl monkeys, as far as we know. A second character that implies the same phylogenetic interpretation, the inferred size of I^1, may be linked with how a taxon exploits an adaptive zone. In the *Aotus* lineage these involve harvesting adaptations, i.e., the uniquely enlarged central incisors of *Aotus* (Rosenberger, 1992).

Lessons from *Xenothrix*, *Soriacebus* and *Lagonimico*

There is a broader context in which a rethinking of *Xenothrix* has importance for platyrrhine systematics. Studies of *Xenothrix* (Rosenberger, 1977; MacPhee, 1996; Horovitz, 1999) tend to agree that it is a pitheciine on account of its mandibular morphology, inferences about the anterior teeth and premolars, and a few details of occlusal morphology. The conundrum has been this: The odd, two-molar dental formula and elongate molar shapes bear little resemblance to any living pitheciine and, until recently, to all fossils. The reasonable default position has been that the molars are autapomorphous, thus irrelevant to cladogeny and to morphotype reconstruction. However, labeling traits as autapomorphies must always be a provisional statement. Discovery of a new fossil sharing that particular trait forces a revision of its polarity status. This is the pitheciine story.

Extending the above analysis to include non-Antillean fossils brings us a step closer to resolving the analytical challenges of the *Xenothrix* dental formula. The Miocene fossil *Soriacebus*, from Argentina, offers new perspective. Its phylogenetic position is a matter of debate (e.g, Rosenberger, 1992; Fleagle *et al.*, 1997*b*; Meldrum & Kay, 1997*a*; Kay *et al.* 1998*a*; Horovitz, 1999). My view is that *Soriacebus* is a pitheciine, based on a suite of traits of the anterior dentition and mandible that are indisputably pitheciine-like, and a second tier of premolar characters that also align the genus with high confidence among pitheciines. Molar morphology is the most serious source of disagreement (see Fleagle *et al.*, 1987, 1997*b*; Kay, 1990). *Soriacebus* lower molars are long and narrow and otherwise unremarkable, in contrast to saki-uakaris, the modern-looking *Cebupithecia* and *Proteropithecia*, and also of *Nuciruptor*. Another feature to emphasize here is that the upper molars of *Soriacebus* are unusual for an atelid in having a small hypocone, which is a sharp contrast to the traditional way we see the pitheciine pattern, as a quadrate large-hypocone tooth. The long lower molars and reduced upper molar morphology of *Xenothrix* and *Soriacebus* are unexpected similarities, and rather unique.

A second genus, *Lagonimico*, provides yet another clue. It, too, presents an interesting character combination (Kay, 1994), with posteriorly deep jaws, small third molars and upper molars lacking any real trace of a hypocone. Using a parsimony algorithm, Kay interpreted *Lagonimico* as a *Callicebus*-sized callitrichine, emphasizing loss of the hypocone among other features. I believe *Lagonimico* is a pitheciine, in part because of its diagnostically deep mandible and flaring gonial region, and the shape of its ascending ramus. The latter uniquely resembles *Callicebus* and *Aotus* in being tall and narrow anteroposteriorly, with a sloping anterior border and a small sigmoid notch. Related features are also seen in *Soriacebus* and *Xenothrix*. The single troubling feature of *Lagonimico* is the tricuspid upper molar pattern.

All these facets come together in a simple, parsimonious hypothesis that binds together *Xenothrix*, *Soriacebus* and *Lagonimico* as pitheciines. The notion is that there is another dimension to the pitheciine radiation that has only surfaced now. These fossils may reflect the ''deep phylogeny'' of pitheciines, even if *Xenothrix* (if not the others) is a closer relative of *Aotus* and *Tremacebus*. In some aspects, the three may reflect the morphological antecedents of the morphotype we were able to distill from comparing extant pitheciines, their fossil isomorphs and information from atelines, the pitheciine outgroup. In another respect, they indicate a new evolutionary pattern in which some pitheciines (*Aotus* and *Xenothrix*) parallel *Callimico* and callitrichins, with a transformation series involving reduction and loss of the third molar.

No splendid isolation

Extinct platyrrhines ranged more widely than the present boundaries of the tropical and subtropical forests of South and Central America, proving that the zoogeographic history of New World monkeys is likely to be interesting and complex. Patagonia has yielded about eight platyrrhine genera, none of which are congeneric with the larger Miocene fauna of Colombia. The relationships of some of these taxa are disputed, but I will focus on three. Based on cranial anatomy, I have argued (Rosenberger, 1979*a*; Fleagle & Rosenberger, 1983) that *Dolichocebus* and *Tremacebus* are early representatives of modern lineages, possibly sister taxa or even ancestors of living genera. I think *Dolichocebus* is closely related to *Saimiri* and *Tremacebus* to *Aotus*.

Kay (1990) and Fleagle *et al.* (1997*b*: 482) presented different views of the relationships of these taxa, and they proposed another way of looking at the collection of Patagonian platyrrhines, summarized as follows:

> Miocene Argentine fossil platyrrhines cannot be readily allied with the commonly recognized clades of living platyrrhines. Rather, they are generally more primitive, each possessing a mosaic of similarities to extant platyrrhine taxa that is incongruent with many current phyletic reconstructions based solely on the anatomy of living New World monkeys.

This is one of several ideas presented by Fleagle, Kay and colleagues about the fossils, yet it echoes the persistent theme that there was a distinct platyrrhine radiation in the south (Kay, 1990; Kay *et al.*, 1998*b*). A generous reading might take the meaning of this statement as: None of the Patagonian taxa are cladistically related to extant forms or their close fossil relatives. A more restrictive reading might be: The Patagonian fossils are a monophyletic group outside the crown group of platyrrhines.

Both hypotheses require a high degree of parallel or convergent evolution, implying that: (1) an *Aotus*-like (and *Xenothrix*-like), nocturnal genus or lineage, exemplified by *Tremacebus*, developed analogously enlarged orbits; (2) a *Saimiri*-like interorbital fenestra (or an annexed, *Cebus*- and *Saimiri*-like conformation of the orbit's medial walls if the fenestrated condition should prove to be misinterpreted) evolved twice among platyrrhines, once in *Dolichocebus*; and, (3) a pitheciin-like dental complex involving incisors and canines, related to hard-fruit eating, evolved independently in *Soriacebus*, which also presents other pitheciine characters of inadequately studied functional significance, such as a deep, thin mandible. It stretches the imagination to think so much parallelism could occur among platyrrhines *within* platyrrhines.

A similar case of mistaken monophyly involves the Greater Antillean primate fauna. MacPhee and colleagues (e.g., MacPhee, 1996; Horovitz & MacPhee, 1999) have argued explicitly that the three Antillean primates, *Xenothrix*, *Antillothrix* and *Paralouatta*, are monophyletic, the descendants of a single ancestral population. As discussed above, I believe *Xenothrix* is closely related to *Aotus*. I also have confidence in the original assessment of *Paralouatta* as a howler relative (Rivero & Arredondo, 1991), based on a comprehensive series of derived cranial features seen nowhere else but in *Alouatta*, in spite of differences in dental anatomy. The latter are likely to reflect the ''deep phylogeny'' of atelines, just as *Soriacebus* morphology, for one, reflects the ''deep phylogeny'' of pitheciines. Here, again, we must weigh the likelihood that two regionally grouped taxa sharing unique morphological patterns with other adaptively specialized platyrrhines living elsewhere are anything but their cousins. Rather than a monospecific origin for Antillean primates, I think the evidence indicates at least two subfamilies belonging to a community of primates got into the Caribbean. Since the crossing distance is also likely to have been small, more than one colonization is not an improbable scenario. In fact, it is likely that there was more than one emigration out of South America and into Central America. An early dispersal produced the community that eventually arrived in the Caribbean. Another introduced the modern Central American forms after the isthmus arose. Their closest relatives are not the Antillean monkeys but the South American species.

Epilogue

The paradigms that dominated this field have shifted in concept and method, promoted partly by a steadily increasing fossil record. With a broad concurrence by morphological and genetic studies, the cebid–atelid model of phylogeny and classification has gained support as a central organizational theme, with callitrichines, pitheciines (with qualifications) and atelines universally recognized as derived, monophyletic subtaxa. The evidence for cebine monophyly is also increasing. Knowledge of the diversity of the pitheciine lineage has greatly increased, owing to a redefinition of their taxonomic composition based on phylogenetic concepts and the discovery of several new fossil genera that pertain to this group.

Approaches to the study of platyrrhine systematics have drifted toward a reliance on parsimony-based numerical cladistic methods but without improving the state of the underlying comparative morphology, which would probably make these methods more valuable. Teeth, the most plentiful of fossils, may still prevail as the favored source of cladistic information – what Fred Szalay calls the ''Tyranny of the Teeth'' – but the evidence produced thus far shows that the dentition alone is an unreliable phylogenetic mentor, especially as the homologous parts of fossils are unevenly represented in the record.

It is prudent not to assume that areas now outside the center of gravity of tropical and subtropical South America were major, independent theatres of platyrrhine evolution. There is no evidence for the scenarios which hold that fossil Patagonian primates, and Antillean primates, are separate monophyletic groups. Each area has at least two genera that belong to two separate families, cladistically. To play devil's advocate in this regard one must, at the very least, directly account for the strong suite of derived morphological features that bind together *Paralouatta* and *Alouatta*, and *Tremacebus* and *Aotus*.

Clearly, the systematics of New World monkeys has emerged from a long dormant state dominated by a scarcity of fossils and a shortage of ideas. The future is promising, for the past 20 years has also proven that fossils can be found in taxonomic abundance. Our methods will become better also, particularly as new technologies improve data input by bringing a new level of clarity to comparative morphology. All these trends are already established. To secure its intellectual future, however, we need to encourage more students to take the path of systematics, particularly in the countries of South and Central America where the living species, and the extinct, are home.

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