Implications of Molecular and Morphological Data for Understanding Ateline Phylogeny

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The ateline monkeys constitute as certain a monophyletic group as there is among primates. The group is intriguing because while their adaptations are well-documented and their monophyly as a group is unquestioned, their phylogenetic interrelationships are controversial. Molecular data indicate a phylogeny at odds with their morphology. Traditional morphological comparisons isolate Alouatta *from the atelins, and link* Ateles *and* Brachyteles *as a sister group to the exclusion of* Lagothrix. *In contrast, several recent molecular studies point to a closer relationship between* Brachyteles *and* Lagothrix *than between* Brachyteles *and* Ateles. *At the heart of the problem lie the assumptions we make about the validity of data and the homology of observed traits. The fossil record further confounds the issue. We must account for the fossil record because it is positive evidence. But we cannot control how much of it there is or how much of it ever will be known. At this point in time, the ateline molecular and fossil record provoke us to examine critically our morphological approach to phylogenetic modeling.*

KEY WORDS: morphology; platyrrhini; phylogeny; homology; homoplasy.

INTRODUCTION

Irresolvable paleoanthropological arguments abound. For example, what was the fate of the Neandertals? Cogent arguments for or against particular hypotheses also abound. In the face of opposing, well-reasoned

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arguments that do not resolve a problem completely, intellectual impasses often result. How much insight might we gain if we viewed such histories as opportunities to rethink a problem?

Questions of ateline monkey evolution lack the glamour of identical questions about apes or humans, by virtue of which they offer a less threatening opportunity to rethink the large problems of how to model phylogeny. The opportunity is not to allege wrongness or unreliability of traditional methods, but instead to explore how much might be learned by approaching the same data sets with different assumptions. The ateline case is most tempting because sound analyses of abundant data have led to opposing models of their evolutionary history.

The ateline monkeys comprise 4 genera of relatively large-bodied, upper canopy dwelling, suspensory-brachiating platyrrhines. *Alouatta* (howling monkeys) are widely distributed throughout the neotropics. *Lagothrix* (woolly monkeys) occur mostly in the high Amazon. *Ateles* (spider monkeys) are ripe fruit specialists with a wide but essentially tropical distribution. *Brachyteles* (woolly spider monkeys) are limited to small remnants of Atlantic Coastal Forest and are highly endangered.

Morphological approaches to ateline phylogenetic modeling have enjoyed wide acceptance. These primates exploit a clear niche in the neotropical forest canopy via suspensory postures and brachiating movements, the skeletal adaptations to which seem readily apparent. Based on logical assumptions that greater commitment in the skeleton to suspension and brachiation reflects how derived the taxon is from the ancestral state, morphologists long ago argued that *Ateles* and *Brachyteles* must be closely related. They also argued that *Lagothrix*, *Ateles* and *Brachyteles* constitute a group distinct from the more quadrupedal *Alouatta* (Fig. 1).

Molecular approaches to ateline phylogenetic modeling have enjoyed a certain objectivity that comes with novelty and new investigators. Not enough time has passed for a new generation of molecular biologists to reinvestigate the taxa, or data, or methodologies. Indeed, just as collegial morphologists investigate separate parts of the skeleton to measure, molecular biologists explore different regions of the genome in pursuit of the same separate but equal insights. Morphologists usually begin with teeth, then others take on the crania, and still others eventually canvas the postcranial skeleton. Molecular biologists range from nuclear to mitochondrial genomes, and within each to different units of study, e.g., chromosomes versus RFLPs versus gene sequences. Several recent studies of ateline molecular biology suggest that *Lagothrix* and *Brachyteles* are sister taxa, which is interesting not only because of the problems this creates for our understanding of morphological similarity but also because so many different laboratories have obtained the same result.
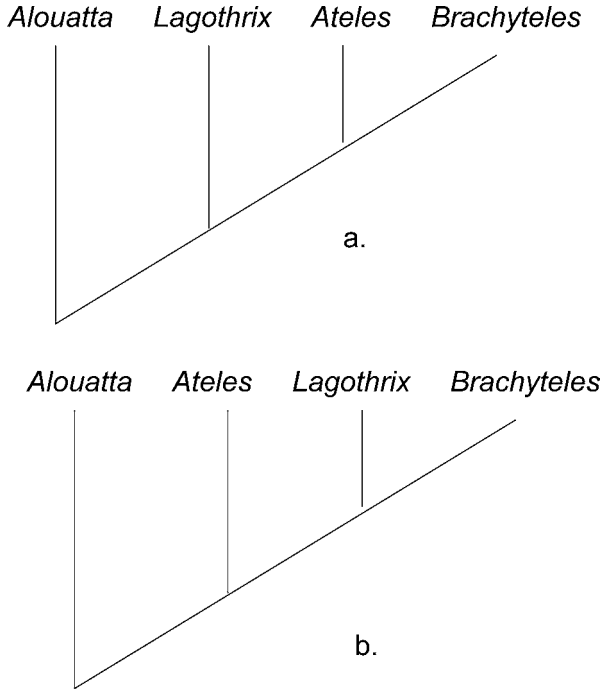
Alouatta   Lagothrix   Ateles   Brachyteles

a.

Alouatta   Ateles   Lagothrix   Brachyteles

b.

Fig. 1. Cladistic relationships among the atelines as supported historically by (a) morphological studies and (b) molecular studies.

I review the history of the morphological and molecular approaches to modeling ateline phylogeny, which established the current impasse. I then suggest a way in which molecular or morphological investigators can resolve it, not in terms of the actual evolutionary history of ateline monkeys, but instead in terms of how we think about it.

HISTORY OF MORPHOLOGICAL RESEARCH

A sense of monophyletic unity among the 4 ateline genera dates to the 19th century and the writings of Spix, Gray, Gregory and Pocock. Attempts to quantify or to modernize these early impressions have largely confirmed the basic distinction of *Alouatta*, the morphologically intermediate nature of *Lagothrix*, and the locomotor similarities of *Ateles* and *Brachyteles*. Prominent researchers even suggested that *Brachyteles arachnoides* should be congeneric with *Ateles* (Fiedler, 1956).

Erikson's (1963) study of brachiation in atelines cemented the similarities between *Ateles* and *Brachyteles* that would compel the next generation of morphologists.

In the modern era 6 dissertations were focused on comparative platyrrhine anatomy. Orlosky (1973) examined dental morphology and noted that teeth of *Ateles* and *Lagothrix* are similar and both greatly contrasted with those of *Brachyteles* in many features (p.155). Rosenberger (1979) followed with a more comprehensive dental analysis of platyrrhines in general, but had limited access to *Brachyteles*. Ford (1982) wrestled with postcranial characters but had only one immature specimen of *Brachyteles*. With little room for any other conclusion she found numerous similarities between *Ateles* and *Lagothrix* and that *Brachyteles* was worthy of its own genus. Hartwig (1993) analyzed cranial morphometry and found that *Lagothrix* remained distinct from a close *Ateles*/*Brachyteles* group and that they were all distinct from *Alouatta*. Cole (1995) provided all of the quantitative rigor that the Hartwig study lacked and concluded that *Ateles* and *Brachyteles* showed synapomorphic transformations for increased brain size. Jones (2004) recently completed a thorough analysis of the evolution of the ateline postcranium, using methods advocated here. As a result her work has not resolved ateline phylogeny as much as casting its analysis in a fresh light.

Before Cole, none of the dissertation studies focused particularly on the atelines. More pressing phylogenetic questions then pertained to other taxa, especially *Cebus* and the Callitrichinae. The obvious distinction of the ateline adaptive radiation, the rarity of *Brachyteles* specimens, and the weight of studies like Erikson's (and later of Rosenberger and Strier, 1989) compelled us to accept the likelihood of a close relationship between *Ateles* and *Brachyteles*. Cole's thesis pivoted more on methodology and less on evolutionary biology, so any doubts about the integrity of *Ateles* and *Brachyteles* as a crown group would wait for the geneticists. Jones (2004) took the first step to integrate them into morphological scenarios.

The early dissertations were more about higher-order interrelationships as reflected in the teeth, postcrania or cranium, and less about intergeneric evolutionary histories. Subsequent publications by the researchers also emphasized the radiation as a whole. The major study by Ford (1986) is a good example. She combined her data set with other morphological data sets and what was known at that time about platyrrhine karyotypes. She argued for a close relationship between *Lagothrix* and *Ateles* based on hind limb traits. She further suggested that a lack of shared character states in the humerus between *Ateles* and *Brachyteles* might indicate that suspensory behavior evolved independently in them. The number of specimens

of *Brachyteles* that she used is unclear. She concluded that "It should be noted that there is little to no evidence that would argue for a closer relationship between *Lagothrix* and *Brachyteles*" (1986:110). This assertion was influenced by perpetuation of the erroneous number of 32 diploid chromosomes for *Brachyteles*, which aligned it with *Ateles* (Chu and Bender, 1962; de Boer, 1974; Koiffmann and Saldanha, 1974).

The most prominent of the post-dissertation reviews to focus on atelines was an innovative combination of morphology and ecology by Rosenberger and Strier (1989). They concluded that a sister group relationship of *Brachyteles* and *Ateles* was very strongly supported. Their approach to character analysis emphasized a judgment of the most likely direction in which specific characters and patterns may have evolved. Rosenberger's judicious use of weighting of characters *a priori* was rooted explicitly in the assumption that *Brachyteles* and *Ateles* were closely related. Reflexively or not, Rosenberger and Strier (1989) argued convincingly for a sister group relationship of *Brachyteles* and *Ateles* by combining individual characters into functional complexes and by stressing that a large suite of postcranial characters devoted to extreme suspension and rapid brachiation constituted overwhelming homology.

Rosenberger and Strier (1989) noted that *Brachyteles* and *Lagothrix* shared a relatively large face and mandible, but attributed the similarity to a primitive condition for atelines. *Ateles* was perceived to display the derived condition of morphological reduction in the masticatory apparatus due to its dietary emphasis on ripe fruit. The simplest explanation for atelin craniodental morphology was to position *Lagothrix* as the ancestral morphotype, from which *Brachyteles* diverged relatively little and *Ateles* presents the highly derived condition, which is consistent with postcranial data that align *Brachyteles* and *Ateles* very tightly.

Ateles and *Brachyteles* share gibbonesque relative limb length ratios and their thumbs are reduced significantly. At that time their diploid chromosome numbers were incorrectly reported to be the same (see Schneider and Rosenberger, 1996). Accordingly, Fleagle (1988) spoke of uncertainties in the higher order relationships of platyrrhines but not at all to the prospect of paraphyly of *Ateles* and *Brachyteles*. In 1999 Fleagle showed a trichotomy of *Lagothrix*, *Brachyteles* and *Ateles* in the phylogenetic diagram and noted the opportunity to learn from molecular data.

Rosenberger (1992) followed the 1989 Rosenberger and Strier study with a model of how feeding niches evolved in atelines. In his model atelines exploit the opportunities for frugivory and folivory in habitats made accessible by adaptations for suspensory climbing and brachiation. *Lagothrix* is a relatively primitive ateline that has not specialized either in the direction of *Alouatta*, i.e., into a deliberate quadrupedal/folivorous niche), or in the

direction of *Ateles*, i.e., obligate brachiation/ripe fruit frugivory. *Brachyteles* and *Ateles* form a sister-group united by an advanced specialization for brachiation; the dental adaptations toward folivory in *Brachyteles* are a recent specialization to conditions imposed in their remnant Atlantic Coastal Forest habitat.

Rosenberger's 1992 assessment was so compelling that morphologists subsequently looked elsewhere for interesting problems. However, genetic approaches to primate evolutionary biology were beginning to mushroom. Without any intrinsic bias or vested interest in the phylogenies constructed by morphologists, molecular anthropologists and biologists began to analyze wide arrays of taxa, including atelines. By the time of the next major attempt to reckon ateline phylogeny, the sister-group relationship of *Brachyteles* and *Ateles* was under scrutiny (Hartwig *et al.,* 1996).

Part of the reason for morphologists to question the sister group of *Brachyteles* and *Ateles* grew out of a brief suggestion that a population of *Lagothrix flavicauda* high in the Peruvian Andes may constitute a distinct genus. Noting the remarks of early naturalists and the apparent robusticity of the rare skeletal material, Groves (personal communication, 1995) renewed the question and argued (Groves, 2001) in favor of a separate generic designation (*Oreonax*). Could *Oreonax* be a kind of intermediary between the woolly monkey and the more robust woolly spider monkey? Despite ready acceptance of the distinction by conservation biologists, morphologists have yet to quantify or publish affirmative data. Ultimately, the molecular affinities of the rare population should establish the best starting point for phylogenetic debate.

Morphological assessments of atelines ebbed until Lockwood (1999) contributed a thoughtful paper on the nature of homoplasy in the pitheciine and ateline postcrania. However, despite the growing molecular evidence in the 1990s for a sister group of *Lagothrix* and *Brachyteles* he advocated no phylogeny: "Postulated relationships within atelins . . . are currently too discordant to resolve what are the most likely relationships" (Lockwood 1999:468).

HISTORY OF MOLECULAR RESEARCH

In the late 1970s and early 1980s, efforts to document the genetic character of South American monkeys were based on karyotypes and protein immunology (Chu and Bender, 1961; de Boer, 1974; Cronin and Sarich, 1975; Baba *et al.,* 1979; Chiarelli, 1980). The researchers mapped out a basic scheme of higher-order relationships that more or

less fit with morphological expectations. But databases often lacked sufficient taxa (Schneider *et al.,* 2001), and early reported karyotypes for *Brachyteles* were incorrect. Substantive analyses prospered when South American scholars, such as Horacio Schneider, entered the field in the early 1990s. They accessed rarer taxa and applied state-of-the-art technology.

Via ε-globin, Schneider *et al.* (1993) confirmed the higher-order relationships proposed from morphology and feeding niche data of Rosenberger (1992). But at finer taxonomic levels some results departed from the morphological scheme, particularly the linkage of *Brachyteles* and *Lagothrix* as a sister group. Schneider and colleagues, citing Pequignot *et al.* (1985), noted that *Brachyteles* and *Lagothrix* each have a diploid chromosome number of 62 (*Ateles* has 32–34). In a study that had mistakenly assumed a diploid chromosome number of 34 for *Brachyteles*, Ford (1986:111) had stated that "...fusion of chromosomes is more likely to occur than fission, and thus...higher chromosome numbers are more likely to be ancestral." This would argue strongly for 62 to be a primitive chromosome number for atelins. Contrarily, Schneider *et al.* (1993:236) believed that "The fact that the diploid number of *Ateles* varies from 32 to 34...suggests that the diploid number of 62 is a synapomorphy for the sister grouping of *Brachyteles* and *Lagothrix*." Polarity of karyotype is as arguable as that of any other trait and it is as likely to be invoked selectively to support or to refute a phylogeny.

The important contribution of the study of Schneider *et al.* (1993) was that it mapped so thoroughly onto the prevailing scenario of adaptive radiation at that time (Rosenberger, 1992). A real sense of synergy and cross-validation between molecular and morphological investigation was on the threshold. The Schneider research group published numerous subsequent studies springing from the morphological platforms of Rosenberger, Ford (1986) and Kay (1990) in a genuine attempt to reconcile genetic and macroscopic evidence. The next study on atelines was by Harada *et al.* (1995), who compared interstitial retinol-binding protein gene (IRBP) and also found a sister group of *Brachyteles* and *Lagothrix*. Eventually Schneider and Rosenberger (1996) published together, a benchmark on new approaches to old problems. But resolution of atelin phylogeny was not to be had then. Even though the 1990s publications overlapped in real time, and included progressive co-authorship, in academic time the morphological school had too much momentum to rein back its emphasis on spider and woolly spider monkey affinities, and the molecular school did not have enough momentum to counter.

The first molecular study outside of the Schneider laboratory was the mitochondrial DNA analysis by Horovitz and Meyer (1995). They used a

series of different character weighting methods but did not have *Brachyteles* in their sample. Meanwhile, Schneider *et al.* (1996) updated their 1993 study by including 5 more species. Results for atelines were unaffected. They speculated that the difference between the molecular and morphological interpretations of the atelin clade were due to the short time span separating the emergence of the three lineages, but they did not explain why a short time span of separation would dissociate the gross morphology from the molecular morphology.

In other words, if the genetic signal for a sister group of *Brachyteles* and *Lagothrix* was not as persuasive as those of *Cacajao* and *Chiropotes*, or of *Callithrix* and *Cebuella* in terms of repeated bootstrap values, perhaps the woolly and woolly spider monkey lineages emerged very recently. But it does not explain how a shallow temporal extent of phylogenic independence would lead to fragile nucleotide similarities but radical gross morphological differences. The opposite would seem to be more likely. Epistemologically, the attempt to reconcile molecules and morphology then demonstrates the essential discordance of the old and the new. The new molecular approach suggests possible cytogenetic mechanisms for its phenetic findings as it resolves its initial, founding, original method and theory. The old morphological approach, long beyond revising its own method and theory, searches for a weakness in the other approach before accepting the results as a call for change.

Horovitz *et al.* (1998) combined molecular and morphological data to attempt a total evidential approach reminiscent of that of Ford (1986). They added a new section of the mitochondrial genome to supplement the database of Horovitz and Meyer (1995) and had *Brachyteles* in the sample. Their results placed *Brachyteles* in a clade with *Lagothrix*, which is distinct from *Ateles*. This agreed with the results of the Schneider laboratory which were, in fact, used as part of the Horovitz and Meyer database. Although their analytical method ultimately may be no stronger than its weakest link (Rosenberger, 2002), it demonstrated that inclusion of another part of the genome yielded results similar to those of the Schneider laboratory.

Several molecular analyses of New World monkeys were published at the end of the 1990s. Von Dornum and Ruvolo (1999) compared nuclear G6PD sequences and placed *Brachyteles* and *Lagothrix* in a clade, with *Ateles* as the nearest taxon followed by *Alouatta*. The clade of *Brachyteles* and *Lagothrix* was the least supported sister group in the analysis—moderate bootstrap support—but still was well-supported overall. They recognized that the molecular evidence needed further support, but that if it was supported then the question of atelin phylogeny was wide open again.

From the Schneider laboratory, Meireles *et al.* (1999) specifically addressed the *Brachyteles-Lagothrix* issue, using $\in$-Globin nucleotide sequences. It supported a clade of *Brachyteles* and *Lagothrix* with 100% bootstrap support. The data set included a much larger number of aligned nucleotide positions than those of previous studies, thus bringing a quantitative weight to the initial results of Schneider *et al.* (1993). Meireles *et al.* (1999) pointed again to the karyotypic similarity between *Brachyteles* and *Lagothrix* and in particular to the variation in *Ateles* ($n = 32-34$) and in *Alouatta* ($n = 44-53$) as proof that the karyotypic similarity between *Brachyteles* and *Lagothrix* is synapomorphic.

A fourth laboratory group (Canavez *et al.,* 1999) used β_2-microglobulin DNA sequences and achieved the same pairing of *Brachyteles* and *Lagothrix* as in all other molecular analyses. Horovitz (1999) added fossil New World monkeys to her database. Unfortunately, the study did not include the nearly complete ateline skeletons of *Protopithecus* and *Caipora*. The fossils that she included were mostly dental remains, which constrained the combined data set and failed to sort one atelin from another. Adding the molecular data simply forced the sister-group of *Brachyteles* and *Lagothrix* because all of the molecular data indicate this and no dental data in the study supported a sister-group within atelins.

The most recent molecular study of ateline taxa from yet another independent investigator (Collins, 2004) reached a different conclusion. Via 2 aspects of the mitochondrial genome and a single copy nuclear gene, Collins (2004) resolved the separation of *Alouatta* from the other genera (grouped there as Atelini). But intergeneric relationships within Atelini could not be resolved, which ultimately lead Collins (2004) to support a trichotomy until more genetic data are considered. An advantage of his study is that it increased the genetic sampling of *Ateles* in the analysis compared to previous studies. Collins (2004) noted that relationships within Atelini changed when different species of *Ateles* were used for analysis. His study is a solid base for a second wave of research that usually follows initial consensus-building.

Schneider *et al.* (2001) summarized the state of the ateline problem in a paradigm-building paper similar to Rosenberger's (1992) summation of adaptive radiations. Indeed, the current state of molecular research is moving beyond primary discovery and toward consensus phylogenies. A subtext of Schneider *et al.* (2001) seemed to be that while some experiments may be methodologically weak and some data sets may be constrained by samples of single individuals, it is hard to argue with a result that appears over and over again, e.g., the sister group of *Brachyteles* and *Lagothrix*. Rosenberger and Strier (1989) essentially made the same appeal

of paradigm, but in reference to the eco-morphological similarities between *Brachyteles* and *Ateles*.

RELEVANCE OF THE FOSSIL RECORD

The fossil record in theory is relevant for any question of phylogeny or evolution, but it accumulates incidentally and extremely sparingly. The fossil record is especially relevant to the question of ateline phylogeny because the 2 most complete fossil New World monkeys are atelines: *Protopithecus* and *Caipora*.

Both genera are large with distinct adaptations to a suspensory/brachiating mode of posture and locomotion (Cartelle, 1993; Hartwig, 1995; Cartelle and Hartwig, 1996; Hartwig and Cartelle, 1996; MacPhee and Horovitz, 2002). Cranially, they are quite different from one another. *Caipora* very closely resembles *Ateles* for all of the distinct features related to neurocranial form and gnathic reduction. The head of *Protopithecus* is somewhat more like *Alouatta*. The foramen magnum is part of an expanded and canted nuchal plane; the anchoring of the face onto the neurocranium is extended but not as severe as in *Alouatta*. The maxilla lacks the extension and curvature that characterize the extreme basicranial extension in *Alouatta*, but like *Alouatta*, its mandible shows a tendency to make room for the underlying hyoid (Fig. 2).

The fact that *Protopithecus* seems to be a dedicated suspensory/brachiator while at the same time being adapted for resonating vocalization is difficult to align with the adaptations of a single living ateline lineage. Either its postcrania evolved in parallel to those of atelins or its cranial configuration evolved in parallel to that of alouattins (Hartwig *et al.,* 1996). Because the skull of *Protopithecus* has a number of unique features in addition to features that converge on the howler condition, the conservative interpretation would be postcranial homology with *Ateles* and *Brachyteles* and hyoid convergence with *Alouatta*, i.e., *Protopithecus* as a howling woolly spider monkey. But the molecular data, taken at face value, argue for a paraphyletic relationship between the 2 extreme brachiators— *Brachyteles* and *Ateles*—which indicates that postcranial similarities, however many or substantial, are just as likely to be convergent. The real impact of *Protopithecus* is that it shows how a single species can exhibit trait complexes believed to be the hallmarks of separate living lineages.

RESOLUTION

The implications of how we have studied ateline phylogeny seem obvious, albeit provocative. Either mophologists have missed the obvious—that

(a)

Fig. 2. The skeletal remains of 2 large Pleistocene atelines suggest that either the highly derived anatomy of suspension and brachiation evolved more than once, or the highly derived vocal apparatus of *Alouatta* evolved more than once. (a) The crania (*Protopithecus*, left; *Caipora*, right) are very similar to one another, in the manner of all atelines, but the mandibles reveal key differences. The mandible of *Protopithecus* (b., top) is contoured to accommodate a large hyoid bone. The mandible of *Caipora* (b., bottom) is virtually indistinguishable, except in size, from that of *Ateles*. The postcranial skeletons of both genera demonstrate a clear and extreme commitment to suspension and brachiation in excess, in some characters, of *Ateles* and *Brachyteles*. The ulna (c., l-r: *Protopithecus*, *Caipora*, *Caipora*, *Protopithecus*) is one among the cluster of signature traits such as limb length ratios, humeral torsion, and relative metacarpal length.

atelin postcranial anatomy evolved in parallel in spider monkeys and woolly spider monkeys—or 3 independent parts of the genome studied by modern, widely accepted molecular biological techniques yield a spurious sister-group relationship between woolly monkeys and woolly spider monkeys.

Calipers and centrifuges will not solve the problem. One method is not the appropriate falsifier or critic of the other. Instead, insight can be found in the effort of Fleagle and McGraw (1999, 2002), who used molecular results as a basis for re-examining morphological assumptions

Fig. 2. Continued.

of phylogeny. Specifically, they searched for and found morphological data to support molecular evidence that surprisingly linked mandrills to a group of mangabeys. The molecular data set up the presumptive relationships, *Macaca* provided a polarity reference, and it was just a matter of defining characters related to what the mandrills and the terrestrial mangabeys had in common a forest-floor foraging habitus.

The ateline case is different in the sense that an abundance of morphological evidence, defined already according to shared foraging ecologies, persuasively links the 2 taxa that molecules separate. To follow the lead of Fleagle and McGraw would be to acknowledge tacitly that molecular

(c)

Fig. 2. Continued.

approaches to phylogenic modeling are infallible, or at the very least much less fallible than are morphological approaches. It would also lead to a better understanding of how morphology evolves.

We are not on the verge of a major methodological breakthrough or paradigm-shift. But we have an opportunity to think about morphology in a different way. The number of times will be few that a consensus of molecular studies will contradict so radically the consensus of morphological studies. Similarly few are the number of times that everyone has agreed on the identification of deeply rooted parallelisms. And yet we know or suspect that morphological homoplasy is more common than the techniques of comparative anatomy can confirm. By allowing consensus molecular results to stand as working model phylogenies we may be able to better anticipate the scope and character of homoplasy within closely related lineages. While it may be humbling to concede the fine line between homology and homoplasy, the possible error risk of using molecules to revise morphological polarities is surely no more alarming than is the prospect that we might misunderstand woolly spider monkeys through and beyond their extinction.

So the resolution in this case is to accept the molecular results as the presumptive relationships from which further analyses should proceed. An appropriate outgroup should be chosen so that morphological characters can be assigned a default polarity. The best equivalent for *Macaca* in South America is probably *Cebus*. Finally, morphological characters will be redefined and reassigned. Characters that unite *Brachyteles* and *Ateles* to the exclusion of *Lagothrix* will be assigned as homoplastic. These must include such venerable homologies as relative limb length ratios, a rudimentary or absent thumb, and labial and clitoral hypertrophy. Those that unite *Brachyteles* and *Lagothrix* to the exclusion of *Ateles*, if any can be found, will be assigned as synapomorphic if they pass the *Cebus* test, and symplesiomorphic if they do not.

In practice this resolution advocates operationalizing the steps used to create phylogenetic trees, but somewhat in reverse. It advocates starting with a reasoned phylogeny and exploring the implications it bears for understanding the anatomy of the taxa involved. The same rules of parsimony that generate the tree from the molecular data will influence how well accepted the morphological implications are. The goal is not to revise a century of laborious morphometrics, but instead to acknowledge that homoplasy is a valid criterion of a last option of explanation. By assuming molecular phylogenies to be presumptively true we may resist atomizing anatomical characters and believing that more characters equals better results. This may be our best chance to decipher parallel and convergent evolution instead of just invoking it when all else fails.

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REFERENCES

Baba, M. L., Darga, L. L., and Goodman, M. (1979). Immunodiffusion systematics of the Primates, part V: the Platyrrhini. *Folia Primatol.* 32: 207–238.

de Boer, L. E. M. (1974). Cytotaxonomy of the Platyrrhini. *Genen en Phaenen* 17: 1–115.

Canavez, F. C., Moreira, M. A. M., Ladasky, J. J., Pissinatti, A., Parham, P., and Seuanez, H. N. (1999). Molecular phylogeny of New World Primates (Platyrrhini) based on β_2-microglobulin DNA sequences. *Molecular Phylogenetics and Evol.* 12: 74–82.

Cartelle, C. (1993). Achado de *Brachyteles* do Pleistoceno final. *Neotropical Primates* 1, 8.

Cartelle, C., and Hartwig, W. C. (1996). A new extinct primate among the Pleistocene megafauna of Bahia, Brazil. *Proc. Nat. Academy Sci.* 93: 6405–6409.

Chiarelli, A. B. (1980). The karyology of South American primates and their relationship to African and Asian species. In Ciochon, R. L., and Chiarelli, A. B. (eds.), *Evolutionary Biology of the New World Monkeys and Continental Drift* Plenum Press, New York. pp. 387–398.

Chu, E. H. Y., and Bender, M. A. (1961). Chromosome cytology and evolution in primates. *Science* 133: 1399–1405.

Cole, T. M. (1995). *Comparative Craniometry of the Atelinae (Platyrrhini, Primates): Function, Development, and Evolution.* University Microfilms, Ann Arbor.

Collins, A. C. (2004). Atelinae phylogenetic relationships: The trichotomy revived? *Am. J. Physical Anthro.* 124: 284–296.

Cronin, J. E., and Sarich, V. M. (1975). Molecular systematics of the New World monkeys. *J. Hum. Evol.* 4: 357–375.

Erikson, G. E. (1963). Brachiation in New World monkeys and in anthropoid apes. *Sympo. Zool. Soc. Lond.* 10: 135–164.

Fiedler, W. (1956). Übersicht über das System der Primaten. *Primatol* 1: 1–266.

Fleagle, J. G. (1988). *Primate Adaptation and Evolution.* Academic Press, San Diego.

Fleagle, J. G. (1999). *Primate Adaptation and Evolution.* (2nd Edn.). San Diego, Academic Press.

Fleagle, J. G., and McGraw, W. S. (1999). Skeletal and dental morphology supports diphyletic origin of baboons and mandrills. *Proc. Nat. Academy Sci.* 96: 1157–1161.

Fleagle, J. G., and McGraw, W. S. (2002). Skeletal and dental morphology of African papionins: Unmasking a cryptic clade. *J. Human Evol.* 42: 267–292.

Ford, S. M. (1982). *A Systematic Revision of the Platyrrhini Based on Features of the Postcranium.* University Microfilms, Ann Arbor.

Ford, S. M. (1986). Systematics of the New World monkeys. In Swindler, D. S., and Erwin, J. (eds.), *Comparative Primate Biology*, *Vol. I, Systematics, Evolution, and Anatomy.* Alan R. Liss, New York. pp. 73–135.

Groves, C. P. (2001). *The Taxonomy of Primates.* Smithsonian Institution Press, Washington, DC.

Harada, M. L., Schneider, H., Schneider, M. P. C., Sampaio, I., Czelusniak, J., and Goodman, M. (1995). DNA evidence on the phylogenetic systematics of New World monkeys: Support for the sister-grouping of *Cebus* and *Saimiri* from two unlinked nuclear genes. *Mole. Phylogenetics Evol.* 4: 331–349.

Hartwig, W. C. (1993). *Comparative Morphology, Ontogeny and Phylogeny of the New World Monkeys (Platyrrhini)*. University Microfilms, Ann Arbor.

Hartwig, W. C. (1995). A new giant monkey from the Pleistocene of Brazil. *J. Hum. Evol.* 28: 189–196.

Hartwig, W. C., and Cartelle, C. (1996). A complete skeleton of the giant South American primate *Protopithecus*. *Nature* 381: 307–311.

Hartwig, W. C., Rosenberger, A. L., Garber, P. W., and Norconk, M. A. (1996). On atelines. In Norconk, M. A., Rosenberger, A. L., Garber, P. S. (eds.), *Adaptive Radiations of Neotropical Primates* Plenum Press, New York. pp. 427–431.

Hershkovitz, P. (1969). Notes on the New World monkeys. *Int. Zool. Yearbook* 12: 3–12.

Horovitz, I. (1999). A phylogenetic study of living and fossil platyrrhines. *Am. Museum Novitates* 3269: 1–40.

Horovitz, I., and Meyer, A. (1995). Systematics of New World monkeys (Platyrrhini, Primates) based on 16S mitochondrial DNA sequences: A comparative analysis of different weighting methods in cladistic analysis. *Molecular Phylo. Evol.* 4: 448–456.

Horovitz, I., Zardoya, R., and Meyer, A. (1998) Platyrrhine systematics: A simultaneous analysis of molecular and morphological data. *Am. J. Phys. Ant.* 106: 261–282.

Jones, A. (2004). *The Evolution of Brachiation in Atelines: A Comparative Study*. University Microfilms, Ann Arbor.

Kay, R. F. (1990). The phyletic relationships of extant and fossil Pitheciinae (Platyrrhini, Anthropoidea). *J. Hum. Evol.* 19: 175–208.

Koiffman, C. P., and Saldanha, P. H. (1974). Cytogenetics of Brazilian monkeys. *J. Hum. Evol.* 3: 275–282.

Koiffmann, C. P., and Saldanha, P. H. (1982). Karyotypic studies in ateline monkeys. *Revista Brasileira de Genetica* 5: 773–792.

Lockwood, C. A. (1999). Homoplasy and adaptation in the atelid postcranium. *Am. J. Phys. Anthr* 108: 459–482.

MacPhee, R. D. E., and Horovitz, I. (2002). Extinct Quaternary platyrrhines of the Greater Antilles and Brazil. In Hartwig, W. C. (ed.), *The Primate Fossil Record*. Cambridge University Press, Cambridge. pp. 189–200.

Meireles, C. M., Czelusniak, J., Schneider, M. P. C., Muniz, J. A. P. C., Brigido, M. C., Ferreira, H. S., and Goodman, M. (1999). Molecular phylogeny of ateline New World monkeys (Platyrrhini, Atelinae) based on γ-globin gene sequences: Evidence that *Brachyteles* is the sister group of *Lagothrix*. *Mol. Phyl. Evol.* 12: 10–30.

Orlosky, F. (1973). *Comparative Dental Morphology of Extant and Extinct Cebidae*. University Microfilms, Ann Arbor.

Pequignot, E. V., Koiffmann, C., and Dutrillaux, B. (1985). Chromosomal phylogeny of *Lagothrix*, *Brachyteles* and *Cacajao*. *Cytogen cell gen* 39: 99–104.

Rosenberger, A. L. (1979). *Phylogeny, Evolution and Classification of New World Monkeys (Platyrrhini, Primates)*. University Microfilms, Ann Arbor.

Rosenberger, A. L. (1992). Evolution of feeding niches in New World monkeys. *Am. J. Phys. Anthr* 88: 525–562.

Rosenberger, A. L. (2002). Platyrrhine paleontology and systematics: The paradigm shifts. In Hartwig, W. C. (ed) *The Primate Fossil Record*. Cambridge University Press, Cambridge. pp. 151–159.

Rosenberger, A. L., and Strier, K. B. (1989). Adaptive radiation of the ateline primates. *J. Hum. Evol.* 18: 717–750.

Schneider, H., Canavez, F. C., Sampaio, I., Moreira, F. A. M., Tagliaro, C. H., and Seuanez, H. N. (2001). Can molecular data place each neotropical monkey in its own branch? *Chromosoma* 109: 515–523.

Schneider, H., and Rosenberger, A. L. (1996). Molecules, morphology, and platyrrhine systematics. In Norconk, M. A., Rosenberger, A. L., and Garber, P. A. (eds.), *Adaptive Radiations of Neotropical Primates.* Plenum Press, New York. pp. 3–20.

Schneider, H., Sampaio, I., Harada, M. L., Barroso, C. M. L., Schneider, M. P. C., Czelusniak, J., and Goodman, M. (1996). Molecular phylogeny of the New World monkeys (Platyrrhini, Primates) based on two ulinked nuclear genes: IRBP Intron 1 and ε-globin sequences. *Am. J. Phy. Anthr* 100: 153–180.

Schneider, H., Schneider, M. P. C., Sampaio, I., Harada, M. L., Stanhope, M., Czelusniak, J., and Goodman, M. (1993). Molecular phylogeny of the New World monkeys (Platyrrhini, Primates). *Molecular Phyl. Evol.* 2: 225–242.

Steiper, M. E., and Ruvolo, M. (2003). New World monkey phylogeny based on X-linked G6PD DNA sequences. *Molecular Phyl. Evol.* 27: 121–130.

von Dornum, M., and Ruvolo, M. (1999). Phylogenetic relationships of the New World monkeys (Primates, Platyrrhini) based on nuclear G6PD DNA sequences. *Molecular Phyl. Evol.* 11: 459–476.