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Evolutionary Morphology, Platyrrhine Evolution, and Systematics

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ABSTRACT

This special volume of the Anatomical Record focuses on the evolutionary morphology of New World monkeys. The studies range from three-dimensional surface geometry of teeth to enamel ultrastructure; from cranioskeletal adaptations for eating leaves and seeds to the histology of taste bud proxies; from the architecture of its bones to the mechanoreceptors of the tail's skin; from the physical properties of wild foods to the feeding biomechanics of jaws and skull; from the shapes of claws and fingertips, and of elbows, to the diversity and morphology of positional behavior; from the vomeronasal organ and its biological roles to links between brains, guts, sociality, and feeding; from the gum-eating adaptations of the smallest platyrrhines to the methods used to infer how big the largest fossil platyrrhines were. They demonstrate the power of combining functional morphology, behavior, and phylogenetic thinking as an approach toward reconstructing the evolutionary history of platyrrhine primates. While contributing new findings pertaining to all the major clades and ecological guilds, these articles reinforce the view that platyrrhines are a coherent ecophylogenetic array that differentiated along niche dimensions definable principally by body size, positional behavior, and feeding strategies. In underlining the value of character analysis and derived morphological and behavioral patterns as tools for deciphering phylogenetic and adaptational history, doubts are raised about a competing small-bore morphological method, parsimony-based cladistic studies. Intentionally designed not to enlist the rich reservoir of platyrrhine evolutionary morphology, an empirical assessment of the costs incurred by this research stratagem reveals inconsistent, nonrepeatable, and often conflicting results. Anat Rec, 294:1955–1974, 2011. © 2011 Wiley Periodicals, Inc.

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> Knowing more and more about less and less may mean that relationships are lost and that the grand pattern and great processes of life are overlooked.
>
> George Gaylord Simpson (1944:xxvii)
> *Tempo and Model in Evolution*

The impetus for this special volume of the Anatomical Record grew out of an excited conversation with one of my good coworkers who has spent his entire professional life studying primate—especially New World monkey—morphology, enlightened by personal experience dissecting primates, collecting their fossils, chasing monkeys in

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the forest, and performing experiments in the lab. My rhetorical question was: “Is morphology dead?” His answer, paraphrasing, was: “It’s never been more alive. Look at all the students going to the museum, coding characters.” To which I replied: “It’s not about making a Grey’s Anatomy of primate morphology. What more have we learned about the animals since all that began?”

The articles assembled here, which focus on platyrrhines, one of the major primate radiations, will hopefully demonstrate that primate morphology is anything but dead, nor is it in abeyance in the era of genomics. Primate morphology is more vibrant than ever, as it should be. We have refined the questions, deployed improved methods, are mastering advanced technologies that probe more deeply into the body and its workings, and continue to discover new fossils that reveal unexpected morphologies which expand the anatomical boundaries circumscribed by extant forms. However, as Simpson warned, it is the relationships among phenomena, the hardest thing to understand and the most important, that remains at risk when investigative agendas are very particularized and synthesis does not follow basic research. At that nodal point, where observation pivots toward meaning, the conversations we have behind the printed word indicates one whole version of morphological inquiry evinces controversy and uncertainty.

I refer to the morphology behind systematics, more specifically to the anatomical basis and methods of phylogeny reconstruction. One needs neither footnotes nor references to validate what is obvious in the pages of the leading journals that publish on primate evolution. Put bluntly: morphological articles dealing with phylogenetics are overwhelmingly biased toward studies that seem to use traits as if they are the parts of inanimate systems, without any reference to a feature’s organic life and history. It is an ironic intellectual twist. The obsolete “descriptive anatomy” on which old-school systematics was built, and which deserved a much needed shot of fresh blood and thinking, has morphed into a nondescriptive anatomy beholden to “character states” that, by intention, are normally construed to be blind to hypotheses, suppositions, and assumptions. The result is a defleshed, binary anatomy. In adopting it, this new school of systematics atomizes and transmographies structural complexity in an effort to satisfy the twin goals of minimizing subjectivity and maximizing sample size, that is, the number of traits used and the number of taxa consulted, en route to producing machine-based cladograms. Is this a good thing? Some say, Yes; others say, No.

Evolutionary morphology, the theme of this volume, is neither a new construct nor a new label (e.g., Szalay, 2000). I use the term here simply as an expression meant to avoid the artificiality of separating the functional properties of characters from their phylogenetic properties. Both aspects are intrinsic to morphology although studying either facet often requires different tools and approaches. However, my contention is that there is more explanatory power in a synthetic morphology where form is brought together with function and phylogeny conceptually. I try to demonstrate this while introducing and contextualizing the articles delivered in the following pages, pointing out where an evolutionary or functional morphological perspective has been important in deciphering and explaining key points in platyrrhine phylogeny and history, as elucidated by anatomy. This approach is a break with the old schools of taxonomy, when nonfunctional paradigms dominated platyrrhine systematics. It is also the antipode of algorithmic, new-school systematics, an explicitly nonfunctionalist approach to phylogeny reconstruction. In my view, no other group of living primates illustrates better the benefits of a synthetic evolutionary morphology approach to systematics than the platyrrhines.

Following Szalay (e.g., 2000) and others, one can also make a distinction between evolutionary morphology and functional morphology as it is now practiced in that the former is inherently concerned with transformation. Functional morphology is surely steeped in evolution, as the explanations we have for “how things work” can be related to selective pressure and differential survival under ecological circumstances. Thus, folivory is seen as adaptive when one lives in a world where leaves are potential food and theoretically beneficial to survival. However, functional morphology does not address how adaptations like folivory arose. This represents a distinct set of questions and an approach that differs from the biomechanical. Tracing the origins of a trait or complex requires phylogenetic thinking, but it would be little more than a sterile exercise if it was not infused with possible explanations of “why” it happened. Evolutionary morphology, as the articles presented herein often show, gets us closer to establishing that crucial relationship between How and Why, which Simpson (1944) would surely have seen as part of the grand pattern and great process behind platyrrhine evolution.

Concerning the articulation of morphology and systematics, to be clear at the outset: I do not wholly reject computer-driven analyses of morphology designed to probe cladistics on philosophical or theoretical grounds. Phylogeny reconstruction is a difficult scientific challenge and all helpful approaches are welcome. However, now that we are about 20 years into the process of applying them to platyrrhines, there is ample empirical evidence to allow an objective assessment of these studies, most of which have used the parsimony method (i.e., PAUP; Swofford, 2002). This leads me to question how well they have been implemented as well as their capacity to perform as intended (see Matthews and Rosenberger, 2008; Rosenberger, 2010b). I also wonder how to evaluate the many inconsistencies they turn out (see below), and if they actually live up to the critical theoretical requirement that they produce explicitly (pure) cladistic results. Do the results of these studies justify the underlying proposition that we should assume as little as possible about the organization and evolution of anatomical characters so as not to contaminate the exercise by making supposedly unnecessary *a priori* postulates?

Such a viewpoint seems merely to shift the menu of complex scientific assumptions—all of science involves assumptions—from the input stage to the analytical. Because of it, hard earned information, hypotheses and causal explanations concerning functional morphology, adaptation and evolutionary history tend to be rejected as valuable evidence. They rarely inform the input routine, character selection and coding, and seem to hold little sway when they challenge output in the form of an alternative cladistic hypothesis. The atomization of morphology required by the algorithmic approach strips morphology of its effective and historical patterns, leading to an objectification which may have an effect opposite of what is intended—fabricating more noise. For in any orderly structural system, the information content of each unit is proportional to the size of the unit within the system and the level of its integration with other parts. Is there any doubt a primate's 10 toenails will say less about history than a whole primate foot functionally interpreted? Or, that the laptop's many keys say less about the manufacturer where it originated than the one motherboard to which each is connected? Ultimately, I am doubtful that some of the logical bases and expectations of the algorithmic agenda has been proven true, that more small-bore observations are commensurate with higher quality research, more accurate results, and the virtue of real objectivity.

In posing this contrast between approaches to phylogenetics, the platyrrhines serve as an object lesson in the value of integrating cladistics with an evolutionary, functional morphology approach to systematics. These themes speak to some of the relationships Simpson (1944) feared were falling between the cracks. More specifically, I take the view that the platyrrhines illustrate how character analysis can contribute to a holistic assessment of evolutionary history that accounts for phylogeny and adaptation within the same theoretical and methodological framework. One of the chief aims of this article is to highlight examples demonstrating this point based on the original studies presented in this volume.

Another aim of this article is to introduce a new classification of the platyrrhines that is designed to better reflect advances made recently, since the first morphology- and cladistics-based overhauls reshaped our thinking in the 1970s and 1980s. I draw particular attention to this point. The need for a revised classification is not based now on new phylogenetic hypotheses. Rather, it reflects major increases in our awareness of taxonomic diversity. There are more than three times as many fossil genera known today than in 1977, for example, and nearly three times as many fossil genera as there are living genera. Up until that point, classifications necessarily had to be anchored in information based on what animals exist today. However, new panoramas of platyrrhine biodiversity are being brought to light. An example. For one of the major modern NWM clades, the Sakis and Uakaris (*Pithecia Chiropotes*, and *Cacajao*), the addition of fossils has totally altered our picture of biodiversity and the ecological role this group has played in platyrrhine evolution (Rosenberger, 2002; Rosenberger et al., 2009). Once seen as a backwater ensemble of limited diversity and a nonfactor in terms of broader classification schemes, the pitheciins now appears to be a remnant of a central ecophylogenetic force in the history of the radiation. Like others who have recently advocated for the position (see below), I now regard this adaptive array as a separate family, Pitheciidae. However, this classification also comes with a caveat, for it can only be provisional. With many more taxa now in need of detailed study, the phylogenetic interrelationships of many fossil platyrrhines are still not well understood.

Structurally, the article is presented in three sections. The first provides a brief background to platyrrhine taxonomy and systematics. The second introduces the volume's papers in a discussion of their new contributions to platyrrhine evolution in the context of an evolutionary morphology perspective. The third section is a targeted summary and critique of the algorithmic approach as it has been applied in morphology-based studies of platyrrhine cladistics.

PART I. BACKGROUND TO PLATYRRHINE SYSTEMATICS

Rosenberger (2002) argued that 1977 dated a paradigm shift in platyrrhinology. With the publication of Hershkovitz's (1977) massive volume on callitrichines (Figs. 1,2), which also included many companion studies of anatomical systems and their evolution among platyrrhines as a whole, the nonfunctional (descriptive) anatomical perspective which dominated taxonomic thought for decades came to a close, along with the *Scala Naturae*-like (gradistic) model of evolution. During the period prior, little progress was made either in classification or phylogenetics since about the 1920s, when scholars such as Pocock (1917, 1920, 1925) and Gregory (1922)—evolutionary morphologists in approach—made important contributions identifying, classifying and explaining "natural groups." In his own approach, Hershkovitz used static keys to organize the classification system, rather than the monophyly principle ushered in via Hennig (1966) and cladistics.

To achieve monophyletic groupings required dynamic analyses of characters, predicated on hypotheses of homology and polarity. In a philosophical shift, systematics embraced transformational thinking, which was consistent with functional morphology, though then, as now, applied rarely in studies of primate systematics. It became important to explain how (in what way) and why features might have changed. These new approaches and views were promoted, in different ways, in cladistic studies of platyrrhines by Ford (e.g., 1980, 1986) and Rosenberger (e.g., 1977, 1979b, 1980). The initial approach advocated by Ford was algorithmic (using Wagner tree parsimony). Rosenberger used character analysis (see Hecht and Edwards, 1977) infused with "adaptational analysis" (see Bock, 1977; Szalay, 1977, 1981; Delson et al., 1977; Szalay and Bock, 1991; Rosenberger, 1992). Homologies and polarities were imputed and tested by the comparative method (i.e., phenetics, anatomical and behavioral correlation, in-group and outgroup commonality, temporal precedence, development, functional-transformational models of adaptation and behavior, etc.). I also weighed characters according to my level of confidence in character analysis decisions, emphasizing the uniqueness of the structures involved and their adaptive roles in the biological gestalt of the taxon. A central methodological concept shared by Ford and Rosenberger was the reconstruction of hypothetical ancestral morphotypes, along with behavioral and adaptive inferences that could be attributed to these hypotheses. Wood and Harrison (2011) have recently re-emphasized the importance of inferring morphotypes as part of the phylogeny reconstruction process.

Classifications illustrate the differences between these pre- and post-Hennigian approaches (Table 1). Hershkovitz (1977) used a large number of suprageneric categories in his scheme, including five family-level (family and subfamily) units devoted to eight genera of fossils

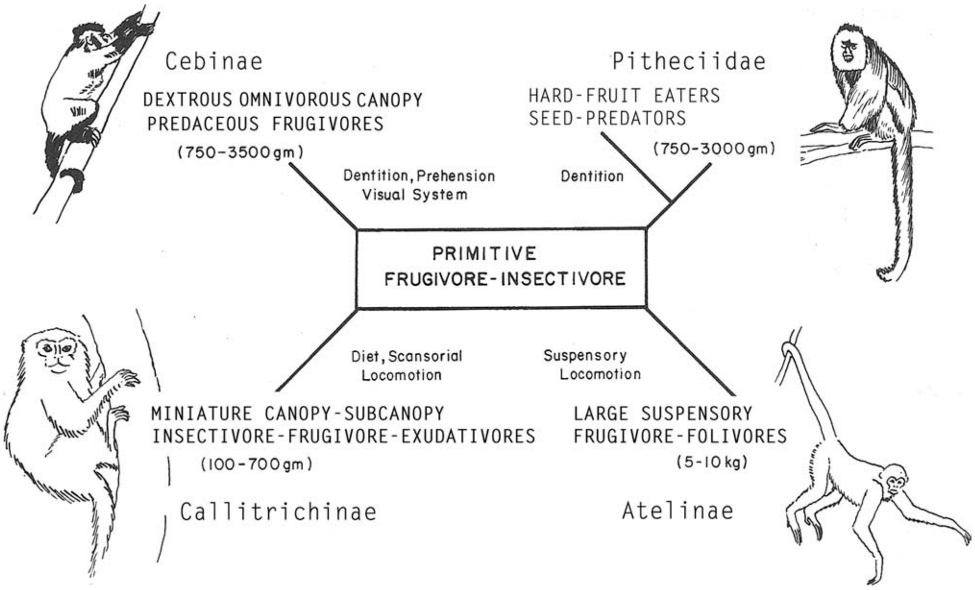

Fig. 1. An ecophylogenetic model of platyrrhine evolution based on the living forms (modified from Rosenberger, 2000). The major axes of differentiation, body size, food, and locomotion are emphasized. See Table 1 for a more specific taxonomic breakdown and a classification that includes fossils.

alone. A similarly large number of higher taxa were used for the living genera. A classification as split as this lacks phylogenetic and adaptive coherence and cannot compliment diversity. The first example of the system I have followed is a composite of formal classifications (e.g., Rosenberger, 1981, 1992) and subsequent taxonomic additions based on new fossils and several topical studies. It is a marked contrast to the Hershkovitz model, organized around a monophyletic two-family system that tiers other monophyletic groups at lower ranks. The increased number of fossils added to the Platyrrhini during this period is important, for accommodating a large number of diverse new taxa would inevitably stress any system based initially on organizing the living forms, as this one was. However, what is most striking is the multiplication of genera related, or potentially related, to the pitheciins *Pithecia*, *Chiropotes*, and *Cacajao*. These three were often collected into a separate subfamily since the middle 1800s (Rosenberger, 1981), but with revised cladistic thinking and the addition of fossils, this group has now swollen to about 14 genera. As noted previously (Rosenberger, 2002), such dramatic changes in knowledge has important implications for considering the role of this clade in the ecological history of platyrrhines.

The second Rosenberger classification in Table 1 is a revision that accommodates the exceptional diversity of the “pitheciid” group by according it full family rank. Recognizing this third family is consistent with the suggestions of molecular systematists who have, since the 1990s, promoted a three-family classification using the same taxonomic concepts as I use here but with one significant difference in content (see Schneider and Rosenberger, 1996). Much of the rest, however, maintains the same structure, although newly discovered fossils have been added. The pitheciids continue to be a challenge systematically, and this new model will

Fig. 2. *Saguinus oedipus* (Cotton-topped tamarin), a small-bodied, clawed callitrichine. From Elliot, 1913.

TABLE 1. A comparison of platyrrhine classifications

Hershkovitz (1977)	Rosenberger (1981–2002)	Rosenberger (present)
Family Callitrichidae	Family Cebidae	Family Cebidae
Callithrix	Subfamily Cebinae	Subfamily Cebinae
Cebuella	*Cebus*	*Cebus*
Saguinus	*Saimiri*	*Saimiri*
Leontopithecus	†*Neosaimiri*	†*Neosaimiri*
Family Callimiconidae	†*Laventiana*	†*Laventiana*
Callimico	†*Dolichocebus*	†*Dolichocebus*
Family Homunculidae	Subfamily Callitrichinae	†*Killikaike*
†*Homuculus*	Tribe Callimiconini	†*Acrecebus*
†*Dolichocebus*	*Callimico*	Subfamily Callitrichinae
Family Cebidae	†*Mohanamico*	Tribe Callimiconini
Subfamily Cebinae	Tribe Sagunini	*Callimico*
Cebus	*Saguinus*	†*Mohanamico*
Subfamily Saimiriinae	Tribe Callitrichini	Tribe Saguinini
Saimiri	*Callithrix*	*Saguinus*
†*Neosaimiri*	*Cebuella*	Tribe Callitrichini
Subfamily Aotinae	*Leontopithecus*	*Callithrix*
Aotus	Subfamily Callitrichinae inc. sed.	*Cebuella*
Subfamily Callicebinae	†*Micodon*	*Leontopithecus*
Callicebus	†*Patasola*	Subfamily Callitrichinae *inc. sed.*
Subfamily Atelinae	Family Cebidae inc. sed.	†*Micodon*
Ateles	†*Branisella*	†*Patasola*
Brachyteles	†*Szalatavus*	Family Cebidae *inc. sed.*
Lagothrix	†*Chilecebus*	†*Branisella*
Subfamily Alouattinae	Family Atelidae	†*Szalatavus*
Alouatta	Subfamily Atelinae	†*Chilecebus*
Subfamily Pitheciinae	Tribe Atelini	Family Atelidae
Pithecia	Ateles	Subfamily Atelinae
Chiropotes	*Brachyteles*	Tribe Atelini
Cacajao	*Lagothrix*	Ateles
Subfamily Tremacebinae	†*Caipora*	*Brachyteles*
†*Tremacebus*	Tribe Alouattini	*Lagothrix*
Subfamily Stirtoniinae	*Alouatta*	†*Caipora*
†*Stirtonia*	†*Paralouatta*	Tribe Alouattini
Subfamily Cebupitheciinae	†*Protopithecus*	*Alouatta*
†*Cebupithecia*	Subamily Pitheciinae	†*Stirtonia*
Family Xenotrichidae	Tribe Pitheciini	†*Paralouatta*
†*Xenothrix*	*Pithecia*	†*Protopithecus*
	Chropotes	†*Solimoea*
Suborder *inc. sed.*	*Cacajao*	Family Pitheciidae
Family Branisellidae	†*Soriacebus*	Subamily Pitheciinae
†*Branisella*	†*Proteropithecia*	Tribe Pitheciini
	†*Nuciruptor*	*Pithecia*
	†*Cebupithecia*	*Chropotes*
	Subfamily Pitheciinae inc. sed.	*Cacajao*
	†*Lagonimico*	†*Proteropithecia*
	†*Carlocebus*	†*Nuciruptor*
	†*Antillothrix*	†*Cebupithecia*
	Tribe Homunculini	Tribe Soriacebinae
	†*Homunculus*	†*Soriacebus*
	Aotus (incl. *A. dindensis*)	†*Mazzonicebus*
	†*Tremacebus*	Subfamily Homunculinae
	Callicebus	†*Homunculus*
	†*Xenothrix*	*Aotus* (incl. *A. dindensis*)
		†*Tremacebus*
		Callicebus
		†*Miocallicebus*
		†*Xenothrix*
		†*Antillothrix*
		†*Insulacebus*
		Subfamily Homunculinae *inc. sed.*
		†*Carlocebus*
		Family Pitheciidae *inc. sed.*
		†*Lagonimico*

undoubtedly benefit from further adjustments as the internal affinities of larger groups (e.g., Tribe Pitheciini) become better known, or when intersubfamily relationships are better understood. For atelids, I have elected to use only one subfamily and two tribes as the terminology is well established and there appears to be no benefit to elevating the latter and adding additional tiers below at this time. As is evident, my philosophy about classification is that it should be consistent with phylogeny, first of all—and, hopefully, with an ecophylogenetic model—but that it also should be balanced as a taxonomic scheme relative to current concepts applied elsewhere. It should not in and of itself attempt to reflect overwhelming adaptive departures detached from a cladistic hypothesis by inflating ranks, as with the separation of the extinct Jamaican genus *Xenothrix* at the family level, which has been advocated (e.g., Hershkovitz, 1970, 1977).

It is pertinent in this regard to comment briefly on other schemes that have recently been published with regard to two taxonomic levels. Following several decades of taxonomic stability, we have entered a period of "taxonomic inflation" (Issac et al., 2004), wherein populations are being accorded full species status largely because new definitions or species concepts are being applied, less so because new knowledge has been gained. Issac et al. note that this phenomenon is more egregiously evident in classifications of New World monkeys than other primates. A similar effect is also evident at the genus and family levels. At least three additional genera of living NWM are currently being recognized beyond the 16 identified by Hershkovitz (1977) and Napier (1976), the cornerstones of modern platyrrhine classification. 1) Van Roosmalen and van Roosmalen (2003) differentially diagnosed *Callibella* (relative to *Cebuella*) based on its slightly larger size and coat color and pattern difference, a methodology that was universally rejected for most of the 20th century. As I interpret them, multivariate analyses of craniomandibular morphology also barely separates the three known specimens allocated to this form from *Cebuella pygmaea* (Aguiar and Lacher, 2003), nor do univariate and multivariate analyses of the postcranium (Ford and Davis, 2009). 2) Rylands et al. (2000) elevated Amazonian marmosets to the genus level (*Mico*) essentially to avoid purported paraphyly of the classical concept of *Callithrix*, but there is no morphological support for this view (see Hershkovitz, 1977). 3) Groves (2001) advanced the notion that *Lagothrix flavicauda* should be elevated to the rank of genus (named *Oreonax*), but this was shown to be based on a flawed parsimony analysis of poorly selected cranial traits (Matthews and Rosenberger, 2008). At a higher level, this inflationary trend has emboldened Rylands and Mittermeier (2009) to recognize five (!) platyrrhine families, with one designed exclusively for genus *Aotus*, and without considering fossils at all.

These taxonomic moves undermine the stability of platyrrhine classification that has been achieved over the last 30 years based on knowledge of morphology, adaptation, molecules, and a consistent interpretation of phylogenetics. Various recent articles review the cladistic models (e.g., Schneider et al., 2001; Schrago, 2007; Osterholtz et al., 2009; Wildman, 2009; Kay et al., 2008; Rosenberger et al., 2009). In my view, there remains one interesting and vexatious problem concerning the affinities of *Aotus*, for which morphology and molecules do not align (e.g., Rosenberger and Tejedor, in press). One school places *Aotus* among pitheciids and the other among cebids *sensu* Rosenberger (1981). A few other discrepancies exist in branching sequences when comparing morphological and molecular dendrograms, each important but less vital than the *Aotus* paradox. Thus, the revised, non-Hershkovitzian picture of platyrrhine systematics that began to emerge in the 1980s based on morphology, began to be corroborated by genetics in the 1990s. And the power of these adjustments has been demonstrated by the capacity of the new system to accommodate many new fossils without requiring still another major overhaul.

PART II. EVOLUTIONARY MORPHOLOGY AND PLATYRRHINE SYSTEMATICS

The global hypothesis that developed during the 1980s is an ecophylogenetic model of platyrrhine evolution (e.g., Rosenberger, 1980, 1981, 2002; Rosenberger et al., 2009). It identifies four monophyletic groups, based on derived characters and character complexes that are also functionally and adaptively important, whose homologies and polarities were informed by functional-adaptive analysis, that is, evolutionary morphology. The three predominant ecological niche parameters that initially characterized these adaptive patterns involved body size, diet, and locomotion. A synopsis is depicted in Fig. 1.

The Size Factor: Body Size and Locomotion

Body size has always figured prominently in narratives of platyrrhine evolution because the group includes the smallest living anthropoid, the 100 g *Cebuella*, and its biggest species, *Brachyteles arachnoides*, is roughly 100-fold larger, weighing about 10 k (Rosenberger, 1992; Ford and Davis, 1992; Peres, 1994). These species are also emblematic of two uniquely platyrrhine locomotory organs, digital claws (the only other exception among euprimates is the clawed aye-aye, *Daubentonia*), and prehensile tails, both foundational features of major NWM clades. Hershkovitz (1977) essentially saw the evolution of size in orthogenetic terms with the smallest platyrrhines being the most primitive and the largest most derived. The idea that the miniature callitrichines are unusual or derived in being so small has been around for a long time (e.g., Pocock, 1917; Gregory, 1922), and a variety of arguments have been put forth in recent decades supporting the hypothesis that they are secondarily dwarfed (e.g., Ford, 1980; Leutenegger, 1980; Martin, 1992). These models tend to identify the special properties and combinations of features in the callitrichine *bauplan* as size-related in comparison with larger extant primates (e.g., clawed digits, tricuspid molars, posterior tooth reduction, chimeric twinning, simplex uterus, large neonates). Many of these features were explicitly considered in character analyses to test homologies, establish polarities, and explain their co-occurrence as parts of an adaptive package to facilitate occupation of a unique small-bodied niche in the platyrrhine radiation. Ford's (1980) synthesis continues to be a useful statement in this regard.

The problem of callitrichine claws has held a particular fascination. More than 100 years ago, Wortman (1904:23, 24) said:

> Whether the lack of opposability of the pollex and hallux [in callitrichines] is to be looked on as a degeneration from a former more perfect condition of prehensility of the extremities, or whether it represents a stage in the process of acquirement of the opposability of these digits, cannot now be determined . . .

Fig. 3. The pitheciids *Aotus vociferans* (Spix's night monkey), left, and *Callicebus personatus* (Masked tit), right. Morphology indicates they are closely related; molecules suggest *Aotus* is more closely related to callitrichines and cebines. From Spix, 1823.

> The habits of the marmosets, while as strictly and completely arboreal as in any of the Primates, resemble those of the squirrels more than those of the monkeys proper . . . the Negro Tamarin (*Midas ureulus*) confines itself mostly to the larger branches, and is frequently seen passing up the perpendicular trunks, clinging to the bark with its claws in a manner not dissimilar to that of the squirrels. This method of climbing is doubtless true of all the marmosets, and the lack of opposability of the hallux and pollex is correlated with the possession of sharp compressed claws instead of flattened nails.

Cartmill's (1974) empirical demonstration of the claw's biomechanical value in the positional behavior of small primates cast new light on the matter to which Wortman was so attuned, and cleared the way for a new consensus to form around the hypothesis that claws and small body size are intertwined derived conditions. This allowed other pieces of the callitrichine puzzle to fall into place. The sensibility of this hypothesis is underscored by the fact that a morphocline of nail-to-claw shapes exists among living platyrrhines, with many species exhibiting transversely arched and prolonged nails on all digits but the hallux, which is uniformly flat nailed.

With new observations and a sensitive quantitative method, Maiolino et al. (2011) reopen the riddle of platyrrhine nails and claws. They show that grooming claws, and a correlatively specialized terminal phalanx to affix them, exist on pedal digit II in at least two non-callitrichine genera, *Aotus* and *Callicebus* (Fig. 3)—something known to the literature but long since forgotten. This places platyrrhines, again, is a position to potentially inform us about the morphotype condition of anthropoids which heretofore was assumed, perhaps incorrectly, to have lost the grooming claw as a synapomorphy: in preserving grooming claws, platyrrhines may have retained the ancestral anthropoid condition. The combined occurrence of nails and grooming claws on the feet of platyrrhines, tarsiers, and living strepsirhines also raises a larger question of homology and transformational process germane to primates more broadly, as we mention. If these structures are phylogenetically continuous with counterparts found in the other great clades of euprimates, an additional question is raised about the actual homologies of the grooming claws. Did platyrrhine grooming claws evolve from the original euprimate grooming claws, which could have arisen directly as modified falculae without passing through a flat-nail character state?

The unique positional behavior of clawed callitrichines does not particularly stand out, as one might expect, in the Youlatos and Meldrum (2011) review of the locomotion of extant NWM and well as the fossil platyrrhines. This is the most up to date survey and evaluation of the platyrrhine locomotor evolution produced during the last 20 years. The authors present a multivariate analysis of frequency data describing locomotion as well as the overall morphology of the astragalus. The astragalus captures the diversity of platyrrhine ankle morphology and sorts fairly well along the lines of the major ecophylogenetic divisions, though not without some interesting overlaps and divergences. Most of the cebids form a cluster, which then links with *Aotus* and *Callicebus*—all springers in the older terminology (e.g., Erikson, 1963).

However, the two most distinct sets in this aspect of their study are the large, quadrupedal, prehensile-tailed, and suspensory atelids and the quadrupeds *Cacajao* and *Chiropotes*, all taxa that use pedal suspension and foot reversal postures. It is rare for studies of positional

Fig. 4. The pitheciids *Chiropotes satanus israelita* (Brown-backed bearded saki), left, *Pithecia pithecia capillimentosa* (White-faced saki), right, are closely related seed-predators. From Spix, 1823.

behavior to examine the transitions between the categories to which we assign animals, but Youlatos and Meldrum use the concept of preadaptation to offer a model pertinent to the evolution of tail-suspension. They suggest the manner of below-branch foot-hanging seen in some pitheciins (Fig. 4), which is accompanied by a draping of the tail (tail-bracing) over the supporting substrate, may represent a behavioral antecedent to the ateline tail-hang. This presupposes an ancient behavioral/adaptive continuity between two sister-clades, pitheciids, and atelids, a notion also promoted by Rosenberger et al. (2011) in suggesting a transition between seed- and leaf-eating.

The positional behavior of *Cebupithecia*, an iconic fossil pitheciin from the middle Miocene of Colombia, is the subject of Organ and Lemelin's (2011) in-depth analysis of tail functional morphology. While it has been known that this species probably did not have a prehensile tail, Organ and Lemelin show the proximal tail region was designed biomechanically to sustain relatively high bending and torsional forces, like prehensile- and semi-prehensile-tailed monkeys, but the distal end was different. They conclude that *Cebupithecia*, like one of the living Saki species, *Pithecia monachus*, as well as *Chiropotes*, was probably capable of tail-bracing postures. Organ and Lemelin also suggest this behavior may have been a primitive feature of the pitheciin clade. This is an intriguing idea because, as they say, there is no evidence for hindfoot reversal in *Cebupithecia*. One other reason why their argument intrigues is that it extends to Medrum's (1998; Youlatos and Meldrum, 2011) preadaptive hypothesis regarding the evolution of the atelid prehensile tail. Identifying the tail-bracing morphology and behavior in a fossil pitheciin and pushing its origins back to the pitheciine morphotype may mean tail bracing was inherited from the last common ancestor shared by pitheciids and atelids.

Returning to the matter of body size, bigness has become a focal point of attention with the remarkable discovery of two large Brazilian subfossils in the 1990s (see MacPhee and Horovitz, 2002). Their existence has essentially doubled the established upper point limit of NWM in terms of body mass. The ecological consequences of this new datum has still to be explored, but occupying a class which places these platyrrhines squarely into a size-niche dimension that parallels Old World monkeys for the first time may be revelatory. In fact, it has even been argued that platyrrhines had already peaked at an intrinsic size limit with *Brachyteles* (Peres, 1994), the largest modern NWM. However, the two subfossils, *Protopithecus* and *Caipora*, are also atelines, and seem to be about twice as large (Hartwig and Cartelle, 1996; Cartelle and Hartwig, 1996).

This inference is now strengthened by Halenar (2011a). She reassesses the body size estimates of *Protopithecus* using a variety of regression models and skeletal elements, including, for the first time, good background samples of platyrrhines to exert tight

Fig. 5. The living predatory cebines include *Saimiri* sp. (Squirrel monkeys), left, and *Cebus apella libidonosus* (Black-striped tufted capuchin), right, related monophyletically to the callitrichines. From Ferreira (1971) and Spix (1823), respectively.

phylogenetic control. Halenar finds that *Protopithecus* was baboon-sized, likely weighing about 20 k. In a related article (Halenar, 2011a), she evaluates the morphology of the distal humerus and proximal ulna using three-dimensional (3D) morphometrics. Here, Halenar finds another unexpected result. *Protopithecus*, an alouattin, while exhibiting limbs that are quite robust and a skull that resembles Howler monkeys in some unusual features, has an elbow that resembles more closely the hyperdynamic suspensory locomotors *Ateles* and *Brachyteles* than the quadrupedal climber *Alouatta*, a genus sometimes described as sluggish. Halenar suggests an adjustment in the model of the ancestral ateline locomotor pattern (see Rosenberger and Strier, 1989), which she envisions as being more acrobatic. She also notes that *Protopithecus* may have been fully capable of some ground use. This compliments the interpretation of MacPhee and Meldrum (2006) with regard to the related Cuban subfossil alouattin *Paralouatta*, which they think may have been semiterrestrial.

One of primatology's most arresting cases of parallel evolution, the independent development of prehensile tails in *Cebus* (Fig. 5) and the atelids (or semiprehensile and prehensile, respectively, depending on one's preferred terminology) is illuminated by new observations made by Organ et al. (2011). For generations, this similarity led zoologists to associate *Cebus* and atelids in classifications, which in today's frame would imply they are monophyletic. Such a perspective posed a serious challenge to the post-Hershkovitzian phylogenetic hypotheses that placed *Cebus* and *Saimiri* with callitrichines as opposed to atelids or any other platyrrhines. Functionally and behaviorally oriented character analysis (Rosenberger, 1983), followed by a diverse series of field studies (see Garber, 2011) as well as morphology projects (e.g., Organ, 2010), showed that the essential *Cebus*-atelid similarities were best interpreted as analogies. Organ and coworkers now demonstrate this phenomenon at the histological level. In the *Cebus* tail, which is fully clothed in fur, the critical mechanicoreceptor cells in the skin are suited mainly for heavy-pressure touch. The glabrous patch of skin on ateline tails, in contrast, are embedded with twice as many receptor types, and it is designed to sense both light and heavy pressure. They hypothesize that the *Cebus* system evolved to support sustained postural behaviors while the atelid's sensitive arrangement evolved to support the delicate timing dynamics of tail-infused locomotion.

The Food Factor: Fossils, Seeds, and More

The assessment of dietary adaptation has become a vital special interest among primatologists—not surprising as the mammalian fossil record is predominantly made up of teeth—and platyrrhine groups are notable for their fealty to distinct foods while also exhibiting a generalist streak. As indicated above, the feeding guilds that have been identified are also clades (Fig. 1), and the particular foods emphasized by callitrichines, cebines, pitheciids, and atelids, and/or the way they

Fig. 6. *Alouatta caraya* female and young (Black and gold hower), left, and *Brachyteles arachnoids* right, are large-bodied, prehensile-tailed atelids. From Spix, 1823.

access them via locomotion and posture, are at the ecological roots of their evolution.

In an effort to infer the diets of fossils using lower molar morphology, Cooke (2011) developed a large dataset of laser surface-scanned 3D models and analyzed their patterns via 3D geometric morphometrics (3DGM). Her project emphasizes the extinct Caribbean forms but also samples mainland Miocene species from Patagonia and Colombia. An interesting facet of Cooke's analysis is the support it offers one of the models explaining selection for molar adaptation, the critical function hypothesis, which was originally formulated in researching platyrrhine molar occlusion (Rosenberger and Kinzey, 1976). Cooke found that the dietary extremes, genera whose foods—leaves, insects, hard or tough fruits, and seeds—would be most difficult to process mechanically, were offset from the other platyrrhines in shape, and more easily classified according to diet using multivariate discriminant functions. Other platyrrhines, with more mixed but largely frugivorous diets, did not sort as well. There are also interesting faunal patterns in Cooke's data, although these need to be judged cautiously in view of the restricted samples used. Yet, the Caribbean and Patagonian primates seem not to present identifiable adaptations to insectivory, folivory, durophagy, or seed predation. These are major dietary patters emblematic of the modern radiation, and they were also established among the middle Miocene La Venta primates of Colombia, which is an ecological antecedent of the current Amazonian primate fauna. While earlier in time and separated far to the south geographically, the absence of several feeding niches among Patagonian fossils is no doubt partially due to sampling, but it also reinforces the idea that the southern cone and the Caribbean, especially, supported ecologically distinctive primate assemblages (Rosenberger et al., 2009).

It is interesting that with Cooke's (2011) system of measurement, which is the most sophisticated attempt thus far to capture the coherent crown geometry of platyrrhine molars, the phenetics, even with the classificatory power of 3DGM, does not consistently reflect phylogenetics at the suprageneric level. However, its does appear to be sensitive to intrageneric and intergeneric relationships in some cases. For example, Cooke confirms the unusual occlusal morphology and molar proportions of the Jamaican *Xenothrix* and finds it clusters closely with the new Hispaniolan fossil *Insulacebus* in shape space (see Cooke et al., 2011). She finds corroboration for congeneric status of modern *Aotus* with a middle Miocene Laventan species, *A. dindensis*, long a matter of controversy (e.g., Kay, 1990; Rosenberger et al., 1990). The sensitivity of the approach is also apparent in another difficult example. It is able see that the Caribbean forms exhibit interesting morphological similarities with the early Miocene Patagonian *Soriacebus* (see Rosenberger, 2002), whose incisor, canine, and premolar functional morphology suggests pitheciine affinities (Rosenberger et al., 1990) despite oddly shaped molars not exhibited among modern NWM or other fossils (but see Tejedor, 2005). This observation goes to the proposition that the Caribbean forms managed to enter the Greater Antilles relatively early in the history of the crown group (see MacPhee and Horovitz, 2002; Rosenberger et al., 2011; Cooke et al., 2011).

These additional links between some Caribbean fossils and the pitheciid NWM, which as noted above are turning out to be a major, highly successful clade within the adaptive radiation, is a fascinating development as the living forms include some of the most anatomically specialized feeders in either Old and New World, the pitheciin seedeaters. As Norconk and Veres (2011) discuss, other primates also rely on seed eating but none seem to have so much of the mouth redesigned to fit this food type, which involves cracking open woody leguminous casings. By providing empirical measures of the toughness and resistance of foods eaten, Noconk and Veres perform a welcome service to morphologists, who have long recognized the explicit connection between selection for anatomical form and the physical properties of the environment with which structures interact. Another remarkable hard fruit adaptation occurs among *Cebus* monkeys, which Cooke (2011) shows is comparable to pitheciins in having flat molar teeth. However, in this case, the most dramatic feeding behaviors mean pounding fruits with tools to extract what the monkeys want to eat, and the molars are histologically reinforced by thick enamel, unlike the pitheciins.

This contrast lends perspective on the recent proposal that the early Miocene Argentine fossil *Soriacebus* evolved a seed-eating adaptation in parallel to the pitheciins (Kay et al., 2008). Kay and coworkers, using a parsimony analysis (see below), found that *Soriacebus* fell outside the monophyletic crown group of NWM, thus requiring an alternative explanation for why they shared such exclusively pitheciin synapomorphies as tall, laterally compressed lower incisors, massive lower canines with a triangular cross section, and a massive pyramidal p2—all part of the breaching and harvesting complex that is becoming fairly well understood in living pitheciins. When their interpretation was challenged (Rosenberger, 2010b), Kay and Fleagle (2010) basically replied that parallelism was common and to be expected among NWM. They proffered the example of grasping tails, which evolved twice. However, the lessons derived from the dentition of *Cebus* illustrates just the converse, how parallelisms arise in different clades as asymmetric morphological equivalents because form is conditioned by other adaptive compromises in each case, in addition to potentially massive differences in their genomes. This principle, an aspect of what Bock (e.g., 1977) called "paradaptation," emerges from functional morphology, but it is explicitly a phylogenetic hypothesis as well. The verisimilitude of the *Soriacebus* and pitheciin anterior dental complex, and the deeply inflated jaws shown by the fossil as well, another potentially correlated pitheciine or pitheciin synapomorphy, suggest both a commonality of function as well as phylogenetic affinity: this is the null hypothesis. It is corroborated by the paradaptive mechanical parallels of the *Cebus* pattern. There, similar biological roles are evident—open the casing, remove the innards, crush it—but those behaviors are performed by a system design constrained, one hypothesizes, by a unique heritage not shared with pitheciins. The convergently evolved methods of *Cebus* cannot enlist incisors or canines to extract the seeds like *Soriacebus* would have and pitheciins actually do. And, the shallow, crushing jaws of *Cebus* are powered by a different muscular arrangement, without a comparable emphasis on the masseters, unlike deep-jawed *Soriacebus* and the pitheciins.

Generally, seeds are viewed as a fundamentally distinct dietary branch of frugivory, but Rosenberger et al. (2011) call attention to some suggestive similarities shared by seedeaters and leafeaters which may have broad consequences pertaining to dietary evolution in platyrrhines and other primates. We present a synthesis of anatomical, behavioral, adaptive and phylogenetic information in asking why the two most folivorous platyrrhines, *Alouatta* and *Brachyteles* (Fig. 6), do not conform in similar fashion to well developed models of primate folivory and herbivory. Howlers tend to, but certainly not the Muriki. The one important constant they share involve teeth highly sensitive to selection for a leafy diet, that is, small incisors and large, crested molars. We propose that even in these "semifolivores," who eat one of the most nutritionally and digestively challenging of primate foods, other nondietary factors interact with selection in the animal's gestalt and some may be more powerful than the large costs of eating leaves, which is why parallelism has not driven them to be more similar to one another. Concerning the origins of their leaf-eating habits, there may be a connection to seed-eating, for seed coats and pericarp tend to contain the same types of chemical deterrents that bother folivores and require gut specializations to deal with, secondary compounds. We propose that a level of seed-eating adaptations in the gut may have been a preadaptation that enabled atelines to shift from a frugivorous to a folivorous diet, and that this kind of a transition could have happened several times in primate evolution. A likely parallel example involves the origins of colobines, but a similar pathway may also have been taken early in primate history, as nontarsiiform euprimates emerged in the Paleogene, perhaps inheriting seed-eating proclivities from a plesiadapiform ancestry.

In all their diversity, seeds and leaves are not the least of dietary challenges experienced by a platyrrhine, for the smallest species are exudativores. Marmosets use the anterior teeth to gouge and wound trees in order to stimulate a flow of edible gum. Some of the unique features of the incisor and canine teeth associated with gum-gouging are well known (e.g., Rosenberger, 2010a; Hogg and Walker, 2011), but how this behavior influences craniomandibular anatomy is a matter of discussion. Forsythe and Ford (2011) find that gouging marmosets differ from nongouging tamarins in only three of 25 metrical features thought to be biomechanically important. They relate the differences to maximizing gape and dissipating loads in the face.

These studies have implicitly corroborated the hypothesis that the suite of craniodental features long thought to be indicative of the primitiveness of callitrichines (e.g., Hershkovitz, 1977) are not continuous with traits found in early primates or primitive mammals but are, instead, novel biomechanical specializations. On the other hand, as the Miocene fossil record of platyrrhines becomes better known, examples of callitrichin-like features are beginning to show up, such as the anteriorly narrow lower jaws and staggered incisors that appear to be present in *Homunculus* and *Branisella*. Full tests of the potential homologies of these similarities are required, and the biomechanical patterns evident at very different levels of biological organization identified by Hogg and Walker (2011) and Forsythe and Ford (2011) should offer valuable perspective in such analyses.

So, too, will be the sophisticated functional morphological research reviewed by Vinyard et al. (2011), a stunning range of elegant lab work—*in vivo* strain gauge assessment of the cranium and jaw; EMG; morphometrics; muscle fiber architecture. Even telemetered EMG studies of Howler monkeys feeding in the wild. Critically important is their finding that "monkeys" of the Old World and New World are not biomechanical equivalents: neither *Cebus* nor *Macaca* can be idealized as typical for purposes of applying dynamic functional information to resolve the attractive questions about how australopiths worked, for example. To their credit, Vinyard et al. also focus on matters that have been studied but produced counterintuitive results which demand further probing and, possibly, revisions of basic assumptions. One such example echoes the results of Forsythe and Ford (2011): absence in gum-gouging marmosets of enhanced resistance to loading the mandibular symphysis.

Correlative Factors: Brains, Guts, and Behavior

As noted, the model of platyrrhine evolution that shaped the previous discussion (Fig. 1) is essentially an ecological hypothesis attempting to explain the shape of the NWM radiation by the animals' differentiation along the principle axes of body size, food, and locomotion. However, there are more layers to this construct. Body size, food, and locomotion meld into the notion of foraging behavior, and foraging strategies trigger considerations of group size, interpersonal behavior, perception, life histories, cognition, and so forth.

For example, NWM are known to rely more heavily on olfactory communication than Old World anthropoids, so much that in some callitrichine species, pheromones are suspected of playing an important role in suppressing ovulation among nonreproducing females, which makes smell a central organizing element of mating and social systems. However, the role of the vomeronasal organ (VNO) in mediating sociosexual behavior is complex and much in need of experimental research. Smith et al. (2011) provide a taxonomically broad morphological perspective on this with their microstructural and macrostructural analysis of the VNO in platyrrhines, which they relate, in part, to selection involving competition for mates. They suggest that relatively smaller (shorter) vomeronasal grooves, the bony trough in which the organ sits, may be associated with monogamy, where sexual selection may be relaxed. However, short grooves are also present in the polyandrous callitrichines, which leads the authors to suggest that the functional division of vomeronasal and main olfactory systems may be less dramatic than supposed. One suspects this may also mean that polyandry in callitrichins evolved from a primitive condition of monogamy, perhaps in concert with the extra parental care necessary for rearing twins. Nevertheless, by showing that VNO size has an osseous correlate, Smith et al. provide a method for tracing it in the fossil record as a way of gaining new glimpses of the behavior of extinct species.

Also investigating the special senses, Muchlinski et al. (2011) test the hypothesis that female *Cebus* monkeys, who must naturally experience higher levels of parental investment than males, ought to be choosier about the food they eat and should therefore be more sensitive tasters. To get at this question, the authors look at sex differences in the histology of the fungiform papillae (FP) on the anterior tongues in a series of capuchins. Their hypothesis is corroborated in finding that females have 50% more FPs per square centimeter than males, and larger surface areas of FPs as well, although both sexes appear to have similar total counts of taste pores (the actual receptors) within the papillae. This is a potentially rich area of research with so many connections to other evolutionary topics that it strains the imagination.

The relationships of dental growth with several life history variables among the cebids, including brain size and body size, as well as ecological aspects, are explored by Hogg and Walker (2011) in a tightly controlled phylogenetic sample that varies in size by about 30 orders of magnitude and includes differing levels of encephalization. Theirs is the first extensive study of enamel growth rates in platyrrhines, and they use three different measures of ontogenetic development. Hogg and Walker suggest that although brain mass strongly influences timing of dental eruption statistically, ecological factors, particularly the age of foraging independence, have a stronger interaction with enamel growth. These results are not entirely consistent with patterns found among strepsirhine primates, which raises a variety of questions requiring additional research. The first next step might be to sample atelids and pitheciids, to see if the platyrrhines as a group are distinct.

Hartwig et al. (2011) examine the evolution of brains and guts in platyrrhines. First off, we present a new robust series of raw measurements on brain weight (and body weight) that encouragingly validate the measurements of a more than 40-year-old data set on brain mass (Stephan and Andy, 1964; Stephan et al., 1981) that has been the primary resource for many subsequent studies on primates. We also show the good correspondence between skeletally based endocranial volume measures and actual brain weights. Then we examine relative brain size in platyrrhines, including all modern genera but *Brachyteles*. A new finding is that *Chiropotes* and *Cacajao*, seed-predators, have elevated brain sizes, approaching and perhaps equaling the high encephalization quotient of *Cebus*, which is famously regarded as one of the most highly encephalized (and intelligent) primates. In suggesting that NWM increased relative brain size in at least three lineages independently, we review some of the ecological and social factors that may have driven these patterns. We also find a complex relationship between relative gut size and differentiation vis-a-vis brain size.

In summary, this selected series of examples relating to the status of evolutionary morphology as a didactic method in the world of NWM, are proof positive of an enlarging, vital research agenda. There is little doubt that the post-Hershkovitzian models of platyrrhine interrelationships and adaptation have shaped the direction of this body of work at several levels, which perhaps has added to the value of their end results. At the same time, while there has been room to challenge these ecophylogenetic models as new data accumulated and were often analyzed by independent methods, the studies reported here tend to reinforce the essential cladistic hypotheses. Whether it is toes or tails or sources of nutrition, ideas about the adaptation and evolution of anatomical features and complexes and adaptive strategies are inevitably rationalized through the phylogenetic perspective, information gained more often than not in the absence of fossils. The research on platyrrhines thus becomes an example of the reciprocity of functional morphology and phylogeny reconstruction, and the potential power of joining the two as an operational, evolutionary morphology approach when appropriate.

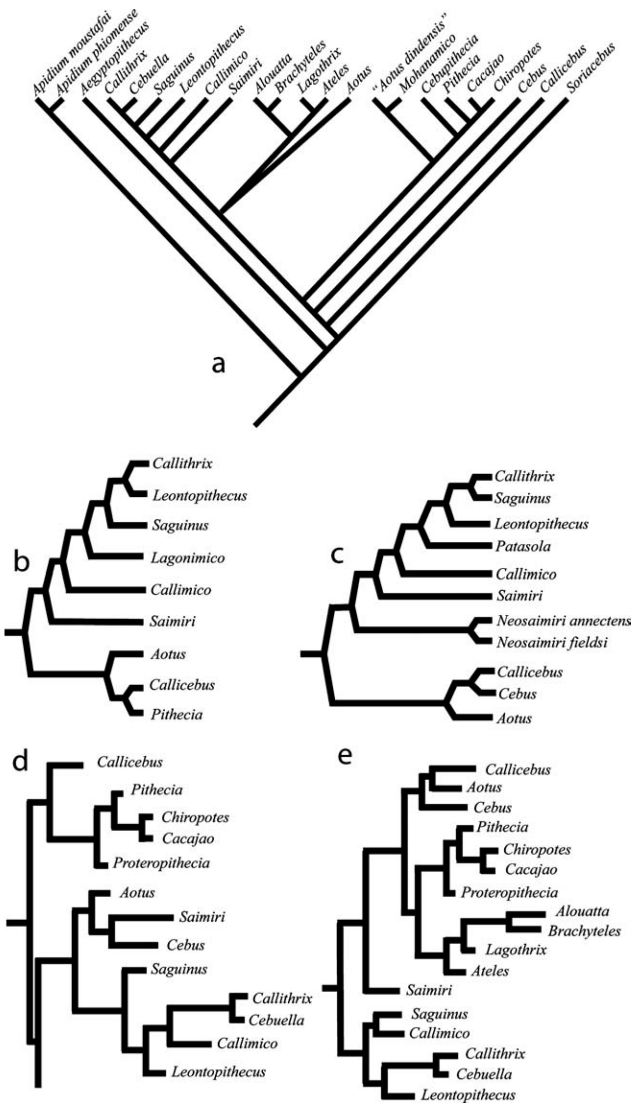

Fig. 7. Five whole or partial maximum parsimony cladograms from several studies produced by Kay and coworkers (see text). (**a**) Kay (1990): 117 dental characters, 19 taxa [genera], Consistency index (CI) = 0.45. (**b**) Kay (1994) *Lagonimico* tree: 18 characters (15 dental), 9 taxa [genera]; CI = 0.65. (**c**) Kay and Meldrum (1997) *Patasola* "preferred" cladogram, 55 dental characters, 11 taxa [10 genera], CI = 0.54. Retention index (RI) = 0.55. (**d**) Kay et al. craniodental tree constrained by molecular backbone tree (Kay et al., 2008, Fig. 20), CI = 0.34. RI = 0.53, 199 characters craniodental. 30 taxa [genera]. (**e**) Kay et al. craniodental tree unconstrained by molecular backbone (Kay et al., 2008, Fig. 21); CI and RI not provided. Compare (a) and (e) for a fuller picture of branch-by-branch discordance of strictly morphology-based parsimony results.

> [T]he cult of impressive technicalities or the cult of precision may get the better of us, and interfere with our search for clarity, simplicity, and truth.
>
> Karl Popper (1983, p. 60)
> *Realism and the Aim of Science*[1]

PART III. EXPERIMENTS IN PARSIMONY

Kay and coworkers (e.g., Kay, 1990, 1994; Kay and Meldrum, 1997; Kay and Cozzuol, 2006; Kay et al., 2008) have been the most ardent users of parsimony algorithms (PAUP; e.g., Swofford, 2002) as a method to reconstruct the cladistics of NWM based on morphology. The effort makes their work an indispensable resource for evaluating the power of this approach in a controlled situation—one lab, using a consistent and expanding dataset based mostly on craniodental features, applied to a single adaptive radiation. It is noteworthy that this approach led Kay et al. (2008) to suggest that nearly all of the early middle Miocene platyrrhines from Patagonia, which comprises a very important collection of fossils key to understanding platyrrhine evolution, belong to a pre-crown radiation of NWM. This idea addresses central questions about the tempo and mode of platyrrhine evolution: How old are the extant lineages and how much have they changed over time? The model proposed by Kay et al. has been presented as an alternative to the Long Lineage Hypothesis (e.g., Rosenberger, 1979a; 2010b; Delson and Rosenberger, 1984), which holds that some of these same Patagonian forms known by interpretable material are actually early representatives of enduring extant clades, in a broad sense representing the ancestral groups from which platyrrhines evolved into the modern guilds as the Amazonian fauna assembled several millions of years later (Rosenberger et al., 2009). More accurately, it addresses a temporal question: When do these long-term lineages, documented by molecular systematists as well (e.g., Opazo et al., 2006; Schrago, 2006; Osterholtz, 2007; Schneider et al., 2001, Wildman, 2009), first appear in the fossil record?

Figure 7 presents summary cladograms of this body of work (e.g., Kay, 1990, 1994; Kay and Meldrum, 1997; Kay et al., 2008), chronologically. The dendrograms appear as published (a, b, and c) or as extracts taken from larger trees (d and e). They were selected to highlight the interpretations of *Callicebus*, one of the more interesting genera whose affinities have historically been problematic (see Rosenberger, 1981; Ford, 1986; Rosenberger and Tejedor, in press). The trees come from four different studies using an expanding dataset involving 15 to 199 craniodental characters, and as many as 30 primate genera. For one study, I reproduce two different dendrograms, one (e) based purely on morphology and another (d) that use a "molecular backbone"

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[1] Cited by Grant and Kluge (2003).

approach to reconstruct morphology, which essentially involves mapping morphological character states onto the topology of an existing molecular tree. The purpose of this particular application was to generate a list of traits useful for placing fossils within a presumably robust cladogram.

The five trees reveal five different linkages for *Callicebus*. The first example (Kay, 1990) should perhaps be treated as an anomaly—a starter tree?—for the outstanding cladistic elements that give it shape have essentially been abandoned by Kay in all subsequent articles (e.g., compare with Fig. 7d,e), save for the recognition (but not the interrelationships) of three monophyletic groups consisting of callitrichines, pitheciins and atelines. For all intents and purposes, when stripped of the wayward interpretations of nonspecialists seeking to force fit classifications, these three clusters of genera have been understood to be coherent units for several generations (Rosenberger, 1981). However, in 1990, Kay interpreted *Callicebus* as a basal member outside the three clades, in a position below *Cebus* at the beginnings of the crown radiation. There is little question today, from morphology and molecules, that both *Callicebus* and *Cebus* are nested well within the Platyrrhini (e.g., Schneider and Rosenberger, 1996; Opazo et al., 2006; Schrago, 2006; Osterholtz, 2007; Schneider et al., 2001, Wildman, 2009).

However, in each of the four other morphology studies in the series *Callicebus* obtains different positions as well, sharing an immediate node with *Pithecia* (b), *Cebus* (c) and *Aotus* (e), or shown as the sister-group to pitheciins (d). There are many interesting aspects to these results. (1) *Aotus* is nearly always in the mix, never being more than one step removed from the *Callicebus* twig or node. *Aotus* and *Callicebus* have long been thought to be closely related (see Rosenberger, 1981). (2) In only one "unconstrained" case (b) is *Callicebus* tied directly to *Pithecia*, but not when the other pitheciins, *Chiropotes* and *Cacajao*, are included in the sample (d and e). Now, the close cladistic association of *Callicebus* and pitheciins is unanimously accepted by morphologists and molecular systematists (e.g., Rosenberger, 1992; Schneider et al., 2001; Opazo et al., 2006; Schrago, 2006; Osterholtz, 2007; Rosenberger et al., 2009; Wildman, 2009). (3) In two post-1990 iterations, *Callicebus*, *Aotus*, and *Cebus* form a exclusive monophyletic group (c and e). This contradicts the powerful cladistic linkage between *Cebus* and *Saimiri*, which is extended to encompass callitrichines as well by essentially all other studies (ibid.). (4) In none of the purely morphological iterations (a–c, e) is *Aotus* more closely related to cebines and callitrichines than to any atelids. The former hypothesis has received nearly universal corroboration from molecular systematists since the middle 1990s (e.g., Schneider et al., 2001; Opazo et al., 2006; Schrago, 2006; Osterholtz, 2007; Wildman, 2009), although I continue to be skeptical of this notion based on morphology, and also because the molecular results seem soft. In a survey of them, *Aotus* is typically linked to cebids via polytomies, and its node receives uncommonly low and variable statistical support (Rosenberger and Tejedor, in press).

These nonrepeated results concerning the interrelationships of *Callicebus* are major inconsistencies among the morphology-based parsimony tress. And, close inspection reveals that the discrepancies are not limited to one genus. They also involve *Saimiri*, *Callimico*, *Leontopithecus*, and so forth. While it is beyond the scope of this study to seek a specific explanation for errant results, it seems clear that no particular outcome can be said to be scientifically credible when it is not replicated, especially by the same methods, in one lab, using a consistently similar body of information. Confidence in any one of the trees, or in particular nodes, could have been gained because each of these iterations, coindependent by their very nature thus highly likely to repeat, was slightly or more progressively tweaked by design, for example, with enlarging matrices of characters and/or taxa but analyzed within the same experimental plan. However, this was not the case. The strongest common denominator among them in terms of broadly accepted and probably accurate results is found in the monophyly of callitrichines, morphologically and behaviorally one of the most derived platyrrhine clades—a finding not only expected but essentially required to avoid disqualification.

The final pair of cladograms was isolated from a larger study because it is instructive in another sense. One of the trees (e) is based exclusively on morphology and the other (d) is built from a molecular backbone. Again, prominent differences are seen with respect to *Callicebus*, *Aotus*, *Cebus*, *Saimiri*, and so forth. For the first time in the series, the morphology (e) suggests *Saimiri* is not related directly to cebids (d), a conclusion that is strongly contradicted by all other phylogenetic studies since the post-Hershkovitz (1977) paradigm shift. However, another aspect reveals the intrinsically limited cladistic signal of the analysis itself. By mapping the characters onto the molecular backbone (d), Kay et al. (2008) were able to obtain a statistical assessment of the "goodness of fit" between morphological characters and the tree. The Consistency index (CI), which is designed to measure the amount of homoplasy, was 0.34, and the retention index (RI), which is meant to measure the amount of synapomorphy, was 0.53. Since plesiomorphy and homoplasy contain no credible cladistic information by definition, the values obtained here indicate about one-third to one-half of the morphological characters mapped onto the molecular tree can be regarded as cladistically irrelevant noise. At most, only about half the tree can be reliably held, from this particular viewpoint, to be built on nodes supported by homologous derived craniodental characteristics.

While I do not assume the molecular tree has precedence over and is more likely to be more "right" than the morphological tree, the question is—What does this poor fit mean? If the molecules are correct, is this repudiation of morphology, or of the particular characters or methods used in the morphological study? It should also be recalled that two of the prior, purely morphological studies achieved much higher CI values, which is partly a function of having smaller matrices, but they also exhibited discordant branching sequences.

Kay et al.'s (2008) research strategy in this last study (d and e) has been critiqued at length (Rosenberger, 2010b; but see Kay and Fleagle, 2010). Various theoretical questions regarding specific sampling protocols and possible artifacts relating to them have been pointed out. However, the backbone methodology is problematic for other, deeper reason as well. It assumes, for example, a symmetrical correspondence between the patterns of molecular and morphological evolution (e.g., Assis and Rieppel, 2010). Moreover, Assis and Rieppel (2010:4) point out an epistemological dilemma associated with the procedure that is inherent in the presumed primacy of the molecular evidence: "Using mapped, rather that tested, characters as synapomorphies cannot lend support to the inference of monophyly, because such "synapomorphies" are empirically empty: they can never be shown to be wrong." In other words, adhering to a backbone methodology makes the results and all contingent anatomical hypotheses oblivious to tests using morphology.

Irrespective of this caveat, Kearney and Rieppel (2006) also note that the procedures used in algorithmic analyses of morphology like the ones discussed here are similar to what Hull (1970) described as an "antitheoretical" method of "look, see, code, cluster" (pg. 31). This was Hulls' summary critique of early formulations of numerical taxonomy, a systematic approach that sought a high level of scientific objectivity but wound up being rejected as sound phylogenetic methodology, partly because nothing is theory-free in science. While acknowledging that practitioners vary in how they apply the method, its main contentions and philosophical positions are quite similar to those embraced by advocates of algorithmic cladistics. To paraphrase Hull (1970:31), their purported value lies in: 1) being based on unweighted or equally weighted characteristics, with no *a priori* weighting; 2) not being biased toward any scientific theory or prior research on the topic, or to ideas applied to character delineation, homologies, and taxonomic clustering.

Several other large points emerge from this assessment of the differing cladograms (Fig. 7). One has been demonstrated many times before in various studies of primates (see references in Rosenberger, 2010b) and other taxa (e.g., Hillis, 1998), including meta-analysis of dozens of morphological studies. The matrix configuration of a parsimony study has a profound influence on results. In other words, when it comes to real world applications, the method may be inherently unstable and unreliable, because no sampling of biodiversity can avoid omitting taxa and lineages that have gone extinct, and the consequences of this loss of information are imponderable but also clearly variable. Thus, we might assume every matrix is a skewed matrix. Wheeler (2005:71) makes this point in another way, which challenges the heart of parsimony as a phylogenetic method grounded in homology, saying: "Given a single cladogram, two features are homologous if their origin can be traced back to a specific transformation of a branch of *that* [Wheeler's emphasis] cladogram, but the same pair of features may not be homologous on alternative cladograms. Homology is entirely cladogram dependent . . . "

Wheeler's (2005) extreme formulation is meant to elucidate a concept of homology but it is also another way of saying parsimony analysis does not guarantee that the states attached to nodes are parts of a genetic continuum of traits or a discrete genetic pathway of descent. It only promises to find the shortest tree possible, that is, a tree with the fewest nodes, based on how select characters are distributed among select taxa. In other words, parsimony is an optimization method. It is not a tool that probes information in search of genetic qualities. It works by antiseptically redistributing character states among taxa in a manner deemed most efficient by predetermined rules, which may have nothing to do with morphological evolution or the evolvability of a particular radiation. Along the way, it brands traits as "synapomorphies," not in the Hennigian sense of shared derived genetic homologies but as common denominators of taxonomic clusters. In reality, these common denominators, which unless homologized and polarized are nothing more than anatomical abstractions, may be primitive, derived, or analogous. As the CI and RI values indicate, the final cladogram is thus supported by an amalgam of cladistic and phenetic information. This is poignantly illustrated by the support values in the morphological cases presented above, and in the poor performance of the craniodental characters when mapped onto the molecular tree.

Does this disqualify parsimony as a tool for phylogeny reconstruction? It should for purists. However, not if we consider parsimony a heuristic device that may bring us a step closer to discovering interrelationships, and accept its many phylogenetic caveats at the same time. It does mean that a parsimony tree cannot be regarded as a true cladogram unless the input characters are stated to be (in theory) homologies, that is, unless it is preceded by character analysis. Why does parsimony work to the extent it does? Perhaps because a minimally adequate number of traits coded at the outset are indeed likely to be homologues. With this kind of "head start," in many cases even purely phenetic resemblances can lead to a natural, monophyletic grouping of related taxa. However, if the parsimony tree is a phenetic-cladistic hybrid, it follows that only some of its nodes are trustworthy. More research, using alternative means, would be required to decide which ones deserve confidence.

Having seen some of the drawbacks of parsimony studies, in the present context the question now becomes: What role might evolutionary morphology have in improving the design of these studies? What roles can functional morphology play, more broadly, in cladistic studies? There are two operative levels in the process of phylogeny reconstruction, the dataset (taxon and character identification and coding) and the analysis (tree building). Functional morphology provides a testing platform for cladistic hypotheses, at the levels of character and clade. If one assumes adaptation is what drives much of morphological evolution, we can test how sensible cladistic hypotheses are by evaluating adaptive continuity and/or discord among potentially related taxa. For example, the association of *Callicebus* with pitheciins is one of the newer features of platyrrhine cladistics, but few researchers recognized any overlapping similarities between these groups until it was determined that they shared in common the unusual pattern of tall, narrow incisors, in addition to some subtle details of upper incisor morphology (Rosenberger, 1979b). This synapomorphic clue attained more cladistic power when it was recognized that the *Callicebus* condition was a good model for an early adaptational "stage" in the evolution of the hyperderived pitheciin incisor-canine battery (Kinzey, 1992; Rosenberger, 1992). At the same time, some of the trenchant differences between *Callicebus* and pitheciins were spelled out as adaptive departures related to the radically derived seed-eating habits evolved among the latter. This offered a rationale as to why close relatives looked less alike than propinquity of descent might predict, and it provided a sound hypothesis for the polarities of hypothesized changes.

In a much simpler example, the power of the hypothesis that *Pithecia*, *Chiropotes*, and *Cacajao* are monophyletic derives not only because one can generate a long list of shared anatomical novelties, but because we understand their anterior teeth as being functionally integrated with the cheek teeth—equally odd in shape—as an adaptive system geared to seed harvesting and processing. Thus, we attribute high "phyletic valence" to the characters. This set of features and analytical concepts has been used to place fossils with very incomplete anatomies, such as the early middle Miocene form *Proteopithecia* from Patagonia (Kay et al., 1998). In fact, the confidence placed in these character hypotheses is so high that *Proteopithecia* is the only Patagonian platyrrhine recognized by Kay et al. (2008) as belonging to the crown NWM clade. The other taxa, represented by characters without clear-cut functional explanations if any at all, he and his coworkers designate as stem platyrrhines. Interestingly, at the same time, they deny that another Patagonian fossil, *Soriacebus*, is also a pitheciine (see above) though it, too, exhibits a number of the same high-weight pitheciin traits.

Obviously, for cases involving taxa characterized by extreme morphologies, functionally interpretable, one might say homologies and polarities are simple enough that conventional character analysis can do the job and algorithms are simply overkill. However, what about the many other cases? One argument invoked to support the use of algorithms seems to be that parallelism and convergence is both so subtle and so common (see Kay and Fleagle, 2010) that the matter should not be left to the alleged subjectivity of conventional morphological methods. While the concern for parallelism is as old as Darwinian systematics itself, the entrenched contemporary view that parallelism is rampant can be attributed to meta-analyses of datasets which have attempted to empirically demonstrate the frequency of parallelism by examining the CI and RI statistics in parsimony projects (e.g., Williams, 2007), as well as to the CI and RI values in individual studies such as the series under discussion here. However, these comparative reports are fraught with difficulties, apart from the fact, recognized by Williams and others, that the measures are not independent of matrix size and cannot thus be compared easily across studies. More serious objections are that high levels of homoplasy appear to be 1) predicated on characters that are themselves nonindependent, and 2) involve traits that may not actually be suitable for higher phylogeny assessments. This situation arises directly from the decision to minimize assumptions about morphology when crafting data matrices. For example, the practice of coding serial homologues, for instance, hypoconulids on first, second and third molars, as three separate characters is one such example appearing in the platyrrhine literature (e.g., Rosenberger, 2010b) that violates several precepts: 1) hypoconulids vary at the population levels within some species and genera, making them difficult to code and untrustworthy at higher taxonomic levels and across clades, where they are prone to functional convergence; 2) the theory of homology dictates that such features strung together across adjacent morphological units constitute one feature, not two or three. According to Sereno (2009:626), and others, "character independence and the mutual exclusivity of character states" are the fundamental assumptions behind character state formulations.

The abundance of parallelisms detected by meta-analyses and individual parsimony studies is an issue, for all agree that it can become a significant nuisance factor in phylogenetic studies. As noted above, in the era of the supermatrix—when a single molar can contribute a dozen states or more—we are likely to find high degrees of parallelism because each one is an artificial subdivision of an integrated functional complex under selection. The essential point is that excising traits from their anatomical systems and treating them all separately strips them of their functional and genetic qualities [to Simpson (1944), relationships], making the effort to reconstruct phylogenetic interrelationships more challenging because it also detaches the analytical process from evolutionary theory. The more and more functional units are subdivided, the more information is lost about their genetic properties and their potential interaction with selective forces; the more noise is added to the system; the higher the measure of homoplasy.

In summary, for platyrrhines, morphology-based parsimony studies do not have a good track record. The "simple" clades can be easily retrieved, as they would likely be on purely phenetic grounds, but problematic genera wander about the trees in an inconsistent manner. Near-repeat studies do not replicate. Knowing these results tend to fail the test of repeatability, they must be viewed skeptically. Meaning, some nodes in a large tree are likely to be reasonable hypotheses of monophyly, but others are not. If there is any rule of thumb that can be applied here, it must be that nodes supported by features that make sense functionally in the lives of the animal are the ones deserving our attention. Those supported by volatile, atomized traits of limited independence and functional value, are to be suspect. As a heuristic device, parsimony analyses have a place, but without testing independently the homologies of the characteristics involved a parsimony tree cannot be accepted as a truly cladistic model. However, the under-performance of these studies in the platyrrhine domain should not be taken as evidence that morphology has failed. Or, that molecules are more reliable as phylogenetic evidence. Or, that parallelism is stultifying. These difficulties lie with the methods we use, not with the morphology itself.

CONCLUSIONS

The diverse set of morphological studies presented here, and fieldwork bearing on morphological questions, continues to expand the body of knowledge concerning the adaptive radiation of NWM. Evolutionary morphological studies of platyrrhine primates now cover a wide range of questions concerning the current ecological and behavioral adaptations of New World monkeys. In both general and specific ways, they add confidence to the models of platyrrhine phylogeny and adaptation that began developing in the 1970s and early 1980s, when platyrrhines first became subject to cladistic studies informed by character analysis. They support the general model of the platyrrhines' current status as an eco-phylogenetic array differentiated along the principle ecological axes of body size, diet, and locomotion, and serve to align other factors such as social organization, brain size, perception, cognition, and so forth. Moreover, they generate testable hypotheses about the adaptive shifts that must have occurred as the platyrrhine panorama unfolded.

One reason for their explanatory power is that the thinking behind these articles is closing the perceived gap between branches of morphology that are often held apart from one another, such as functional morphology and biomechanics, allometry, histology, systematics, and phylogeny reconstruction, while also addressing matters of ecology, behavior, and life history that articulate with anatomy. The result is a more expansive evolutionary morphology. Its perspective provides a robust platform for generating and testing hypotheses about platyrrhine evolution, how and why groups and characteristics changed over time, in addition to serving morphology's more conventional *raison d'être*, to investigate how things are structured, how they operate and how to categorize anatomical diversity. Evolutionary morphology also provides a primary way to rationalize false cladistic signals by exposing parallelisms as independently evolved paradaptations.

The notion of evolutionary morphology ties phylogeny and adaptation together as a matter of method. Many of the hypotheses about the cladistic interrelationships of platyrrhines are made plausible because there are strong adaptive hypotheses behind the characteristics put forth to support the phylogenetic models, with functional morphology proving a deeper understanding of the connections between form and biological role, and because the groups so identified occupy an understandable place in nature. Many of the homologies and polarities proposed as cladistic evidence in the first place were identified as being of potential value because of their evident adaptive significance.

Molecular systematics offers an independent empirical test of morphology-based phylogenetic results, a direct acid test of the hypothesized relationships and an indirect check of the evidence behind them. Overall, there is broad concordance between molecular and evolutionary morphological models, although some question marks—areas ripe for further research—still remain. What do I mean by broad concordance? Four major clades have been identified, and most workers see them as comprising two basic divisions of the radiation. Two of the four are unanimously agreed to be sister-taxa. There is consensus on how the major subclades within these groups sort out. Many of the links between pairs and triplets of genera are agreed on. That the molecules and morphology are also in sync in terms of the time scale inferred for the origins of these clades adds confidence and mutual corroboration of the phylogenetic outlines.

The main morphological method competing with the character analysis approach to phylogeny reconstruction over the past 20 years has been parsimony-based cladistics. These projects suffer from inconsistency, as shown by following the results obtained for the genus *Callicebus* in a series of related craniodental studies from the same lab. Cladistically, differences in the placement of *Callicebus* may be as small as one-node shifts or one-branch swaps, but they also get quite large: a cladistic position nested deeply inside versus one at the very edge of crown platyrrhines. In a taxonomic sense, the parsimony studies have aligned *Callicebus* with at least two different families. A number of other genera (e.g., *Saimiri*, *Cebus*, *Aotus*, *Leontopithecus*, and *Saguinus*) are also variably placed, nontrivially, in these assessments.

The NWM parsimony studies have also been shown empirically to have a low cladistic yield at the character level, that is, relatively few true synapomorphies, for the trees tend to exhibit low levels of homology. The reasons for this are not easy to determine, but various critiques of how the method has been used in primate studies, including platyrrhines, have pointed out a preponderance of issues. These could plague any phylogenetic study but they are more acute in rigid machine-based treatments. Among them: disparities in taxonomic samples used; a reliance on population-level traits for higher phylogeny studies; matrices biased by taxon and character choices; excessive use of nonindependent, correlated, and redundant characters; and, especially acute for studies involving fossils, matrices skewed by material limitations.

This relatively poor performance calls out for caution, especially when this approach is used to address, within a constrained taxonomic framework, the phylogenetics of individual, poorly known fossils. Without a complimentary assessment of the evidence by character analysis or evolutionary morphology, which has been shown to have a good track record, these projects are inevitably handicapped by compromised samples: an overabundance of missing biological information and an overatomized anatomy. Such is the case for several middle Miocene fossils of the circum-Amazonian basin. Examples are *Lagonimico* (said to be a giant tamarin, but more likely a pitheciid) and *Solimoea* (said to be a primitive atelin but more likely an aloauttin). Similarly, questionable results have been obtained in assessing a whole group of older fossils from Patagonia. Based on a very unevenly preserved information base, and using a molecular backbone approach in an effort to extract cladistically informative anatomical traits from the whole panoply of modern platyrrhine craniodental diversity, all the fossils were determined to be outside the crown clade. In this case, the resemblances between *Tremacebus* and *Aotus*, and *Soriacebus* and pitheciins, of features shown to be powerful ecophylogenetic indicators by evolutionary morphology, were rejected with little or no consideration, even though the trees' homoplasy indices were high.

These examples call into question the trustworthiness of morphology-based parsimony as a tool for cladistics, certainly as the ultimate arbiter. If platyrrhines are taken as an example, it has yet to be shown that parsimony-based methods, which tend to shun attaching evolutionary interpretations of homology, polarity, and adaptation as evidence inputs, have greater resolving power than a morphology which concentrates on fewer characters and is laden with interconnected evolutionary hypotheses. It has yet to be shown that anatomical information purged of its structural-functional context, that is, evidence of its genetic covariation and inheritance, outperforms methods that fuse morphology, phylogeny, and adaptation. Or, that sheer quantity of information, including characters and taxa devoid of evolutionary context, redundancies, or those immaterial to the question at hand because they are autapomorphic for other groups, yields more robust results than character analyses that fuse morphology and adaptation within a properly constructed phylogenetic framework.

As some have noted, the philosophical basis of algorithmic, morphology-based cladistics is akin to the "look, see, code, cluster" foundations of the now defunct school of numerical taxonomy. In other words, there is ample room for improvement. On the other hand, the rich evolutionary morphological tradition that is taking root in studies of the platyrrhines, like those presented herein, suggests progress could be made even by inserting only one additional term to the protocol: look, see, *interpret*, code, and cluster.

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