



The status of platyrrhine phylogeny: A meta-analysis and quantitative appraisal of topological hypotheses



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ABSTRACT

Phylogenetic or species trees reflect the branching process of lineages and have direct and indirect interest for several branches of evolutionary anthropology. Estimating phylogenetic trees is a necessary first step toward understanding the factors responsible for the ecological and phenotypic diversification of a primate clade. The platyrrhines have become well known as a phylogenetic challenge. Since the 1990s, platyrrhine phylogenetic studies have increasingly analyzed DNA sequences, or other molecular datasets. Several researchers have claimed with confidence that platyrrhine phylogenetic history has been 'resolved' using these molecular data, but the concordance among these studies has never been quantified. Here, we perform a meta-analysis of published platyrrhine trees using topological information and multivariate methods. Specifically, we examine the claim that platyrrhine phylogeny has been determined and explore the relationships between phylogenies and dataset types used for phylogenetic inference (nuclear DNA, mtDNA, Alu sequences, morphology or mixed data). We compare topologies summarizing 31 major neontological studies of the platyrrhines produced since 1975. The analysis reveals that major disparities are rather common among the hypotheses regarding the higher-level relationships of platyrrhines. We also find that the global concordance that appears to emerge at the generic level is less impressive when one looks more finely at particular relationships. Moreover, correspondence among trees appears to be related to the 'type' of dataset analyzed, which suggests that the biological properties of distinct datasets have an inherent influence on the likelihood of producing similar reconstructions of phylogenetic relationships. This serves to remind us that the main questions surrounding the phylogeny reconstruction program begin with experimental design, for both molecular and morphological datasets. Thus, previous claims that platyrrhine genus-level topology have been 'resolved', or that calibrated molecular trees are sufficiently accurate representations of phylogenetic history that they overpower morphological interpretations of fossils, must be considered premature.

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Introduction

For decades following Darwin's (1859) seminal work, naturalists have used phenotypic traits to infer the branching process and lineage histories of species, depicting them as phylogenetic trees. Phylogenetic trees are hypotheses describing the ancestor–descendent relationship of species and the branching order that traces the common ancestry of taxa (e.g., Barton et al., 2007; Yang and Rannala, 2012). The most fundamental elements of a phylogenetic tree are composed of: 1) a hierarchical network, or

topology, representing a sequence of linkages that traces lineage splits, or the latter's underlying speciation events; and, 2) branch lengths between the nodes at tree bifurcations and those leading to terminal taxa, which represent the time dimension of phyletic evolution within evolving lineages, between ancestors and descendants, or the duration of a separated lineage. Together, these attributes describe the underlying history of species evolution and divergence of an evolutionary radiation, and may offer insight into biological and ecological factors that have shaped its history.

Before the emergence of DNA sequencing technologies, primate phylogenies were estimated almost exclusively from morphological characters, relying to an important extent on anatomy preserved in the fossil record (see Purvis, 1995). Today, phylogenetic relationships are inferred using a variety of datasets, and for multiple reasons. In addition to its original purpose of estimating the

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relationships among species to build the tree of life, phylogeny has become integrated with many branches of biology, being fundamental for ecological and evolutionary studies (Felsenstein, 1985; Purvis, 1995; Nunn, 2011; Yang and Rannala, 2012). In this larger and more holistic role, coupled with the widespread availability of molecular data derived from many living species and the development of powerful new tools including Hennigian, statistical and computational approaches (e.g., Lemey et al., 2009; Yang and Rannala, 2012), there has been a marked shift in the phylogenetic research program. Topologies have become the essential quest of reconstructed phylogenies, and concern for branch length, within-lineage changes or ancestral-descendant evolution illuminated by the fossil record is now less studied in comparison, except when internode lengths are used to generate a timescale. Fossils, it seems, have also taken a back seat as a prioritized source of phylogenetic information for groups like the platyrrhines that are well represented by extant species and their DNA (e.g., Kay et al., 2008; Kay, 2013).

Probing the power of phylogenetic hypotheses and testing their veracity is, of course, a fundamental requirement of primate systematics research. In the realm of morphology an excellent recent example is Carter et al. (2014), which assessed the suitability of employing character coding systems designed for discriminating among human populations to investigate the phylogenetic relationships among *Australopithecus* species. Many other examples can be cited wherein tests have employed alternative outgroups or sample compositions to demonstrate how trees can be perturbed. Similarly, for studies using molecules, as recently reviewed by Schneider and Sampaio (2013) with respect to platyrrhines, or New World monkeys (NWM), progressive testing has been done by adding newly sampled species or genes, or applying different analytical algorithms.

New world monkeys: a précis of the phylogenetic problems

Like other large, morphologically diverse extant primate radiations – Malagasy strepsirrhines being the classic complement – the platyrrhines have become well known as a phylogenetic challenge. The phylogenetics of this group has been widely discussed among paleontologists and neontologists (e.g., Rosenberger, 1984; Kay, 1990; Opazo et al., 2006; Wildman et al., 2009; Perelman et al., 2011; Rosenberger and Tejedor, 2013). As with other primate groups, before phylogeny reconstruction gained prominence as a distinct research endeavor, ideas of affinities were expressed in classifications. Two useful twentieth century markers of this period are Simpson's (1945) arrangement of primates and Hershkovitz's (1977) arrangement of platyrrhines. These respective efforts, one by a paleontologist who was a taxonomic generalist (Mammalia) and the other by a neontologist who was a regional specialist (South American mammals), set the stage for modern phylogenetic projects. Studies developed by others during the 1970s slowly began to alter these and other rather vague schema, which lacked a workable level of phylogenetic control from the genus-level on up. Several were inherently phenetic (though presented as phylogenetic), based on immunological distance or chromosome morphology (e.g., DeBoer, 1974; Baba et al., 1975; Cronin and Sarich, 1975; Chiarelli, 1980). The most influential studies, however, used anatomical data under more rigorous cladistic protocols (Rosenberger, 1979; Ford, 1980; Rosenberger, 1984; Dunlap et al., 1985; Ford, 1986; Kay, 1990; Horovitz et al., 1998). Although they obtained somewhat different results, the outlines of a modern view of platyrrhine interrelationships, quite different from earlier notions, emerged clearly by the early 1980s (see Rosenberger, 2002; Schneider and Sampaio, 2013). Because the platyrrhine fossil record remained almost trivial even then – and it

is no more than a very modest one today – these studies were rooted mainly in neontological data.

Since the 1990s, platyrrhine phylogenetic studies have increasingly analyzed DNA sequences or other molecular datasets (e.g., Schneider et al., 1993, 1996; Goodman et al., 1998; Horovitz et al., 1998; Opazo et al., 2006; Wildman et al., 2009; Perelman et al., 2011). Concurrently, as technologies advanced, computational phylogenetics and molecular systematics progressively became the methods of choice. Many of these were focused studies, targeting NWM, and they eventually included excellent samples of platyrrhine generic diversity. Others, also summarized in this report, were primate-wide projects that presented a dense sampling of NWM placed in cladistic context. But as our analysis shows, despite well-founded initial expectations, the rich influx of molecular data continues to generate different, mutually exclusive topological arrangements among genera, families and subfamilies, even though the four major groups (callitrichines, cebines, pitheciins, atelids) that comprise 14 of the 16 genera we recognize are now agreed by all to be monophyletic. Specifically, several studies present alternative topologies depicting the affinities of *Aotus*, at the family-level and even within one hypothesized family-level clade, and the interrelationships between pitheciids (including at least, among the modern forms, *Callicebus*, *Pithecia*, *Chiropotes* and *Cacajao*) and other families is controversial (e.g., Schneider et al., 2001; Opazo et al., 2006; Wildman et al., 2009; Perelman et al., 2011). While such differences are generally acknowledged among molecular systematists, these and other inconsistencies challenge the claim held by several advocates from this school that NWM phylogenetic history has been 'resolved' (Hodgson et al., 2009; Wildman et al., 2009; Perelman et al., 2011). Perhaps because of such conviction there has been no systematic effort to objectively evaluate variations among the published trees, an exercise that one would think might lead to a deeper understanding of the platyrrhine branching process and/or difficulties in the methods of phylogeny reconstruction.

Objectives

In this study of the status of platyrrhine phylogeny, we take a novel approach. Rather than assessing the constituent parts of phylogenetic trees from the bottom up, we examine existing hypotheses holistically from the top down, via meta-analysis, by quantifying the similarities and differences of the resulting trees in their entirety. To our knowledge, this is the first time such an approach has been applied to primate phylogenetics. Our strategy is to measure the congruence and disparities of published phylogenetic trees using topological information and multivariate statistical methods. Our aim is to probe the underlying causes of the varied tree topologies, and to explore possible reasons for this phenomenon. Our operating presumption is that an objective, quantitative assessment of tree topologies based on different phenotypic datasets (e.g., molecular and morphological) has the potential to improve both the methods of phylogenetic inference and our understanding of platyrrhine evolution. It may lead to a better understanding of the discrepancies and perhaps enable us to isolate problems of method and experimental design. Consequently, we first explore the notion held by several researchers that the genus-level and higher phylogeny of NWM has been 'resolved.' Second, we test the hypothesis that variation exhibited among published phylogenetic trees is related to the types of data used in the analyses (i.e., nuclear DNA, mtDNA, Alu sequences, morphology or mixed [morphology plus molecular data]).

As a first step, we employ two distinct approaches to quantitatively describe the properties that underlie tree topology. One examines the linkage structure, that is, who is related to whom, or

overall tree topology. To do this, we use the [Robinson and Foulds \(1981; RF\)](#) distance that provides a metric of the overall topological resemblance of selected phylogenetic trees ([Fig. 1](#)). The second feature examines how the array of nodes combines to determine a particular tree shape characteristic, its symmetry or asymmetry. Are trees one-sided, with many nodes descending from one lineage, or are the nodes more equally distributed between and/or among bifurcating lineages? For this, we employ a modified version of [Colless's \(1982\)](#) index of cladogram balance ([Fig. 1](#)). Topologies dominated by nodes situated along a single lineage produce highly parallel, pectinate series of branches (a 'Hennigian comb') and are considered highly imbalanced. Balanced trees are more symmetrical, with a relatively even number of dichotomous divisions arising from the alternate main branches ([Fig. 1](#)). Finally, we explore overall tree structure, based on the RF distances, using Principal Coordinates and Unweighted Pair-Group Average cluster analyses.

Materials and methods

We assembled 31 topologies from the literature, which represent the majority of phylogenetic studies published since the 1970s ([Table 1](#); [Appendix A Supplementary Online Material \[SOM\] text 1 and 2](#)). We use the term 'phylogeny' in the current sense of cladistic relationships. Other studies are mentioned in the text where relevant. The topologies themselves are not all from independent studies. Some projects were evidently ongoing over a period of time, and some produced topologies as alternative hypotheses after processing the data in more than one way inside of individual papers. However, these quasi-repetitive selections are rare. As a rule, no more than two topologies per publication were selected under these conditions. We divided the projects into several categories based on data type and data quantity. We labeled the four main

data types as morphology, molecules, mixed, and trees. 'Morphology' is self-explanatory. The 'molecular' datasets were divided into four groups based on numbers of base pairs: Small DNA (SDNA), Middle DNA (MDNA) and Big DNA (BDNA) ([Table 1](#)). We also distinguished data sets using nuclear DNA and mtDNA, and studies based on SINEs (Short Interspersed Elements, or Alu sequences). The 'mixed' category comprised studies that combined nuclear DNA, mtDNA, and morphology. The 'trees' category refers to one important study that produced a single 'super tree' by synthesizing many existing trees.

For statistical purposes, the comparison of trees requires that all topologies have the same size and content, i.e., trees must comprise the same taxa in identity and number. Also, since we are focused on both genus-level and higher phylogeny, several decisions and modifications of the original trees were necessary for standardization. For example, when relationships were presented as questionable, by a dotted line, but no alternatives were given, we treated that hypothesis as equivalent to the other relationships presented in that tree. For examining higher phylogeny, we collapsed the subordinate branches of family- and subfamily-level clades. Specific cases that depart from this protocol are explained below. With regard to the requirement of equivalence among the taxonomic units of the trees, one genus that was consistently absent from many of the ones we evaluated was *Cebuella*, so we effectively collapsed *Cebuella* into *Callithrix*. Other genera recently recognized by some workers, such as *Mico*, *Callibella* and *Sapajus*, were also excluded. None of these three genera were part of the roster of trees we examined and their taxonomic status is debated anyway. We are confident that these decisions have no real analytical consequences because there is little question that forms like *Mico* and *Callibella* are part of a closely related monophyletic group of species already represented by *Callithrix*, and that *Sapajus* and *Cebus* are another closely related monophyletic group.

At the family and subfamily levels, we employed the following groupings: Cebinae (*Cebus*, *Saimiri*), Callitrichinae (*Callithrix*, *Leontopithecus*, *Saguinus*, *Callimico*), Pitheciinae/Pitheciidae (*Callicebus*, *Pithecia*, *Chiropotes*, *Cacajao*), Atelidae (*Ateles*, *Brachyteles*, *Lagothrix*, *Alouatta*). We use Cebidae for Cebinae + Callitrichinae, knowing that opinions vary about the generic composition of the family: some studies include *Aotus* in this group while other studies do not. As with the case of pitheciids, whose composition is also debated with *Aotus* situated at the crux (e.g., [Rosenberger, 2002](#); [Kay et al., 2008](#)), we emphasize that we use these taxonomic schemes for consistency. The topologies depicted below should also be consulted to clarify when *Callicebus* is included or excluded from the pitheciids or pitheciine group. In general, we endeavored to identify *Aotus* and *Callicebus* as separate taxonomic units in order to explicate how the affinities of *Aotus* are presented with respect to callitrichines, cebines and pitheciines.

The focal topologies of the meta-analysis, all of which are rooted, were transcribed into Newick format ([SOM text 1](#)). A tree produced by [Canavez et al. \(1999; Fig. 2\)](#) serves as an example. In Newick terms it is represented as follows: ((((((*Cacajao*,*Chiropotes*),*Pithecia*),*Callicebus*), (*Alouatta*,*Ateles*),(*Lagothrix*,*Brachyteles*))))),((*Aotus*,(*Cebus*,*Saimiri*)),(*Saguinus*,(*Leontopithecus*,(*Callimico*,*Callithrix*)))))). The taxonomic names represent the terminal taxa of the tree and the interior nodes pertaining to monophyletic groups are codified by matched parentheses. The paired taxa or clades descending from a node are separated by a comma. In the trees, because we only display topological relationships, branch lengths between nodes are arbitrarily uniform for visual consistency.

We divided the full set of NWM topologies into three groups to compare and quantify relationships with particular questions in mind. First, we assembled 26 comprehensive trees that treat the 15

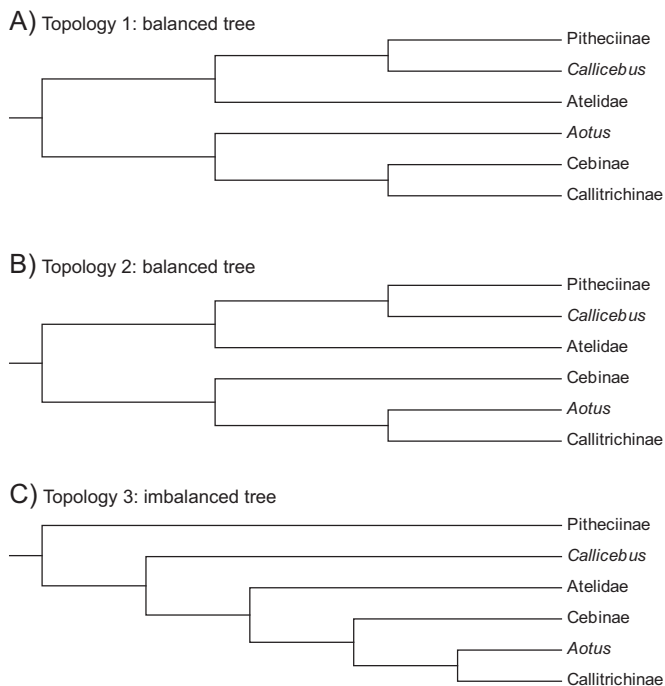


Figure 1. Different tree shapes or topologies. A) and B) display symmetrical or balanced trees showing a topological difference in the relationship between *Aotus* and cebids. C) displays a tree topology that is different from the previous two trees and is totally asymmetrical or imbalanced. The topological differences can be measured with the [Robinson and Foulds \(1981; RF\)](#) distance. The more specific differences in symmetry observed in C) can be quantified using a modified version of [Colless's \(1982\)](#) index of cladogram balance.

Table 1
Topologies (Tree) obtained from the literature (Reference) for our analyses, which represents the majority of phylogenetic studies published since the 1970s. In the table we also display the specific figure (Fig.) for the tree in the original study (Reference), the category for each tree based on data type and data quantity (Group dataset), the size of molecular (Loci) and morphological (Characters) dataset and the method used to infer the tree in the original study (Method).

Tree	Reference	Fig.	Group dataset	Loci (Base pair)	Characters	Method
Canavez1999	Canavez et al. (1999)	3	Small DNA	1 (1706)	0	M. Parsimony
Goodman1998	Goodman et al. (1998)	1	Small DNA	1 (1700)	0	M. Parsimony
VonDornum1999	Von Dornum and Ruvolo (1999)	7	Small DNA	1 (1286)	0	M. Parsimony
Barroso1997	Barroso et al. (1997)	2	Small DNA	1 (1843)	0	M. Parsimony
Schneider1993	Schneider et al. (1993)	4	Small DNA	1 (1928)	0	M. Parsimony
Schneider1996	Schneider et al. (1996)	4	Small DNA	2 (3771)	0	M. Parsimony
Horovitz1998c	Horovitz et al. (1998)	3a	Small DNA	2 (3771)	0	M. Parsimony
Schneider2000	Schneider (2000)	1	Small DNA	4 (6600)	0	M. Parsimony
Pyrchitko2005	Pyrchitko et al. (2005)	2a	Small DNA	1 (2700)	0	M. Parsimony
Harada1995	Harada et al. (1995)	6	Small DNA	2 (3771)	0	M. Parsimony
Opazo2006a	Opazo et al. (2006)	3	Middle DNA	7 (8598)	0	M. Likelihood
Opazo2006b	Opazo et al. (2006)	2	Middle DNA	7 (8598)	0	M. Parsimony
Schrage2007	Schrage (2007)	1	Middle DNA	6 (7295)	0	Bayesian Inference
Chatterjee2009a	Chatterjee et al. (2009)	4	Middle DNA (mt)	7 (6138)	0	Bayesian Inference
Chatterjee2009b	Chatterjee et al. (2009)	1	Middle DNA (mt)	7 (6138)	0	Bayesian Inference
Finstermeier2013	Finstermeier et al. (2013)	1	Big DNA (mt)	37 (13,281)	0	M. Likelihood and Bayesian
Fabre2009	Fabre et al. (2009)	4	Big DNA	27 (42,000)	0	M. Likelihood
Perelman2011	Perelman et al. (2011)	1	Big DNA	54 (34,927)	0	M. Likelihood
Perez2012	Perez et al. (2012)	1	Big DNA	68 (47,233)	0	Bayesian Coalescent
Springer2012	Springer et al. (2012)	1	Big DNA	79 (61,199)	0	M. Likelihood
Wildman2009	Wildman et al. (2009)	4	Big DNA	20 (17,809)	0	M. Parsimony; M. Likelihood; Bayesian
Osterholz2009	Osterholz et al. (2009)	2	SINE	0	128	Character analysis
Ray2005	Ray et al. (2005)	3	SINE	0	190	M. Parsimony
CroninSarich1975	Cronin and Sarich (1975)	?	SINE	?	?	Character analysis
Horovitz1998b	Horovitz et al. (1998)	4	Mixed	?	76	M. Parsimony
Horovitz1998a	Horovitz et al. (1998)	3b	Morphology	0	76	M. Parsimony
Kay1990	Kay (1990)	3	Morphology	0	117	M. Parsimony
Rosenberger1984	Rosenberger (1984)	1	Morphology	0	>100	Character analysis
Ford1986	Ford (1986)	1	Morphology	0	>150	Wagner tree and character analysis
Kay2008	Kay et al. (2008)	21	Morphology	0	268	M. Parsimony
Purvis1995	Purvis (1995)	5	Trees	0	112	Super tree, Parsimony

genera (see Fig. 2), with *Cebuella* and *Mico* included in *Callithrix* when necessary, as noted. This dataset, hereafter *15genera*, was designed to explore arrangements representing the full diversity of the extant radiation. The second dataset, hereafter *5high-taxa*, was generated to focus on the topologies of the main platyrrhine clades and the affinities of the controversial *Aotus* with respect to them. Apart from *Aotus*, these taxa include cebines, callitrichines, atelids

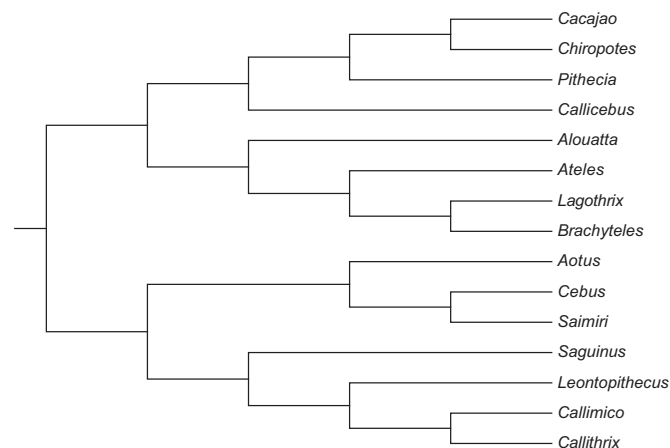


Figure 2. Tree representation. The topological representation of the Canavez et al. (1999) phylogeny is used as an example of how rooted tree topology is translated into Newick format for our meta-analysis, as follows: ((((((Cacajao,Chiropotes),-Pithecia),Callicebus), (Alouatta,(Ateles,(Lagothrix,Brachyteles))))),(Aotus,(Cebus,Saimiri)),(Saguinus,(Leontopithecus,(Callimico, Callithrix))))).

and pitheciids. Again, unless indicated, the pitheciids include *Pithecia*, *Chiropotes*, *Cacajao* and *Callicebus*. A third dataset, hereafter *6taxa*, further separates out *Callicebus*, which has been variously linked to *Aotus* and to pitheciids (*Pithecia*, *Chiropotes*, *Cacajao*) under a variety of higher-taxon schemes.

The topological congruence between trees (see Fig. 1), their overall topological differences, was quantified using the RF distance, which is also called the symmetric difference metric. This distance measure calculates the number of internal branches or links that exist in one tree but not in the other. Considering two trees, T_1 and T_2 , the distance is defined as:

$$RF(T_1, T_2) = |L_1/L'_1| + |L_2/L'_2|,$$

where L_1 and L_2 are the set of all links on T_1 and T_2 , respectively. L'_1 is the set of all links in L_1 that has a match in L_2 , and L'_2 is the set of all links in L_2 that has a match in L_1 . Therefore, this distance describes all of the unmatched links for both trees (Robinson and Foulds, 1981; Kuhner and Felsenstein, 1994). Robinson and Foulds distances were estimated in the Tree distance program, version 3.695, of the PHYLIP package (Felsenstein, 2005).

We then used Principal Coordinates (PCo) and Unweighted Pair-Group Average (UPGMA) cluster analyses to summarize the matrices of pairwise RF distances between trees and to visualize the patterns of topological differences among them. The PCo analysis is employed to find the eigenvalues and eigenvectors of the distance matrices among all trees (Legendre and Legendre, 1998). The eigenvectors, or PCo scores, are used to plot the topological differences among these trees in Euclidean space. The UPGMA is then used as a hierarchical clustering algorithm to produce a

dendrogram whose structure corresponds with the pairwise distances among the trees (Sneath and Sokal, 1963). This algorithm first generates a group, or cluster 1, between the pair of trees with minimal RF distance. Then, the average distance is calculated between the cluster 1 and the other distances in the RF matrix, clustering the pair of trees (or tree versus cluster 1) with minimal RF distance. This step is repeated until all of the trees are grouped. The PCo and UPGMA analyses were performed in PAST ver. 2.17 (Hammer et al., 2001).

Finally, we used a modification of Colless's (1982) index of cladogram balance to measure tree asymmetry (see Fig. 1). Colless's index sums, over all $(n - 1)$ nodes in a topology with n tips, the numbers of tips subtended by the right-hand (TR) and left-hand (TL) branches at each node and normalizes them. However, we only measured the balance parameter between the main clades in a platyrrhine tree by defining a modified index of main topology balance (Imtb):

$$\text{Imtb} = \text{ABS}(\text{TR} - \text{TL})/n - 2,$$

where TR and TL represent the number of tips in the right-hand (inferior in our horizontal tree displays) and left-hand (superior) branches stemming from the main node (the tree root), respectively. The index may range from 0 (completely balanced) to 1 (completely unbalanced).

Results

The PCo ordination of the 26 topologies based on *15genera* is shown in Fig. 3, while the UPGMA structure is shown in Fig. 4. These analyses display clusters of trees (Fig. 5) that are generally concordant with data type. It is important to point out that although Purvis1995 is a summary of other trees, Purvis's original trees (Purvis, 1995) were mainly based on morphological characters. The two main clusters in both analyses broadly separate morphological from molecular studies. They are divided along PCo1, which represents 45.5% of the variance. The morphological trees exhibit much more dispersion along PCo2, which comprises 13.5% of the variance. The PCo and UPGMA for *6taxa* datasets (SOM Figs. 1 and 2) display similar clustering to the *15genera* dataset in confirming a basic distinction between morphological and molecular trees. Although the pattern is weaker, similar clustering is

observed in the *5high-taxa* dataset (SOM Figs. 3 and 4). The morphological and molecular trees tend to differ in the following ways: 1) the positions (sometimes shown as equally likely options: Ford, 1986) of *Aotus* and *Callicebus*, 2) the relationships between Atelidae and the other main clades, 3) whether or not Cebinae is holophyletic (i.e., not including *Aotus*), 4) the composition of Cebidae (Cebinae + Callitrichinae, with or without *Aotus*), and 5) the relationships among genera within the atelid and callitrichine clades (Fig. 5). Moreover, the morphological and molecular trees differ in symmetry (Fig. 6), with a high proportion (2/6 cases, 33%) of morphology trees being completely imbalanced (Imtb = 1.00: Ford, 1986; Kay, 1990), while the molecular trees present values of intermediate and balanced shapes, with rare exceptions.

Among the molecular datasets there are two large clusters. The main groupings of trees are built from Small versus Big plus Middle nuclear DNA (Figs. 3 and 4). Mitochondrial DNA and SINE trees stand more or less between these larger clusters, presenting the smallest metrical distances in our analysis. The thrust of these topologies supports the division of platyrrhines into the four widely accepted clades (Atelidae, Pitheciidae [including *Callicebus*], Callitrichinae, Cebinae) and the inclusion of *Aotus* within the monophyletic group composed of cebines and callitrichines (Fig. 5). However, the BDNA trees differ in the position of *Aotus* within that larger group. *Aotus* is seen as a branch that is either external to Cebidae (e.g., Perez et al., 2012), external to Cebinae (e.g., Wildman et al., 2009), or external to Callitrichinae (e.g., Perelman et al., 2011; Fig. 5). The BDNA studies favor the position of pitheciids as a basal platyrrhine lineage with respect to atelids plus cebines, with callitrichines appearing as a monophyletic sister-group. The BDNA studies also generate intermediately balanced trees. In contrast, the other molecular trees favor monophyly of pitheciids plus atelids, with totally balanced trees (Fig. 6). Within the Atelidae there is uniformity among the molecular trees regarding *Alouatta* as a sister-group to the clade of *Ateles*, *Brachyteles* and *Lagothrix*, with *Brachyteles* and *Lagothrix* linked together. The internal relationships with callitrichines and pitheciids are also consistent across the BDNA studies. Conversely, the trees based on SDNA hypothesize a closer phylogenetic relationship between atelids and pitheciids, and suggest several alternatives regarding *Aotus*, Callitrichinae and Cebinae.

The PCo and UPGMA for *6taxa* and *5high-taxa* datasets display clusters and inconsistencies that are similar to the *15genera* dataset

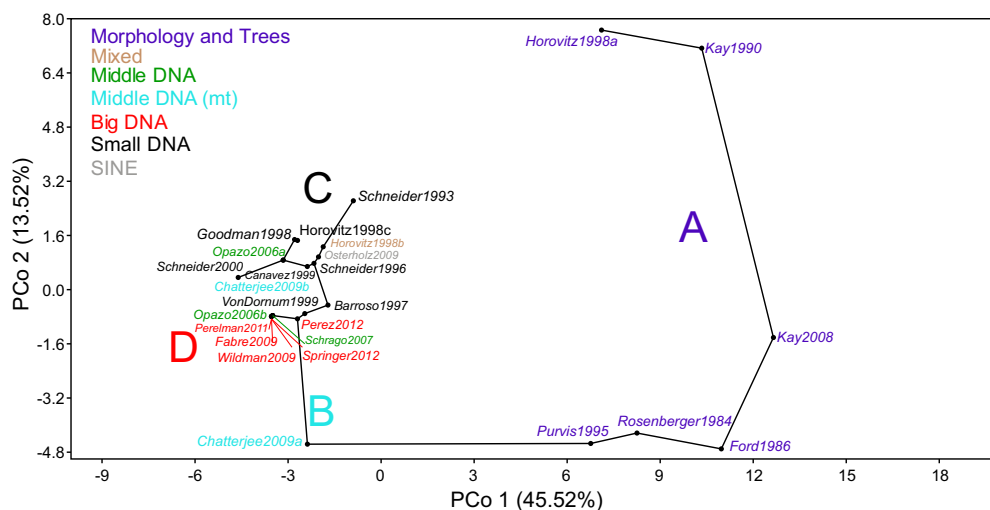


Figure 3. *15genera* PCo result. PCo ordination of the 26 topologies based on *15genera* datasets, showing the main dispersion axes of morphological and molecular trees, as well as the main clusters (A–D) of trees in Fig. 4.

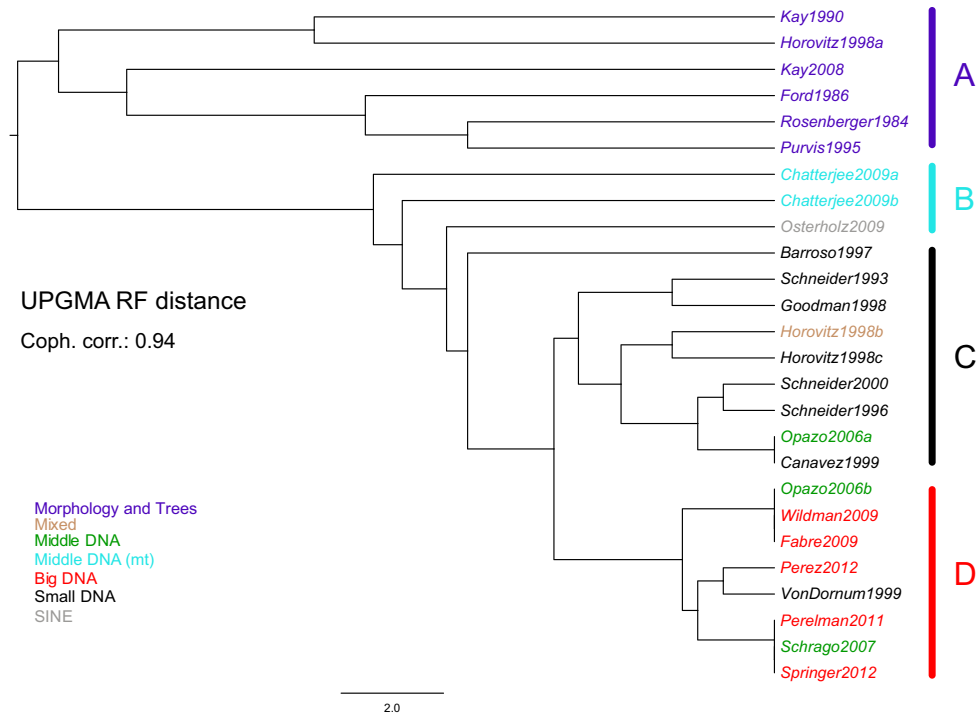


Figure 4. *15genera* cluster result. The UPGMA structure of the 26 topologies based on *15genera* datasets, showing the main clusters (A–D) of trees that separate morphological from molecular studies.

for the molecular trees (SOM Figs. 1–4). However, there is an important difference that emerges from these analyses. The *6taxa* dataset more strongly emphasizes the separation of the morphology trees from the molecular trees than the *5high-taxa* dataset. This is due to different placements of *Callicebus* among morphologists, against the uniform position of this genus in the molecular studies. This is clearly shown by PCo 1, which explain 29% of total tree variance in *5high-taxa* and 41% of tree variance in *6taxa* datasets.

Discussion

While a few reviews have been concerned with the topological accord and discord evident among platyrrhine phylogenetic trees (e.g., Schneider, 2000; Rosenberger, 2002), and many original studies mention complementary projects that agree or disagree at some level, this report is the first, to our knowledge, that attempts to provide an empirical, uniform, quantitative examination to assess the correspondence of a large sample of such trees. We compared topologies summarizing 31 major neontological studies of the platyrrhines produced since 1975. The stated hypothesis of recent years (Hodgson et al., 2009; Wildman et al., 2009; Perelman et al., 2011) claiming that platyrrhine phylogeny has been ‘resolved’ is not supported by our analysis, which reveals that major disparities are rather common in interpreting their higher-level interrelationships. We also find that global concordance at the generic level is less impressive when one looks more finely at particular relationships (Figs. 3–5). Moreover, we confirm our second expectation: the degree of correspondence among trees appears to be related to the ‘type’ of dataset analyzed. This suggests that the biological properties of distinct datasets influence the likelihood of obtaining similar reconstructions of phylogenetic relationships. Therefore, even as the most recent phylogenetic trees tend to converge on similar results, this may be due partially to methodological artifact.

Why are there differences among the topologies based on different datasets?

There are several possible explanations for the disparities we observed among the trees estimated using different datasets. One overarching theoretical issue explains why there is a high likelihood that inconsistencies will be introduced as data sources diversify. Molecular sequences and morphological characters can each have an evolutionary history that is not inextricably tied to the underlying branching processes of species (Maddison, 1997; Rannala and Yang, 2008; Degnan and Rosenberg, 2009; Heled and Drummond, 2010; Knowles and Kubatko, 2010). In some cases, speciation and phenotypic divergence—both morphological and molecular—may not be tightly correlated biological phenomena. Rather, they are dependent upon the particular evolutionary history of a clade in a specific ecological context, with the populations’ own evolutionary rates and demographic histories (Felsenstein, 1985; Degnan and Rosenberg, 2009; Heled and Drummond, 2010; Knowles and Kubatko, 2010; Lanier et al., 2013). When we add new datasets of molecular sequences, morphological or concatenated data into the platyrrhine phylogenetic research program (Table 1), the chances of replicating precisely the topological patterns of other studies may reduce because the individual sequences or morphological characters could have had different evolutionary histories, and thus produce different reconstructed topological configurations (Perez et al., 2012). At the same time, when there is large overlap in the datasets used, the results are expected to be highly similar.

Our results show that morphological and molecular trees differ significantly, both within and between datasets, in the placement of *Aotus*, with regard to the affinities of pitheciids vis à vis the other clades, and at other nodes as well. Since the *Aotus* problem is tied up with the pitheciid question, this is an indication that discrepancies are especially impactful at points of deep divergence among the platyrrhine lineages (Opazo et al., 2006; Perez et al., 2012). It

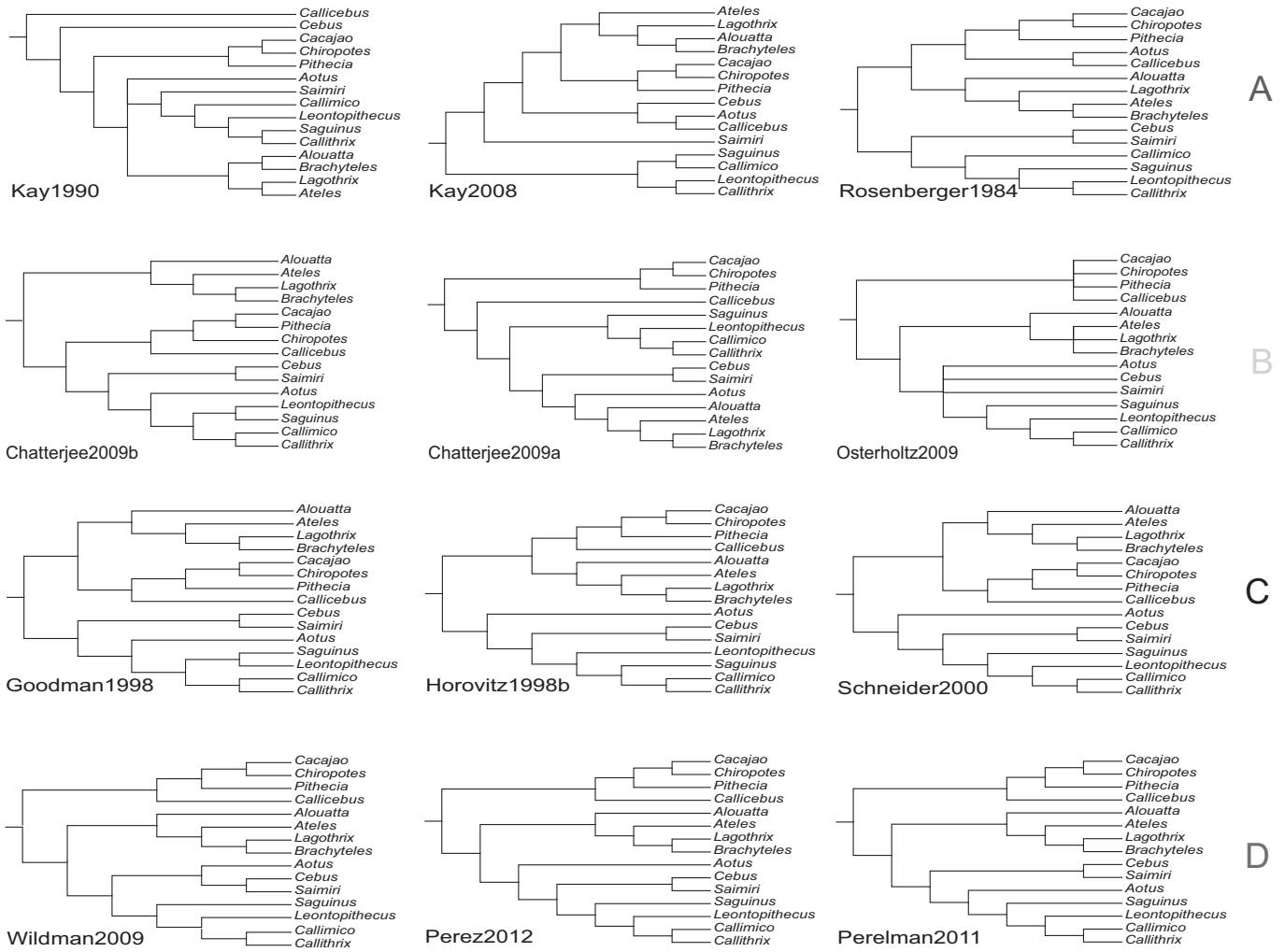


Figure 5. Platyrrhine tree topologies. Topologies based on 15genera datasets representing the main clusters observed in Figs. 3 and 4.

highlights the complexity of the evolutionary processes that may have acted during the early phases when extant NWM underwent their radiation (Aristide et al., 2013). For example, differences between morphological and molecular variation, in particular, have been addressed in this context using geometric morphometric and phylogenetic comparative methods (Perez et al., 2011; Aristide et al., 2013). These studies show that morphological divergence among platyrrhines was concentrated early in its evolutionary radiation, suggesting that phylogenetic relationships estimated using morphological data could differ from molecular phylogenetic trees due to ecological factors acting during an early period of rapid differentiation (Aristide et al., 2013). Therefore, these ecological factors also are important to explain because single genes or morphological structures showed discordant relationships at the points of deep divergence in the platyrrhine trees (Figs. 3–5; Liu et al., 2008; Perez et al., 2012).

Another possible explanation for disparity in topology relates to the outcomes being driven by differences in the analytical methods employed (Felsenstein, 2004). Some reconstruction methods can potentially generate an incorrect phylogenetic tree when the assumptions of the methods are violated (Huelsenbeck, 1997). This was pointed out for Maximum Parsimony by Felsenstein (1978), who showed that when a true tree exhibits long branches in complimentary clades, this method will converge on a false phylogeny in which the long branches are inadvertently linked

together (see Huelsenbeck, 1997). However, this does not appear to be the main reason for discord among the platyrrhine trees (but see Rosenberger and Tejedor, 2013) because Maximum Parsimony actually produced several different topologies using the molecular datasets (Table 1). Moreover, when these molecular datasets were

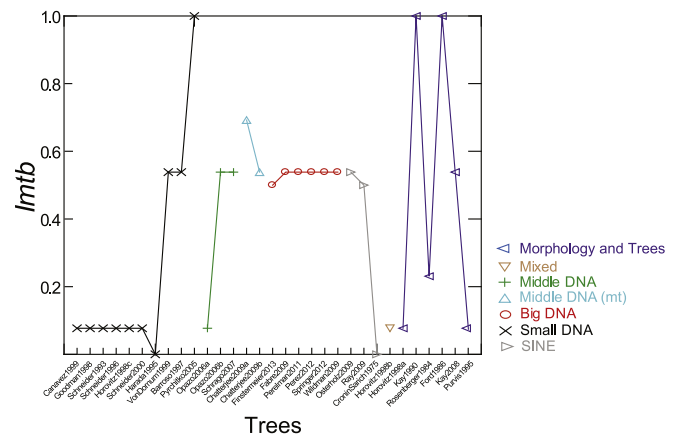


Figure 6. Imtb result. Plot of the index of main topology balance (Imtb) for all studied topologies, showing the differences in symmetry of the morphological and molecular trees.

analyzed using other techniques, such as Maximum Likelihood or Bayesian inference, they generated similar topologies (e.g., Wildman et al., 2009).

A third possible explanation for the levels of disparity in the phylogenetic trees is taxon sampling (e.g., Matthews and Rosenberger, 2008; Nabhan and Sarkar, 2012; and references cited therein). Taxon sampling can greatly influence phylogenetic inference. It can also highly influence the informal confidence levels placed on the phylogenetic hypotheses of groups like the platyrrhines, where the vast majority of studies are based on extant species and employ the same families of data and method. Although the sampling of genera utilized in the studies examined here is an appropriate, statistically robust accounting of modern taxa, this assemblage does not comprise either a representative or a random sample of the NWM branching process through geological time. It is a subsample from a universe where an untold number of taxa and lineages have become extinct (see more below). Moreover, some extant genera or clades may be oversampled (e.g., the *Callithrix/Mico/Cebuella* clade versus *Callimico*) because they have out-survived others, perhaps due to their ecological flexibility, speciose biodiversity ratio, or both. Therefore, the extant NWM provide a limited and biased picture of the full diversity of platyrrhines through geological time and this can potentially prejudice estimations of platyrrhine phylogeny. The size of the data loss is also impossible to know, but the fossil record suggests that 16 living genera are a small fraction of platyrrhine diversity historically (Fleagle and Tejedor, 2002; Rosenberger et al., 2009; Fleagle, 2014).

For specific clades, this problem may be exaggerated. For example, the still meager fossil record suggests that the moderns inadequately reflect historical biodiversity of pitheciids. They may account for three to five genera today, but well over a dozen extinct forms have already been found (see Tejedor, 2008; Rosenberger et al., 2009; Cooke et al., 2011; Tejedor, 2013). In the light of these unknowns, it may well be that some relationships routinely inferred in studies of extant samples of the platyrrhines could be artifacts of uneven and skewed taxonomic sampling. This caveat applies equally to morphology and to molecules, of course. Particularly, we can ask, are all parts of the tree similarly affected by data gaps? Does this bias the relationships between major clades? Does it affect inter-generic relationships within modern clades?

Taxonomic undersampling could be a critical problem when the missing samples would have involved intermediates between clades or taxa separated by a wide phenetic gap among the living. This may be the case for *Callimico*, a morphologically unique genus represented by a single species within a clade (callitrichines) comprising many species (more than a dozen) distributed among four other modern genera. *Callimico* appears to be a relatively old lineage that diverged from its nearest relatives ca. 13 Ma (millions of years ago) according to the molecules (Aristide et al., 2013). A member of its lineage also appears to have been present in La Venta at about that time (Rosenberger et al., 1990; Fleagle and Tejedor, 2002). In the same way, *Aotus* is a morphologically unique genus belonging to an ancient clade, at least ca. 20 Ma according to Aristide et al. (2013), and occurring at La Venta as well in the form of *Aotus dindensis* (Setoguchi and Rosenberger, 1987). The long branches of *Aotus* and *Callimico* suggest the possibility of high extinction rates associated with the origins and differentiation of these two clades as there are few if any indications of morphological intermediacy, which is perhaps a correlated historical phenomenon. Regarding *Aotus*, while discrete shared derived morphological traits have been proposed relating the genus to *Callicebus* (e.g., Rosenberger and Tejedor, 2013), and this is supported by various morphometric phenetic studies (see Rosenberger et al., 2013), no matter to which taxa *Aotus* might be most closely related – a pitheciid or a cebid – there are trenchant anatomical

gaps that indicate taxonomic intermediacy has been lost to sampling error. How this influences the estimation of phylogeny in both of these cases is hard to say.

Is there a best dataset?

In our efforts to find the ‘truest of the true’ trees, we cannot forget that the branching history of extant platyrrhine species is a reflection of circumstances that took place in the remote past, and that our statistical sample of living species is a biased collection of taxa that have survived extinction, as noted. In other words, although it is common sense in systematics, the ‘true’ shape of platyrrhine phylogeny will never be observable and may never be able to be reconstructed. Critical relevant data may be forever unobtainable (Sober, 1988). Therefore, phylogenetic trees are by definition hypotheses, or estimates, inferred from specific datasets using specific computational methods (Lemey et al., 2009; Yang and Rannala, 2012), and finding that platyrrhine trees are quite variable and dependent on data type should not be surprising. Nevertheless, it is constructive to discuss reasons why some datasets may be better than others among the many that have been assembled. It can be argued, for example, that because the evolution of a particular phenotypic trait, or complex – both morphological and molecular – depends on branching processes as well as a unique set of evolutionary and ecological processes (Felsenstein, 1985; Maddison, 1997; Rannala and Yang, 2008), a dataset relating to ecological adaptation might show a high correlation with the actual topological history of an ecologically successful radiation. This implies that particular datasets have their own valence for specific clades (e.g., Lockwood et al., 2004). This, too, is a common sense rule of thumb long understood or presumed by systematists.

Several platyrrhine studies have suggested that the genealogical tree based on a molecular sequence or a concatenation of sequences are the best options for inferring platyrrhine branching history (Schneider et al., 2001; Hodgson et al., 2009; Osterholz et al., 2009; Perelman et al., 2011). However, coalescent theory suggests that the inferred genealogy of a sequence represents a single realization of a stochastic process and is determined by factors such as demographic history and natural selection (Rosenberg and Nordborg, 2002; Degnan and Rosenberg, 2009). Moreover, theoretical works find that when there are high levels of discordance among gene trees, such as for platyrrhines, the frequently employed concatenation method can result in an inaccurate species tree as more data are added (Liu et al., 2008; Degnan and Rosenberg, 2009). Similarly, the topology of concatenated morphological phylogenies for platyrrhines is generally determined by the characters that dominate the matrix (e.g., Rosenberger, 2002). A recent NWM species tree estimate based on coalescent methods (Perez et al., 2012) shows that when we consider gene tree discordance, phylogenetic methods produced poorly supported (i.e., non-resolved) relationships for the nodes with low concordance between gene trees.

Therefore, the coalescent model suggests that phylogenetic methods that have been employed, such as the concatenation of molecular and morphological datasets, may not be the best option because there exists a high level of discord among gene and morphological trees (Liu et al., 2008; Degnan and Rosenberg, 2009; Perez et al., 2012). In such cases, phylogenetic hypotheses may display ‘gene trees’ or ‘morphological trees’ rather than ‘species trees,’ or the branching history of platyrrhine species. Because of these issues, it is advisable that future studies of platyrrhine species tree estimation ought to explore more sophisticated models and methods based on the multi-species coalescence theory (Liu et al., 2008; Degnan and Rosenberg, 2009; Heled and Drummond, 2010;

Knowles and Kubatko, 2010), which considers tree discordance during the inference process.

Two interesting examples of discrepancies between molecular and morphological trees

Returning to our précis of the phylogenetic problems in platyrrhine systematics, there are two key clades where discrepancies between phylogenetic hypotheses based on morphological and molecular evidence are manifest in differing placements of individual genera, and where the biological correlates and implications of these conflicts deserve to be discussed in more detail. First, an interesting and noteworthy example of discord involves *Callimico*, a species at the center of platyrrhine evolution, classification and phylogeny for much of the twentieth century (see Hershkovitz, 1977). The morphology of *Callimico*, long understood to be a mosaic of marmoset- and tamarin-like traits combined with traits exhibited by all other extant NWM, was key to understanding that cebines and callitrichines are joined as a monophyletic group. This was the first pointer toward the new conception of platyrrhine phylogeny and evolution that is widely adopted today (see Schneider and Rosenberger, 1996; Rosenberger, 2002; Schneider and Sampaio, 2013). Recently Cortés-Ortiz (2009) reviewed the various molecular alternatives for *Callimico* and other callitrichine genera. Like the majority of molecular trees produced since the 1990s (Fig. 5), Cortés-Ortiz favors the view that *Callimico* is nested within Callitrichinae as a sister-taxon to *Callithrix* (with *Cebuella*), in spite of the detailed countervailing morphological evidence she provides (see also Wildman et al., 2009). This hypothesis not only makes it very difficult to reconcile anatomical character evolution across multiple systems (see Garber et al., 1996; Cortés-Ortiz, 2009), it also undermines a phylogenetic keystone that has already proven crucial to unraveling platyrrhine phylogeny.

In its simplest form, the reconsideration of *Callimico* systematics in the 1970s and 1980s, which followed work well articulated by Gregory (1922), amounted to the recognition that key features of callitrichine morphology were not primitive for platyrrhines but derived. *Callimico* features such as a 0.5 kg body size, a *k*-strategy/single-birth reproductive system, three-molar dental formula and molar hypocones all appear to be more primitive than the patterns shared by all four of the other callitrichine genera, who are almost always smaller in body mass, are *r*-strategist that produce twins, exhibit two molars and lack hypocones. Imagining parallel changes in body size trajectories in the two other lineages, via selection or drift, is the least difficult parameter to rationalize given this phylogenetic hypothesis. Parallel evolution of tooth reduction and loss would seem to be somewhat more difficult to accommodate. But perhaps the most challenging notion requires the parallel evolution of multiple embryo production and dizygotic, chimeric twinning. The highly specialized bidiscoidal placentae seen in marmosets and tamarins (see Rutherford and Tardif, 2009) results in genetic exchanges between the developing fetal twins and a host of associated anatomical, behavioral and selective correlates. It is unlikely to have evolved twice among a closely related group of genera within a single clade. A simple way to reconcile logically the character conflict is to doubt the veracity of the *Callimico* + *Callithrix/Cebuella* topological hypothesis, which should be followed up by a probe into why the molecules and/or analytical methods employed appear to have produced a false phylogenetic signal. Cortés-Ortiz (2009) suggested that a false signal could have been produced in connection with a relatively rapid divergence of these lineages, leading to ancestral lineage sorting, as we have suggested as well (Perez et al., 2012, 2013).

Secondly, much has been written concerning the debate revolving about *Aotus* (e.g., Rosenberger, 2002; Rosenberger and

Tejedor, 2013). It is not trivial that the alternative hypotheses sometimes place *Aotus* in different family-level clades (e.g., Rosenberger, 1984; Ford, 1986; Opazo et al., 2006; Wildman et al., 2009). However, it is highly interesting and important that this seemingly profound disparity in platyrrhine phylogeny concerns a single genus, only one out of 16 extant genera. But it also involves a swap between two of the main branches in platyrrhine phylogeny, two out of four. Further, it is clear that the molecular evidence is rather soft on the interrelationships of *Aotus*. The survey of 17 molecular trees indicates (Table 1; SOM text 1; SOM Figs. 3 and 4) that there are four common options among these studies: 1) *Aotus* is linked with others in a polytomy, i.e., 'unresolved', 31% of the trees; 2) *Aotus* is placed as a basal cebine, 29%; 3) *Aotus* is placed as a basal callitrichine, 23%; 4) *Aotus* is placed as a basal cebid, 17%. The polytomies link *Aotus* to cebines and callitrichines most often, to callitrichines, or, to atelids. In addition to the molecular studies, cladistic analyses of chromosome banding patterns have also yielded varying solutions (de Oliveira et al., 2012), where *Aotus* is linked by synapomorphy either with cebines or with *Callicebus*. Thus, while on the face of it the morphology and molecules would appear to be saying different things, a closer look at the molecular results reveals widely varying interpretations even within that approach.

It is important to point out that morphologists also have presented varying interpretations of *Aotus*. Taking the most active workers, Ford, Kay and Rosenberger have each presented different platyrrhine trees, with Kay's being the most contrasting (Rosenberger, 2002; see Fig. 3). While Ford (1986) and Rosenberger (1984) agree that *Aotus* and *Callicebus* are likely sister-genera, albeit not necessarily in symmetrically composed monophyletic groups, Kay has presented as many as five alternatives since 1990 (see Rosenberger, 2011), in different studies using varying taxonomic compositions depending on their aims. These are: 1) in a trichotomy with atelids and callitrichines + *Saimiri*, 2) at a basal position of a clade restricted to *Callicebus* and *Pithecia*, 3) at a basal position in a clade restricted to *Cebus* and *Callicebus*, 4) at a basal position in a clade restricted to *Cebus* and *Saimiri*, 5) as a sister-genus to *Callicebus* in a clade where *Cebus* is basal. It should also be pointed out that the morphological studies of Ford, Kay and Rosenberger depend on a considerable amount of data overlap, although these data were analyzed by very different methods: Ford using Wagner's parsimony method, Kay preferring Maximum Parsimony PAUP, and Rosenberger using conventional character analysis. However, all employ more than 100 dental characters, often with the same polarities, presented by Rosenberger (1979). This suggests that the disparate interpretations of *Aotus* interrelationships arise from the treatment of the data rather than the data themselves.

Perez et al. (2012) suggested that the discrepancies among molecular and morphological trees in the placement of *Aotus* may be a consequence of the relatively rapid divergence of the main platyrrhine lineages (see also Steiper and Ruvolo, 2003), which may be related in part to ancestral lineage sorting or selection. The discord may also be influenced by several evolutionary and ecological processes acting during the platyrrhine diversification. Either way, this lack of consistency suggests that *Aotus* should be a major focus of attention as we try to further reconstruct the puzzle of platyrrhine phylogeny (e.g., Rosenberger et al., 2009; Perez et al., 2012; Aristide et al., 2013).

Conclusions

Our impression is that over the past 50 years of primate phylogeny reconstruction it has become the cultural norm to judge morphology against molecules, as if one or the other offers the

superior biological dataset. This would be a mistake. Both datasets generate hypotheses, not truths. The beauty of having different ways of reconstructing relationships is that they provide independent phylogenetic hypotheses. The conundrum of 'gene trees' versus 'species trees' has recently come to the forefront as an implication of coalescent theory and the recognition that several factors influence tree structure, including horizontal gene transfer, long branch attraction and incomplete lineage sorting (Rannala and Yang, 2008). The same can be pointed out for morphology. Several works have shown that specific morphological traits can display convergent evolution linked to ecological convergence between non-related clades during the branching process (e.g., Moen et al., 2013). This serves to remind us that the main questions surrounding the platyrrhine phylogeny reconstruction program begin with experimental design (e.g., Goldman, 1998; Townsend et al., 2008), for both molecular and morphological datasets.

Our quantitative examination of a large sample of platyrrhine trees suggests the perils of using molecular phylogenetic scaffolds as a framework for analyzing the evolution of morphological traits in the process of phylogeny reconstruction (e.g., Kay, 2013). If molecular evolution and morphological evolution are uncoupled from speciation, as some maintain, the application of molecular scaffolds may, in fact, be invalid. Either way, the phylogenetic disparities we document among platyrrhine trees tell us that dogmatic proclamations of platyrrhine genus-level topology being 'resolved' (Wildman et al., 2009; Perelman et al., 2011), or that calibrated molecular trees are sufficiently accurate representations of phylogenetic history that they overpower morphological interpretations of fossils (Hodgson et al., 2009), must be considered premature.

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Appendix A. Supplementary online material

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2014.08.009>.

References

- Aristide, L., Rosenberger, A.L., Tejedor, M., Perez, S.I., 2013. Modeling lineage and phenotypic diversification in the New World monkey (Platyrrhini, Primates) radiation. *Mol. Phylogenet. Evol.* In press.
- Baba, M.L., Goodman, M.D., H., Moore, G.W., 1975. Origins of the Ceboidea from an immunological perspective. *J. Hum. Evol.* 4, 89–102.
- Barroso, C.M.L., Schneider, H., Schneider, M.P.C., Sampaio, I., Harada, M.L., Czelusniak, J., Goodman, M., 1997. Update on the phylogenetic systematics of New World monkeys: Further DNA evidence for placing the pygmy marmoset (*Cebuella*) within the genus *Callithrix*. *Int. J. Primatol.* 18, 651–674.
- Barton, N.H., Briggs, D.E.G., Eisen, J.A., Goldstein, D.B., Patel, N.H., 2007. *Evolution*. Cold Spring Harbor Laboratory Press, New York.
- Canavez, F.C., Moreira, M.A.M., Ladoski, J.L., Pissinatti, A., Parhan, P., Seuanez, H.N., 1999. Molecular phylogenetics of New World primates (Platyrrhini) based on β 2-microglobulin DNA sequences. *Mol. Phylogenet. Evol.* 12, 74–82.
- Carter, K., Worthington, S., Smith, T.M., 2014. Non-metric dental traits and hominin phylogeny. *J. Hum. Evol.* 69, 123–128.
- Chatterjee, H.J., Ho, S.Y.W., Barnes, I., Groves, C., 2009. Estimating the phylogeny and divergence times of primates using a supermatrix approach. *BMC Evol. Biol.* 9, 259.
- Chiarelli, A.B., 1980. The karyology of South American primates and their relationship to African and Asian species. In: Ciochon, R.L., Chiarelli, A.B. (Eds.), *Evolutionary Biology of New World Monkeys and Continental Drift*. Plenum, New York, pp. 387–398.
- Colless, D.H., 1982. Review of phylogenetics: The theory and practice of phylogenetic systematics, by E. O. Wiley. *Syst. Zool.* 31, 100–104.
- Cooke, S.B., Rosenberger, A.L., Turvey, S., 2011. An extinct monkey from Haiti and the origins of the Greater Antillean primates. *Proc. Natl. Acad. Sci.* 108, 2699–2704.
- Cortés-Ortiz, L., 2009. Molecular phylogenetics of Callitrichinae with emphasis on marmosets and *Callimico*. In: Ford, S.M., Porter, L.M., Davis, L.C. (Eds.), *The Smallest Anthropoids: The Marmoset/Callimico Radiation*. Developments in Primatology: Progress and Prospects. Kluwer Academic Press, New York, pp. 3–24.
- Cronin, J.E., Sarich, V.M., 1975. Molecular systematics of the New World monkeys. *J. Hum. Evol.* 4, 357–375.
- Darwin, C., 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London.
- de Oliveira, E.H., Neusser, M., Müller, S., 2012. Chromosome evolution in New World monkeys (Platyrrhini). *Cytogenet. Genome Res.* 137, 259–272.
- DeBoer, L.E.M., 1974. Cytotaxonomy of the Platyrrhini (Primates). *Genen en Phaenen* 17, 1–115.
- Degnan, J.H., Rosenberg, N.A., 2009. Gene tree discordance, phylogenetic inference and the multispecies coalescent. *Trends Ecol. Evol.* 24, 332–340.
- Dunlap, S.S., Thorington, R.W., Azziz, M.A., 1985. Forelimb anatomy of New World monkeys: myology and the interpretation of primitive anthropoid models. *Am. J. Phys. Anthropol.* 68, 499–517.
- Fabre, P.H., Rodrigues, A., Douzery, E.J.P., 2009. Patterns of macroevolution among Primates inferred from a supermatrix of mitochondrial and nuclear DNA. *Mol. Phylogenet. Evol.* 53, 808–825.
- Felsenstein, J., 1978. Cases in which parsimony or compatibility methods will be positively misleading. *Syst. Zool.* 27, 401–410.
- Felsenstein, J., 1985. Phylogenies and the comparative method. *Am. Nat.* 125, 1–15.
- Felsenstein, J., 2004. *Inferring Phylogenies*. Sinauer, Massachusetts.
- Felsenstein, J., 2005. PHYLIP (Phylogeny Inference Package) version 3.6. Distributed by the author. Department of Genome Sciences, University of Washington, Seattle.
- Finstermeier, K., Zinner, D., Brameier, M., Meyer, M., Kreuz, E., Hofreiter, M., Roos, C., 2013. A mitogenomic phylogeny of living primates. *PLoS One* 8 (7), e69504.
- Fleagle, J.G., 2014. *Primate Adaptation and Evolution*. Academic Press, New York.
- Fleagle, J.G., Tejedor, M.F., 2002. Early platyrrhines of southern South America. In: Hartwig, W.C. (Ed.), *The Primate Fossil Record*. Cambridge University Press, Cambridge, pp. 161–174.
- Ford, S.M., 1980. Callitrichids as phyletic dwarfs, and the place of Callitrichidae in Platyrrhini. *Primates* 21, 31–43.
- Ford, S.M., 1986. Systematics of the New World monkeys. In: Swindler, D.R., Erwin, J. (Eds.), *Comparative Primate Biology, Systematics, Evolution and Anatomy*, Volume 1. Alan R. Liss, New York, pp. 73–135.
- Garber, P.A., Rosenberger, A.L., Norconk, M.A., 1996. Marmoset misconceptions. In: Norconk, M.A., Rosenberger, A.L., Garber, P.A. (Eds.), *Adaptive Radiations of Neotropical Primates*. Plenum Press, New York, pp. 87–95.
- Goldman, N., 1998. Phylogenetic information and experimental design in molecular systematics. *Proc. Roy. Soc. B* 265, 1779–1786.
- Goodman, M., Porter, C.A., Czelusniak, J., Page, S.L., Schneider, H., Shoshani, J., Gunnell, G., Groves, C.P., 1998. Toward a phylogenetic classification of primates based on DNA evidence complemented by fossil evidence. *Mol. Phylogenet. Evol.* 9, 585–598.
- Gregory, W.K., 1922. *The Origins and Evolution of the Human Dentition*. William and Wilkins, Baltimore.
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4 (1), 9. http://paleo-electronica.org/2001_1/past/issue1_01.htm.
- Harada, M.L., Schneider, H., Schneider, M.P.C., Sampaio, I., Czelusniak, J., 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. *Mol. Phylogenet. Evol.* 4, 331–349.
- Heled, J., Drummond, A.J., 2010. Bayesian inference of species trees from multilocus data. *Mol. Biol. Evol.* 27, 570–580.
- Hershkovitz, P., 1977. *Living New World Monkeys, Part 1 (Platyrrhini)*, with an Introduction to Primates. Chicago University Press, Chicago.
- Hodgson, J.A., Sterner, K.N., Matthews, L.J., Burrell, A., Jani, R.A., Raaum, R.L., Stewart, C.-B., Distotell, T.R., 2009. Successive radiations, not stasis, in the South American primate fauna. *Proc. Natl. Acad. Sci.* 106, 5534–5539.
- Horowitz, I., Zardoya, R., Meyer, A., 1998. Platyrrhine systematics: a simultaneous analysis of molecular and morphological data. *Am. J. Phys. Anthropol.* 106, 261–281.
- Huelsenbeck, J.P., 1997. Is the Felsenstein zone a fly trap? *Syst. Biol.* 46, 69–74.
- Kay, R.F., 1990. The phyletic relationships of extant and fossil Pitheciinae. *J. Hum. Evol.* 19, 175–208.
- Kay, R.F., 2013. Biogeography in deep time – What do phylogenetics, geology, and paleoclimate tell us about early platyrrhine evolution? *Mol. Phylogenet. Evol.* In press.
- Kay, R.F., Fleagle, J.G., Mitchell, T.R.T., Colbert, M., Bown, T., Powers, D.W., 2008. The anatomy of *Dolichocebus gaimaneensis*, a stem platyrrhine monkey from Argentina. *J. Hum. Evol.* 54, 323–382.
- Knowles, L.L., Kubatko, L.S., 2010. *Estimating Species Trees: Practical and Theoretical*. Wiley-Blackwell, New York.
- Kuhner, M.K., Felsenstein, J., 1994. A simulation comparison of phylogeny algorithms under equal and unequal evolutionary rates. *Mol. Biol. Evol.* 11, 459–468.
- Lanier, H.C., Huang, H., Knowles, L.L., 2013. How low can you go? The effects of mutation rate on the accuracy of species-tree estimation. *Mol. Phylogenet. Evol.* 70C, 112–119.

- Legendre, P., Legendre, L., 1998. Numerical Ecology. Elsevier, Amsterdam.
- Lemey, M., Salemi, M., Vandamme, A.-M., 2009. The Phylogenetic Handbook: A Practical Approach to Phylogenetic Analysis and Hypothesis Testing. Cambridge University Press, Cambridge.
- Liu, L., Pearl, D.K., Brumfield, R.T., Edwards, S.V., 2008. Estimating species trees using multiple-allele DNA sequence data. *Evolution* 62, 2080–2091.
- Lockwood, C.A., Kimbel, W.H., Lynch, J.M., 2004. Morphometrics and hominoid phylogeny: support for a chimpanzee-human clade and differentiation among great ape subspecies. *Proc. Natl. Acad. Sci.* 101, 4356–4360.
- Maddison, W.P., 1997. Gene trees in species trees. *Syst. Biol.* 46, 523–536.
- Matthews, L.J., Rosenberger, A.L., 2008. Taxonomic status of the yellow tailed woolly monkey, *Lagothrix flavicauda* – an object lesson in the implementation of PAUP[®]. *Am. J. Phys. Anthropol.* 137, 245–255.
- Moen, D.S., Irschick, D.J., Wiens, J.J., 2013. Evolutionary conservatism and convergence both lead to striking similarity in ecology, morphology, and performance across continents in frogs. *Proc. R. Soc. B* 280, 20132156.
- Nabhan, A.R., Sarkar, I.N., 2012. The impact of taxon sampling on phylogenetic inference: a review of two decades of controversy. *Brief. Bioinform.* 13, 122–134.
- Nunn, C.L., 2011. The Comparative Method in Evolutionary Anthropology and Biology. The University of Chicago Press, Chicago and London.
- Opazo, J.C., Wildman, D.E., Pritchko, T., Johnson, R.M., Goodman, M., 2006. Phylogenetic relationships and divergence times among New World monkeys (Platyrrhini, Primates). *Mol. Phylogenet. Evol.* 40, 274–280.
- Osterholz, M., Walter, L., Roos, C., 2009. Retropositional events consolidate the branching order among New World monkey genera. *Mol. Phylogenet. Evol.* 50, 507–513.
- Perelman, P., Johnson, W.E., Roos, C., Seuánez, H.N., Horvath, J.E., Moreira, M.A.M., Kessing, B., Pontius, J., Roelke, M., Rumpfer, Y., Schneider, M.P.C., Silva, A., O'Brien, S.J., Pecon-Slattery, J., 2011. A molecular phylogeny of living primates. *PLoS Genet.* 7, e1001342.
- Perez, S.I., Klaczko, J., Rocatti, G., dos Reis, S.F., 2011. Patterns of cranial shape diversification during the phylogenetic branching process of New World monkeys (Primates: Platyrrhini). *J. Evol. Biol.* 24, 1826–1835.
- Perez, S.I., Klaczko, J., dos Reis, S.F., 2012. Species tree estimation for a deep phylogenetic divergence in the New World monkeys (Primates: Platyrrhini). *Mol. Phylogenet. Evol.* 65, 621–630.
- Perez, S.I., Tejedor, M.F., Novo, N.M., Aristide, L., 2013. Divergence times and the evolutionary radiation of New World monkeys (Platyrrhini, Primates): An analysis of fossil and molecular data. *PLoS One* 8 (6), e68029.
- Pritchko, T., Johnson, R.M., Wildman, D.E., Gumucio, D., Goodman, M., 2005. The phylogenetic history of New World monkey beta globin reveals a platyrrhine beta to delta gene conversion in the atelid ancestry. *Mol. Phylogenet. Evol.* 35, 225–234.
- Purvis, A., 1995. A composite estimate of primate phylogeny. *Phil. Trans. Roy. Soc. B* 348, 405–421.
- Rannala, B., Yang, Z., 2008. Phylogenetic inference using whole genomes. *A. Rev. Genom. Hum. Genet.* 9, 217–231.
- Ray, D.A., Xing, J., Hedges, D.J., Hall, M.A., Laborde, M.E., Anders, B.A., White, B.R., Stoilova, N., Fowlkes, J.D., Landry, K.E., Chemnick, L.G., Ryder, O.A., Batzer, M.A., 2005. Alu insertion loci and platyrrhine primate phylogeny. *Mol. Phylogenet. Evol.* 35, 117–126.
- Robinson, D.F., Foulds, L.R., 1981. Comparison of phylogenetic trees. *Math. Biosci.* 53, 131–147.
- Rosenberg, N.A., Nordborg, M., 2002. Genealogical trees, coalescent theory and the analysis of genetic polymorphisms. *Nat. Rev. Genet.* 3, 380–390.
- Rosenberger, A.L., 1979. Phylogeny, Evolution and Classification of New World Monkeys (Platyrrhini, Primates). University Microfilms, Ann Arbor.
- Rosenberger, A.L., 1984. Fossil New World Monkeys dispute the molecular clock. *J. Hum. Evol.* 13, 737–742.
- 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. 151–160.
- Rosenberger, A.L., 2011. Evolutionary morphology, Platyrrhine evolution and systematics. *Anat. Rec.* 294, 1955–1974.
- Rosenberger, A.L., Setoguchi, T., Shigehara, N., 1990. The fossil record of callitrichine primates. *J. Hum. Evol.* 19, 209–236.
- Rosenberger, A.L., Tejedor, M.F., 2013. The misbegotten: long lineages, long branches and the interrelationships of *Aotus*, *Callicebus* and the saki-uakaris. In: Barnett, A., Veiga, L., Ferrari, S., Norconk, M. (Eds.), *Evolutionary Biology and Conservation of Titis, Sakis and Uacaris*. Cambridge University Press, Cambridge, pp. 13–22.
- Rosenberger, A.L., Tejedor, M.F., Cooke, S., Halenar, L., Pekkar, S., 2009. Platyrrhine ecophylogenetics, past and present. In: Garber, P.A., Estrada, A., Biccamarques, J.C., Heymann, E.W., Strier, K.B. (Eds.), *South American Primates: Comparative Perspectives in the Study of Behavior, Ecology and Conservation*. Springer, New York, pp. 69–113.
- Rosenberger, A.L., Klukkert, Z.S., Cooke, S.B., Rimoli, R., 2013. Rethinking *Antillothrix*: The mandible and its implications. *Am. J. Primatol.* 75, 825–836.
- Rutherford, J.N., Tardif, S.D., 2009. Developmental plasticity of the microscopic placental architecture in relation to litter size variation in the common marmoset monkey (*Callithrix jacchus*). *Placenta* 30, 105–110.
- Schneider, H., 2000. The current status of the New World monkey phylogeny. *Anais da Academia Brasileira de Ciências* 72 (2).
- Schneider, H., Rosenberger, A.L., 1996. Molecules, morphology and platyrrhine systematics. In: Norconk, M.A., Rosenberger, A.L., Garber, P.A. (Eds.), *Adaptive Radiations of Neotropical Primates*. Plenum Press, New York, pp. 3–19.
- Schneider, H., Sampaio, I., 2013. The systematics and evolution of New World primates – A review. *Mol. Phylogenet. Evol.* In press.
- Schneider, H., Schneider, M.P.C., Sampaio, I., Harada, M.L., Stanhope, M., Goodman, M., 1993. Molecular phylogeny of the New World monkeys (Platyrrhini, Primates). *Mol. Phylogenet. Evol.* 2, 225–242.
- Schneider, H., Sampaio, I., Harada, M.L., Barroso, C.M.L., Schneider, M.P.C., Czelusniak, J., Goodman, M., 1996. Molecular phylogeny of the New World monkeys (Platyrrhini, Primates) based on two unlinked nuclear genes: IRBP intron 1 and ϵ -globin sequences. *Am. J. Phys. Anthropol.* 100, 153–179.
- Schneider, H., Canavez, F.C., Sampaio, I., Moreira, M.A.M., Tagliaro, C.H., Seuánez, H.N., 2001. Can molecular data place each Neotropical monkey in its own branch? *Chromosoma* 109, 515–523.
- Schrage, C.G., 2007. On the time scale of New World Primate diversification. *Am. J. Phys. Anthropol.* 132, 344–354.
- Setoguchi, T., Rosenberger, A.L., 1987. A fossil owl monkey from La Venta, Colombia. *Nature* 326, 692–694.
- Simpson, G.G., 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.* 85, 1–350.
- Sneath, P.H.E., Sokal, R.R., 1963. Principles of Numerical Taxonomy. Freeman & Co., San Francisco.
- Sober, E., 1988. Reconstructing the Past: Parsimony, Evolution, and Inference. Bradford/MIT Press, Cambridge.
- Springer, M.S., Meredith, R.W., Gatesy, J., Emerling, C.A., Park, J., Rabosky, D.L., Stadler, T., Steiner, C., Ryder, O.A., Janečka, J.E., Fisher, C.A., Murphy, W.J., 2012. Macroevolutionary dynamics and historical biogeography of primate diversification inferred from a species supermatrix. *PLoS One* 7 (11), e49521.
- Steiper, M.E., Ruvolo, M., 2003. New World monkey phylogeny based on X-linked G6PD DNA sequences. *Mol. Phylogenet. Evol.* 27, 121–130.
- Tejedor, M.F., 2008. The Origin and Evolution of Neotropical Primates. *Arquivos do Museu Nacional, Rio de Janeiro* 66, 251–269.
- Tejedor, M.F., 2013. Sistemática, evolución y paleobiogeografía de los primates Platyrrhini. *Revista del Museo de La Plata (Sección Zoología)* 20, 20–39.
- Townsend, T.M., Alegre, R.E., Kelley, S.T., Wiens, J.J., Reeder, T.W., 2008. Rapid development of multiple nuclear loci for phylogenetic analysis using genomic resources: an example from squamate reptiles. *Mol. Phylogenet. Evol.* 47, 129–142.
- Wildman, D.E., Jameson, N.M., Opazo, J.C., Yi, S.V., 2009. A fully resolved genus level phylogeny of Neotropical primates (Platyrrhini). *Mol. Phylogenet. Evol.* 53, 694–702.
- Yang, Z., Rannala, B., 2012. Molecular phylogenetics: principles and practice. *Nat. Rev. Genet.* 13, 303–314.