



# Modeling lineage and phenotypic diversification in the New World monkey (Platyrrhini, Primates) radiation



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## ABSTRACT

Adaptive radiations that have taken place in the distant past can now be more thoroughly studied with the availability of large molecular phylogenies and comparative data drawn from extant and fossil species. Platyrrhines are a good example of a major mammalian evolutionary radiation confined to a single continent, involving a relatively large temporal scale and documented by a relatively small but informative fossil record. Here, we present comparative evidence using data on extant and fossil species to explore alternative evolutionary models in an effort to better understand the process of platyrrhine lineage and phenotypic diversification. Specifically, we compare the likelihood of null models of lineage and phenotypic diversification versus various models of adaptive evolution. Moreover, we statistically explore the main ecological dimension behind the platyrrhine diversification. Contrary to the previous proposals, our study did not find evidence of a rapid lineage accumulation in the phylogenetic tree of extant platyrrhine species. However, the fossil-based diversity curve seems to show a slowdown in diversification rates toward present times. This also suggests an early high rate of extinction among lineages within crown Platyrrhini. Finally, our analyses support the hypothesis that the platyrrhine phenotypic diversification appears to be characterized by an early and profound differentiation in body size related to a multidimensional niche model, followed by little subsequent change (*i.e.*, stasis).

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## 1. Introduction

The study of lineage and phenotypic diversification in living clades with relatively recent divergences has supported models of adaptive radiation (Simpson, 1953; Schluter, 2000) that predict selective influences arising from ecological opportunity and circumstances (Gavrillets and Losos, 2009; Losos and Mahler, 2010). This process frequently results in great phenotypic variation and species richness relative to a short time frame of phylogenetic divergence (Schluter, 2000; Gavrillets and Losos, 2009; Losos and Mahler, 2010). It is also suspected that similar processes of adaptive radiation have driven the initial diversification of clades that originated in the distant past, for example, at the ordinal and subordinal levels in mammalian clades (Gavrillets and Losos, 2009; Losos and Mahler, 2010). In such cases, ecological opportunity may decrease during the radiation as niches are filled, leading to stasis.

Several evolutionary radiations have been carefully studied with recently developed mathematical models applied to molecu-

lar phylogenies and comparative data from extant species (Nee, 2006; Gavrillets and Losos, 2009; Losos and Mahler, 2010). However, it is becoming clear that our capacity to successfully model and understand the diversification processes of ancient clades is limited when only neontological data are considered (Quental and Marshall, 2010; Slater et al., 2012). New World monkeys (Parvorder Platyrrhini), one of the three major groups of living and fossil primates, are a good example of a major mammalian evolutionary radiation that occupies a large temporal scale (*i.e.*, 20–40 million years ago or megannums [Ma] in Central and South America), exhibits a remarkable phenotypic variation (*e.g.*, a body mass spanning two orders of magnitude, from 0.1 to more than 10 kg) and presents a relatively small but informative fossil record (Fleagle, 1999; Fleagle and Tejedor, 2002; Tejedor, 2008). Morphological and phylogenetic studies have hypothesized that the diversification of this monophyletic group was mainly linked to the action of deterministic-selective factors related to ecological variables (Rosenberger, 1992; Marroig and Cheverud, 2001; Rosenberger et al., 2009). However, there is no general agreement about the main ecological dimension—*e.g.*, diet, locomotion or a multidimensional niche—behind the platyrrhine diversification (Rosenberger, 1992; Allen and Kay, 2012; Youtatos and Meldrum, 2011; Perez

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et al., 2011). It has also been suggested that the marked phenotypic diversification of platyrrhines occurred relatively quickly during the initial branching process of the main extant clades in connection with ecological niche opportunity (i.e., an early-burst platyrrhine radiation), followed by a slowdown in evolutionary rates which resulted in the widespread retention of the formative patterns that are characteristic of these lineages (i.e., evolutionary stasis; Rosenberger, 1992; Rosenberger et al., 2009; Perez et al., 2011).

Although some recent studies of evolutionary radiations have included information from the fossil record along with phylogenies and comparative data of extant species in a mathematical modeling framework (Slater et al., 2010, 2012; Etienne et al., 2011), such approach to the study of the dynamic processes of lineage origin and extinction, and phenotypic diversification, has not been applied to explore the platyrrhine evolutionary radiation. Here, we present comparative evidence using data on extant and fossil species to explore alternative evolutionary models in an effort to better understand the process of platyrrhine lineage and phenotypic diversification. Specifically, we compare the likelihood of null models of lineages and phenotypic diversification versus various models of adaptive evolution. Moreover, we explore the main ecological dimension behind the platyrrhine diversification. If the platyrrhine diversification conforms to the adaptive radiation theory, we expect that differentiation of the major extant platyrrhine lineages was concentrated relatively early in the history of the clade and that phenotypic variation—measured as body size—was partitioned among subclades early in their phylogenetic history as well, as a major driver or consequence of ecological niche partitioning and niche-filling. As a starting point, we first estimate a chronophylogenetic tree for most extant platyrrhine species using molecular data and Bayesian methods (Drummond et al., 2006). Then, using this tree and comparative statistical methods we explore the pattern of lineage diversification through time (Nee et al., 1992; Harmon et al., 2003; Ricklefs, 2007; Stadler, 2011a), investigate the pattern of body size diversification through time and the fit of a series of evolutionary models (Harmon et al., 2003; Butler and King, 2004). Finally, given that the inference of the tempo and mode of diversification of a clade using only extant species can be biased (Quental and Marshall, 2010; Slater et al., 2012), we compare the results based on extant species with the estimated body masses and number of lineages inferred from the platyrrhine fossil record. Summarizing, our work contributes to the discussion of platyrrhine evolution and diversification in three different ways: (1) we present one of the most complete molecular phylogenies of extant platyrrhine species to date, sampling published data on 108 taxa and estimating a chronophylogenetic tree for 78 putative “good” species; (2) we mathematically model the pattern of lineage and phenotypic diversification of the platyrrhine clade; and (3) we combine data about extant and fossil species in a novel way not employed before in studies of the platyrrhines to better understand the process of their diversification.

## 2. Materials and methods

### 2.1. Molecular divergence among species and phylogenetic inference

Phylogenetic trees are used in almost every branch of evolutionary biology. In particular, in comparative analyses they are needed to avoid misinterpreting historical contingencies as causal relationships and to understand the patterns of diversification (Nee, 2006; Losos, 2011; Yang and Rannala, 2012). In our study, the phylogenetic tree itself is not of direct interest but it is a necessary first step for the following statistical comparative analyses. Previous phylogenetic studies have estimated the platyrrhine phylogenetic tree using ca. 50% (58 species, Chatterjee et al., 2009; or

64 species, Perelman et al., 2011) or 60% (73 species, Fabre et al., 2009) of species recognized by Groves (2001). However, most of the methods in comparative analyses assume that a large fraction of the extant species in the clade under study are included in the dataset (Pybus and Harvey, 2000; Ricklefs, 2007; Cusimano et al., 2012). On the other hand, the use of many different definitions of species in primate systematics has led to a fluctuating taxonomy in platyrrhines (e.g. Groves, 2004; Rylands et al., 2012) and concerns on taxonomic inflation have arisen (Rosenberger, 2012). Since speciation events are not instantaneous, the decision onto how finely distinguish lineages is rather arbitrary (Ricklefs, 2007). For this reason, we decided to set up a reproducible criterion for distinguishing species based on a minimum molecular divergence threshold. A total of 108 platyrrhine species and subspecies were initially considered for analysis based on the availability of DNA sequences on the Genbank database (Supplementary Table A.1). Cytochrome *b* (CytB) DNA sequences were downloaded from Genbank for 90 specimens (based on availability) that were previously accepted as valid species or subspecies in the platyrrhine literature (Groves, 2001). We estimated molecular distance among the 90 specimens within each genus using Mega 5 (Tamura et al., 2011) and established a likely point (3%) of minimum divergence among species (Fouquet et al., 2007; Clemente-Carvalho et al., 2011). After this procedure, we excluded taxa with low molecular divergence (mainly subspecies) and considered as full species those taxa previously regarded as subspecies that were above the distance threshold. Specifically, 26 taxa were excluded from analysis based on the existence of a low molecular distance, because they probably represent geographic variants of other species included in the dataset (Supplementary Table A.1). The final dataset included 78 species, as 14 taxa from the Perelman et al. (2011) dataset that did not have an available CytB sequence were included based on the fact that they are broadly recognized as full species. Another four species were excluded because their large proportion of missing data could hinder the analysis. Thus, our dataset comprised a great percentage (ca. 80%) of the likely extant platyrrhine species.

To estimate the chronophylogenetic tree for the 78 platyrrhine species we analyzed the dataset obtained for the platyrrhine species and three outgroups (*Macaca mulatta*, *Pan troglodytes*, *Homo sapiens*) from GenBank (see Wildman et al., 2009; Perelman et al., 2011). The analyzed dataset is a DNA concatenated matrix for 81 species with a total of 25,361 bp, including 15 selected nuclear genes from Perelman et al. (2011) with few missing data, and 11 non-coding sequences from Wildman et al. (2009) (Supplementary Table A.2). The dataset also includes IRBP and  $\xi$ -globin genes and four mitochondrial sequences (CytB, 16s, 12s and COII). Several available gene sequences (e.g. from Perelman et al. (2011)) were not included in our phylogenetic estimation because a great number of species lacked data for those genes. The sequences of each gene were aligned using ClustalW and manually corrected with BioEdit 7.0.0 software (Hall, 2004). Accession numbers for the mitochondrial, IRBP and  $\xi$ -globin sequences are shown in Supplementary Table A.1.

We performed a concatenated Bayesian analysis based on the molecular dataset to estimate chronophylogenetic relationships among the 81 primate species. jModelTest 0.1 (Posada, 2008) was employed to determine the most appropriate model of sequence evolution for each analyzed gene sequences estimated under the Akaike Information Criterion with correction for sample size (AICc). The best fit models for studied genes are shown in the Supplementary Table A.2. The Bayesian chronophylogenetic analysis was performed using BEAST v1.6.1 (Drummond and Rambaut, 2007). The analysis was carried out using Markov Chain Monte Carlo (MCMC) simulations for 200,000,000 generations and a sample frequency of 20,000. The convergence was determined

using the program Tracer v1.5 (Rambaut and Drummond, 2007) and the first 1250 sampled trees were excluded. We used a relaxed molecular clock model, which allows substitution rates to vary across branches according to an uncorrelated lognormal distribution (Drummond et al., 2006; Drummond and Rambaut, 2007). Six fossil calibrations were selected (see Perez et al., 2013). Fossil calibration for *Homo-Pan* divergence (minimum time 5.7 Ma, maximum time 10 Ma; LogNormal distribution with offset 5.7, mean 0.5 and standard deviation 0.5) and Anthropoidea (minimum time 33.70 Ma, maximum time 65.80 Ma; LogNormal distribution with offset 33.7, mean 2.4 and standard deviation 0.55) were obtained from Benton et al. (2009). Minimum divergence time of Alouattinae, Cebinae and Aotinae were set at 12.5 Ma, based on *Stirtonia*, *Neosaimiri* and *Aotus dindensis*, three fossils attributable to Alouattinae, Cebinae and Aotinae, respectively (Kay et al., 2008; Tejedor, 2008). We used a LogNormal distribution with offset 12.5, mean 1.8 and standard deviation 0.4 for the Alouattinae, Cebinae and Aotinae constraints. Minimum divergence time of Pitheciidae was set at 15.7 Ma (LogNormal distribution with offset 15.7, mean 1.5 and standard deviation 0.5), based on *Proteropithecina neuquensis*, a fossil attributable to Pitheciidae (Kay et al., 1998). Maximum divergence time was set at 26 Ma, based on the absence of Pitheciidae, Alouattinae, Cebinae and Aotinae fossils in or previous to the Deseadan fauna of Salla, Bolivia, and other South American formations of the same age. Both minimum and maximum calibration bounds were set to the probability that the true divergence time outside the bounds is small, but non-zero (dos Reis et al., 2012; Perez et al., 2013). Although a calibrated tree could be important for discussing some aspects of the results, the following analyses are insensitive to the total length of the tree, i.e. based on relative times (see discussion below). We computed the maximum clade credibility (MCC) tree in TreeAnnotator 1.4.8 (Drummond and Rambaut, 2007). FigTree v1.3.1 was used to plot the phylogenetic tree.

## 2.2. Lineage diversification pattern analysis

The number of species in a clade is the result of speciation and extinction processes acting since the origin of that clade. The most direct way of studying this diversity dynamic is to analyze the fossil record. However, the information contained in molecular phylogenetic trees of extant species allow us to estimate speciation and extinction rates in the absence of an appropriate fossil record (Harvey et al., 1994; Nee et al., 1994; Ricklefs, 2007; Stadler, 2011a). This information can be recovered by analyzing the fit of different mathematical models of diversification to the reconstructed phylogeny.

Following this approach, we first quantitatively tested, using the widely used  $\gamma$  statistic (Pybus and Harvey, 2000), whether the pattern of lineage diversification in the platyrrhine tree departs from what is expected under the most simple model, Pure-Birth (PB), in which each species has a constant probability  $\lambda$  (speciation rate) of generating another species in each point in time and there is no extinction (Nee, 2006). Under this model, the number of species  $N(t)$  after  $t$  units of time, starting from  $N(0)$  species is expected to grow exponentially:  $N(t) = N(0)e^{\lambda t}$ . The  $\gamma$  statistic measures the difference between the average sum of branch lengths between each internal node and the root, and the midpoint of the tree (Pybus and Harvey, 2000). This statistic has mean of 0 for trees generated under a PB process, and significant negative values indicate a decelerating lineage accumulation rate toward present times, or, in other words, that branching events are concentrated disproportionately early in the phylogeny, as is expected in scenarios of adaptive radiation (Gavrillets and Losos, 2009).

To further assess the diversification model that best explains the observed diversity pattern and to estimate possible changes

in diversification rates across the platyrrhine tree we compared the fit, using the Akaike Information Criterion (AIC), of the observed branching sequence to various models of lineage accumulation. AIC is calculated as  $-2\ell + 2K$  where  $\ell$  is the maximum likelihood value of the data and  $K$  is the number of parameters in the model. AIC represents a compromise between fit and complexity of the model (Burnham and Anderson, 2002). The tested models were the following: (i) PB and birth-death (BD; with parameters  $\lambda$  and  $\mu$  [extinction rate]), as constant-rates lineage accumulation models (although some of these models allow for discrete  $\lambda$  shifts at specific points in time), and (ii) linear (DDL) and exponential (DDX) density-dependent processes (as variable  $\lambda$  models with no extinction) (Rabosky and Lovette, 2008a). Because the importance of extinction in shaping lineage origination curves may be underestimated in the DDX and DDL models, we also included a density-dependent model with a non-zero  $\mu$  (DDD + E; Etienne et al., 2011). Density-dependent models assume that the diversification rate ( $\lambda - \mu$ ) decreases as the lineage population reaches some threshold density. If there are ecological limits to diversity, a slowdown in lineage diversification rate would be expected in an adaptive radiation scenario, since ecological opportunity may decrease as niches are filled (Rabosky and Lovette, 2008b; Gavrillets and Losos, 2009; Etienne et al., 2011). Also, since  $\lambda$  and  $\mu$  may have changed through time in response to different external factors, we also included the recently proposed birth-death-shift (BDS) method by Stadler (2011b), which can estimate whether and when a shift in rates occurred in the tree.

To account for incomplete sampling in our tree, we added the missing splitting events to the analyzed tree, using the maximum likelihood  $\lambda$  and  $\mu$  estimations from the MCC tree, assuming that they occurred between 1 and 5 Ma. Using this approach, we simulated 200 completely sampled trees and repeated the  $\gamma$  test and the model fitting analyses (Cusimano et al., 2012). To also account for uncertainty in phylogenetic reconstruction, analyses were repeated over a random sample of 100 trees drawn from the post-burn in set of the BEAST analysis.

Finally, we visually inspected the time pattern of lineage accumulation by plotting the number of ancestral lineages in our phylogenetic tree (in a log scale) versus time (lineage-through-time plot, LTT; Ricklefs, 2007), and compared it, using simulations, to the expected pattern under the PB and BD (keeping track of extinct lineages) models of diversification.

All analyses were conducted with the LASER (Rabosky, 2006), TreePar and TreeSim (Stadler, 2011b,c), and APE (Paradis et al., 2004) packages for R 2.15.1 (R-Development Core Team, 2012).

In order to develop a generic origination trajectory for the fossil record, we assembled geochronologic ages from the literature for 23 fossil platyrrhine genera ranging from the Deseadan South American Land Mammal Age (SALMA) to the Laventan SALMA, spanning from 26 to 11.8 Ma (Fleagle and Tejedor, 2002; Tejedor, 2008; Rosenberger et al., 2009). This data was then used to build origination estimates (as numbers of genera confined to an interval plus those that cross the top boundary of the interval; Foote, 2000) for each SALMA. To test for possible biases due to a poor sampling of the fossil record, we applied the Spearman's rank correlation test as described in Barrett et al. (2009). Briefly, the number of genera for each time slice (as SALMAs) is expected to be positively correlated with the number of sampled geological formations if sampling is affecting the shape of the origination curve.

## 2.3. Phenotypic diversification analyses

Platyrrhine monkeys are one of the most phenotypically diverse groups of living primates. In particular, body size can range from roughly 100 g in *Cebuella pygmaea* to more than 10 kg in some atelids, with hypothesized ecological and functional correlates. Thus,



size, with all its intrinsic biological attributes, represents a good example of the significant phenotypic diversity found in platyrrhines. We obtained body mass data from the literature for the 78 extant species in our phylogeny and 15 fossil species (estimated from dental measurements and regression formulae; [Supplementary Table A.3](#)). As male and female body mass were highly correlated ( $R^2 = 0.986$ ) among the living species average body mass were used in the analyses. Male and female data were pooled and log-transformed for all analyses.

To explore the time pattern of body mass variation, we first calculated a mean relative disparity-through-time (DTT) plot for our phylogeny as described by [Harmon et al. \(2003\)](#). Disparity is measured as  $D = \Sigma(d_i)/n - 1$  where  $d_i$  is pairwise Euclidean distance between species and  $n$  is the number of species. First, disparity was calculated for the entire platyrrhine clade, and then for each subclade. Disparity of each subclade was standardized by dividing it by the disparity of the entire clade (relative disparity; [Harmon et al., 2003](#)). Finally, the mean relative disparity for each point in time is calculated for all subclades present at that time. Then we compared the observed body mass disparity through time to that expected if character evolution had followed a Brownian motion (random) model of diversification by simulating body size evolution 1000 times across our tree. Disparity values near 0 imply that most of the phenotypic variation is partitioned among subclades rather than within each subclade (e.g. among families, subfamilies, etc. rather than within each family, subfamily, etc.), whereas values near 1 imply the opposite, indicating that subclades have independently evolved to occupy similar places of morphological space ([Harmon et al., 2003](#)). Phenotypic disparity is expected to be partitioned among subclades early in an early niche-filling scenario of adaptive radiation. We also calculated the morphological disparity index (MDI, [Harmon et al., 2003](#)), which quantifies the overall difference between the observed and expected curves of disparity through time. Negative values are expected under an adaptive radiation scenario, indicating lower subclade disparity than in the random evolution model. The DTT analysis is implemented in the GEIGER package ([Harmon et al., 2008](#)) for R.

Body mass is proposed to be strongly related to diet among platyrrhines ([Rosenberger, 1980, 1992](#); [Marroig and Cheverud, 2001](#); [Perez et al., 2011](#)). To explore this hypothesis, we applied the model selection approach of [Butler and King \(2004\)](#) to compare the relative fit (measured with Akaike Information Criterion, AIC; see above) of a stochastic model (Brownian motion, BM; [Felsenstein, 1985](#)) versus seven models of adaptive evolution (Ornstein–Uhlenbeck, OU; [Hansen, 1997](#)) to the body size variation. In the BM model, body size evolves up the phylogeny via random walk and disparity accumulates over time ([Felsenstein, 1985](#)). To model adaptive evolution in platyrrhine size variation, we implemented seven Ornstein–Uhlenbeck models (OU; [Hansen, 1997](#)) with either one, three, four or five optima. Specifically, we implemented a random walk with a single stationary peak modeled as an Ornstein–Uhlenbeck process (OU1), such that the size have a tendency to return to a median value ([Hansen, 1997](#); [Butler and King, 2004](#)), and six OU models with several optima formulated based on previous hypotheses about the main ecological dimension behind the platyrrhine diversification. The parameters of the evolutionary models were estimated by maximum likelihood:  $\sigma$  (the intensity of the random changes in body size),  $\alpha$  (the rate of changes toward an optimum, or the strength of selection),  $\theta k$  (optimal value for the body size in each niche optimum  $k$ ).

To build the ecological models, or adaptive evolution hypotheses, we first assigned each extant species to an ecological niche according to published works ([Rosenberger, 1992](#); [Norconk et al., 2009](#); [Youlatos and Meldrum, 2011](#); [Allen and Kay, 2012](#)), which describe different ecological groups. For uni-dimensional niche hypotheses, data concerning diet composition (i.e., average annual

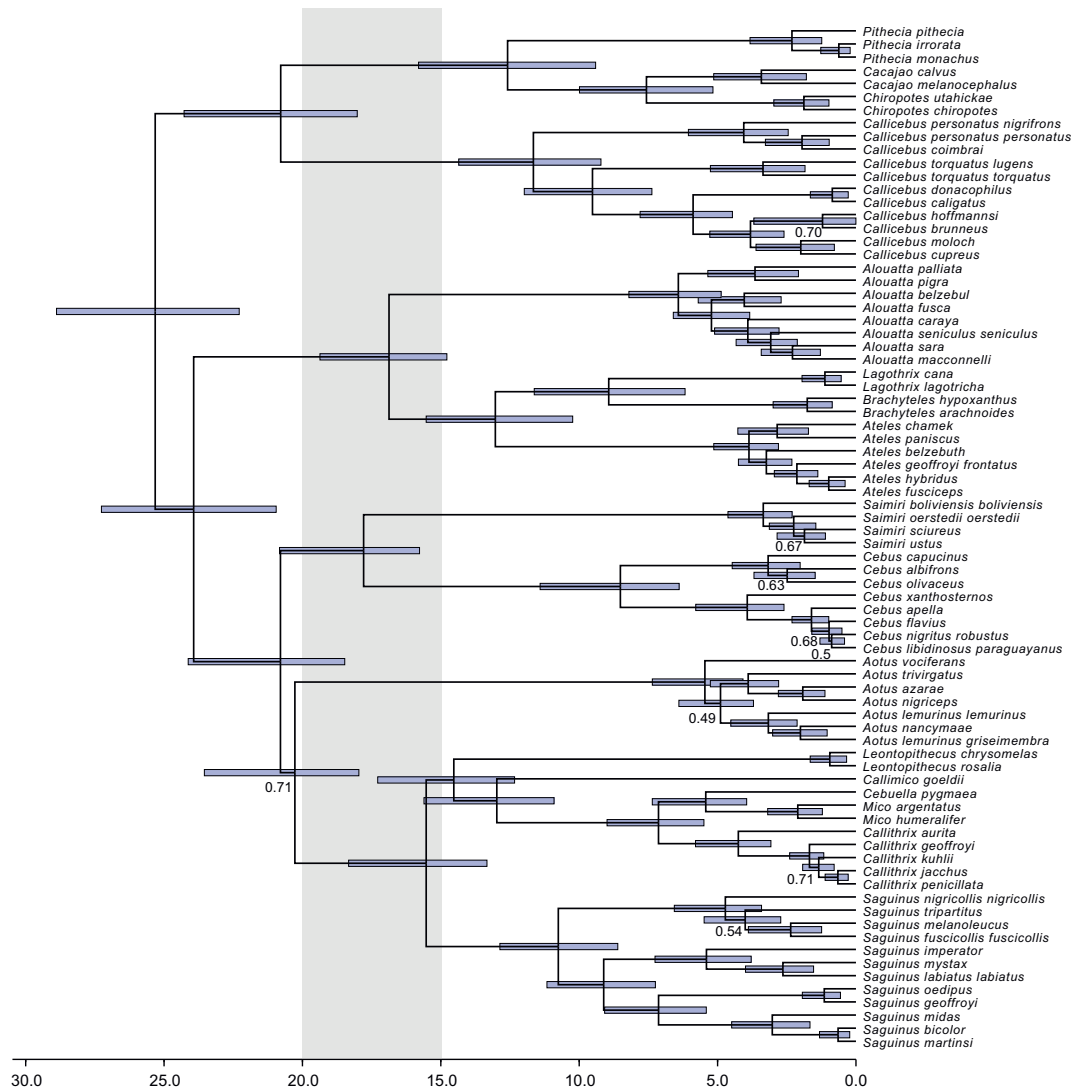
percentages of plant parts and insects in the diets of platyrrhine genera), diet quality (i.e., percentage of structural plant parts [leaves and stems], reproductive plant parts [fruits, seeds, flowers, nectar and gums] and animal matter in the diet) and locomotion (i.e., percentages of arboreal quadrupedal walk, clamber and bridge, clawed locomotion and suspensory locomotion) of platyrrhine genera and species were taken from [Norconk et al. \(2009\)](#), [Allen and Kay \(2012\)](#) and [Youlatos and Meldrum \(2011\)](#), respectively. We then calculated the principal component (PC) scores for each data set to reduce the number of ecological variables and avoid multicollinearity; these PCs describe broad variation in ecology (i.e., diet composition, diet quality and locomotion PCs) and were used to group species in the different ecological niches (see below). It is important to remark that although these niche models are based on real datasets, they are hypotheses modeling the ancestral partition of platyrrhine niches. OU processes model the effect of different selective regimes (ecological niches in this case) acting along the branches of a phylogenetic tree and thus can be used to test for phenotypic diversification related to ecological factors ([Butler and King, 2004](#)), using data that is strongly phylogenetically structured. In our analyses, character states for all internal branches were estimated using a maximum likelihood approach. Finally, we explored body mass variation for the ancient Patagonian and younger La Ventana (Colombia) fossil species in relation with the best supported model. The OU analysis is implemented in the OUCH package ([Butler and King, 2004](#)) for R and was performed using the function `OUaverage` from [Jaffe et al. \(2011\)](#).

To account for uncertainty in phylogenetic reconstruction, DTT and OU analyses were performed over a random sample of 100 trees drawn from the post-burn in set of the BEAST analysis.

### 3. Results

Our chronophylogenetic tree of platyrrhines is in general agreement with other recent relationship estimations ([Fig. 1](#); [Opazo et al., 2006](#); [Wildman et al., 2009](#); [Perelman et al., 2011](#); [Perez et al., 2012](#)), which support the division of platyrrhines into three monophyletic families (Atelidae, Cebidae and Pitheciidae) and suggest a sister-group phylogenetic relationship between Atelidae and Cebidae ([Opazo et al., 2006](#); [Wildman et al., 2009](#)). We found *Aotus* to be phylogenetically related to Callitrichinae, as did [Perelman et al. \(2011\)](#), but with low node support. The affinities of *Aotus* are contentious as several molecular and morphological studies do not align ([Perez et al., 2012](#); [Rosenberger and Tejedor, 2013](#)). Because of this controversy, we repeated all the statistical analyses varying the phylogenetic position of *Aotus* (as a sister clade of Cebidae or Cebinae, as most studies report). The results were almost identical (data not shown). Our results are also consistent with other molecular assessments, which indicate the branches connecting the main platyrrhine lineages are short, suggesting that the diversification of the main living platyrrhine clades could indeed represent a rapid sequential radiation (but see below; [Fig. 1](#); [Opazo et al., 2006](#); [Wildman et al., 2009](#); [Perez et al., 2012](#)). The divergence time estimation suggest that the last common ancestor (LCA) of extant platyrrhine primates existed at ca. 25 Ma, with the 95% confidence limit for the node ranging from ca. 22.5–29 Ma. This result is in contrast with other recent estimations, mainly to the influential [Hodgson et al. \(2009\)](#) study, which suggested a LCA for crown platyrrhines at ca. 19 Ma.

Based on the  $\gamma$  statistic over 100 random trees drawn from the post-burn in set, we found no evidence of a decelerating lineage accumulation rate toward present times in the overall origination pattern of the platyrrhine clade (mean  $\gamma = 0.493$ ,  $p = 0.679$ ). This result is robust to incomplete sampling (mean  $\gamma = 0.290$ ,



**Fig. 1.** Maximum clade credibility (MCC) chronophylogenetic tree from the BEAST analysis for 78 species of platyrrhine monkeys. Blue bars on the tree indicate 95% confidence intervals for estimated node ages. Support is indicated for nodes with  $<0.8$  posterior Bayesian probability. Shaded area shows estimated temporal range for Patagonian fossil lineages.

$p = 0.612$ ). Moreover, the best supported model of lineage diversification was a pure-birth model with one rate shift: an abrupt slowdown in speciation rates at 0.42 Ma (Table 1). Such recent rate shifts may not be significant since incomplete species sampling and taxonomic inflation can affect the shape of the most recent portion of the tree; however, when accounting for incomplete sampling, a slowdown is also recovered at similar dates (Supplementary Table A.4). Overall, this result shows, based on the extant species tree, that through more than 99% of the time since its ori-

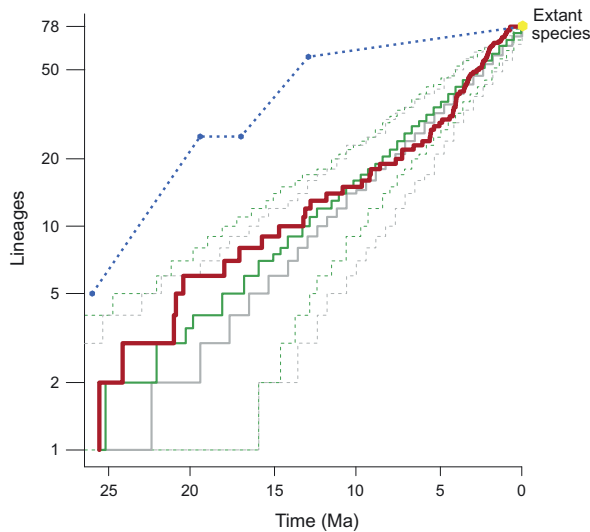
gins, crown platyrrhines diversified at a constant rate. On the other hand, for the BD models, the maximum likelihood extinction rate is probably underestimated, an acknowledged issue of diversification models. The absence of an evident early pulse of lineage origination is also visually seen in the LTT plot for extant species (Fig. 2). However, the fossil lineages origination curve seems to show a different picture: a relatively rapid increase in the number of species followed by an apparent slowdown in the origination rate, a pattern reminiscent of a density-dependent diversification

**Table 1**

Mean parameter estimates and comparison of the fit of different lineage diversification models to 100 trees randomly drawn from the post-burn in fraction of the BEAST analysis (numbers in parentheses are standard deviations; SD). Ma: mega annum.  $r$ : net diversification rate (speciation–extinction; per million years);  $a$ : turnover (extinction/speciation). Rates go from past to present. AIC: Akaike Information Criterion score; wAIC: Akaike weights. For the BDS analysis, the best fitting model is given.

Model	Rate shift times (Ma)	$r$	$a$	AIC	wAIC
Pure-birth (2 rates)	0.42 (0.16)	0.17 (0.01); 0.04 (0.05)	–	–90.03 (9.26)	0.516
BDS (1 shift)	0.42 (0.16)	0.12 (0.01); 0.04 (0.05)	0.44 (0.13); 0.15 (0.16)	–88.75	0.273
Pure-birth (1 rate)	–	0.16 (0.01)	–	–86.55 (8.69)	0.091
Birth–death	–	0.14 (0.01)	0.22 (0.11)	–85.11 (8.83)	0.044
DDX	–	0.12 (0.02)	–	–85.05 (8.82)	0.043
DDL	–	0.16 (0.03)	–	–84.56 (8.69)	0.034
DDD + E <sup>a</sup>	–	0.52	0.34	–69.94	0.000

<sup>a</sup> Calculated only for the MCC tree.

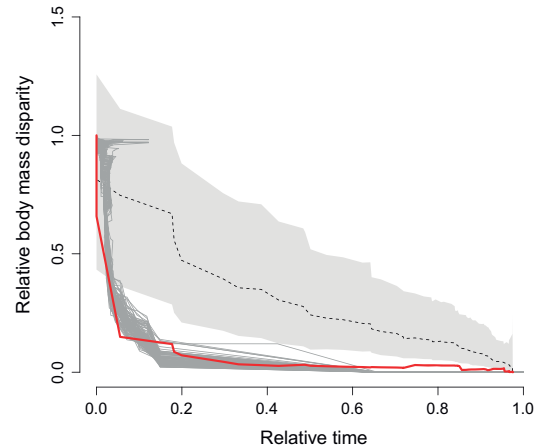


**Fig. 2.** Semi-logarithmic plots of lineage accumulation through time (LTT plot). Red bold solid line: LTT plot based on the MCC tree of extant species. Dark green/light gray solid and thin dashed lines: median and 95% confidence intervals for the expected distribution under a PB or BD model, respectively, simulated using the maximum likelihood rates estimated from the MCC tree. Extinct lineages are included in the BD curve. Blue dashed line: observed fossil-based lineage origination curve. The number of species in extinct taxa was estimated by applying a conservative mean species/genus ratio of the living taxa (*i.e.*, five) (Quental and Marshall, 2010). Difference between the area under the MCC tree/Fossil curve and BD curve = 5.05/30.68; PB curve = 0.48/26.11. Area between Fossil and MCC curves = 25.63. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

trajectory (Fig. 2, blue dashed line). This pattern is even stronger when compared to simulated trees under the PB and BD models, even considering that the BD curve includes extinct lineages (Fig. 2). Furthermore, this minimum estimated diversity through time is likely to be very conservative, since it lacks a large fossil record from the early Miocene of Amazonia, an area that was certainly populated with platyrrhine representatives (Marivaux et al., 2012). The Spearman's correlation coefficient between genera per SALMAs and the sampled geological formations showed a non-significant value ( $r = 0.286$ ,  $p = 0.65$ ), suggesting that the observed increase in fossil genera over time is not due to sampling bias.

Fig. 3 shows the DTT plot for the body mass data. Average subclade disparity along the entire history of the group is lower than expected under a BM model of mass evolution. Values drop near 0 since the early divergence of the platyrrhines, and show little variation over time. An MDI value of  $-0.255$  also confirms quantitatively this result. This outcome indicates a strong pattern where most size variation occurs among the main platyrrhine subclades, which tend to occupy more isolated regions of body mass morphospace, consistent with an early radiation and niche-filling scenario.

The PCs scores displayed in Fig. 4 were used to group species in the different ecological niches. We defined 4 and 3 niches for diet composition (OU-dietC4 and OU-dietC3, respectively); 5 and 4 niches for diet quality (OU-dietQ5 and OU-dietQ4, respectively); and 3 niches for locomotion (OU-Loc3; Fig. 4). Finally, a multidimensional niche model was built based on the Rosenberger (1992) hypothesis; this hypothesis is mainly a combination of diet composition and locomotion niche dimensions and defines 5 broad ancestral ecological niches (OU-MD5; Fig. 4). The overall fit of the models of body mass evolution to these hypothetical niches is shown in Table 2. The OU model with 5 body mass optima (OU-MD5), based on the multivariate niche hypothesis of Rosenberger (1980, 1992), was the best supported, with an Akaike weight well above the other candidate models, which performed poorly in



**Fig. 3.** Relative disparity-through-time plot (DTT) for body mass in the 78 platyrrhine species. Solid red line shows disparity calculated for the MCC platyrrhine tree. Black dashed line shows median expected disparity under the null hypothesis of random evolution of body size (data generated by 1000 simulations). Shaded area shows the 95% range for the simulations. Dark gray lines: disparity for 100 trees randomly sampled from the post-burn in fraction of the BEAST analysis. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

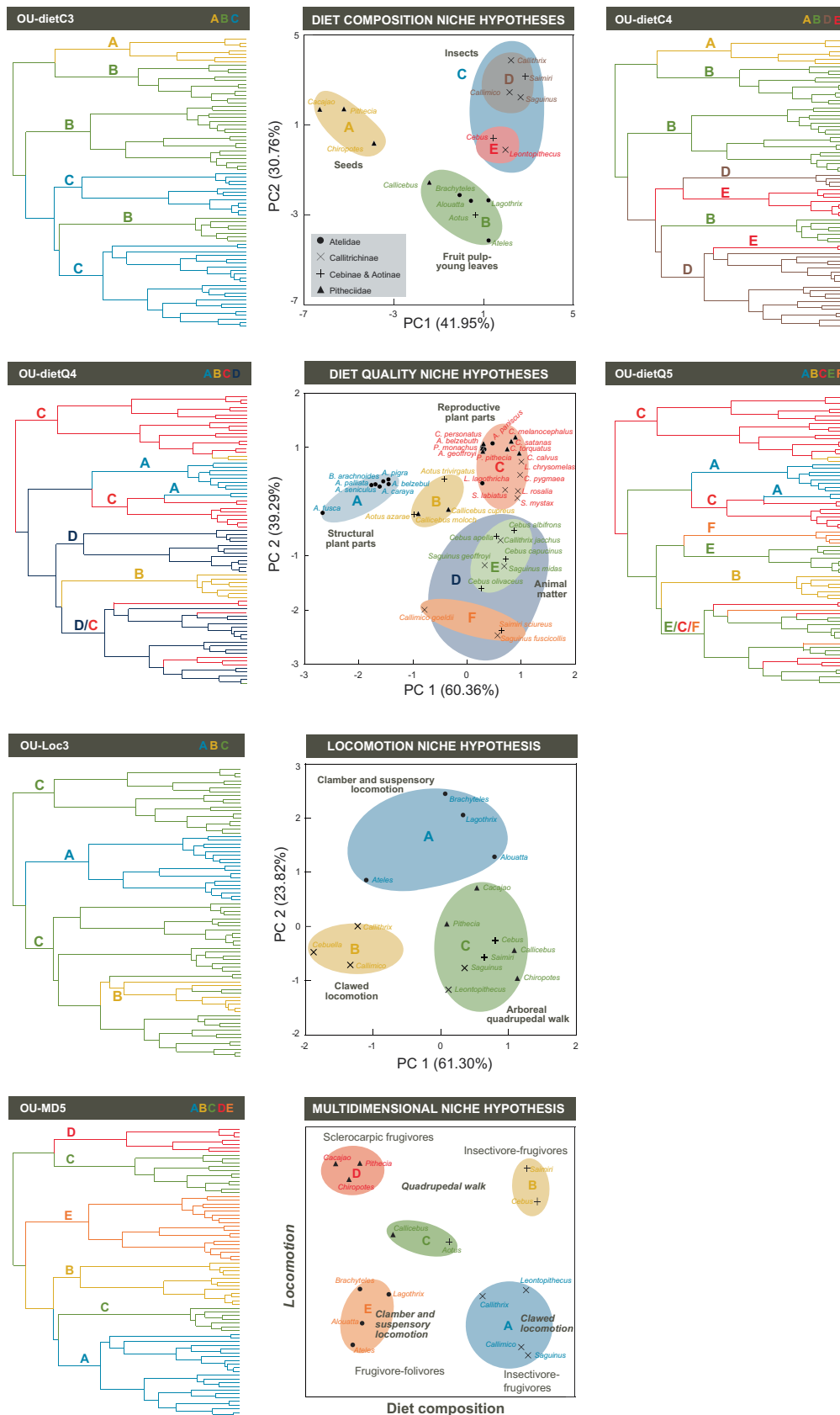
comparison. Taking into consideration the proposed phylogenetic relationships of the fossils with extant clades (Rosenberger, 1992; Fleagle, 1999; Fleagle and Tejedor, 2002; Rosenberger et al., 2009), body mass estimates for fossil platyrrhines, particularly La Venta genera, show a similar pattern of variation to that observed for each of the ecological categories of the OU-MD5 model (Fig. 5).

#### 4. Discussion

The process of diversification of the platyrrhines has been investigated phylogenetically and morphologically (e.g., Rosenberger, 1992; Fleagle, 1999; Marroig and Cheverud, 2001; Hodgson et al., 2009; Wildman et al., 2009; Perez et al., 2011, 2012, 2013). Many of these studies have interpreted the diversification of extant New World monkeys as an adaptive radiation in which the major lineages diversified early and into various alternative ecological niches that continue to exist today (see discussion in Rosenberger, 1992; Rosenberger et al., 2009; Tejedor, 2013). In all cases, the initial time of the diversification process of extant platyrrhine species is emphasized (e.g., Kay et al., 2008; Hodgson et al., 2009; Rosenberger, 2012; Perez et al., 2013). Previous works suggest that diversification of platyrrhines conforms to key expectations of a model of adaptive radiation—diversity or time-dependent lineage origination associated with phenotypic diversification of ecologically relevant traits such as body size. However, to our knowledge, this is the first statistical effort to model the phenotypic and lineage diversification of platyrrhines using a large and representative species sample and combining molecular phylogenies, fossil data and a comparative phylogenetic approach. In the following sections, we discuss our results on the pattern of lineage branching and phenotypic diversification, its relationships with previously hypothesized ecological variables and the importance of the previously suggested initial times of branching to understand this diversification process.

##### 4.1. Lineage diversification

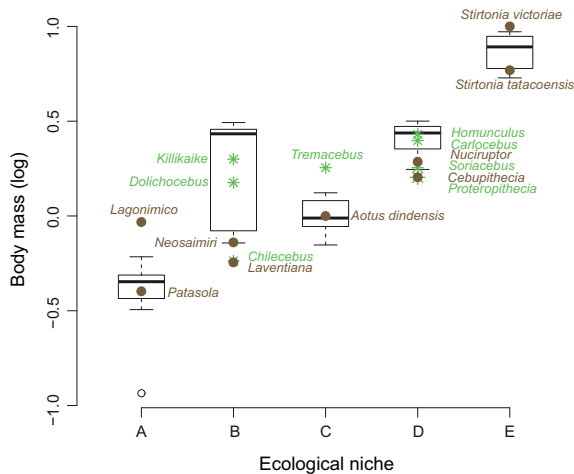
As it has been suggested often for platyrrhines (e.g., Hodgson et al., 2009; Wildman et al., 2009), a central prediction of the adaptive radiation model based on young radiations is that a large



**Fig. 4.** Adaptive regime models for evolution of body mass (OU models). Each species was assigned a niche based on a Principal Component analysis (PC, center figures) according to different hypotheses. Axes represent the principal component scores used to reduce the number of variables and avoid multicollinearity. Diet composition niche hypotheses: based on Norconk et al. (2009) diet data. Diet quality niche hypotheses: based on Allen and Kay (2012). Locomotion niche hypothesis: based on Youtatos and Meldrum (2011). Multidimensional niche hypothesis: based on Rosenberger (1992). Note that this hypothesis is not based on a PC analysis. Ancestral states in the trees were reconstructed using a maximum likelihood criterion. See text for details on each model.

**Table 2**  
Performance of alternative models of body mass evolution in the platyrrhine diversification. Models were fit over 100 trees randomly drawn from the post burn-in fraction of the BEAST analysis. Refer to text for description of models. AICc: Median and standard deviation (SD, in parentheses) for Akaike Information Criterion scores corrected for sample size. ΔAICc: difference between each model median AICc score and the best fitting model AICc score; wAICc: weighted AICc. α: median and SD for the strength of selection parameter estimation (see Methods).

Model	AICc	ΔAICc	wAICc	α
OU-MD5	488.23 (9.58)	0	0.9988	1.91 (1.06)
OU-Loc3	503.48 (13.17)	14.24	0.0008	0.27 (0.24)
OU-DietC4	504.61 (13.44)	15.37	0.0004	0.23 (0.26)
BM	509.48 (13.48)	20.24	0	–
OU-DietC3	512.97 (12.82)	23.73	0	0.12 (0.18)
OU-DietQ4	514.14 (12.77)	24.90	0	0.13 (0.20)
OU-DietQ5	515.77 (12.85)	26.53	0	0.13 (0.20)
OU1	516.76 (12.78)	27.52	0	0.06 (0.07)



**Fig. 5.** Log body mass for 78 extant species and fossil genera of platyrrhine monkeys following the multidimensional niche hypothesis (Rosenberger, 1992; OU-MD5, see text and Fig. 4). Fossil genera were assigned to each category according to proposed phylogenetic relationships based on morphology (Tejedor, 2008, 2013; Rosenberger et al., 2009); however, the phylogenetic relationships of Patagonia fossils are strongly disputed (Kay et al., 2008). Circles: La Venta fossils; asterisks: Patagonian fossils.

number of lineages are accumulated during the early stages of a clade’s evolutionary history, followed by a slowdown in species origination rates (Gavrillets and Losos, 2009; Losos and Mahler, 2010). Contrary to the previous proposals, our study did not find evidence of a rapid lineage accumulation in the phylogenetic tree of extant platyrrhine species. However, it has been repeatedly argued that high extinction rates and other factors might erase the signal of a decrease in lineage diversification rates estimated from phylogenies based on extant species, and that including information from the fossil record is thus essential to account for this (Pybus and Harvey, 2000; Rabosky and Lovette, 2008b; Quental and Marshall, 2010; Slater et al., 2012). In this sense, in our study the fossil-based diversity curve seems to show a slowdown in diversification rates toward present times (Fig. 2). When the oldest known fossil lineages (mostly from Patagonia) are considered, the number of lineages increases noticeably compared to those inferred to exist at that time from the molecular phylogeny, and an early pulse (approximately between 20 and 15 Ma) in the origination of platyrrhine lineages may become observable (Fig. 2). Moreover, diversity levels through time estimated from the fossil record are likely underestimated. On the other hand, the absence of a meaningful correlation between the number of fossil genera and platyrrhine-bearing rock formations suggests that this pattern is

paleontologically robust and that the platyrrhines present a small but representative fossil record. The observed pattern in the extant diversity curve may be linked to the extinction of the Patagonian primates or their retraction towards the northwest after 15 Ma (Middle Miocene; Tejedor, 2013). Platyrrhines are climate-sensitive mammals that certainly responded to the paleoenvironmental changes in South America after the Middle Miocene, when the environments shifted towards more arid and cooler conditions in Patagonia and the current configuration of Andes and Amazonian originated, generating the extinction of numerous lineages within (Rosenberger et al., 2009) or outside the extant main clades (Kay et al., 2008). Globally, these findings may suggest that high extinction levels played a key role in shaping the extant assemblage of platyrrhine species, and that the observed lineage diversity pattern can be reconciled with the predictions of the adaptive radiation theory only when considering that a significant part of the early platyrrhine diversity became extinct. On the other hand, the observed slowdown in diversification rates near present times, even when incomplete taxa sampling was considered, may be linked to our inability to detect recent lineage splitting events. In this sense, this rate slowdown at Pleistocene times has also been recovered in a recent analysis of a phylogeny of all primates (Springer et al., 2012) in which different taxonomic arrangements were considered, thus further indicating that evolutionary relevant splitting events may be overlooked by our current taxonomic criteria.

4.2. Phenotypic diversification

Our results concerning the temporal pattern of body mass variation are generally consistent with the expectation that the size variation was partitioned among subclades early in the phylogenetic history of the platyrrhines. The plot in Fig. 3 shows how size disparity is high during the early branching process, probably related to changes in ecological conditions, such as ecological opportunity (Harmon et al., 2003). Strikingly, the magnitude of size disparity during the early branching process of platyrrhines is unusually high compared with most previous studies we are aware of (e.g., Harmon et al., 2003; Slater et al., 2010; Derryberry et al., 2011; Weir and Mursleen, 2013), confirming the distinctiveness of the platyrrhine radiation (Delson and Rosenberger, 1984).

The AIC analysis used to test whether body mass evolved according to a stochastic model or to the occupation of different ecological niches shows interesting results. Particularly, Brownian motion, the non-adaptive and simplest (i.e., with fewer parameters) model, has limited support (Table 2). The models of phenotypic diversification within each dietary and locomotion niche (OU-dietQ, OU-dietC and OU-Loc3 models, Fig. 4) exhibit poor performance with respect to other models (Table 2). The model of phenotypic diversification during differentiation of the main lineages and subsequent evolutionary stasis within the multidimensional ecological niches (OU-MD5 model; Rosenberger, 1992; Rosenberger et al., 2009) has the best performance (Table 2). These results differ from previous works pointing out that platyrrhine size diversification is mainly related to diet variation (e.g., Marroig and Cheverud, 2001; Perez et al., 2011). Conversely, we show that the diet ecological dimension alone is not enough to explain the platyrrhine body mass diversification. These outcomes support a more complex scenario where platyrrhine evolution is likely related to size changes among the main lineages linked to a multidimensional niche (Rosenberger, 1980, 1992).

Moreover, size variation among the platyrrhine fossil species show a similar pattern of variation—particularly the most complete La Venta fossil assemblage—to that obtained analyzing the extant species. This supports the notion of a niche filling at La Venta times, as extant species body size partitioning is already evident in ancient lineages. However, the interpretation of this result is



highly dependent on the assignment of fossil species to the extant platyrrhine clades (see below). Taken together, this results may be suggestive of the early platyrrhine lineages diversifying in sympatry, as intraclade competition probably constrained body size evolution.

Functional studies pointed out that there are natural size thresholds dividing the platyrrhine dietary-locomotory niches (Rosenberger, 1980, 1992; Fleagle, 1999; Youlatos and Meldrum, 2011). The causal relationship among these variables is debated; for example, Hershkovitz, (1977) suggested that the platyrrhine radiation was an evolution of body size, with locomotor and dietary consequences, while other authors suggested the inverse relationship (e.g., Perez et al., 2011). In any case, a central prediction of the adaptive radiation hypothesis is that phenotypes diversify early in the branching process in connection with ecological dimensions (Schluter, 2000; Losos and Mahler, 2010). Thus, the ecological opportunity that could have existed during the early phylogenetic history of platyrrhines within South America probably was a very important factor promoting body size changes among the main lineages; after the initial great diversification, these lineages probably maintained relatively stable size classes linked to their ecological niches. Although ecological opportunity might have driven the early size changes, and narrowed the range of adaptive options later as niches became filled via intra-clade speciation, various additional factors could have shaped subsequent stasis, including stabilizing selection, genetic constraints owing to pleiotropy, developmental or functional constraints and the enduring isolation of the continent which lacked a diversity of other arboreal competitors, among others (Gavrillets and Losos, 2009; Wiens et al., 2010).

#### 4.3. The timing of platyrrhine diversification

Although obtaining absolute dates for the platyrrhine tree was not the main focus of this report since most of the analyses conducted here are only concerned with relative times, having an accurate estimation of the time of origin of the extant taxa is an important step for incorporating the paleontological information. In a recently published article (Perez et al., 2013), we used different approaches to confidently estimate the absolute time of origin of extant platyrrhines and their main lineages. Results showed that the most recent common ancestor of extant lineages probably existed between 21–29 to 27–31 Ma, according to two different methodologies, thus indicating that the oldest known Patagonian fossils fall well inside the age range of crown platyrrhines. These dates are broadly concordant with previous works (e.g., Opazo et al., 2006; Wilkinson et al., 2011). Particularly, if we accept these dates for the initial branching of extant platyrrhines, we could relate the shape of extant phylogeny and the lineages diversification results to the extinction and paleoenvironmental changes in South-America after the Middle Miocene, as is suggested by the analyses of extant and fossil platyrrhine lineages (Fig. 2; Hoorn et al., 2010).

Although the question of the Patagonian forms being extinct members of extant lineages or representatives of a separate radiation cannot be resolved only with dating approaches, the absolute dates obtained in Perez et al. (2013), and other previous works, allow for the first hypothesis to be plausible, thus linking the extant species tree with the fossils' temporal distribution. It has to be noted though, that other available divergence time estimations (e.g., Hodgson et al., 2009; Chiou et al., 2011) support a different interpretation of the relationship of the oldest fossil species with extant lineages (but see Perez et al. (2013) for a discussion). In this latter case our results about the shape of platyrrhine lineages and phenotypic diversification are still valid.

## 5. Conclusions

The temporal pattern of lineage accumulation and the mode of phenotypic evolution described here based on the extant platyrrhine species might seem contradictory since, as described above, one of the adaptive radiation scenarios predicts an early burst of species origination accompanied by a marked phenotypic diversification. Although both processes may be unlinked, when we also consider the fossil record information this contradiction diminishes as a pattern of an early burst of species diversification arises. This result also shows how the signature of an adaptive radiation may have been erased from the phylogenetic structure of extant species—perhaps by high rate of extinction among lineages after the earlier diversification—but be still retained in the patterns of phenotypic variation, as recent examples have suggested (e.g., Slater et al., 2010; Derryberry et al., 2011). Furthermore, body mass niches appear to have been filled very early in the history of the clade, with a pattern that is remarkably stronger than that seen in other groups. This point also is confirmed by the inclusion of information from the fossil record. Therefore, using a novel approach, as well as fossil and extant species, our analyses support the hypothesis that the platyrrhine tempo and mode of diversification appears to be characterized by an early and profound differentiation in body size related to a multidimensional niche model, followed by little subsequent change (i.e., stasis) in body size. It also suggests an early high rate of extinction among lineages within crown Platyrrhini.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ympev.2013.11.008>.

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