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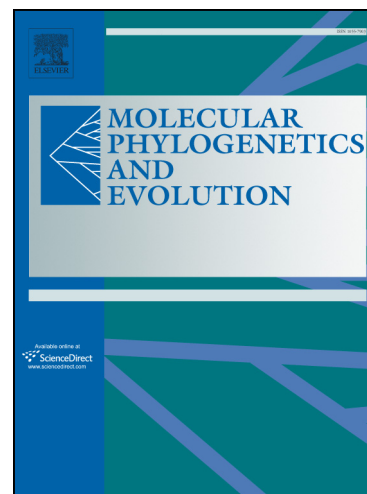
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1   **Modeling lineage and phenotypic diversification in the New World monkey**

2   **(Platyrrhini, Primates) radiation**

3

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17   Short title: Modeling platyrrhine diversification

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1   ABSTRACT

2   Adaptive radiations that have taken place in the distant past can now be more

3   thoroughly studied with the availability of large molecular phylogenies and comparative

4   data drawn from extant and fossil species. Platyrrhines are a good example of a major

5   mammalian evolutionary radiation confined to a single continent, involving a relatively

6   large temporal scale and documented by a relatively small but informative fossil record.

7   Here, we present comparative evidence using data on extant and fossil species to

8   explore alternative evolutionary models in an effort to better understand the process of

9   platyrrhine lineage and phenotypic diversification. Specifically, we compare the

10 likelihood of null models of lineage and phenotypic diversification versus various

11 models of adaptive evolution. Moreover, we statistically explore the main ecological

12 dimension behind the platyrrhine diversification. Contrary to the previous proposals,

13 our study did not find evidence of a rapid lineage accumulation in the phylogenetic tree

14 of extant platyrrhine species. However, the fossil-based diversity curve seems to show a

15 slowdown in diversification rates toward present times. This also suggests an early high

16 rate of extinction among lineages within crown Platyrrhini. Finally, our analyses support

17 the hypothesis that the platyrrhine phenotypic diversification appears to be characterized

18 by an early and profound differentiation in body size related to a multidimensional

19 niche model, followed by little subsequent change (*i.e.*, stasis).

20 *Keywords*: body size; adaptive radiation; fossil record; niche-filling

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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 (Gavrilets 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; Gavrilets 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 (Gavrilets 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 molecular phylogenies and comparative data from extant species (Nee, 2006; Gavrilets 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 Marshal, 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 & Tejedor, 2002; Tejedor, 2008).

1 Morphological and phylogenetic studies have hypothesized that the diversification of

2 this monophyletic group was mainly linked to the action of deterministic-selective

3 factors related to ecological variables (Rosenberger, 1992; Marroig and Cheverud, 2001;

4 Rosenberger et al., 2009). However, there is no general agreement about the main

5 ecological dimension —*e.g.*, diet, locomotion or a multidimensional niche— behind the

6 platyrrhine diversification (Rosenberger, 1992; Allen and Kay, 2011; Youlatos and

7 Meldrum, 2011; Perez et al., 2011). It has also been suggested that the marked

8 phenotypic diversification of platyrrhines occurred relatively quickly during the initial

9 branching process of the main extant clades in connection with ecological niche

10 opportunity (*i.e.*, an early-burst platyrrhine radiation), followed by a slowdown in

11 evolutionary rates which resulted in the widespread retention of the formative patterns

12 that are characteristic of these lineages (*i.e.,* evolutionary stasis; Rosenberger, 1992;

13 Rosenberger et al., 2009; Perez et al., 2011).

14   Although some recent studies of evolutionary radiations have included

15 information from the fossil record along with phylogenies and comparative data of

16 extant species in a mathematical modeling framework (Slater et al., 2010, 2012; Etienne

17 et al., 2011), such approach to the study of the dynamic processes of lineage origin and

18 extinction, and phenotypic diversification, has not been applied to explore the

19 platyrrhine evolutionary radiation. Here, we present comparative evidence using data on

20 extant and fossil species to explore alternative evolutionary models in an effort to better

21 understand the process of platyrrhine lineage and phenotypic diversification.

22 Specifically, we compare the likelihood of null models of lineages and phenotypic

23 diversification versus various models of adaptive evolution. Moreover, we explore the

24 main ecological dimension behind the platyrrhine diversification. If the platyrrhine

1   diversification conforms to the adaptive radiation theory, we expect that differentiation

2   of the major extant platyrrhine lineages was concentrated relatively early in the history

3   of the clade and that phenotypic variation —measured as body size— was partitioned

4   among subclades early in their phylogenetic history as well, as a major driver or

5   consequence of ecological niche partitioning and niche-filling. As a starting point, we

6   first estimate a chronophylogenetic tree for most extant platyrrhine species using

7   molecular data and Bayesian methods (Drummond et al., 2006). Then, using this tree

8   and comparative statistical methods we explore the pattern of lineage diversification

9   through time (Nee et al., 1992; Harmon et al., 2003; Ricklefs, 2007; Stadler, 2011a),

10   investigate the pattern of body size diversification through time and the fit of a series of

11   evolutionary models (Harmon et al., 2003; Butler and King, 2004). Finally, given that

12   the inference of the tempo and mode of diversification of a clade using only extant

13   species can be biased (Quental and Marshal, 2010; Slater et al., 2012), we compare the

14   results based on extant species with the estimated body masses and number of lineages

15   inferred from the platyrrhine fossil record. Summarizing, our work contributes to the

16   discussion of platyrrhine evolution and diversification in three different ways: 1) we

17   present one of the most complete molecular phylogenies of extant platyrrhine species to

18   date, sampling published data on 108 taxa and estimating a chronophylogenetic tree for

19   78 putative "good" species; 2) we mathematically model the pattern of lineage and

20   phenotypic diversification of the platyrrhine clade; and 3) we combine data about extant

21   and fossil species in a novel way not employed before in studies of the platyrrhines to

22   better understand the process of their diversification.

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1 **2. Materials and methods**

2 *2.1. Molecular divergence among species and phylogenetic inference*

3   Phylogenetic trees are used in almost every branch of evolutionary biology. In

4 particular, in comparative analyses they are needed to avoid misinterpreting historical

5 contingencies as causal relationships and to understand the patterns of diversification

6 (Nee, 2006; Losos, 2011; Yang and Rannala, 2012). In our study, the phylogenetic tree

7 itself is not of direct interest but it is a necessary first step for the following statistical

8 comparative analyses. Previous phylogenetic studies have estimated the platyrrhine

9 phylogenetic tree using ca. 50% (58 species, Chatterjee et al., 2009; or 64 species,

10 Perelman et al., 2011) or 60% (73 species, Fabre et al., 2009) of species recognized by

11 Groves (2005). However, most of the methods in comparative analyses assume that a

12 large fraction of the extant species in the clade under study are included in the dataset

13 (Pybus and Harvey, 2000; Ricklefs, 2007; Cusimano et al., 2012). On the other hand,

14 the use of many different definitions of species in primate systematics has led to a

15 fluctuating taxonomy in platyrrhines (e.g. Groves, 2004, Rylands et al., 2011) and

16 concerns on taxonomic inflation have arisen (Rosenberger, 2012). Since speciation

17 events are not instantaneous, the decision on to how finely distinguish lineages is rather

18 arbitrary (Ricklefs, 2007). For this reason, we decided to set up a reproducible criterion

19 for distinguishing species based on a minimum molecular divergence threshold. A total

20 of 108 platyrrhine species and subspecies were initially considered for analysis based on

21 the availability of DNA sequences on the Genbank database (Supplementary Table A.1).

22 Cytochrome *b* (CytB) DNA sequences were downloaded from Genbank for 90

23 specimens (based on availability) that were previously accepted as valid species or

24 subspecies in the platyrrhine literature (Groves, 2005). We estimated molecular distance

1   among the 90 specimens within each genus using Mega 5 (Tamura et al., 2011) and

2   established a likely point (3%) of minimum divergence among species (Fouquet et al.,

3   2007; Clemente-Carvalho et al., 2010). After this procedure, we excluded taxa with low

4   molecular divergence (mainly subspecies) and considered as full species those taxa

5   previously regarded as subspecies that were above the distance threshold. Specifically,

6   26 taxa were excluded from analysis based on the existence of a low molecular distance,

7   because they probably represent geographic variants of other species included in the

8   dataset (Supplementary Table A.1). The final dataset included 78 species, as 14 taxa

9   from the Perelman et al. (2011) dataset that did not have an available CytB sequence

10   were included based on the fact that they are broadly recognized as full species. Another

11   four species were excluded because their large proportion of missing data could hinder

12   the analysis. Thus, our dataset comprised a great percentage (*ca.,* 80%) of the likely

13   extant platyrrhine species.

14   To estimate the chronophylogenetic tree for the 78 platyrrhine species we

15   analyzed the dataset obtained for the platyrrhine species and three outgroups (*Macaca*

16   *mulatta*, *Pan troglodytes*, *Homo sapiens*) from GenBank (see Wildman et al., 2009, and

17   Perelman et al., 2011). The analyzed dataset is a DNA concatenated matrix for 81

18   species with a total of 25,361 bp, including 15 selected nuclear genes from Perelman et

19   al. (2011) with few missing data, and 11 non-coding sequences from Wildman et al.

20   (2009) (Supplementary Table A.2). The dataset also includes IRBP and ξ-globin genes

21   and four mitochondrial sequences (CytB, 16s, 12s and COxII). Several available gene

22   sequences (*e.g.* from Perelman et al., 2011) were not included in our phylogenetic

23   estimation because a great number of species lacked data for those genes. The

24   sequences of each gene were aligned using ClustalW and manually corrected with

1   BioEdit 7.0.0 software (Hall, 2004). Accession numbers for the mitochondrial, IRBP

2   and ξ-globin sequences are shown in Supplementary Table A.1.

3   We performed a concatenated Bayesian analysis based on the molecular dataset

4   to estimate chronophylogenetic relationships among the 81 primate species. jModelTest

5   0.1 (Posada, 2008) was employed to determine the most appropriate model of sequence

6   evolution for each analyzed gene sequences estimated under the Akaike Information

7   Criterion with correction for sample size (AICc). The best fit models for studied genes

8   are shown in the Supplementary Table A.2. The Bayesian chronophylogenetic analysis

9   was performed using BEAST v1.6.1 (Drummond and Rambaut, 2007). The analysis was

10   carried out using Markov Chain Monte Carlo (MCMC) simulations for 200,000,000

11   generations and a sample frequency of 20,000. The convergence was determined using

12   the program Tracer v1.5 (Rambaut and Drummond, 2007) and the first 1,250 sampled

13   trees were excluded. We used a relaxed molecular clock model, which allows

14   substitution rates to vary across branches according to an uncorrelated lognormal

15   distribution (Drummond et al., 2006; Drummond and Rambaut, 2007). Six fossil

16   calibrations were selected (see Perez et al., 2013). Fossil calibration for *Homo-Pan*

17   divergence (minimum time 5.7 Ma, maximum time 10 Ma; LogNormal distribution

18   with offset 5.7, mean 0.5 and standard deviation 0.5) and Anthropoidea (minimum time

19   33.70 Ma, maximum time 65.80 Ma; LogNormal distribution with offset 33.7, mean 2.4

20   and standard deviation 0.55) were obtained from Benton et al. (2009). Minimum

21   divergence time of Alouattinae, Cebinae and Aotinae were set at 12.5 Ma, based on

22   *Stirtonia, Neosaimiri* and *Aotus dindensis*, three fossils attributable to Alouattinae,

23   Cebinae and Aotinae, respectively (Kay et al., 2008; Tejedor, 2008). We used a

24   LogNormal distribution with offset 12.5, mean 1.8 and standard deviation 0.4 for the

1   Alouattinae, Cebinae and Aotinae constraints. Minimum divergence time of Pitheciidae

2   was set at 15.7 Ma (LogNormal distribution with offset 15.7, mean 1.5 and standard

3   deviation 0.5), based on *Proteropithecia neuquenensis*, a fossil attributable to

4   Pitheciidae (Kay et al., 1998). Maximum divergence time was set at 26 Ma, based on

5   the absence of Pitheciidae, Alouattinae, Cebinae and Aotinae fossils in or previous to

6   the Deseadan fauna of Salla, Bolivia, and other South American formations of the same

7   age. Both minimum and maximum calibration bounds were set to the probability that

8   the true divergence time outside the bounds is small, but non-zero (dos Reis et al., 2012;

9   Perez et al., 2013). Although a calibrated tree could be important for discussing some

10   aspects of the results, the following analyses are insensitive to the total length of the

11   tree, *i.e.* based on relative times (see discussion below). We computed the maximum

12   clade credibility (MCC) tree in TreeAnnotator 1.4.8 (Drummond and Rambaut, 2007).

13   FigTree v1.3.1 was used to plot the phylogenetic tree.

14

15   *2.2. Lineage diversification pattern analysis*

16   The number of species in a clade is the result of speciation and extinction

17   processes acting since the origin of that clade. The most direct way of studying this

18   diversity dynamic is to analyze the fossil record. However, the information contained in

19   molecular phylogenetic trees of extant species allow us to estimate speciation and

20   extinction rates in the absence of an appropriate fossil record (Harvey et al, 1994; Nee et

21   al, 1994; Ricklefs 2007; Stadler, 2011a). This information can be recovered by

22   analyzing the fit of different mathematical models of diversification to the reconstructed

23   phylogeny.

24   Following this approach, we first quantitatively tested, using the widely used γ

1   statistic (Pybus and Harvey, 2000), whether the pattern of lineage diversification in the

2   platyrrhine tree departs from what is expected under the most simple model, Pure-Birth

3   (PB), in which each species has a constant probability λ (speciation rate) of generating

4   another species in each point in time and there is no extinction (Nee, 2006). Under this

5   model, the number of species N(t) after t units of time, starting from N(o) species is

6   expected to grow exponentially: $N(t) = N(o)e^{\lambda t}$. The γ statistic measures the difference

7   between the average sum of branch lengths between each internal node and the root and

8   the midpoint of the tree (Pybus and Harvey, 2000). This statistic has mean of 0 for trees

9   generated under a PB process, and significant negative values indicate a decelerating

10   lineage accumulation rate toward present times, or, in other words, that branching

11   events are concentrated disproportionally early in the phylogeny, as is expected in

12   scenarios of adaptive radiation (Gavrilets and Losos, 2009).

13   To further assess the diversification model that best explains the observed

14   diversity pattern and to estimate possible changes in diversification rates across the

15   platyrrhine tree we compared the fit, using the Akaike Information Criterion (AIC), of

16   the observed branching sequence to various models of lineage accumulation. AIC is

17   calculated as $-2\ell+2K$ where ℓ is the maximum likelihood value of the data and K is the

18   number of parameters in the model. AIC represents a compromise between fit and

19   complexity of the model (Burnham and Anderson, 2002). The tested models were the

20   following: (i) PB and birth-death (BD; with parameters λ and μ [extinction rate]), as

21   constant-rates lineage accumulation models (although some of these models allow for

22   discrete λ shifts at specific points in time), and (ii) linear (DDL) and exponential (DDX)

23   density-dependent processes (as variable λ models with no extinction) (Rabosky and

24   Lovette, 2008a). Because the importance of extinction in shaping lineage origination

1   curves may be underestimated in the DDX and DDL models, we also included a

2   density-dependent model with a non-zero μ (DDD+E; Etienne et al., 2011). Density-

3   dependent models assume that the diversification rate (λ- μ) decreases as the lineage

4   population reaches some threshold density. If there are ecological limits to diversity, a

5   slowdown in lineage diversification rate would be expected in an adaptive radiation

6   scenario, since ecological opportunity may decrease as niches are filled (Rabosky and

7   Lovette, 2008b; Gavrilets and Losos, 2009; Ettiene et al., 2011). Also, since λ and μ

8   may have changed through time in response to different external factors, we also

9   included the recently proposed birth-death-shift (BDS) method by Stadler (2011b),

10   which can estimate whether and when a shift in rates occurred in the tree.

11   To account for incomplete sampling in our tree, we added the missing splitting

12   events to the analyzed tree, using the maximum likelihood λ and μ estimations from the

13   MCC tree, assuming that they occurred between 1 and 5 Ma. Using this approach, we

14   simulated 200 completely sampled trees and repeated the γ test and the model fitting

15   analyses (Cusimano et al., 2012). To also account for uncertainty in phylogenetic

16   reconstruction, analyses were repeated over a random sample of 100 trees drawn from

17   the post-burn in set of the BEAST analysis.

18   Finally, we visually inspected the time pattern of lineage accumulation by

19   plotting the number of ancestral lineages in our phylogenetic tree (in a log scale) versus

20   time (lineage-through-time plot, LTT; Ricklefs 2007), and compared it, using

21   simulations, to the expected pattern under the PB and BD (keeping track of extinct

22   lineages) models of diversification.

23   All analyses were conducted with the LASER (Rabosky, 2006), TreePar and

24   TreeSim (Stadler, 2011b,2011c), and APE (Paradis et al. 2004) packages for R 2.15.1

1   (R-Development Core Team, 2012).

2   In order to develop a generic origination trajectory for the fossil record, we

3   assembled geochronologic ages from the literature for 23 fossil platyrrhine genera

4   ranging from the Deseadan South American Land Mammal Age (SALMA) to the

5   Laventan SALMA, spanning from 26 to 11.8 Ma (Fleagle and Tejedor, 2002; Tejedor,

6   2008; Rosenberger et al., 2009). This data was then used to build origination estimates

7   (as numbers of genera confined to an interval plus those that cross the top boundary of

8   the interval; Foote, 2000) for each SALMA. To test for possible biases due to a poor

9   sampling of the fossil record, we applied the Spearman's rank correlation test as

10   described in Barrett et al. (2009). Briefly, the number of genera for each time slice (as

11   SALMAs) is expected to be positively correlated with the number of sampled

12   geological formations if sampling is affecting the shape of the origination curve.

13

14   *2.3. Phenotypic diversification analyses*

15   Platyrrhine monkeys are one of the most phenotypically diverse groups of living

16   primates. In particular, body size can range from roughly 100 grams in *Cebuella*

17   *pygmaea* to more than 10 kg in some atelids, with hypothesized ecological and

18   functional correlates. Thus, size, with all its intrinsic biological attributes, represents a

19   good example of the significant phenotypic diversity found in platyrrhines. We obtained

20   body mass data from the literature for the 78 extant species in our phylogeny and 15

21   fossil species (estimated from dental measurements and regression formulae;

22   Supplementary Table A.3). As male and female body mass were highly correlated (R^2=

23   0.986) among the living, species average body mass were used in the analyses. Male

24   and female data were pooled and log-transformed for all analyses.

1   To explore the time pattern of body mass variation, we first calculated a mean

2   relative disparity-through-time (DTT) plot for our phylogeny as described by Harmon et

3   al. (2003). Disparity is measured as $D = \Sigma(d_i)/n-1$ where d_i is pairwise Euclidean

4   distance between species and n is the number of species. First, disparity was calculated

5   for the entire platyrrhine clade, and then for each subclade. Disparity of each subclade

6   was standardized by dividing it by the disparity of the entire clade (relative disparity;

7   Harmon et al., 2003). Finally, the mean relative disparity for each point in time is

8   calculated for all subclades present at that time. Then we compared the observed body

9   mass disparity trough time to that expected if character evolution had followed a

10   Brownian motion (random) model of diversification by simulating body size evolution

11   1,000 times across our tree. Disparity values near 0 imply that most of the phenotypic

12   variation is partitioned among subclades rather than within each subclade (*e.g.* among

13   families, subfamilies, etc. rather than within each family, subfamily, etc.), whereas

14   values near 1 imply the opposite, indicating that subclades have independently evolved

15   to occupy similar places of morphological space (Harmon et al., 2003). Phenotypic

16   disparity is expected to be partitioned among subclades early in an early niche-filling

17   scenario of adaptive radiation. We also calculated the morphological disparity index

18   (MDI, Harmon et al., 2003), which quantifies the overall difference between the

19   observed and expected curves of disparity through time. Negative values are expected

20   under an adaptive radiation scenario, indicating lower subclade disparity than in the

21   random evolution model. The DTT analysis is implemented in the GEIGER package

22   (Harmon et al., 2008) for R.

23   Body mass is proposed to be strongly related to diet among platyrrhines

24   (Rosenberger, 1980, 1992; Marroig and Cheverud, 2001; Perez et al., 2011). To explore

1 this hypothesis, we applied the model selection approach of Butler and King (2004) to

2 compare the relative fit (measured with Akaike Information Criterion, AIC; see above)

3 of a stochastic model (Brownian motion, BM; Felsenstein, 1985) vs. seven models of

4 adaptive evolution (Ornstein-Uhlenbeck, OU; Hansen, 1997) to the body size variation.

5 In the BM model, body size evolves up the phylogeny via random walk and disparity

6 accumulates over time (Felsenstein, 1985). To model adaptive evolution in platyrrhine

7 size variation, we implemented seven Ornstein-Uhlenbeck models (OU; Hansen, 1997)

8 with either one, three, four or five optima. Particularly, we implemented a random walk

9 with a single stationary peak modeled as an Ornstein–Uhlenbeck process (OU1), such

10 that the size have a tendency to return to a median value (Hansen, 1997; Butler and

11 King, 2004), and six OU models with several optima formulated based on previous

12 hypotheses about the main ecological dimension behind the platyrrhine diversification.

13 The parameters of the evolutionary models were estimated by maximum likelihood: σ

14 (the intensity of the random changes in body size), α (the rate of changes toward an

15 optimum, or the strength of selection), θk (optimal value for the body size in each niche

16 optimum k).

17   To build the ecological models, or adaptive evolution hypotheses, we first

18 assigned each extant species to an ecological niche according to published works

19 (Rosenberger, 1992; Norconk et al., 2009; Youlatos and Meldrum, 2011; Allen and Kay,

20 2011), which describe different ecological groups. For uni-dimensional niche

21 hypotheses, data concerning diet composition (i.e., average annual percentages of plant

22 parts and insects in the diets of platyrrhine genera), diet quality (i.e., percentage of

23 structural plant parts [leaves and stems], reproductive plant parts [fruits, seeds, flowers,

24 nectar and gums] and animal matter in the diet) and locomotion (i.e., percentages of

1 arboreal quadrupedal walk, clamber and bridge, clawed locomotion and suspensory

2 locomotion) of platyrrhine genera and species were taken from Norconk et al. (2009),

3 Allen and Kay (2011) and Youlatos and Meldrum (2011), respectively. We then

4 calculated the principal component (PC) scores for each data set to reduce the number

5 of ecological variables and avoid multicollinearity; these PCs describe broad variation

6 in ecology (i.e., diet composition, diet quality and locomotion PCs) and were used to

7 group species in the different ecological niches (see below). It is important to remark

8 that although these niche models are based on real datasets, they are hypotheses

9 modelling the ancestral partition of platyrrhine niches. OU processes model the effect of

10 different selective regimes (ecological niches in this case) acting along the branches of a

11 phylogenetic tree and thus can be used to test for phenotypic diversification related to

12 ecological factors (Buttler and King, 2004), using data that is strongly phylogenetically

13 structured. In our analyses, character states for all internal branches were estimated

14 using a maximum likelihood approach. Finally, we explored body mass variation for the

15 ancient Patagonian and younger La Ventan (Colombia) fossil species in relation with the

16 best supported model. The OU analysis is implemented in the OUCH package (Buttler

17 and King, 2004) for R and was performed using the function OUaverage from Jaffe et

18 al. (2011).

19   To account for uncertainty in phylogenetic reconstruction, DTT and OU analyses

20 were performed over a random sample of 100 trees drawn from the post-burn in set of

21 the BEAST analysis.

22

23 **3. Results**

24   Our chronophylogenetic tree of platyrrhines is in general agreement with other

1   recent relationship estimations (Fig. 1; Opazo et al., 2006; Wildman et al., 2009;

2   Perelman et al., 2011; Perez et al., 2012), which supports the division of platyrrhines

3   into three monophyletic families (Atelidae, Cebidae and Pitheciidae) and suggests a

4   sister-group phylogenetic relationship between Atelidae and Cebidae (Opazo et al.,

5   2006; Wildman et al., 2009). We found *Aotus* to be phylogenetically related to

6   Callitrichinae, as did Perelman et al. (2011), but with low node support. The affinities of

7   *Aotus* are contentious as several molecular and morphological studies do not align

8   (Perez et al., 2012; Rosenberger and Tejedor, 2013). Because of this controversy, we

9   repeated all the statistical analyses varying the phylogenetic position of *Aotus* (as a

10   sister clade of Cebidae or Cebinae, as most studies report). The results were almost

11   identical (data not shown). Our results are also consistent with other molecular

12   assessments, which indicate the branches connecting the main platyrrhine lineages are

13   short, suggesting that the diversification of the main living platyrrhine clades could

14   indeed represent a rapid sequential radiation (but see below; Fig. 1; Opazo et al., 2006;

15   Wildman et al., 2009; Perez et al., 2012). The divergence time estimation suggest that

16   the last common ancestor (LCA) of extant platyrrhine primates existed at *ca.* 25 Ma,

17   with the 95% confidence limit for the node ranging from *ca.* 22.5–29 Ma. This result is

18   in contrast with other recent estimations, mainly to the influential Hodgson et al. (2009)

19   study, which suggested a LCA for crown platyrrhines at *ca.* 19 Ma.

20   Based on the γ statistic over 100 random trees drawn from the post-burn in set,

21   we found no evidence of a decelerating lineage accumulation rate toward present times

22   in the overall origination pattern of the platyrrhine clade (mean $\gamma = 0.493$, $p = 0.679$).

23   This result is robust to incomplete sampling (mean $\gamma = 0.290$, $p = 0.612$). Moreover, the

24   best supported model of lineage diversification was a pure-birth model with one rate

1   shift: an abrupt slowdown in speciation rates at 0.42 Ma (Table 1). Such recent rate

2   shifts may not be significant since incomplete species sampling and taxonomic inflation

3   can affect the shape of the most recent portion of the tree; however, when accounting for

4   incomplete sampling, a slowdown is also recovered at similar dates (Supplementary

5   Table A.4). Overall, this result shows, based on the extant species tree, that through

6   more than 99% of the time since its origins, crown platyrrhines diversified at a constant

7   rate. On the other hand, for the BD models, the maximum likelihood extinction rate is

8   probably underestimated, an acknowledged issue of diversification models. The absence

9   of an evident early pulse of lineage origination is also visually seen in the LTT plot for

10   extant species (Fig. 2). However, the fossil lineages origination curve seems to show a

11   different picture: a relatively rapid increase in the number of species followed by an

12   apparent slowdown in the origination rate, a pattern reminiscent of a density-dependent

13   diversification trajectory (Fig. 2, blue dashed line). This pattern is even stronger when

14   compared to simulated trees under the PB and BD models, even considering that the BD

15   curve includes extinct lineages (Fig. 2). Furthermore, this minimum estimated diversity

16   through time is likely to be very conservative, since it lacks a large fossil record from

17   the early Miocene of Amazonia, an area that was certainly populated with platyrrhine

18   representatives. The Spearman's correlation coefficient between genera per SALMAs

19   and the sampled geological formations showed a non-significant value (r=0.286, $p =$

20   0.65), suggesting that the observed increase in fossil genera over time is not due to

21   sampling bias.

22   Figure 3 shows the DTT plot for the body mass data. Average subclade disparity

23   along the entire history of the group is lower than expected under a BM model of mass

24   evolution. Values drop near 0 since the early divergence of the platyrrhines, and show

1 little variation over time. An MDI value of -0.255 also confirms quantitatively this

2 result. This outcome indicates a strong pattern where most size variation occurs among

3 the main platyrrhine subclades, which tend to occupy more isolated regions of body

4 mass morphospace, consistent with an early radiation and niche-filling scenario.

5   The PCs scores displayed in the figure 4 were used to group species in the

6 different ecological niches. Particularly, we defined 4 and 3 niches for diet composition

7 (OU-dietC4 and OU-dietC3, respectively); 5 and 4 niches for diet quality (OU-dietQ5

8 and OU-dietQ4, respectively); and 3 niches for locomotion (OU-Loc3; Fig. 4). Finally, a

9 multidimensional niche model was built based on the Rosenberger (1992) hypothesis;

10 this hypothesis is mainly a combination of diet composition and locomotion niche

11 dimensions and defines 5 broad ancestral ecological niches (OU-MD5; Fig. 4). The

12 overall fit of the models of body mass evolution to these hypothetical niches is shown in

13 Table 2. The OU model with 5 body mass optima (OU-MD5), following the

14 multivariate niche hypothesis of Rosenberger (1980, 1992), was the best supported, with

15 an Akaike weight well above the other candidate models, which performed poorly in

16 comparison. Taking into consideration the proposed phylogenetic relationships of the

17 fossils with extant clades (Rosenberger, 1992; Fleagle, 1999; Fleagle and Tejedor, 2002;

18 Rosenberger et al., 2009), body mass estimates for fossil platyrrhines, particularly La

19 Venta genera, show a similar pattern of variation to that observed for each of the

20 ecological categories of the OU-MD5 model (Fig. 5).

21

22 **4. Discussion**

23   The process of diversification of the platyrrhines has been investigated

24 phylogenetically and morphologically (*e.g.,* Rosenberger, 1992; Fleagle, 1999; Marroig

1   and Cheverud, 2001; Hodgson et al., 2009; Wildman et al., 2009; Perez et al., 2011,

2   2012, 2013). Many of these studies have interpreted the diversification of extant New

3   World monkeys as an adaptive radiation in which the major lineages diversified early

4   and into various alternative ecological niches that continue to exist today (see

5   discussion in Rosenberger 1992; Rosenberger *et al.* 2009; Tejedor, 2012). In all cases,

6   the initial time of the diversification process of extant platyrrhine species is emphasized

7   (*e.g.,* Kay et al., 2008; Hodgson et al., 2009; Rosenberger, 2012; Perez et al., 2013).

8   Previous works suggest that diversification of platyrrhines conforms to key expectations

9   of a model of adaptive radiation —diversity or time-dependent lineage origination

10   associated with phenotypic diversification of ecologically relevant traits such as body

11   size. However, to our knowledge, this is the first statistical effort to model the

12   phenotypic and lineage diversification of platyrrhines using a large and representative

13   species sample and combining molecular phylogenies, fossil data and a comparative

14   phylogenetic approach. In the following sections, we discuss our results on the pattern

15   of lineage branching and phenotypic diversification, its relationships with previously

16   hypothesized ecological variables and the importance of the previously suggested initial

17   times of branching to understand this diversification process.

18

19   *4.1. Lineage diversification*

20   As it has been suggested often for platyrrhines (*e.g.*, Hodgson et al., 2009;

21   Wildman et al., 2009), a central prediction of the adaptive radiation model based on

22   young radiations is that a large number of lineages are accumulated during the early

23   stages of a clade's evolutionary history, followed by a slowdown in species origination

24   rates (Gavrilets and Losos, 2009; Losos and Mahler, 2010). Contrary to the previous

1   proposals, our study did not find evidence of a rapid lineage accumulation in the

2   phylogenetic tree of extant platyrrhine species. However, it has been repeatedly argued

3   that high extinction rates and other factors might erase the signal of a decrease in

4   lineage diversification rates estimated from phylogenies based on extant species, and

5   that including information from the fossil record is thus essential to account for this

6   (Pybus and Harvey, 2000; Rabosky and Lovette, 2008b; Quental and Marshall, 2010;

7   Slater et al., 2012). In this sense, in our study the fossil-based diversity curve seems to

8   show a slowdown in diversification rates toward present times (Fig. 2). When the oldest

9   known fossil lineages (mostly from Patagonia) are considered, the number of lineages

10   increases noticeably compared to those inferred to exist at that time from the molecular

11   phylogeny, and an early pulse (approximately between 20 and 15 Ma) in the origination

12   of platyrrhine lineages may become observable (Fig. 2). Moreover, diversity levels

13   through time estimated from the fossil record are likely underestimated. On the other

14   hand, the absence of a meaningful correlation between the number of fossil genera and

15   platyrrhine-bearing rock formations suggests that this pattern is paleontologically robust

16   and that the platyrrhines present a small but representative fossil record. The observed

17   pattern in the extant diversity curve may be linked to the extinction of the Patagonian

18   primates or their retraction towards the northwest after 15 Ma (Middle Miocene;

19   Tejedor, 2012). Platyrrhines are climate-sensitive mammals that certainly responded to

20   the paleoenvironmental changes in South America after the Middle Miocene, when the

21   environments shifted towards more arid and cooler conditions in Patagonia and the

22   current configuration of Andes and Amazonian originated, generating the extinction of

23   numerous lineages within (Rosenberger et al. 2009) or outside the extant main clades

24   (Kay et al., 2008). Globally, these findings may suggest that high extinction levels

1 played a key role in shaping the extant assemblage of platyrrhine species, and that the

2 observed lineage diversity pattern can be reconciled with the predictions of the adaptive

3 radiation theory only when considering that a significant part of the early platyrrhine

4 diversity became extinct. On the other hand, the observed slowdown in diversification

5 rates near present times, even when incomplete taxa sampling was considered, may be

6 linked to our inability to detect recent lineage splitting events. In this sense, this rate

7 slowdown at Pleistocene times has also been recovered in a recent analysis of a

8 phylogeny of all primates (Springer et al., 2012) in which different taxonomic

9 arrangements were considered, thus further indicating that evolutionary relevant

10 splitting events may be overlooked by our current taxonomic criteria.

11

12 *4.2. Phenotypic diversification*

13   Our results concerning the temporal pattern of body mass variation are generally

14 consistent with the expectation that the size variation was partitioned among subclades

15 early in the phylogenetic history of the platyrrhines. The plot in the Figure 3 shows how

16 size disparity is high during the early branching process, probably related to changes in

17 ecological conditions, such as ecological opportunity (Harmon et al., 2003). Strikingly,

18 the magnitude of size disparity during the early branching process of platyrrhines is

19 unusually high compared with most previous studies we are aware of (*e.g.,* Harmon et

20 al., 2003; Slater et al., 2010; Derryberry et al., 2011; Weir and Mursleen, 2012),

21 confirming the distinctiveness of the platyrrhine radiation (Delson and Rosenberger,

22 1984).

23   The AIC analysis used to test whether body mass evolved according to a

24 stochastic model or to the occupation of different ecological niches shows interesting

1   results. Particularly, Brownian motion, the non-adaptive and simplest (*i.e.,* with fewer

2   parameters) model, has limited support (Table 2). The models of phenotypic

3   diversification within each dietary and locomotion niche (OU-dietQ, OU-dietC and OU-

4   Loc3 models, Fig. 4) exhibit poor performance with respect to other models (Table 2).

5   The model of phenotypic diversification during differentiation of the main lineages and

6   subsequent evolutionary stasis within the multidimensional ecological niches (OU-MD5

7   model; Rosenberger, 1992; Rosenberger et al., 2009) has the best performance (Table

8   2). These results differ from previous works pointing out that platyrrhine size

9   diversification is mainly related to diet variation (e.g., Marroig and Cheverud, 2001;

10   Perez et al., 2011). Conversely, we show that the diet ecological dimension alone is not

11   enough to explain the platyrrhine body mass diversification. These outcomes support a

12   more complex scenario where platyrrhine evolution is likely related to size changes

13   among the main lineages linked to a multidimensional niche (Rosenberger, 1980, 1992).

14   Moreover, size variation among the platyrrhine fossil species show a similar

15   pattern of variation —particularly the most complete La Venta fossil assemblage— to

16   that obtained analyzing the extant species. This supports the notion of a niche filling at

17   La Venta times, as extant species body size partitioning is already evident in ancient

18   lineages. However, the interpretation of this result is highly dependent on the

19   assignment of fossil species to the extant platyrrhine clades (see below). Taken together,

20   this results may be suggestive of the early platyrrhine lineages diversifying in simpatry,

21   as intraclade competition probably constrained body size evolution.

22   Functional studies pointed out that there are natural size thresholds dividing the

23   platyrrhine dietary-locomotory niches (Rosenberger, 1980, 1992; Fleagle, 1999;

24   Youlatos and Meldrum, 2011). The causal relationship among these variables is debated;

1   for example, Hershkovitz (1977) suggested that the platyrrhine radiation was an

2   evolution of body size, with locomotor and dietary consequences, while other authors

3   suggested the inverse relationship (*e.g.*, Perez et al. 2011). In any case, a central

4   prediction of the adaptive radiation hypothesis is that phenotypes diversify early in the

5   branching process in connection with ecological dimensions (Schluter, 2000; Losos and

6   Mahler, 2010). Thus, the ecological opportunity that could have existed during the early

7   phylogenetic history of platyrrhines within South America probably was a very

8   important factor promoting body size changes among the main lineages; after the initial

9   great diversification, these lineages probably maintained relatively stable size classes

10   linked to their ecological niches. Although ecological opportunity might have driven the

11   early size changes, and narrowed the range of adaptive options later as niches became

12   filled via intra-clade speciation, various additional factors could have shaped subsequent

13   stasis, including stabilizing selection, genetic constraints owing to pleiotropy,

14   developmental or functional constraints and the enduring isolation of the continent

15   which lacked a diversity of other arboreal competitors, among others (Gavrilets and

16   Losos, 2009; Wiens et al., 2010).

17

18   *4.3. The timing of platyrrhine diversification*

19   Although obtaining absolute dates for the platyrrhine tree was not the main focus

20   of this report since most of the analyses conducted here are only concerned with relative

21   times, having an accurate estimation of the time of origin of the extant taxa is an

22   important step for incorporating the paleontological information. In a recently published

23   article (Perez et al., 2013), we used different approaches to confidently estimate the

24   absolute time of origin of extant platyrrhines and their main lineages. Results showed

1   that the most recent common ancestor of extant lineages probably existed between 21–

2   29 to 27–31 Ma, according to two different methodologies, thus indicating that the

3   oldest known Patagonian fossils fall well inside the age range of crown platyrrhines.

4   These dates are broadly concordant with previous works (*e.g.,* Opazo et al., 2006;

5   Wilkinson et al., 2011). Particularly, if we accept these dates for the initial branching of

6   extant platyrrhines, we could relate the shape of extant phylogeny and the lineages

7   diversification results to the extinction and paleoenvironmental changes in South-

8   America after the Middle Miocene, as is suggested by the analyses of extant and fossil

9   platyrrhine lineages (Fig. 2; Hoorn et al., 2010).

10   Although the question of the Patagonian forms being extinct members of extant

11   lineages or representatives of a separate radiation cannot be resolved only with dating

12   approaches, the absolute dates obtained in Perez et al. (2013), and other previous works,

13   allow for the first hypothesis to be plausible, thus linking the extant species tree with the

14   fossils' temporal distribution. It has to be noted though, that other available divergence

15   time estimations (*e.g.,* Hodgson et al., 2009; Chiou et al., 2011) support a different

16   interpretation of the relationship of the oldest fossil species with extant lineages (but see

17   Perez et al. [2013] for a discussion). In this latter case our results about the shape of

18   platyrrhine lineages and phenotypic diversification are still valid.

19

20   **5. Conclusions**

21   The temporal pattern of lineage accumulation and the mode of phenotypic

22   evolution described here based on the extant platyrrhine species might seem

23   contradictory since, as described above, one of the adaptive radiation scenarios predicts

24   an early burst of species origination accompanied by a marked phenotypic

1   diversification. Although both processes may be unlinked, when we also consider the

2   fossil record information this contradiction diminishes as a pattern of an early burst of

3   species diversification arises. This result also shows how the signature of an adaptive

4   radiation may have been erased from the phylogenetic structure of extant species —

5   perhaps by high rate of extinction among lineages after the earlier diversification—but

6   be still retained in the patterns of phenotypic variation, as recent examples have

7   suggested (*e.g.,* Slater et al., 2010; Derryberry et al., 2011). Furthermore, body mass

8   niches appear to have been filled very early in the history of the clade, with a pattern

9   that is remarkably stronger than that seen in other groups. This point also is confirmed

10   by the inclusion of information from the fossil record. Therefore, using a novel

11   approach, as well as fossil and extant species, our analyses support the hypothesis that

12   the platyrrhine tempo and mode of diversification appears to be characterized by an

13   early and profound differentiation in body size related to a multidimensional niche

14   model, followed by little subsequent change (*i.e.*, stasis) in body size. It also suggests an

15   early high rate of extinction among lineages within crown Platyrrhini.

16

17   **Acknowledgments**

23

24

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14   **Figure Legends**

15   **Figure 1.** Maximum Clade Credibility (MCC) chronophylogenetic tree from the

16   BEAST analysis for 78 species of platyrrhine monkeys. Blue bars on the tree indicate

17   95% confidence intervals for estimated node ages. Support is indicated for nodes with <

18   0.8 posterior Bayesian probability. Shaded area shows estimated temporal range for

19   Patagonian fossil lineages.

20

21   **Figure 2**. Semi-logarithmic plots of lineage accumulation through time (LTT plot). Red

22   bold solid line: LTT plot based on the MCC tree of extant species. Dark green/light gray

23   solid and thin dashed lines: median and 95% confidence intervals for the expected

24   distribution under a PB or BD model, respectively, simulated using the maximum

1   likelihood rates estimated from the MCC tree. Extinct lineages are included in the BD

2   curve. Blue dashed line: observed fossil-based lineage origination curve. The number of

3   species in extinct taxa was estimated by applying a conservative mean species/genus

4   ratio of the living taxa (i.e., five) (Quental and Marshal, 2010). Difference between the

5   area under the MCC tree/Fossil curve and BD curve = 5.05/30.68 ; PB curve =

6   0.48/26.11. Area between Fossil and MCC curves = 25.63. For interpretation of the

7   color references in this figure, the reader is referred to the online version.

8

9   **Figure 3**. Relative disparity-through-time plot (DTT) for body mass in the 78

10   platyrrhine species. Solid red line shows disparity calculated for the MCC platyrrhine

11   tree. Black dashed line shows median expected disparity under the null hypothesis of

12   random evolution of body size (data generated by 1000 simulations). Shaded area shows

13   the 95% range for the simulations. Dark gray lines: disparity for 100 trees randomly

14   sampled from the post-burn in fraction of the BEAST analysis. For interpretation of the

15   color references in this figure, the reader is referred to the online version.

16

17   **Figure 4.** Adaptive regime models for evolution of body mass (OU models). Each

18   species was assigned a niche based on a Principal Component analysis (PC, center

19   figures) according to different hypotheses. Axes represent the principal component

20   scores used to reduce the number of variables and avoid multicollinearity. Diet

21   composition niche hypotheses: based on Norconk et al. (2009) diet data. Diet quality

22   niche hypotheses: based on Allen and Kay et al. (2011). Locomotion niche hypothesis:

23   based on Youlatos and Meldrum (2011). Multidimensional niche hypothesis: based on

24   Rosenberger (1992). Note that this hypothesis is not based on a PC analysis.

1   Ancestral states in the trees were reconstructed using a maximum likelihood criterion.

2   See text for details on each model. For interpretation of the color references in this

3   figure, the reader is referred to the online version.

4

5   **Figure 5**. Log body mass for 78 extant species and fossil genera of platyrrhine monkeys

6   following the multidimensional niche hypothesis (Rosenberger, 1992; OU-MD5, see

7   text and Fig. 4). Fossil genera were assigned to each category according to proposed

8   phylogenetic relationships based on morphology (Tejedor, 2008, 2012; Rosenberger et

9   al., 2009); however, the phylogenetic relationships of Patagonia fossils are strongly

10   discussed (Kay et al., 2008). Circles: La Venta fossils; asterisks: Patagonian fossils.

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Pithecia pithecia
Pithecia irrorata
Pithecia monachus
Cacajao calvus
Cacajao melanocephalus
Chiropotes utahickae
Chiropotes chiropotes
Callicebus personatus nigrifrons
Callicebus personatus personatus
Callicebus coimbrai
Callicebus torquatus lugens
Callicebus torquatus torquatus
Callicebus donacophilus
Callicebus caligatus
Callicebus hoffmannsi
Callicebus brunneus
Callicebus moloch
Callicebus cupreus
Alouatta palliata
Alouatta pigra
Alouatta belzebul
Alouatta fusca
Alouatta caraya
Alouatta seniculus seniculus
Alouatta sara
Alouatta macconnelli
Lagothrix cana
Lagothrix lagotricha
Brachyteles hypoxanthus
Brachyteles arachnoides
Ateles chamek
Ateles paniscus
Ateles belzebuth
Ateles geoffroyi frontatus
Ateles hybridus
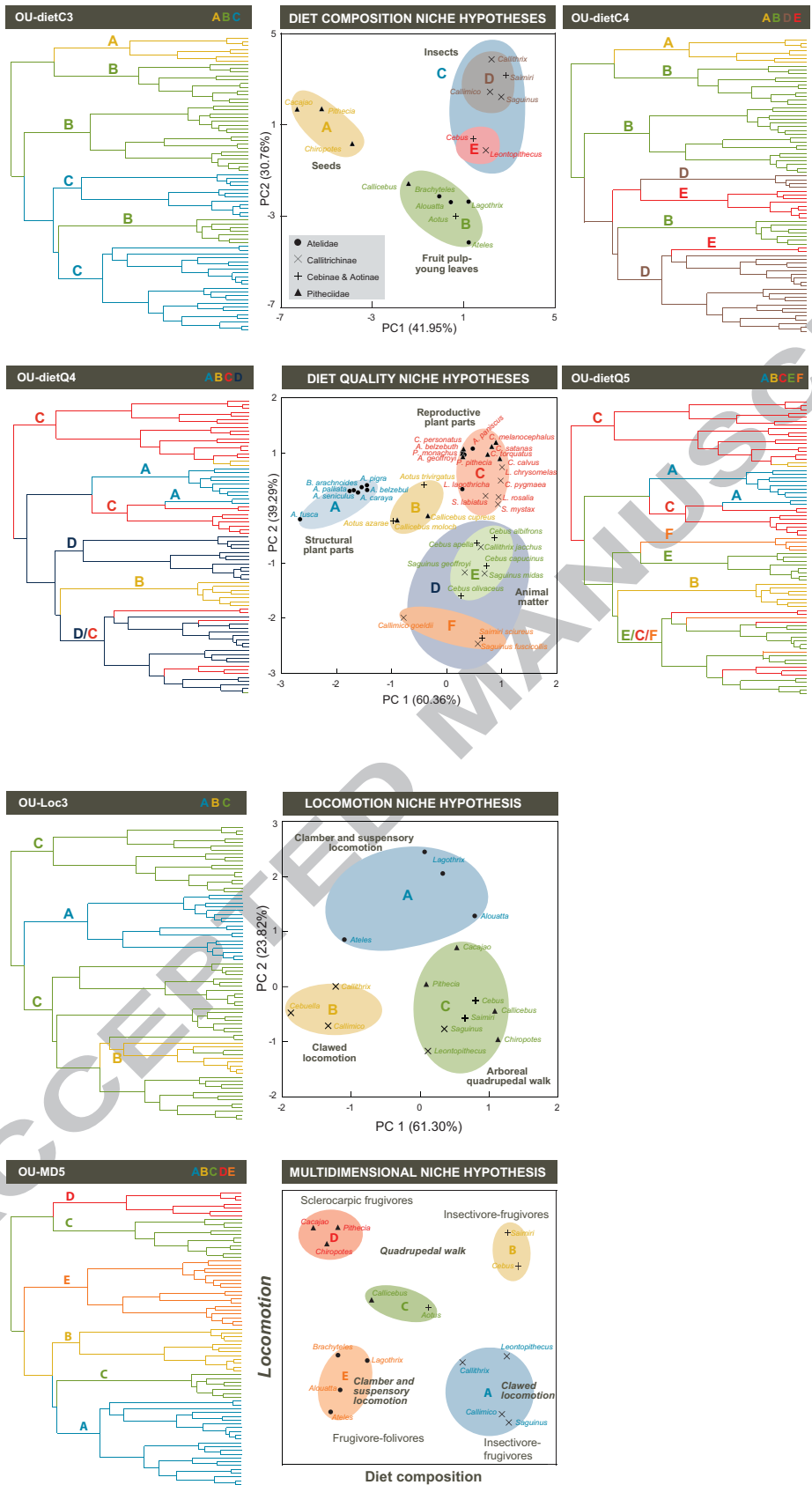*Ateles fusciceps*
Saimiri boliviensis boliviensis
Saimiri oerstedii oerstedii
Saimiri sciureus
Saimiri ustus
Cebus capucinus
Cebus albifrons
Cebus olivaceus
Cebus xanthosternos
Cebus apella
Cebus flavius
Cebus nigritus robustus
Cebus libidinosus paraguayanus
Aotus vociferans
Aotus trivirgatus
Aotus azarae
Aotus nigriceps
Aotus lemurinus lemurinus
Aotus nancymaae
Aotus lemurinus griseimembra
Leontopithecus chrysomelas
Leontopithecus rosalia
Callimico goeldii
Cebuella pygmaea
Mico argentatus
Mico humeralifer
Callithrix aurita
Callithrix geoffroyi
Callithrix kuhlii
Callithrix jacchus
Callithrix penicillata
Saguinus nigricollis nigricollis
Saguinus tripartitus
Saguinus melanoleucus
Saguinus fuscicollis fuscicollis
Saguinus imperator
Saguinus mystax
Saguinus labiatus labiatus
Saguinus oedipus
Saguinus geoffroyi
Saguinus midas
Saguinus bicolor
Saguinus martinsi

0.70
0.67
0.63
0.68
0.5
0.49
0.71
0.71
0.54

30.0   25.0   20.0   15.0   10.0   5.0   0.0
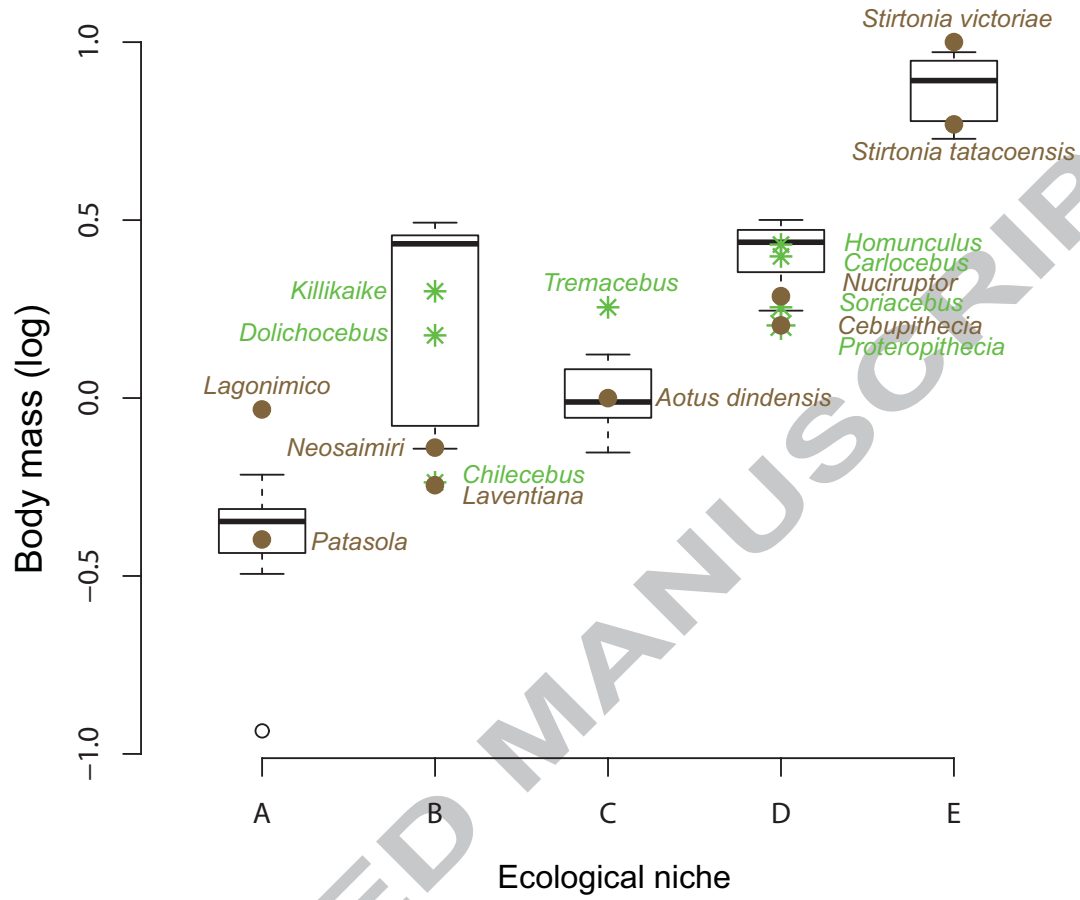
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1   Table 1. Mean parameter estimates and comparison of the fit of different lineage

2   diversification models to 100 trees randomly drawn from the post-burn in fraction of the

3   BEAST analysis (numbers in parentheses are standard deviations; SD). Ma: mega

4   annum. r: net diversification rate (speciation – extinction; per million years); a: turnover

5   (extinction/speciation). Rates go from past to present. AIC: Akaike Information

6   Criterion score; wAIC: akaike weights. For the BDS analysis, the best fitting model is

7   given. *calculated only for the MCC tree.

| 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*	-	0.52	0.34	-69.94	0.000

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1   Table 2. Performance of alternative models of body mass evolution in the platyrrhine

2   diversification. Models were fit over 100 trees randomly drawn from the post burn-in

3   fraction of the BEAST analysis. Refer to text for description of models. AICc: Median

4   and standard deviation (SD, in parentheses) for Akaike Information Criterion scores

5   corrected for sample size. ΔAICc: difference between each model median AICc score

6   and the best fitting model AICc score; wAICc: weighted AICc. α: median and SD for

7   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)

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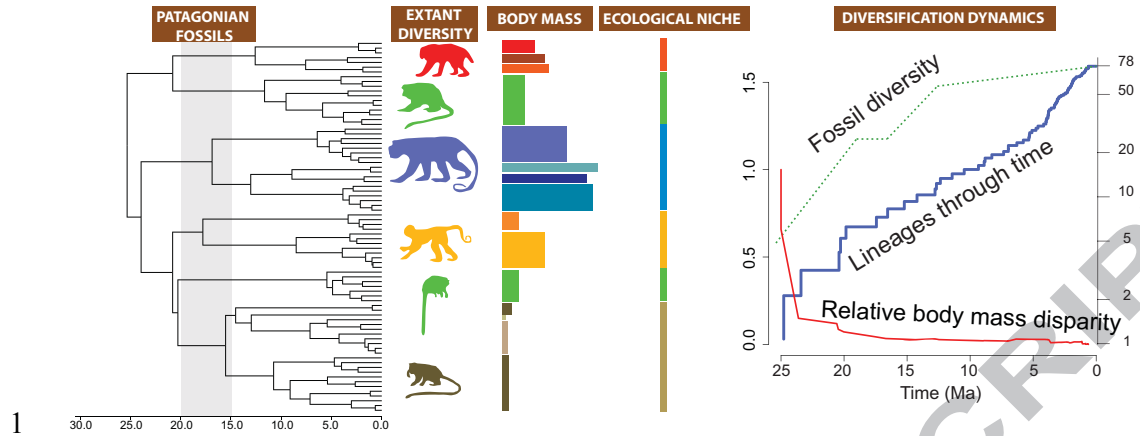
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3 Graphical abstract

4

1 **Highlights**

2   We estimate a dated platyrrhine phylogenetic tree for ca. 80% extant species.
3   Extant lineage diversification shows a constant rate of accumulation.
4   In contrast, body size diversification shows a pattern of early niche partition
5   followed by stasis.
6   Body size evolved according to the occupation of a multidimensional niche.
7   When oldest fossils are included, an early pulse of lineage origination appears.
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