



Early evolutionary diversification of mandible morphology in the New World monkeys (Primate, Platyrrhini)



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ARTICLE INFO

Article history:

Received 24 August 2016

Accepted 3 August 2017

Keywords:

Paleontology

Neontology

Phenotypic evolution

Mandible

Fossils

Neotropical

ABSTRACT

New World monkeys (order Primates) are an example of a major mammalian evolutionary radiation in the Americas, with a contentious fossil record. There is evidence of an early platyrrhine occupation of this continent by the Eocene–Oligocene transition, evolving in isolation from the Old World primates from then on, and developing extensive morphological and size variation. Previous studies postulated that the platyrrhine clade arose as a local version of the Simpsonian ecospace model, with an early phase involving a rapid increase in morphological and ecological diversity driven by selection and ecological opportunity, followed by a diversification rate that slowed due to niche-filling. Under this model, variation in extant platyrrhines, in particular anatomical complexes, may resemble patterns seen among middle–late Miocene (10–14 Ma) platyrrhines as a result of evolutionary stasis. Here we examine the mandible in this regard, which may be informative about the dietary and phylogenetic history of the New World monkeys. Specifically, we test the hypothesis that the Simpsonian ecospace model applies to the platyrrhine mandible through a geometric morphometric analysis of digital images of the jaws of extant and extinct species, and we compare these results to those obtained using a phylogenetic comparative approach based on extant species. The results show a marked phylogenetic structure in the mandibular morphology of platyrrhines. Principal component analyses highlight the morphological diversity among modern forms, and reveal a similar range of variation for the clade when fossil specimens are included. Disparity-Through-Time analysis shows that most of the shape variation between platyrrhines originated early in their evolution (between 20 and 15 Ma). Our results converge with previous studies of body mass, cranial shape, the brain and the basicranium to show that platyrrhine evolution might have been shaped by an early increase in morphological variation followed by a decelerated rate of diversification and evolutionary stasis.

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1. Introduction

New World monkeys, or platyrrhines, are one of the main clades of the order Primates and an example of a major mammalian evolutionary radiation in the Americas. The clade is considered to be monophyletic and has a relatively long evolutionary history of nearly 30 million years (Ma) spanning South and Central America, and the Caribbean (e.g., Rosenberger et al., 2009; Perez et al., 2013; Opazo et al., 2006). The fossil record of platyrrhines is contentious, but there is well supported paleontological evidence of their presence in the late Oligocene (ca. 26 Ma; Fleagle and Tejedor,

2002) or even in the late Eocene (>35 Ma; Bond et al., 2015). Therefore, the clade's earliest representatives probably invaded the continent by the Eocene–Oligocene transition, ~35 Ma, and evolved in isolation from the Old World primates from then on (e.g., Rosenberger, 2002; Tejedor and Rosenberger, 2008; Fleagle, 2013; Perez et al., 2013). While taxonomic interpretations differ, a picture of their diversity depicts a radiation within the Americas that evolved into several lineages that comprise approximately 125 extant species in 16 or 17 genera and five main clades (i.e., families or subfamilies; Wilson and Reeder, 2005; Perelman et al., 2011; Aristide et al., 2015a).

Together with the large species diversity, platyrrhines have occupied a wide range of ecological niches, showing considerable diversity in many ecologically interpretable traits (e.g., Terborgh, 1983; Kinzey, 1997; Fleagle, 2013). Particularly, the clade presents

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large variety in: a) diet composition, including different proportions of exudates, fruit pulp, seeds, leaves, and insects; b) diet quality, from low quality diets based mainly on leaves to higher quality diets based on protein-rich insects and seeds; c) social group size and organization, varying in group size from 2 to 200 individuals; and d) mating patterns, with monogamous, polyandrous, and polygynous systems. Moreover, they evolved a diversity of body sizes (with species ranging from ~100 g to ~10 kg [e.g., Hershkovitz, 1977; Ford and Davis, 1992; Rosenberger, 1992; Fleagle, 2013; Aristide et al., 2015a]), body shapes (Youlatos and Meldrum, 2011), dental morphologies (Rosenberger, 1992; Winchester et al., 2014) and cranial morphologies (Perez et al., 2011; Aristide et al., 2015b).

Previous studies have suggested that the marked morphological and ecological diversity of platyrrhines originated relatively early in the evolutionary history of the group, during the initial branching processes corresponding with the time of the origin of the main extant clades (see Delson and Rosenberger, 1984; Rosenberger, 1979, 1980, 1992, 2002). Specifically, these studies have postulated a local version of the Simpsonian eco-space model (Simpson, 1944; Benton, 2015; see Aristide et al., 2015a), where an early phase of rapid increase in morphological and ecological diversity – correlating with a high rate of evolutionary innovation – is driven by powerful selection and ecological niche opportunity (Losos and Mahler, 2010). In Simpson's model, after the initial phase, the rate of evolutionary diversification slows down as niches are filled. Some taxa may become extinct while new species may emerge within clades, mainly by subdividing niches already pioneered by the ancestral species. It has also been proposed that the anatomical and adaptive character of the extant platyrrhine genera and species may resemble the morphological and ecological variation seen in Miocene fossil forms due to long periods of relative evolutionary stasis (Rosenberger, 1979, 1992; Rosenberger et al., 2009; Aristide et al., 2015a).

Here, we analyze the mandible to test the above proposals. Rosenberger (1980, 1992) suggested that during the initial differentiation of platyrrhines, two fundamental patterns of jaw morphology arose (Fig. 1). As now seen among the extant forms, in the cebid clade (excluding *Aotus*, a genus now often classified as a cebid but then considered what modern classifications call a pitheciid), the lower border of the corpus is approximately horizontal, paralleling the occlusal plane, and the angular region forms a right angle (Fig. 1b). In atelids and pitheciids, and specifically in *Aotus*, the profile is different. The jaw deepens posteriorly and tends to become wider in the anteroposterior direction in the region of the mandibular angle (Fig. 1a). In extreme variations, as in pitheciids such as *Callicebus* (and occasionally *Aotus*), and in the atelid *Alouatta*, the mandible is greatly deepened below the molars and the gonial region is widened in depth and anteroposterior length.

These two patterns may be the ancestral conditions of the major clades (Rosenberger, 1980, 1992), as they predominate among the genera included in these clades. However, there are also exceptions in both mandibular morphologies that appear to converge on the alternative condition. For example, the cebid *Leontopithecus* presents a jaw profile that tends to deepen posteriorly, while *Chiropotes* and *Cacajao* tend to display the opposite silhouette; *Aotus*, if considered to be a cebid, would also be an example, having a more pitheciid-like morphology. There are alternative explanations for the evolution of patterns of mandibular morphology in platyrrhines. It is well established that the lower jaw is biomechanically and adaptively important, and presumed to reflect diet to certain degree (e.g., Hylander, 1979, 1985; Anapol and Lee, 1994; Ravosa, 1996; Ross et al., 2012; Meloro et al., 2015). Specifically for platyrrhines, Rosenberger (1980, 1992) pointed out the correspondence between mandible morphology and diet. The extant cebids have frugivorous and insectivorous feeding habits and have a light-weight feeding mechanism, while atelids have frugivorous-foivorous habits and show a heavy-duty masticatory system (Rosenberger, 1980). This suggests that the evolutionary pattern of the mandible does not correspond with a neutral (Brownian motion) expectation. Alternatively, previous work based largely on the living species pointed out that patterns of mandibular morphology track the phylogenetic history of platyrrhines (e.g., Rosenberger, 1977, 1992; Meloro et al., 2015; Terhune et al., 2015), suggesting that its diversification might not depend mainly on diet or biomechanical factors. This suggests that platyrrhine mandible evolution was a deeply complex process.

In particular, the timing and mode of evolution of such platyrrhine mandible morphological patterns are far from being understood, and the fossil record is the only direct source of evidence to explore them. For platyrrhines, the record remains relatively small but is nonetheless informative. The earliest platyrrhine fossils date to the late Eocene (*Perupithecus ucayaliensis*, found recently at Santa Rosa, Peru; Bond et al., 2015) and late Oligocene (*Branisella boliviana* and *Szalatavus attricuspis*, both found at Salla, Bolivia; Wolff, 1984; Rosenberger et al., 1991; Fleagle, 2013). The phylogeny of these fossils is not well determined. Moreover, the Patagonian region of Argentina and Chile has produced several platyrrhine fossils from early and middle Miocene deposits (e.g., *Chilecebus carrascoensis*, *Dolichocebus gaimanensis* and *Tremacebus harringtoni*, from the early Miocene; *Soriacebus ameghinorum*, *Carlocebus intermedius* and *Homunculus patagonicus*, from the middle Miocene). Here, too, while these taxa are undisputedly platyrrhine, their phyletic interrelationships are under debate (e.g., Kay, 1990; Kay et al., 2008; Rosenberger, 2010; Fleagle, 2013; Rosenberger and Tejedor, 2013). Due to this controversial taxonomy, in this study we do not include Patagonian fossil mandible specimens in the sample, considering only the generally accepted crown platyrrhine clade and its fossils.

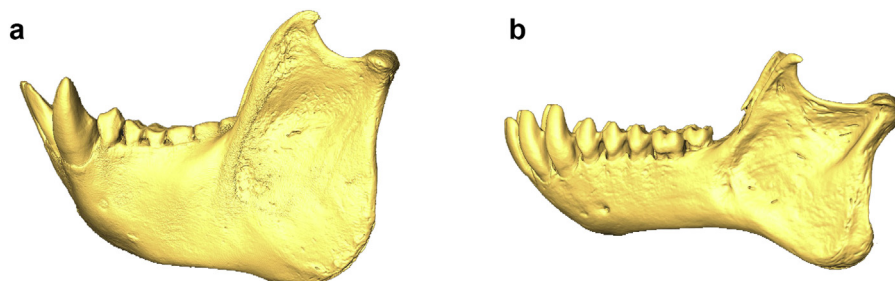


Figure 1. Image showing the two mandible shape patterns proposed by Rosenberger (1980, 1992) in lateral view. (a) An example of the atelid and pitheciid pattern represented by a *Cacajao calvus* mandible specimen. (b) An example of the cebid pattern represented by a *Callithrix penicillata* mandible specimen.

Younger platyrrhines found from the site of La Venta in the Magdalena River valley of Colombia, which date from the middle and late Miocene (10–14 Ma), present a different picture. This primate fauna is essentially of Amazonian aspect, including genera that probably represent the ancestors or close relatives of several living genera; they can certainly be allocated to existing low-level taxonomic clades – subfamilies and tribes (e.g., Hartwig and Meldrum, 2002; Rosenberger et al., 2009). The locality of La Venta has yielded several fossil platyrrhines, including *Nuciraptor rubricae*, believed to belong to the pitheciine clade (Meldrum and Kay, 1997), *Aotus dindensis*, the mandible morphology of which strikingly resembles that of extant *Aotus* (Setoguchi and Rosenberger, 1987), *Neosaimiri fieldsi*, similar to extant *Saimiri* (Takai, 1994), *Lagonimico conclutatus*, described by Kay (1994) as a giant tamarin, although Rosenberger (2002), based on mandible morphology, allocated this species to the pitheciine clade, and *Laventiana annectens*, similar to *Neosaimiri* and extant *Saimiri* (Rosenberger, 1984).

Platyrrhine evolution is also documented by several Pleistocene and Holocene fossils, mostly found in caves in Brazil and the Caribbean. There are well represented skeletal remains of the atelids *Cartelles coimbrafilhoi* (Halén and Rosenberger, 2013) and *Caipora bambuorum* (Cartelle and Hartwig, 1996; Fleagle and Tejedor, 2002; Fleagle, 2013), both from Brazil. Other Pleistocene and recent fossils have been recovered from different islands of the Caribbean, though their evolutionary relationships are disputed. Here we summarize our perspective of Caribbean monkey phylogeny (for alternative hypotheses see Kay, 2015). *Xenothrix mcgregori*, known from the latest-Pleistocene and perhaps recent remains found in Jamaica, is a difficult taxon, but prior studies (Rosenberger, 2002; Cooke et al., 2011) coalesce around the idea that *X. mcgregori* was a Jamaican monkey broadly related to *Aotus* (see Rosenberger et al., 2013). The Pleistocene–recent *Antillothrix bernensis* from the Dominican Republic is included in the pitheciid clade due primarily to its mandibular morphology (Rosenberger et al., 2013). The Pleistocene *Paralouatta varonai* (the genus also represented by a bone of Miocene age), from Cuba, was a large platyrrhine thought, based on the cranium, to be part of the alouattin clade (Rosenberger et al., 2009). Some authors suggest that these Caribbean primates belong to a single monophyletic clade, Xenothrichidae (see Hershkovitz, 1974; Macphee and Fleagle, 1991), while others support various dispersal events from the nearby mainland, with millions of years of independent evolution between Caribbean and mainland platyrrhines (e.g., Rosenberger, 2002).

In this study, we quantitatively examine the hypothesis of an early morphological diversification of the platyrrhines through an analysis of morphometric variation in the mandible of extant and fossil species, and compare the results to those obtained using a phylogenetic comparative approach based on extant species. Particularly, we explore the phylogenetic structure and the pattern of morphological diversification through time. To test the hypothesis of early morphological diversification and evolutionary stasis in mandibular morphology, we use a molecular phylogeny of the extant platyrrhines estimated using a dataset of multiple coding and non-coding DNA sequences (Perelman et al., 2011; Aristide et al., 2015a), geometric morphometric techniques to study shape variation of the mandible (Mitteroecker and Gunz, 2009), and phylogenetic comparative methods (Blomberg et al., 2003; Harmon et al., 2003). This combination of phylogenetic comparative methods applied to extant species and the direct study of the fossil and extant taxa is considered one of the most efficient approaches to explore the pattern of morphological diversification of a clade (Gavrillets and Losos, 2009; Alvarez et al., 2011).

2. Materials and methods

2.1. Samples

Two different datasets were used, both based on digital images (see protocol below) from which landmark coordinates were collected. The first dataset consisted of 252 adult mandibles from 32 extant species belonging to the five main platyrrhine clades (Atelidae, Pitheciidae, Callitrichinae, Cebinae and Aotinae; Table 1, Supplementary Online Material [SOM] Table S1). Aotinae, a controversial taxon usually including only the extant genus *Aotus*, is employed here to minimize confusion with current literature. See Rosenberger and Tejedor (2013) for an alternative view of its systematics and classification. The specimens were obtained from the Mastozoology Sections of Museo de La Plata (MLP), Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN), the Museu Nacional do Rio de Janeiro (MNRJ) and the American Museum of Natural History (AMNH). The second dataset included nine hemi-mandibles from fossil specimens obtained from images of casts and published reports (Table 2, SOM Table S2; Setoguchi and Rosenberger, 1987; Kay, 1994; Meldrum and Kay, 1997; Hartwig and Meldrum, 2002; Rosenberger et al., 2012, 2013). While our basic photographic protocol (see SOM) for producing digital images for this project was not followed in the publications cited, the hemi-mandible is a relatively flat structure in platyrrhines, therefore, the two-dimensional coordinate dataset faithfully captures comparable, pertinent shape information without bias (more information about error and reliability is given below). When possible, we examined more than one photograph of each fossil specimen, including a published photograph of the original specimen and an image of the cast taken for us, to be confident about

Table 1
Extant species sample used in the morphometric analyses.

Species	n	Clade	Institution ^a
<i>Aotus azarae</i>	18	Aotinae	MACN
<i>Aotus nigriceps</i>	5	Aotinae	MNRJ
<i>Alouatta caraya</i>	20	Atelidae	MACN
<i>Alouatta palliata</i>	2	Atelidae	MACN
<i>Ateles belzebuth</i>	3	Atelidae	MACN
<i>Brachyteles arachnoides</i>	4	Atelidae	MNRJ
<i>Brachyteles hypoxanthus</i>	2	Atelidae	MNRJ
<i>Lagothrix lagotricha</i>	3	Atelidae	MACN
<i>Leontopithecus rosalia</i>	6	Atelidae	MACN
<i>Callimico goeldii</i>	1	Callitrichinae	MNRJ
<i>Callithrix jacchus</i>	22	Callitrichinae	AMNH; MACN
<i>Callithrix penicillata</i>	4	Callitrichinae	MNRJ
<i>Leontopithecus chrysomelas</i>	4	Callitrichinae	MNRJ
<i>Mico argentatus</i>	1	Callitrichinae	MACN
<i>Mico chrysoleucus</i>	4	Callitrichinae	MNRJ
<i>Saguinus fuscicollis</i>	6	Callitrichinae	MACN
<i>Cebuella pygmaea</i>	1	Callitrichinae	MNRJ
<i>Cebus albifrons</i>	8	Cebinae	MACN
<i>Cebus apella</i>	4	Cebinae	MACN; MLP
<i>Cebus libidinosus</i>	20	Cebinae	MACN
<i>Cebus nigritus</i>	8	Cebinae	MACN
<i>Saimiri boliviensis</i>	9	Cebinae	MACN
<i>Saimiri sciureus</i>	2	Cebinae	MACN
<i>Cacajao calvus</i>	3	Pitheciidae	MNRJ
<i>Cacajao melanocephalus</i>	4	Pitheciidae	MNRJ
<i>Callicebus donacophilus</i>	12	Pitheciidae	MACN
<i>Callicebus personatus</i>	5	Pitheciidae	MNRJ
<i>Chiropotes albinus</i>	10	Pitheciidae	AMNH
<i>Chiropotes satanas</i>	28	Pitheciidae	AMNH
<i>Pithecia irrorata</i>	21	Pitheciidae	AMNH
<i>Pithecia pithecia</i>	8	Pitheciidae	AMNH
<i>Saguinus midas</i>	4	Pitheciidae	AMNH
TOTAL	252		

^a Abbreviations defined in text.

landmark placements. The fossils represent at most nine different genera (Table 2). Five of these species (*A. dindensis*, *L. conclutatus*, *L. annectens*, *N. fieldsi* and *N. rubricae*) were recovered at La Venta. These fossils can be easily allocated to modern platyrrhine groups (e.g., Hartwig and Meldrum, 2002). The other four species are Pleistocene to Holocene in age and come from the Caribbean or east central Brazil: *A. bernensis*, *X. mcgregori*; *P. varonai*; *C. bambuiorum*.

2.2. Phylogenetic data

Phylogenetic trees have direct or indirect interest for several branches of biology and anthropology (e.g., Lemey et al., 2009; Wiens, 2009; Yang and Rannala, 2012) and their estimation is a necessary first step for understanding the factors responsible for the ecological and phenotypic diversification of a clade (e.g., Felsenstein, 1985; Wiens, 2009; Losos, 2011). In this study, we based our phylogenetic analysis on the fossil-calibrated chronophylogenetic tree previously published in Aristide et al. (2015a), obtained using Bayesian methods on a concatenated dataset of 25,361 DNA bp, including coding and non-coding sequences and selecting six fossil calibrations.

2.3. Geometric morphometric analysis of extant and ancient specimens

Geometric morphometric techniques were used to study variation in the mandibular morphology of extant and fossil platyrrhine species. Two-dimensional coordinates were captured from digital images of the left hemi-mandible in lateral view, standardizing these images for mandible and camera lens plane position and distance to camera lens (See SOM; Zelditch et al., 2004). In some cases, the left side was missing or damaged. This issue was solved by using the reflected image of the right side. tpsDIG 2.12 software (Rohlf, 2015) was used to digitize 41 two-dimensional coordinates of landmarks and semilandmarks (Fig. 2). Since several fossil specimens preserved only the mandibular corpus, a subset of eight landmarks and 10 semilandmarks was used to characterize its shape (Fig. 2; see SOM for landmark and semilandmark definitions). The mandibular corpus, comprising the horizontal ramus and the alveolar region from incisors to molars (Atchley and Hall, 1991) and, in this study also including the region that many researchers call the symphysis, is a well-defined anatomical module that makes an important contribution to morphological variation of the full mandible (Cheverud et al., 2004; Alvarez et al., 2011).

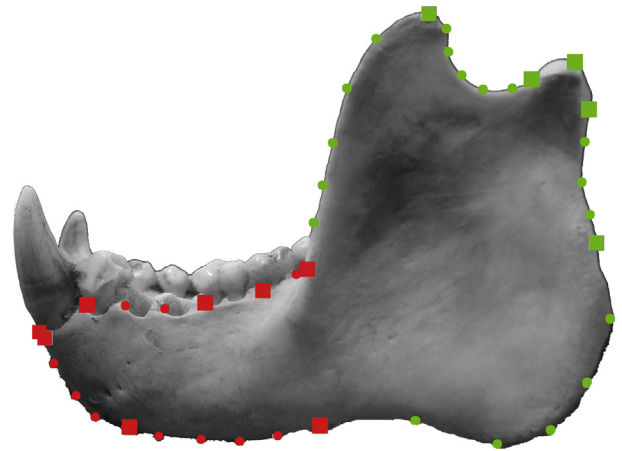


Figure 2. Mandible landmarks (squares) and semilandmarks (circles) recorded from New World monkeys using tpsDig. Red squares and circles were included in mandibular corpus analyses. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Once the coordinates were recorded, the geomorph package (Adams and Otárola-Castillo, 2013) for R (R Development Core Team, 2015) was used to align the landmarks and semilandmarks by means of Generalized Procrustes analysis and the sliding method (with bending energy criterion; Perez et al., 2006; Gunz and Mitteroecker, 2013). This allowed us to eliminate variation due to differences in scaling, rotation and position of the specimens (i.e., non-shape variation) and to estimate the consensus shapes for each species, evaluating shape differences among them. The Procrustes shape coordinates resulting from the alignment were analyzed using principal component analysis (PCA) to reduce morphospace dimensionality. A PCA consists of the generation of uncorrelated axes describing major tendencies in shape variation within the sample. The resulting axes are lineal combinations of the original Procrustes coordinates derived from a rigid rotation of the morphospace. In this way the coordinates are not distorted during computation (Mitteroecker and Gunz, 2009). The estimation of the PCA was carried out with the extant species' mean shape or consensus.

We also performed a PCA including extant and fossil specimens. It was estimated by projecting the fossil specimens onto the extant consensus species' principal component (PC) space. For this, we first estimated a Generalized Procrustes superposition of the mandibular corpus shape coordinates belonging to extant

Table 2

Fossil specimens used in the morphometric analyses.^a

Specimen	Site information	Date	Cast available	Photo source
<i>Aotus dindensis</i>	Locality 9–86 A, El Dinde area, Tatacoa Desert, Huila Department, Colombia.	Middle Miocene; 12–15 Ma	Yes; AMNH	Setoguchi and Rosenberger (1987) Kay (1994)
<i>Lagonimico conclutatus</i>	Locality 90, La Victoria Formation, Tatacoa Desert, Huila Department, Colombia.	Middle Miocene; ≈ 13.5 Ma	No	
<i>Laventiana annectens</i>	Masato Site, Villavieja Formation, La Venta Area, Huila Department, Colombia	Middle Miocene; 10–12.5 Ma	Yes; AMNH	Hartwig and Meldrum, 2002
<i>Neosaimiri fieldsi</i>	Honda Group, Villavieja Formation, La Venta Area, Huila Department, Colombia	Middle Miocene; 12–16 Ma	Yes; AMNH	Hartwig and Meldrum, 2002
<i>Nuciraptor rubricae</i>	Duke Locality 32, Honda Group, Villavieja Formation, La Venta Area, Huila Department, Colombia	Middle Miocene 12.8 ± 0.2 Ma	No	Meldrum and Kay (1997)
<i>Antillothrix bernensis</i>	La Jeringa Cave, Parque Nacional del Este, La Altagracia Province, Dominican Republic	Late Holocene; 3850 ± 150 BP	Yes; AMNH	Rosenberger et al. (2013)
<i>Caipora bambuiorum</i>	Toca da Boa Vista Cave, Bahia State, Brazil	Pleistocene/recent	No	Rosenberger et al. (2012)
<i>Paralouatta varonai</i>	Cueva Alta, Cuba	Early Quaternary	Yes, AMNH	Macphee and Horovitz (2008)
<i>Xenothrix mcgregori</i>	Long Mile Cave, Jamaica	Quaternary, until ≈ 1700 AD	No	Rosenberger (1977)

^a BP = Before Present; AMNH = American Museum of Natural History.

consensus species and fossil specimens all together, obtaining the Procrustes coordinates corresponding to both samples. We then subtracted the fossil specimens' coordinates and generated a PC space with the extant species only. This way, the obtained space represents the major patterns in mandible variation for the extant species only, without influence from the fossil species. As a final step, the shape data of fossil specimens were projected onto this PC space. To better describe the shape differences among extant and fossil species, we estimated a Minimum Spanning Tree (MST) based on the Euclidean distance (total shape variation) matrix and displayed it on the PC1 plus PC2 morphospace. Additionally, we calculated between-group PCs (Mitteroecker and Bookstein, 2011) to better describe the shape variation within species. In this analysis we used the consensus of extant species to generate the PC shape space and then projected all the specimens, both extant and fossils. All the procedures were performed using the geomorph (Adams and Otárola-Castillo, 2013) and stats package for R (R Development Core Team, 2015).

Finally, to examine the range of morphological variation in living and fossil taxa, we calculated Foote's disparity measurement (D , Foote, 1993; Neige, 2003) and the variance of the Procrustes distances (V), a measure similar to D . The D is estimated as the distance from the mean shape of each species to the consensus mean shape of all species. Conversely, the variance is calculated directly over the column of Euclidean distances between the studied species. Also, confidence intervals were obtained by means of bootstrap iterations, as implemented in the geomorph R package.

2.4. Measurement error

We assessed measurement error through Procrustean Randomization Test (PROTEST), a permutation test used for comparing multivariate data sets by means of a Procrustes statistic, minimizing the sum-of-squared differences between configurations in a multivariate space, followed by the randomization and permutation of values between sets and the posterior estimation of the statistical significance of the Procrustean fit (Peres-Neto and Jackson, 2001). We carried out four distinct PROTEST analyses to evaluate a) intra-observer error due to landmark and semilandmark digitizing; b) error associated with mandible orientation; c) differences between two or three-dimensional datasets; and d) error related to the use of images obtained from publications and fossil casts. For the intra-observer error estimation, a single set of 17 photographs of platyrrhine mandible specimens in lateral view (each corresponding to a different genus) was used to digitize landmarks and semilandmarks in two distinct sessions separated by a two week period. To test error due to orientation we digitized landmarks and semilandmarks in two datasets, containing the same 17 platyrrhine mandible specimens in each set, differing in their orientation: the first dataset was oriented aligning the sagittal plane in parallel with the camera lens, while in the second set the mandibular corpus was parallel to the lens. To analyze differences between the use of two or three-dimensional mandible samples (see Alvarez and Perez, 2012), we digitized landmarks and semilandmarks onto two datasets of 34 mandible specimens each (two per genus). The first set was three-dimensional, and the second sample was two-dimensional. For this analysis we employed a sample of Computed Tomography (CT) scans obtained in the Mastozoology Sections of Museo de La Plata (MLP), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN) and the Digital Morphology Museum of the Kyoto University Primate Research Institute (DMM, KUPRI). Finally, to test the error due to the use of images obtained from publications and fossil casts, we used two datasets containing the same specimens

but differing in the source from which they were obtained. One sample was based on original published images and the other was based on our own photographs of casts. We performed a Procrustes fit on the coordinates taken during each sampling and compared the ordinations produced by each. As a measure of association we used the sum of the squared residuals corresponding to each ordination (Gower, 1971; Perez et al., 2006). Finally, to test the statistical significance of the Procrustean fit we carried out the permutation procedure PROTEST (Jackson, 1995; Peres-Neto and Jackson, 2001). Procrustes analysis and PROTEST were implemented using geomorph (Adams and Otárola-Castillo, 2013) and vegan (Oksanen et al., 2014) packages for R v3.3.1.

2.5. Phylogenetic comparative analysis of extant specimens

We first tested for the association between size and mandible shape variation among extant species using a Phylogenetic Generalized Least-Square (PGLS) analysis, which takes into account the expected lack of independence among species (Martins and Hansen, 1997; Rohlf, 2001). We fit the PC scores of shape coordinates to the Log-Body Mass (Log-BM; Aristide et al., 2015a) using the regression model: $S = XB + e$, where S is the PC score matrix describing mean differences between species, X is the Log-BM matrix, B is the matrix of partial regression coefficients, and e is the error term. To account for phylogenetic non-independence, this regression analysis assumes that e has a covariance matrix (C) derived from the phylogenetic tree of the studied species (Martins and Hansen, 1997; Rohlf, 2001). The PGLS analysis was run using the package caper (Orme, 2013) in the software R.

In order to examine the relationship between phylogeny and phenotypic variation in the mandible, we measured the phylogenetic signal of jaw morphology among extant platyrrhine species. Phylogenetic signal is the tendency of more closely related species to be more similar with respect to a given trait than more distantly related species; expressed in another way, it is a measure of the statistical dependency between the trait value and the phylogenetic tree. Since we used multidimensional data (Procrustes shape coordinates), we estimated a multivariate generalization of Blomberg's K statistic, K_{mult} method, which is used for quantifying and evaluating phylogenetic signal in multidimensional traits like shape under a Brownian motion evolutionary model (Blomberg et al., 2003; Adams, 2014). We also estimated the Blomberg's K statistic on the scores from PC axes 1 and 2. The phylogenetic signal was calculated using the picante (Kembel et al., 2010) and geomorph (Adams and Otárola-Castillo, 2013) packages in R.

With the objective of visualizing changes in shape variables of the mandibular corpus and the hemi-mandible during phylogenetic history, we mapped and plotted the extant species PC1 scores on the estimated phylogenetic tree in .nwk format, estimating ancestral character states through a maximum likelihood (ML) based procedure, which assumes that characters evolve under a Brownian motion model. This way, two species will be expected to be different from one another in proportion to the time elapsed since sharing a common ancestor (Felsenstein, 1985). The ML estimate of the root is equivalent to the root node estimated during a contrasts algorithm, so, by re-rooting the tree at each node, ML at every node in the tree was calculated. The mapping of PC1 scores on the phylogenetic tree was carried out using the phytools (Revell et al., 2012) package for R.

To visualize the phenotypic variation pattern of the mandible within and among the platyrrhine clades through their phylogenetic history – including time and branching pattern – we generated a disparity-through-time (DTT) plot using a platyrrhine

chronophylogenetic tree in *.nwk* format and extant species PC scores, for PC1 and for PC1 and PC2 together. Disparity can be estimated using the mean Euclidean distances between species. It is calculated for each clade as a whole, and then for each subclade defined by a node in the phylogeny. Then, the relative disparity is calculated as the subclade disparity in relation to the whole disparity. Relative mean disparity – in other words the average of all relative disparities from all subclades whose ancestral lineages were present at the moment of divergence – was estimated for every divergence event through the phylogeny. Relative disparity values near to 0 imply that subclades contain relatively less variation than the clade's total variation. Values close to 1 imply that subclades include a substantial proportion of total variation of the clade (Harmon et al., 2003). In an early niche-filling scenario (i.e., the adaptive radiation or Simpsonian ecospace model) for platyrrhines, we would expect phenotypic disparity to be split among the main subclades (i.e., the subfamilies). The DTT analysis was performed using the *geiger* package (Harmon et al., 2008) for R.

3. Results

The results of the PROTEST procedure for measurement error associated with intra-observer error showed a statistical significance of the Procrustes fit between both ordinations (Fit Correlation value = 0.9865, $p < 0.001$), indicating that the differences between measurement sessions are not statistically significant. Moreover, our second PROTEST analysis testing measurement error related to distinct mandible orientations also showed high correlation between ordinations (0.9676, $p < 0.001$), suggesting the non-significance of such differences. Since the mandible is relatively flat yet still contains three-dimensional structure, we tested the error between 2D and 3D measurements with a PROTEST analysis as well. This result showed a Procrustes correlation of 0.9991 ($p < 0.001$; SOM Fig. S1), suggesting that the differences due to the number of dimensions registered is not significant. Finally, the results of the PROTEST analysis between published images and the photographs of fossil casts displayed a high correlation (0.9923; $p < 0.001$), suggesting that both datasets are useful for these morphometric analyses.

In the PC analysis based on the complete mandibles of the living species, the first two PCs explain about 64% of total variation (PC1: 47.39%; PC2: 16.89%; Fig. 3a). The major differences in morphology involve the changes in the relative size of angular region, which is smaller toward the most positive values of PC1. The mandibular corpus uncovers variation related to its dorsoventral height, which is more compressed for the most positive values of PC1. The subfamily Callitrichinae (specifically *Cebuella pygmaea*) is located on the extreme edge of PC1, though the cluster shows a large spread along both PC axes. On the opposite end of PC1 are the pitheciids and the atelids with a deeper mandibular corpus, combined with a larger angular region. The most negative values on PC1 belong to *Callicebus donacophilus* and *Alouatta caraya*. The Pitheciidae are located toward the positive end of PC2, while all Atelidae fall into negative values. The spread of Cebinae reflects a clear division between *Cebus* and *Saimiri* species, the latter showing more positive values on PC1 and negative values on PC2, while *Cebus* species exhibit intermediate values on PC1 and positive values on PC2. Also, *Saimiri* species fall within the Callitrichinae morphospace. Aotinae are located between Pitheciidae and *Cebus* species, with negative values on PC1 and positive values on PC2. *Aotus* exhibits a larger angular process, and a more dorsoventrally compressed mandibular corpus. The wide separation displayed between the two *Aotus* species is noteworthy, since *Aotus azarae* falls closer to pitheciids and *Aotus nigriceps* closer to cebids, suggesting that the two opposite phylogenetic hypotheses regarding its position within the

platyrrhines (see Rosenberger and Tejedor, 2013) are represented in the shape data. The PGLS results show that shape variation of complete mandibles (PC1–6 [~90% of shape variation]) is not strongly associated with variation in body size ($R^2 = 0.14$; $p = 0.02$), although the association is stronger when we consider the variation in PC1 ($R^2 = 0.45$; $p < 0.001$) or PC1 plus PC2 ($R^2 = 0.49$; $p < 0.001$).

The results of the PCA of the mandibular corpus of living species showed that the first two PCs explained ~65% of total variation (PC1: 35.83%; PC2: 29.85%; Fig. 3b). The most significant morphological differences are in the relative dorsoventral height of the mandibular corpus, which is relatively more compressed for the most positive values of PC1. The species' distribution along PC1 is similar to that displayed on the PCA of the complete mandible, though there is a difference in the position of the atelids, which display more intermediate values on this axis. This apparently indicates that mandibular corpus morphology is an acceptable discriminator between this family and the pitheciids. Moreover, aotines, with intermediate values on PC1 and positive values on PC2, are located inside the atelid distribution in morphospace. Pitheciids, with a more expanded mandibular corpus, display a wide distribution along PC2, thus marking a difference with the previous PCA based on the complete mandible. The PGLS results show that shape variation of the mandibular corpus (PC1–4 [~90% of variation]) is not associated with variation in body size ($R^2 = 0.005$; $p = 0.68$), the PC1 plus PC2 display a very low association with Log-BM ($R^2 = 0.10$; $p < 0.04$), and the PC1 shows a significant but relatively low association with Log-BM ($R^2 = 0.23$; $p < 0.003$). Thus, even though the results are significant, R^2 values are too low to seriously consider this association in future discussions.

Summarizing, results of the PC analyses of the complete mandible and the mandibular corpus of the extant species reveal a large amount of morphological variation. Additionally, the distribution pattern of the species in morphospace allows us to infer the existence of a marked phylogenetic structure in platyrrhine mandibular morphology. The quantified phylogenetic signal for the extant species mandibular corpus based on multivariate data (Procrustes shape coordinates, $K_{\text{mult}} = 0.479$; $p = 0.001$) implies that the taxa are phenotypically less similar to each other than expected under Brownian motion (Adams, 2014). The K statistic for univariate data for PC1 ($K = 1.518$; $p = 0.001$) and PC2 ($K = 0.818$; $p = 0.001$) indicates a strong phylogenetic signal.

The mapping of the PC1 scores for the mandibular corpus on the phylogeny (Fig. 4), according to phylogeny and a Brownian motion model, estimated that the relatively short and deep mandibles of Pitheciidae may have appeared early in the clade's phylogenetic history (~15–20 Ma), with negative values of PC1 at the node of this family origin. Among them, *Callicebus* and *Chiropotes* might seem to have evolved independently through a process of increased shortening and deepening of the mandible body. In the case of *Chiropotes* and *Cacajao*, corpus depth and robusticity is exaggerated. The atelids, as well as *Aotus* species, show intermediate values for PC1. Similarly, the cebine *Saimiri* and the callitrichines *Cebuella*, *Callithrix*, *Mico* and *Callimico* may have undergone a significant lengthening of the mandibular corpus while retaining the shallowest jaws among platyrrhines. It is important to highlight that this method estimates ancestral node values without using the information from the fossil record. Nevertheless, it is a remarkable tool for formulating new hypotheses on the platyrrhine past shapes, verifiable with the known fossil record.

The DTT-plots, obtained for PC1 only (Fig. 5a) and for the first two PCs obtained from extant species (Fig. 5b), indicate that the average disparity of mandibular morphology within the subclades is lower than the expected under a Brownian motion model as the evolution of platyrrhines unfolded. Both DTT-plots show that the average disparity values drop near 0 early in the crown platyrrhine

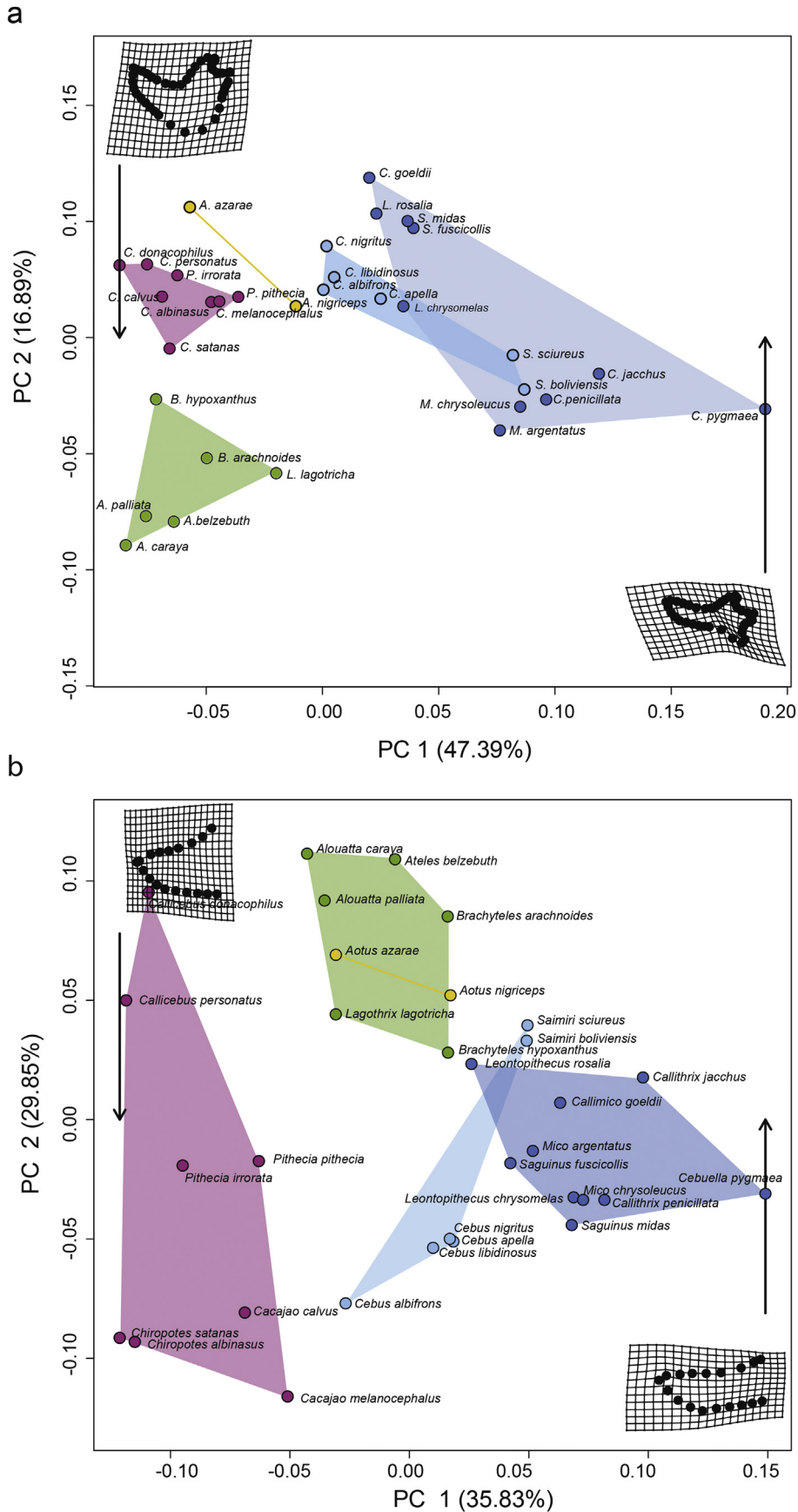


Figure 3. Ordination of the 32 platyrrhine extant species in the spaces defined by the first two principal component (PC) scores using two-dimensional morphometric data from mean species configurations, plus grid changes showing the lateral profile shape changes along the first and second PC for the complete mandible (a) and mandibular corpus (b). Dots represent a consensus individual for each species. Filled polygons indicate each extant family and subfamily.

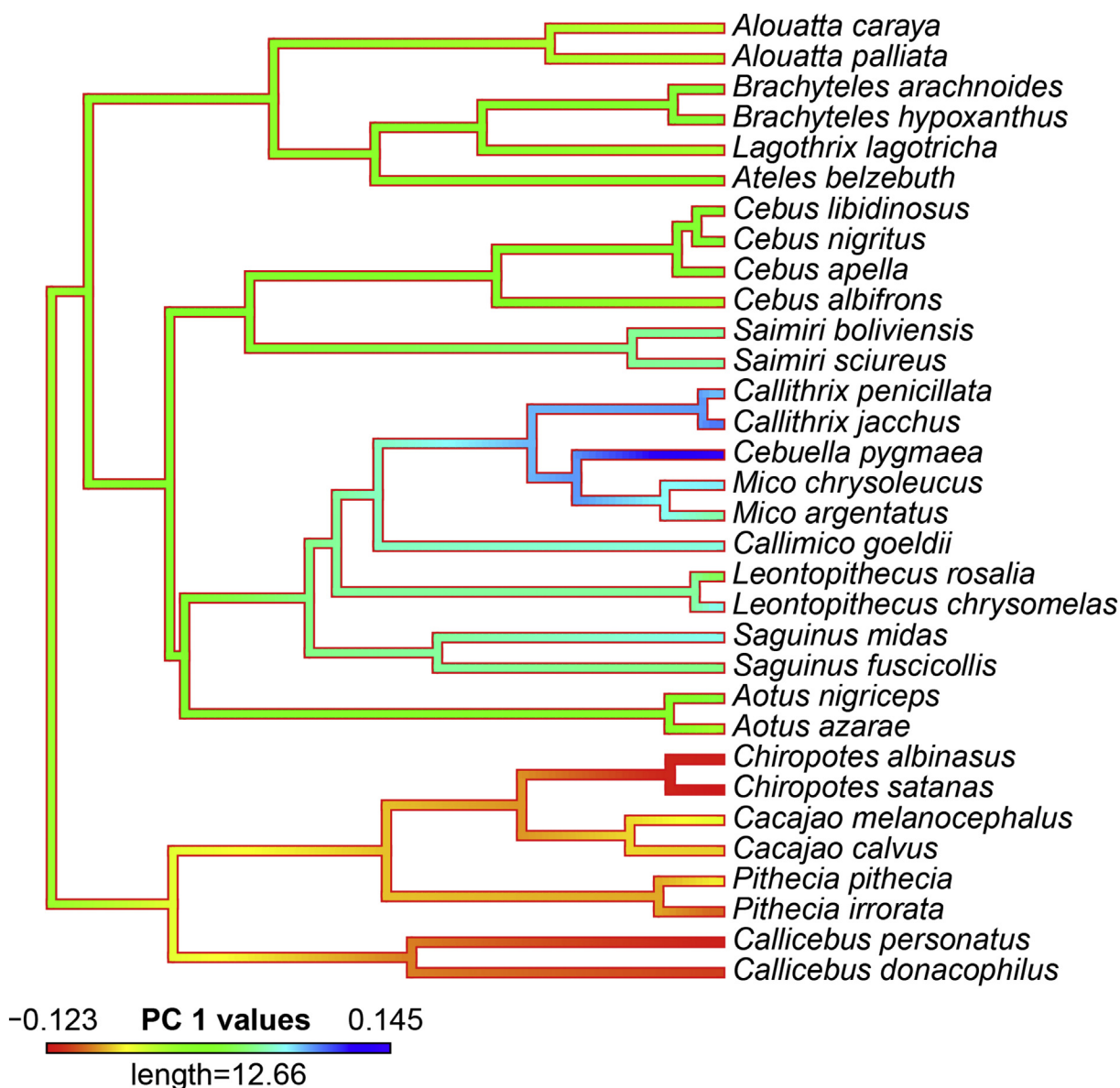


Figure 4. The first principal component (PC) scores using two-dimensional morphometric data from mean species configurations of the extant platyrrhine sample mapped on the phylogeny. Scale below indicates values of PC1 and its color guides. Maximum likelihood procedure assuming Brownian motion model for character evolution was used for estimating values at nodes and branches of the tree. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

diversification, showing little variation through time. Particularly, examining PC1 and PC2, the DTT-plot suggests that the diversification in mandible shape among the main platyrrhine clades occurred ~20–15 Ma (Fig. 5b). This means that most of the mandible shape variation that can be seen between the main platyrrhine subclades, which are clearly differentiated in morphospace, seems to appear as expected in a niche-filling paradigm, i.e., as in Simpson's model. Thus, morphological differentiation between subclades might have arisen close to the origin of the crown platyrrhine taxon.

The PCA performed with extant consensus species and the posterior projection of the fossils' morphological data (Fig. 6) showed that the first two PCs explain about 69.5% of total variation (PC1:42.55%; PC2:26.98%; Fig. 6). The distribution of species in shape space is similar to the ordination along PC1 and PC2 of analysis of extant species. The analysis shows that some of the La

Venta fossils (*N. rubricae*, *N. fieldsi*, *L. annectens*, *A. dindensis*) are located near callitrichines and cebines, while Pleistocene/Holocene fossils and *L. conclutatus* are positioned closer to the atelids and aotines. The position of *A. dindensis* in PC space, which overlaps with that of *Callithrix jacchus*, is relatively separated from extant *Aotus* species and closer to *N. fieldsi* and *Mico*, *Leontopithecus* and *Saguinus* species. Moreover, the MST gave us a better view of shape relationships among other species, which are only approximated in the reduced morphospace described by PC1 and PC2. In particular, *N. rubricae* is also close to *Mico*, *Leontopithecus* and *Saguinus* species and *A. bernensis* is close to *X. mcgregori* and to extant atelids, although they seem distant in the PC1 plus PC2 morphospace (Fig. 6). The between group PCA projecting the individual observations on the morphospace of the species mean shape (excluding fossils) shows that the fossil specimens are within the range of variation expected for current families (Fig. 7).

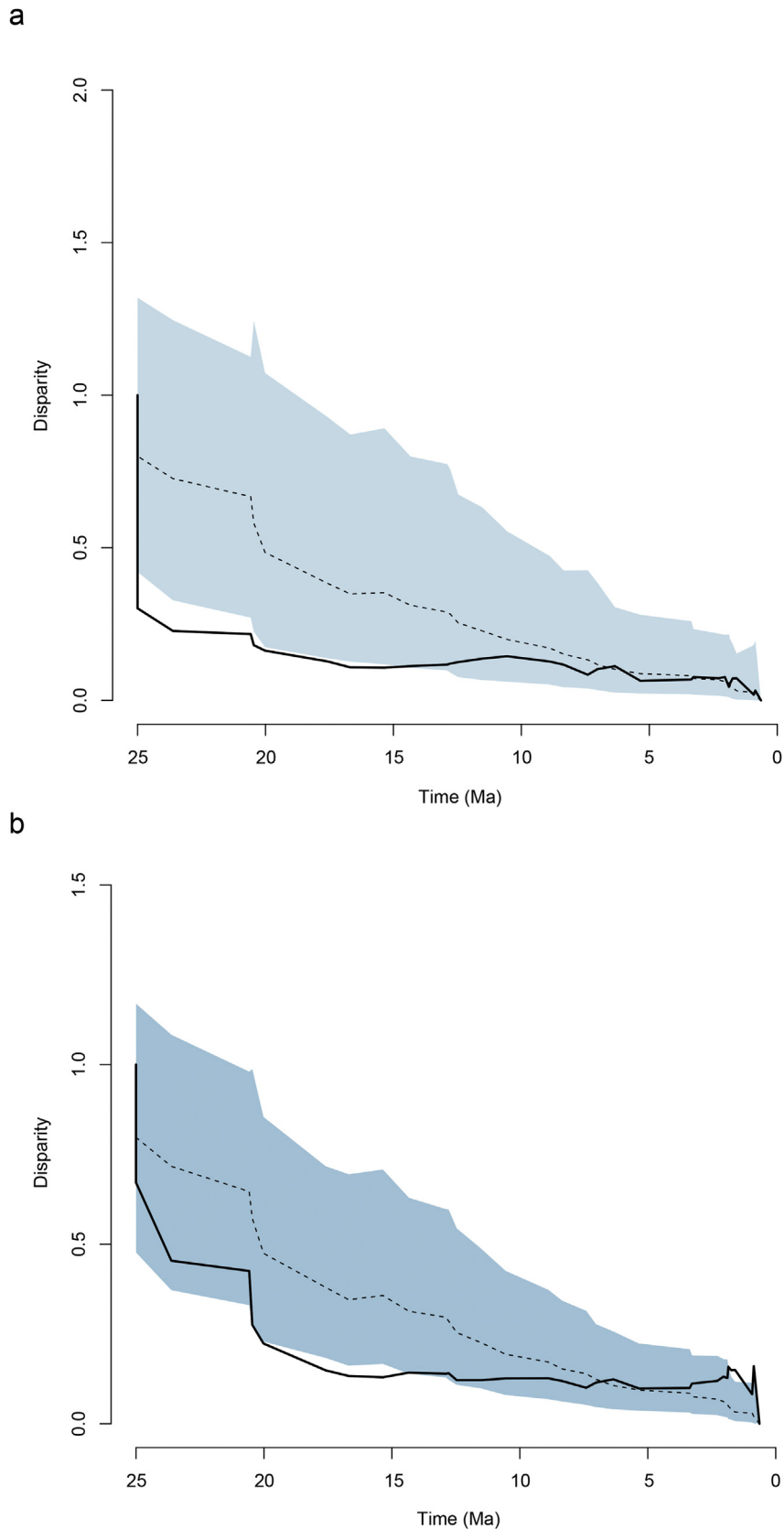


Figure 5. Disparity-through-time plot of principal component (PC) axis 1 (a) and PC axes 1–2 (b) of the two-dimensional morphometric data of the extant platyrrhine sample. Average value at a given point in time is the average disparity of subclades whose ancestral lineages were present at that time relative to the disparity of the entire clade. Higher values of relative disparity correspond to a greater average volume of morphospace occupied by subclades relative to the morphological disparity of the whole clade. The mean of simulated disparity under a Brownian motion model is shown by the dotted line. The shaded area represents the 95% confidence interval of the simulated data. Time equals 25 Ma at the beginning of the simulation, corresponding to the beginning of platyrrhine diversification. Relative time increases to the right along the x-axis. For the fossil calibration of the phylogenetic tree used on this analysis, six fossils were used (see [Aristide et al., 2015a](#)).

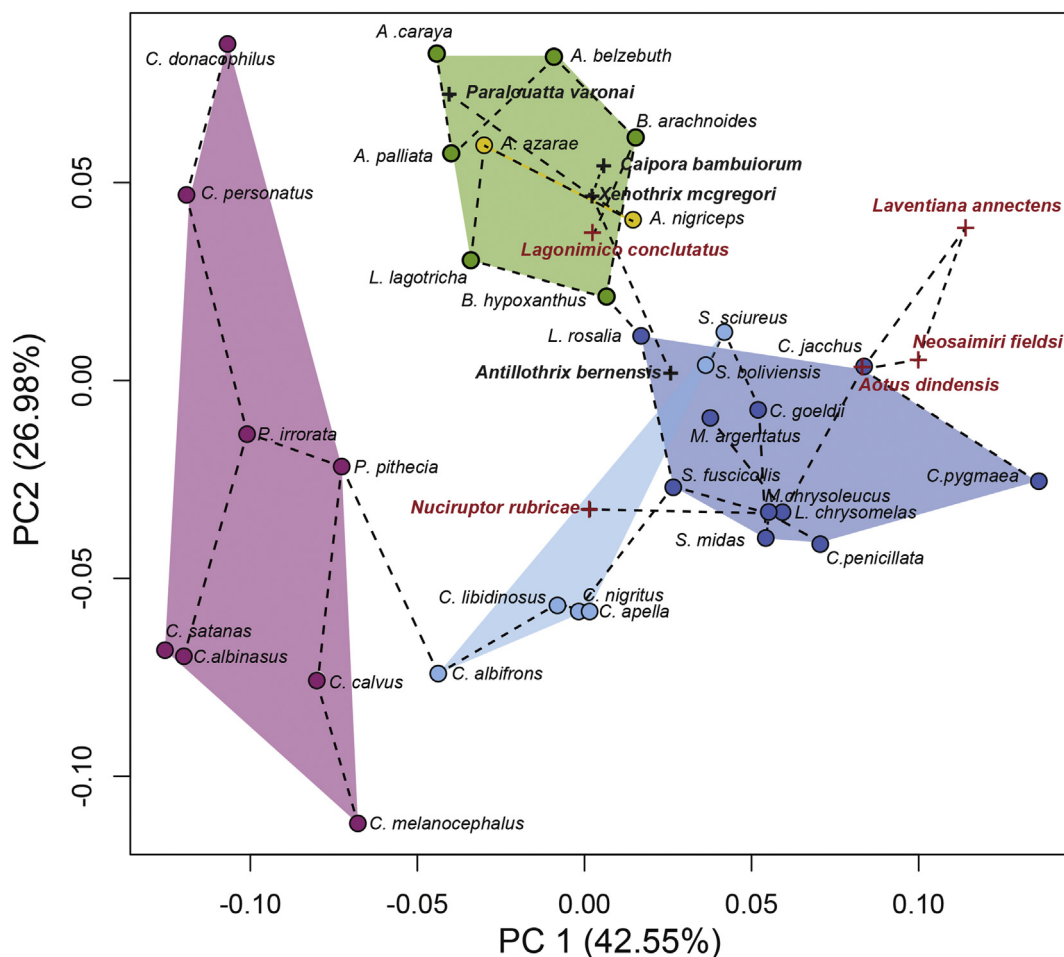


Figure 6. Ordination of the 32 platyrrhine extant species in the space defined by the principal component (PC) 1 and 2 scores of the mean species configurations for the mandibular corpus, with the projection of nine fossil specimens onto the morphospace. The dots represent individuals or a consensus individual for each extant species, while the crosses represent fossil individuals (red: La Venta fossils; dark gray: Pleistocene/Holocene fossils). Dotted lines represent a Minimum Spanning Tree (MST), calculated using a Euclidean distance matrix. Filled polygons encompass extant families and subfamilies. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

In recent years, the origin and maintenance of morphometric variation among platyrrhine species, as also found in other clades, have been mainly studied using a statistical (phylogenetic) comparative approach on extant species (e.g., Perez et al., 2009, 2011; Mahler et al., 2010). We show that it is important to analyze extant and fossil morphological data, since it allows us to consider past morphological variation in relation to extant species variation. Although several efforts previously used this type of sampling to calculate the age of lineages, species origination and extinction rates, or changes in body size among past platyrrhine species (Fleagle and Tejedor, 2002; Perez et al., 2013; Aristide et al., 2015a), our report is one of the first to include fossil evidence in the morphometric and phylogenetic comparative analyses in platyrrhines.

As in previous studies analyzing the mandibles of fossil and extant species from other mammalian clades (e.g., Alvarez et al., 2011), the relatively poor preservation of fossil platyrrhine mandibles made it difficult to analyze this structure beyond the corpus or alveolar region. However, the results obtained were similar to the results obtained analyzing the mandible as a whole. Moreover, we are encouraged that the pattern of shape variation among the hemi-mandibles of extant genera described in two dimensions did not differ significantly from the picture obtained with the hemi-

mandibles in three dimensions. In several ways, our quantitative analysis also corresponds well with previous trait analyses of mandible evolution (Rosenberger, 1977, 1992; Tejedor and Rosenberger, 2008; Rosenberger and Tejedor, 2013). Despite the fact that some forms of variation were not considered in this study, for example the relative size of the mandibular corpus and ramus (which has been of considerable importance for describing certain primate groups; Rosenberger and Tejedor, 2013), or the effects of taphonomy on the fossils, our results suggest that the use of mandibular corpus morphometric data in two dimensions, including previously published mandible images of fossil specimens, is adequate to describe patterns of mandibular variation in the platyrrhine species.

Regarding the fossils, several findings are highly interesting (Figs. 6 and 7). There are consistent clusterings in morphospace, also evident in the MST. *Paralouatta* is associated with *Alouatta* among atelids, *Caipora* and *Lagonimico* fall close to *Brachyteles* among atelids, and *Xenothrix* and *Antillothrix* align close to one another and in association with aotines and atelids. These are species with atelid- or primitive pitheciid-style (e.g., roughly *Pithecia*-like) mandibles. Placement of *Laventiana* and *Neosaimiri* toward the extreme end of the cebid distribution also corresponds with predictions based on character analysis, and the position of *Neosaimiri* fairly close to *Saimiri* adds to the strength of this result.

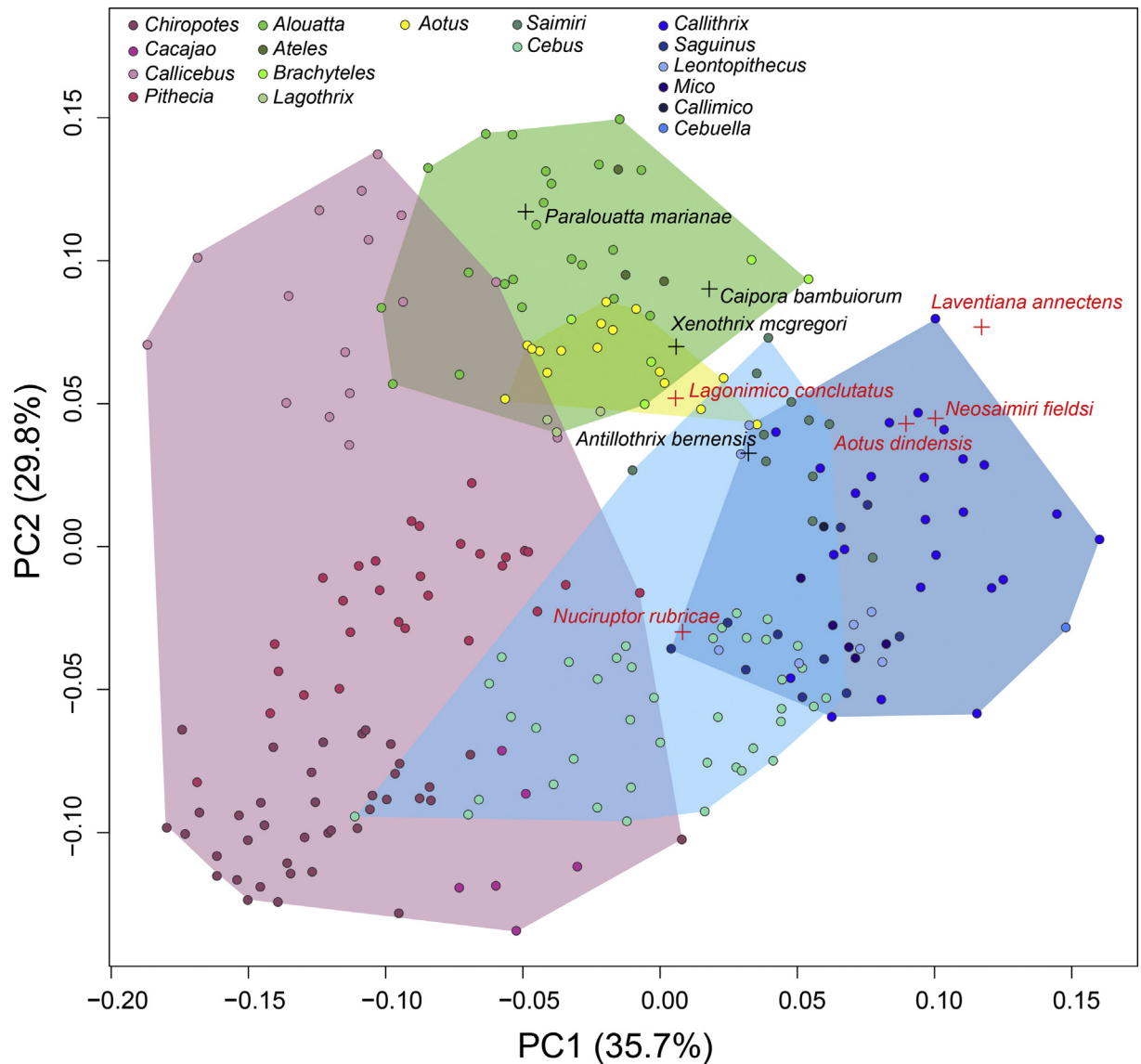


Figure 7. Ordination of the platyrrhine extant specimens in the space defined by the between-groups PC 1 and 2 scores of the mean species configurations for the mandibular corpus, with the projection of nine fossil specimens onto the morphospace. The dots represent individuals for each extant species, while the crosses represent fossil individuals (red: La Venta fossils; dark gray: Pleistocene/Holocene fossils). Filled polygons encompass extant families and subfamilies. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

On the other hand, the wide separation of *Antillothrix* from *Callicebus* is unexpected and does not align with other morphometric work, which showed the specimen as falling in the overlapping multidimensional space of *Callicebus* and *Aotus* (Rosenberger et al., 2013). Further investigation is required here. Similarly, *A. dindensis* falls relatively distant from the extant aotines. *Nuciruptor* appears to be situated in a novel shape space, although this may be interpreted as one anchored by pitheciines, with whom it is likely affiliated (Meldrum and Kay, 1997). The mandible of *Nuciruptor*, however, is more primitive than that of the modern pitheciines included here, so this result should not cause much debate. In general, fossils for which mandibular morphology is known seem to conform to the two patterns of platyrrhine mandibular morphology described above. One is a cebid pattern, and the other is an atelid-pitheciid pattern, which also encompasses the morphology of *Aotus*.

Recent studies using morphometrics of other systems that used extant platyrrhine species and phylogenetic comparative methods have demonstrated a strong relationship between phenotypic

variation and species phylogeny (Perez et al., 2011; Aristide et al., 2015a, 2015b; Meloro et al., 2015). These findings add evidence to the global hypothesis of an early diversification followed by evolutionary stasis in platyrrhine evolution, a position advocated by Rosenberger (e.g., 1980, 1992), which was based on one of the first morphological trait analyses developed within the context of functional-ecological information. The broad cladistic outlines of that hypothesis have been widely accepted since it has been largely confirmed by molecular studies (Schneider and Rosenberger, 1996). Prior notions of platyrrhine evolution, i.e., by Hershkovitz (1977), were fraught with phylogenetic error, so the interaction – or correspondence – between phylogeny, morphology and adaptation was obscured. Until then, in primatology, it was rare for systematists and functional morphologists to see phylogeny and adaptation as intimately intertwined processes – two sides of the same coin as Szalay (2000) exhorted poignantly – where clues to revealing both facets reside in the same sets of characters, and both research domains benefit when characters are analyzed as if they are one.

The phylogenetic signal analyses performed here on extant species allowed us to observe a strong relationship between phylogenetic structure and mandibular morphology. *K* values for the main trends of morphological variation were near to 1, as expected in characters evolving according to a Brownian motion evolutionary model (Losos, 2008). This is similar to the results of previous studies for complete mandible shape variation (Meloro et al., 2015). Additionally, the DTT plot, and mostly the one using evidence from the PC1 of extant species, shows high mandible variation during the early branching process, suggesting that morphological disparity of the mandible might have been partitioned among subclades early in the phylogenetic history of the crown platyrrhines (see Rosenberger, 1980, 1992). Therefore, we confirm for the mandibular corpus a strong phylogenetic structure that is also observed among platyrrhine species for other phenotypic traits and systems, such as body size, brain size and basicranial anatomy (Perez et al., 2011; Aristide et al., 2015a, 2015b).

The ordination present in the PCA of extant species and fossil specimens showed that during the early stages of platyrrhine diversification the mandible displays slightly larger amounts of variation, occupying a similar dispersion in morphospace and implying that mandible shapes similar to that of extant species might have been present at least since La Venta time (15–12 Ma). This result is concordant with the DTT-plot of PC1 and PC2 of extant species that suggests that diversification among the main clades in mandible shape occurred between 20 and 15 Ma (Fig. 5b). This idea is also suggested by the nearness of fossil and extant species disparity values ($D_{\text{extant}} = 0.026$; $D_{\text{extant+fossils}} = 0.029$; $V_{\text{extant}} = 0.0029$; $V_{\text{extant+fossils}} = 0.0031$). These analyses, plus the mapping and plotting of PC1 onto the phylogeny, may support the idea that there was an early differentiation of the varied mandibular morphologies that characterize each platyrrhine subclade in the present, followed by a marked stability in the evolution of these characters. Results like these may indicate that some lineages, such as *Aotus* and *Callicebus*, have retained elements of ancestral crown platyrrhine mandibular morphologies throughout their long history, as suggested by the Long Lineage Hypothesis (see Rosenberger, 2010).

Therefore, our analyses support the expectation that the morphological diversity of extant platyrrhine genera and species is similar to or slightly smaller than the diversity observed among the Miocene taxa (~15–12 Ma ago). This result could suggest a long period of relative evolutionary stasis in mandible morphology after the early diversification of platyrrhines (Rosenberger, 1979, 1984; Rosenberger et al., 2009; Meloro et al., 2015; Aristide et al., 2015a). The early phase of modern crown platyrrhine evolution was probably characterized by a rapid diversification in morphological and ecological traits, driven by natural selection and ecological niche opportunity. The similarity in the variation among fossil and extant species also suggests that, after the initial phase, the rate of morphological diversification slowed down as niches were filled by diversifying ecomorphological clades. Moreover, it is possible that the platyrrhines may have gone through different processes of diversity loss in the past, thus reducing morphological disparity compared to that seen today. It is important to remark that even when fossil specimens analyzed in this study do not represent the earliest phase of platyrrhine diversification, their morphological resemblance to extant species may indicate at least 15 Ma of evolutionary stasis.

Summarizing, we show here that the conjoint study of extant and fossil species, in combination with the use of phylogenetic comparative methods, offers a deep quantifiable description of the diversification pattern through time and a refined understanding of platyrrhine evolutionary history. Our results suggest that the beginnings of platyrrhine diversification might be an example of the

Simpsonian ecospace model (Simpson, 1944), where similar or higher levels of morphological variation relative to that observed among the extant species are expected in the remote past, when the ecological niche space for a platyrrhine had not been exploited and the initial invasion could begin. Future advances in the studies of the morphological differentiation of platyrrhines would be enhanced with the recovery of additional and better-preserved fossil specimens and the employment of alternative phylogenetic comparative modeling approaches. This would increase the sample size, the analyzed morphological traits and the accessible time range, and it would allow us to test different evolutionary scenarios for platyrrhine diversification.

Acknowledgments

We thank D. Flores (Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Argentina) and D. Verzi (Museo de La Plata, Argentina) for granting access to the platyrrhine skeletal collections under their care. Raquel Lamela-Lopez photographed some of the mandible used in this study. We also thank three anonymous reviewers who contributed greatly to improving the manuscript. This research was supported by a grant from FONCYT (PICT-2014-1810; 2015–2018), CONICET (PIP 112-200901-00132; 2014–2016) and UNLP (PI- N787 2015–2018).

Supplementary Online Material

Supplementary online material related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2017.08.008>.

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