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Morphometric variation of extant platyrrhine molars: taxonomic implications for fossil platyrrhines

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ABSTRACT

The phylogenetic position of many fossil platyrrhines with respect to extant ones is not yet clear. Two main hypotheses have been proposed: the *layered* or *successive radiations* hypothesis suggests that Patagonian fossils are Middle Miocene stem platyrrhines lacking modern descendants, whereas the *long lineage* hypothesis argues for an evolutionary continuity of all fossil platyrrhines with the extant ones. Our geometric morphometric analysis of a 15 landmark-based configuration of platyrrhines' first and second lower molars suggest that morphological stasis, may explain the reduced molar shape variation observed. Platyrrhine lower molar shape might be a primitive retention of the ancestral state affected by strong ecological constraints thoughout the radiation the main platyrrhine families. The Patagonian fossil specimens showed two distinct morphological patterns of lower molars, *Callicebus*-like and *Saguinus*-like, which might be the precursors of the extant forms, whereas the Middle Miocene specimens, though showing morphological resemblances with the Patagonian fossils, also diplayed new, derived molar patternss, *Alouatta*-like and *Pitheciinae*-like, thereby suggesting that despite the overall morphological stasis of molars, phenotypic diversification of molar shape was already settled during the Middle Miocene.

INTRODUCTION

Platyrrhine evolution is controversial. However, most researchers agree that they most likely constitute a monophyletic clade derived from African ancestors (Fleagle and Kay, 1997; Takai et al., 2000; Kay et al., 2004; Oliveira et al., 2009; Bond et al., 2015), although the phylogenetic position of some living taxa and the affinities of some fossil specimens are still uncertain. Currently, two different viewpoints have been proposed regarding the evolutionary history of the earliest platyrrhines and their overall relationships with extant forms. The "long lineages" hypothesis argues that the oldest known Patagonian fossils (16–20 Ma) are to be included within the extant Platyrrhines (Rosenberger, 1979, 1980, 1981, 1984; Rosenberger et al., 2009; Tejedor, 2013), whereas the "layered or successive radiations" hypothesis suggests that these fossils constitute a geographically isolated stem group , phylogenetically unrelated to the crown platyrrhines, that went extinct (along with some Antillean species) (Kay, 2010; 2014; Kay and Fleagle, 2010; Kay et al., 2008). According to Kay (2014), the divergence of modern lineages occurred in the tropics. The Late Oligocene and Early Miocene platyrrhines would have branched off from the ancestral lineage when climatic conditions in Patagonia became unfavorable and the Andean uplift was a potential barrier to their dispersal. However, Tejedor (2013) has suggested that *Chilecebus* (20 Ma), a fossil specimen (Tejedor, 2003) from the western Andean cordillera, south of Santiago de Chile, indicates that the Andean mountains did not constitute a biogeographic barrier. Tejedor (2013) argued that a paleobiogeographic corridor throughout western South America would have allowed for a continental connectivity between the north and the southernmost fossil platyrrhines. Unfortunately, dating of the fossil specimens and fossil-based approaches for calibrating the molecular phylogeny support both models. Perez et al. (2013) have estimated a crown platyrrhine origin at around 29 Ma (27- 31), which allows for the inclusion of the fossil Patagonian primates into a crown Platyrrhini lineage showing evolutionary continuity with the Middle Miocene lineages. In contrast, Hodgson et al. (2009) have dated their origin between 16.8 and 23.4 Ma, suggesting an unlikely relationship of the early Miocene fossils with the crown platyrrhine clade (but see different temporal models in Goodman et al., 1998; Opazo et al., 2006; Chatterjee et al. 2009; Perelman et al. 2011; Wilkinson et al. 2011; Jameson Kiesling et al. 2014).

Molar morphology has been widely used to determine the phylogenetic positions of extinct specimens with respect to living forms (e.g., Kay, 1990; Rosenberger et al., 1991a, b; Benefit, 1993; Meldrum and Kay, 1997; Miller and Simons, 1997; Horovitz and MacPhee, 1999; Kay and Cozzuol, 2006; Kay et al., 2008), since tooth development is under strong genetic control (Jernvall and Jung, 2000). Recent studies have reported that molar shapes carries strong phylogenetic signals, and can be useful tool for establishing taxonomic affinities between extant and extinct catarrhine primates (Nova Delgado et al., 2015a; Gamarra et al., 2016), and also in some Platyrrine taxa (Nova Delgado et al., 2015b), with closely related species exhibiting common phenotypic traits.

Affinities of the fossil platyrrhine primates based on dental morphology

Until now, a total of 31 Early Miocene Platyrrhini fossil genera have been so far reported in the South American continent and the Caribean: 11 in La Venta (Colombia), 8 in the Argentinian Patagonia, 4 in the Greater Antilles, 5 in Brazil, and 1 each in Chile, Bolivia and Peru (Tejedor, 2013; Bond et al., 2015). *Neosaimiri*, *Laventiana* (La Venta, Colombia) and *Dolichocebus* (Chubut Province, Argentina) have been included in Cebinae (Rosenberger, 2011). *Neosaimiri* is considered a direct ancestor of the extant *Saimiri* due to its similar molar shape (Rosenberger et al., 1990a; 1991a). Its molars exhibit sharp cusps, well-developed distal cusps, buccal cingulum, a strong buccal flare, and a distinct post-entoconid notch on molars only found in *Saimiri* and *Laventiana* (Rosenberger et al., 1991a, 1991b; Takai, 1994; Tejedor, 2008). *Laventiana* is sometimes considered a synonym of *Neosaimiri* (Takai, 1994; Meldrum and Kay, 1997), although it has been suggested to be more primitive than *Neosaimiri* (Rosenberger et al., 1991b). *Laventiana*'s teeth closely resemble those of *Saimiri* and *Cebus-Sapajus*; it shows thick-enamel bunodont molars exhibiting a small buccal cingulum and an angular cristid obliqua, lacking buccal flare (Rosenberger et al., 1991b). *Dolichocebus* has been suggested to be a member of the *Saimiri* lineage, mainly for its interorbital fenestra considered a derived feature in squirrel monkeys (Tejedor, 2008; Rosenberger et al., 2009; Rosenberger, 2010). However, Kay and colleagues (Kay et al., 2008; Kay and Fleagle, 2010) argued that *Dolichocebus* is a stem platyrrhine and that the description of the orbital region was probably affected by postmortem damage.

On the other hand, *Aotus dindensis* was first described as a sister taxon of extant *Aotus* (Setoguchi and Rosenberger, 1987), although Kay (1990) has suggested that it is probably conspecific with *Mohanamico hershkovitzi*, which may be closely related to the callitrichines, especially *Callimico*, due to their morphological similarities in the canine and the second premolar. *Aotus dindensis* is included into the Pitheciidae (Rosenberger et al., 1990a) within the Homunculinae subfamily, along with *Aotus, Callicebus* and some Argentinian and Caribbean fossil primates (Rosenberger, 1981, 2002, 2011). However, molecular phylogenetic analyses have repeatedly rejected a link between *Aotus* and Pitheciids (.e.g Hodgson et al., 2009; Osterholz et al., 2009; Wildman et al., 2009), placing it as a basal cebid. Tejedor and Rosenberger (2008) proposed that *Homunculus* is likely an ancestral pitheciid because although it shows a primitive dental morphology, it notably resembles that of *Callicebus.* The two taxa show rectangular-shaped molars, small incisors and non-projecting canines, a trait shared with *Carlocebus* (Fleagle, 1990). Nonetheless, unlike *Callicebus*, the molars of *Homunculus* exhibit well-marked crests and prominent cusps (Tejedor, 2013), and an unusual paraconid on the lower first molar (also found in *Dolichocebus*; Kay et al., 2008). Another fossil from the early Miocene known as *Soriacebus* was initially included by Rosenberger (1990) as an early pitheciinae, due to its resemblance on the anterior dentition (Fleagle et al., 1987; Fleagle, 1990; Fleagle and Tejedor, 2002; Tejedor, 2005). However, some dental traits of *Soriacebus* (premolars-molars size, lower molar trigonid, and reduction hypocone) bear resemblance also with the callitrichines. Indeed, Kay (1990) argues that such similarities traits found between *Soriacebus* and pitheciins or with callitrichines are due to homoplasy, rather than phylogenetic relationships among such lineages (Kay, 1990). According to Kay (1990) *Soriacebus, Carlocebus*, *Homunculus* as all Patagonian fossils should be considered stem platyrrhines.

Xenothrix is a Late Pleistocene Caribbean fossil from Jamaica that shows a callitrichine-like dental formula (2132; MacPhee and Horovitz, 2004), low relief molars and a narrowing of intercuspal distance and augmentation of the mesial and distal crown breadths (Cooke et al., 2011), a feature also seen in *Insulacebus toussaintiana*, another Caribbean primate. Rosenberger (2002) argued that *Xenothrix* is closely related to *Aotus* and *Tremacebus* by the enlargement of the orbits and the central incisors, while MacPhee and Horovitz (2004) suggested a possible Pitheciidae affinity, due to its low relief molar pattern. Nonetheless, the puffed cusps and the lack of crenulation on the molar crown discriminate the Jamaican fossil from the Pitheciidae, suggesting that is likely that *Xenothrix* does not belong to crown platyrrhine group (Kay, 1990; Kinzey, 1992).

Cebupithecia and *Nuciruptor*, two Colombian Middle Miocene genera, also share some traits with the extant Pitheciidae family, mostly in the anterior dentition but also in their low molar cusps and poorly developed crests (Kay, 1990; Meldrum and Kay, 1997). *Nuciruptor* does not exhibit several of the shared traits among Pitheciines (projecting canine and small or absent diastema). *Cebupithecia*, although considered to be more derived than *Nuciruptor* (Meldrum and Kay 1997), was interpreted by Meldrum and Kay (1997) as an example of convergent evolution and, thus, not a direct ancestor of extant pitheciines. Finally, *Stirtonia* (originally from Colombia but also recovered from Acre State, Brazil) exhibits similar dental size and morphology to extant *Alouatta*; showing molar teeth with sharp and well-formed crests, a long cristid oblique, small trigonid, and spacious talonid basin (Hershkovitz 1970; Kay et al., 1987; Kay and Frailey, 1993; Kay and Cozzuol, 2006; Kay, 2014).

Numerous studies have examined landmark-based geometric morphometrics (GM) of molar shape for studying patterns of inter-specific variation and their implication in phylogeny and ecological adaptations (e.g., Bailey 2004; Cook 2011; Gómez-Robles et al., 2007, 2008, 2011; Martinón-Torres et al., 2006; Singleton et al. 2011; White 2009 Nova Delgado et al., 2015a,b; Gamarra et al., 2016). However, in Platyrrhine primates, GM of molar shape has mainly focused on dietary adaptations (Cooke, 2011), rather than to predict the phylogenetic attribution of unclassified specimens (Nova Delgado et al., 2015a).

The aim of the present study is to use two-dimensional (2D) GM to quantify and analyze occulsal shape variation of lower molars (M_1 and M_2) of extant Platyrrhini primates to asesses the affinities of the Patagonian, Colombian and Antillanean fossil taxa with the extant forms and to estimating the efficiency of molar shape for discriminating fossil specimens.

MATERIAL AND METHODS

Images of the dental crowns, in occlusal view and including a scale line, of 12 holotypes fossil platyrrhine specimens and one fossil from Fayum (*Proteopithecus sylviae*), were obtained from the literature (Table 2). The platyrrhine fossil specimens included 12 genera (*Soriacebus*, *Dolichocebus*, *Homunculus*, *Carlocebus*, *Neosaimiri*, *Laventiana*, *Mohanamico*, *Aotus*, *Stirtonia*, *Nuciruptor*, *Cebupithecia*, and *Xenothrix*), discovered in Argentina, Colombia and Jamaica, and dated to between Holocene and early Miocene (Table 1).

The extant comparative samples consisted in 802 adult individuals representing all recognized platyrrhine groups (3 families, 18 genera, 61 species,; Table 2), whose 2D and 3D morphometric variability of lower molars has alredy been analysed in some platyrrine species (Nova Delgado et al., 2015b) Dental casts were obtained from original specimens housed at Museu de Zoologia Universidade de São Paulo (MZPS), Museu Nacional do Rio de Janeiro (MNRJ) in Brazil, and from Hacienda La Pacífica (HLP) in Costa Rica. The casts were made following published protocols (see Galbany et al., 2004, 2006). 2D images of molar occlusal surfaces of the extant specimens were taken with a Nikon D70 digital camera fitted with a 60-mm optical lens held horizontally on the stand base, at a minimum distance of 50 cm. The dental crown was imaged with a 0° of tilt with the cervical line perpendicular to the camera focus (Nova Delgado et al., 2015a). Images of fossil dental crowns were obtained from the literature and imported to Adobe Photoshop, where they were scaled to the same resolution (400 dpi). The images both for the extant and the fossil specimens were scaled to 5mm and standardized to right side, with the mesial border facing to the right, the distal border to the left, and the lingual and buccal sides facing upward and downward, respectively. All images were saved at high resolution (1600 × 1200 pixel) in JPEG format.

Geometric morphometric analysis

Geometric Morphometrics (GM) quantifies shape differences between biological structures using a set of digitized homologous points (landmarks) in two-dimensional or three-dimensional spaces (Bookstein 1991; Adams et al. 2004; Slice 2005). Landmarks are numerical values (coordinates) that reflect the location and orientation of each specimen in the morphospace (Slice, 2007). The two-dimensional (2D) landmark protocol used in this study has been previously used in different research performed in molars of catarrhines and platyrrhines (Nova Delgado et al., 2015a, b; Gamarra et al., 2016), which included the same standardized definitions scaled and orientation. The configuration consisted of 15 landmarks: molar occlusal polygon was defined by the four tips of the cusps (protoconid, metaconid, hypoconid and entoconid).The crown outline was represented by eight landmarks, which included two landmarks on fissure intersections; four corresponding to maximum crown curvatures; and two in the mid mesio-distal line on the crown perimeter. Further, three landmarks were used to represent the positions of crests (Table 3 and Fig. 1) (Cooke, 2011). Landmark recording was performed with TPSDig v 1.40 (Rohlf, 2004) and landmark coordinates were then imported into MorphoJ (Klingenberg, 2011). The most commonly employed method to remove the information unrelated to shape variation is the generalized procrustes analysis (GPA) (Rohlf, 1999, 2005). GPA is based on a least squares superimposition approach that involves scaling, translation and rotation effects so that the distances between the corresponding landmarks are minimized (Rohlf and Slice, 1990; Goodall, 1991; Rohlf and Marcus 1993; Rohlf, 1999; Adams et al., 2004). After the procrustes superimposition, the covariance matrix of all the compared shapes is used to derive a Principal Components Analysis (PCA) (Zelditch et al., 2004).

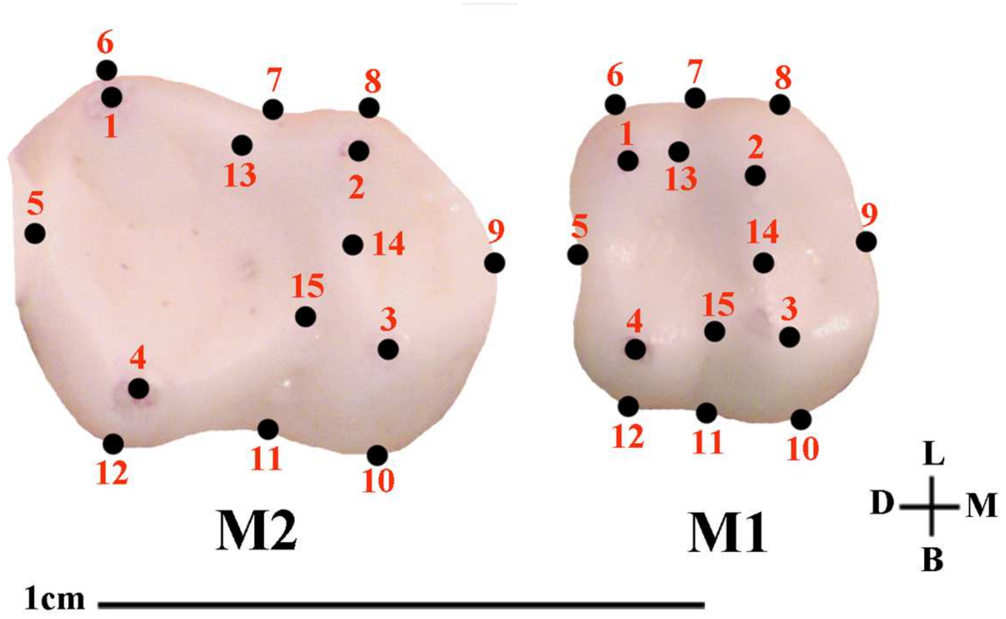

Figure 1. Set of landmarks used in the geometric morphometrics analyses. a) M_2; *Alouatta guariba* 23177 MNRJ; b) M_1: *Sapajus libidinosus* 23246 MNRJ.

The PCA of M_1 and M_2 morphometric variability of the extant species were used to explore dental affinities of fossil specimens within the extant comparative platyrrhine sample. The resulting PCs were used to conduct Linear Discriminant Function analysis (LDA). Because PCA transforms original high-dimensional data, and removes the irrelevant and redundant dimensions (Zelditch et al., 2004). LDA maximizes differences between groups but allows classifying isolated cases based on their distances to the group centroids of the extant taxa. The probability that a case belongs to a particular group is proportional to the distance to the group centroid (Kovarovic et al., 2011). The reliability of the classification was estimated from the *post-hoc* correct classification probability after cross-validation (*pcc*), and the *a posteriori* probability score was used as the probability that a fossil belongs to a particular group. Several LDAs were made considering different discriminant factors: 1) family (Cebidae, Atelidae, Pitheciidae), 2) the subfamily-level classification proposed by Groves (2005) (Subfamily G) (Cebinae, Saimiriinae, Callitrichinae, Pitheciinae, Callicebinae, Aotinae, Atelinae, Alouattinae), 3) the subfamily classification by Rosenberger (2011) (Subfamily R) (Cebinae, Callitrichinae, Pitheciinae, Homunculinae, Atelinae) (Table 4), and 4) a genus level (*Cebus*, *Sapajus*, *Saimiri*, *Callithrix*, *Mico*, *Cebuella*, *Callimico*, *Leontopithecus*, *Saguinus*, *Aotus*, *Callicebus*, *Cacajao*, *Chiropotes*, *Pithecis*, *Lagothrix*, *Brachyteles*, *Atelles*, *Allouatta*). The LDA analyses were carried out with SPSS v.15 (SPSS, Inc. 2006).

RESULTS

Principal components analyses

The first two PCs of the PCA analysis of M_1 for all platyrrhines (Fig. 2) explain 42.06 % of total shape variance (PC1 30.60%; PC2 11.46%). Positive scores on PC1 correspond to molars with a broad occlusal polygons and a mesiodistally rectangular outline; whereas a negative PC1 score are characterized by a relatively quadrangular outline and slight buccolingually rectangular occlusal polygon resulted by displacement of distal cusps (entoconid and hypoconid) to mesio-lingually and mesial cusps (metaconid and protoconid) to distal-lingually side respectively. Positive scores on PC2 molar indicate a rectangular occlusal polygon and a mesiodistally rectangular outline, whereas negative score on PC2 reflect molars with relatively quadrangular outline and slight rectangular occlusal polygon more widely displaced to buccally side.

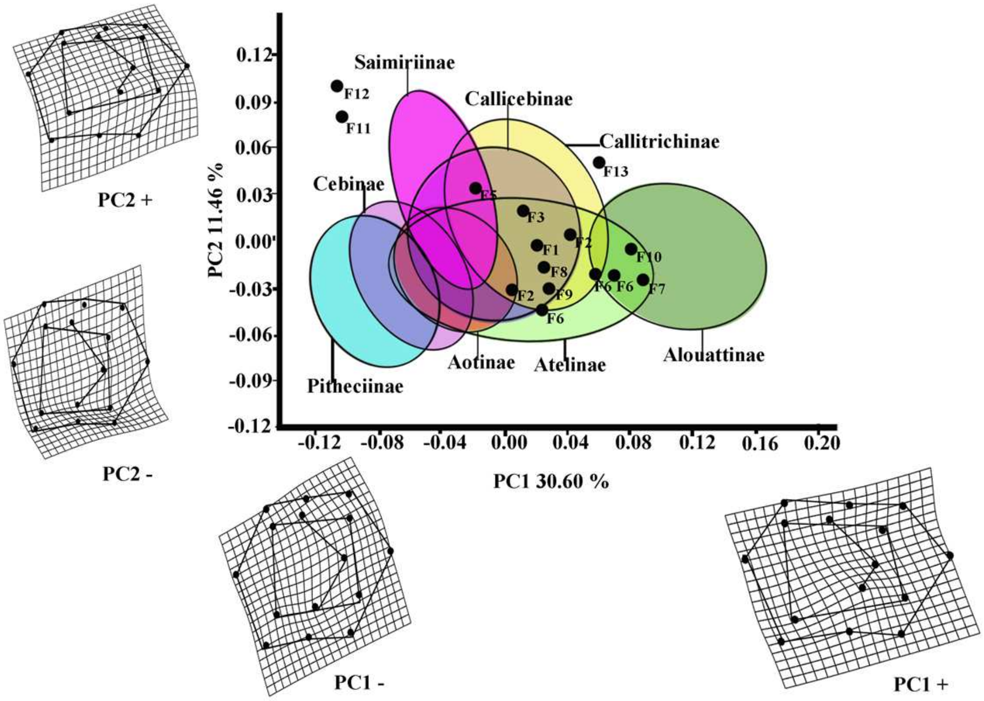

Figure 2. Scatterplot of the first two principal components (PCs) derived from the PCA of M_1 shape variability of Platyrrhini. Grids indicate the deformations associated with the extreme values of each principal component. Ellipses represent the subfamily-level classification proposed by Groves (2005). The letters F and numbers in figure represent the fossils listed in Table 1.

Despite the PCA does not discriminate groups, the plot of PC1 *versus* PC2 (Fig. 2, including 95% confidence ellipses of the subfamily groups) shows differences between subfamilies. Alouattinae clearly cluster on the positive scores of PC1, whereasontrast Pithecinae and Cebinae greatly overlap on the most negative score of PC1. The rest of the groups (Saimirinae, Callicebinae, Callitrichidae, Atellidae and *Aotinae*) show intermediate values for PC1 and greatly overlap. For the second PC function (PC2), all groups greatly overlapp, though

Saimirinae, Callitrichinae and Callicebinae show somewhat higher PC2 scores than the rest. Most of the fossil specimens showed positive PC1 scores, except *Carlocebus* (F5) and especially *Nuciruptor* (F11) and *Cebupithecia* (F12) that had negative PC1 and positive PC2 scores. Most extinct forms overlapped with the extant platyrrhines, within Callicebinae, Callitrichinae and Atellinae, except *Xenothrix* (F13), *Nuciruptor* and *Cebupithecia*.

The first two PCs for M_2 (Fig. 3) accounted for 42.80% of the total variance (PC1: 28.58%; PC2: 14.22%). The molar shape changes for positive and negative PC1 scores for M_2 were relatively similar to those observed for M_1, whereas positive PC2 scores for M_2 corresponded to the negative ones on PC2 for M_1, and negative ones on PC2 for M_2 were equivalent to the positive score of PC2 for M_1. The PC1 *versus* PC2 plot (Fig. 3) showed similar distributions of the subfamilies to those for M_1, although greater separations between groups were observed. Alouattinae showed the largest, positive scores for PC1, and Pitheciinae and Cebinae the most negative scores, with the other groups showing again intermediate values. Callitrichinae and Saimiriiane were placed mainly on the negative score of the PC2 axis, although overlapped somewhat with the other groups. Most fossil specimens again clustered on positive scores for PC1 and PC2, mainly within the dispersion of Callitrichinae, although *Stirtonia* (F10), and some specimens of *Neosaimiri* clearly fell within the Alouattinae clade, *Dolichocebus* (F3) within Saimiriinae, and *Nuciruptor* (F11) was closer to Cebinae and Pitheciinae on the negative scores of PC1. *Homunculus* (F4) did not fell at all within any extant taxa, showing highly possitive PC2 scores.

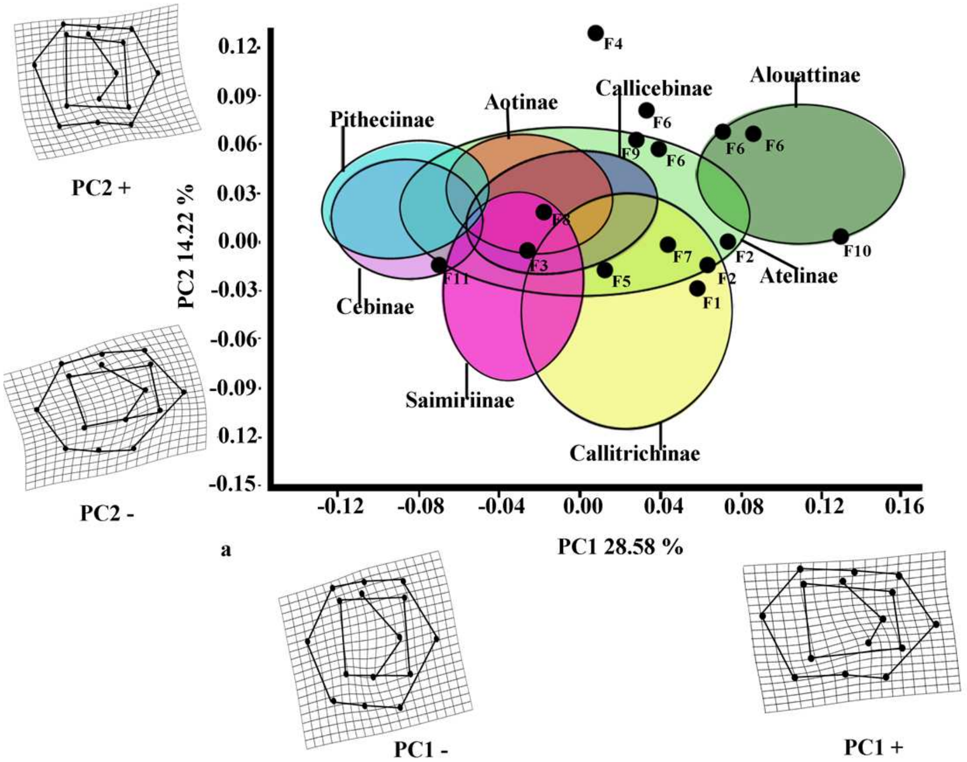

Figure 3. Scatterplot of the first two principal components (PCs) derived from the PCA of M_2 shape variability of Platyrrhini. Grids indicate the deformations associated with the extreme values of each principal component**.** Ellipses represent the subfamily-level classification proposed by Groves (2005). The letters F and numbers in figure represent the fossils listed in Table 1.

Discriminant analyses of the fossil speciomens

The *post-hoc* percentages of correct classification after cross-validation (*pcc*) were high both for M_1 (Table 4a, range = [85.7−88.0%]) and M_2 (Table 4b, range = [84.7−90.6%]). In both cases the highest *pcc* value was obtained when Groves' *subfamily* factor was discriminated. The range of differences between *pcc* values before and after cross-validation was [1.3−4.7] and in both teeth the *genus* discrimiant factor showed the highest decrease in *pcc*. The difference in *pcc* values between Groves' (Cebinae, Saimiriinae, Callitrichinae, Pitheciinae, Callicebinae, Aotinae, Atelinae, Alouattinae) and Rosenberger's (Cebinae, Callitrichinae, Pitheciinae, Homunculinae, Atelinae) *pcc* values were 2.3% for M_1 and 1.6% for M_2 (Table 5). The percentage of total variance explaine by the first two discriminant functions (DF1, DF2; Table 4) for all discriminat factors ranged from 63.3% (*genus*) to 100% (*family*) for M_1, and from 66.1% (*genus*) to 100% (*family*) for M_2. The highest percentage of total variance explained by DF1 was 56.0% (*family*) for M_1 and 68.3% (*family*) for M_2, and the highest one for DF2 was 44.0% (*family*) for M_1 and 32.8% (*subfamily R*) for M_2.

Regarding the classification of the fossils specimens, the ranges of the *a priori* classification probabilities varied depending on the discriminant factor used (Table 5; Fig. 4 shows the landmark configurations of the fossil specimes analysed). *Mohanamico* showed a high probability of belonging to the callitrichines clade, as well as *Carlocebus*, although the probability was smaller for M_2. Both *Neosaimiri* and *Soriacebus* showed high probabilities of belonging to the callitrichines for M_1, though to Callicebinae/ Homunculinae for M_2. *Cebupithecia* (M_2 not available) and *Nuciruptor* neotypes showed a high probability of belonging to the pitheciid clade in LDAs. In contrast, *Xenothrix* (M_2 not available) likely belonged to *Callithrix*, despite in the PCA this fossil specimen did not fall within Callitrichinae range. *Stirtonia* was assigned to the Atelidae clade, and to *Alouatta* at the genus level, except for Rosenberger' *subfamily* factor for M_2. *Laventiana* was also classified into the atelids for M_1, but was more closely related to callitrichines for M_2. *Aotus dindensis* showed a high probability of belonging to *Aotus* taxa for M_1, but *Callicebus* was the group with the greatest affinity for M_2. Finally, *Proteopithecus* showed a high resemblance with *Saimiri* for M_1, but with *Callimico* for M_2.

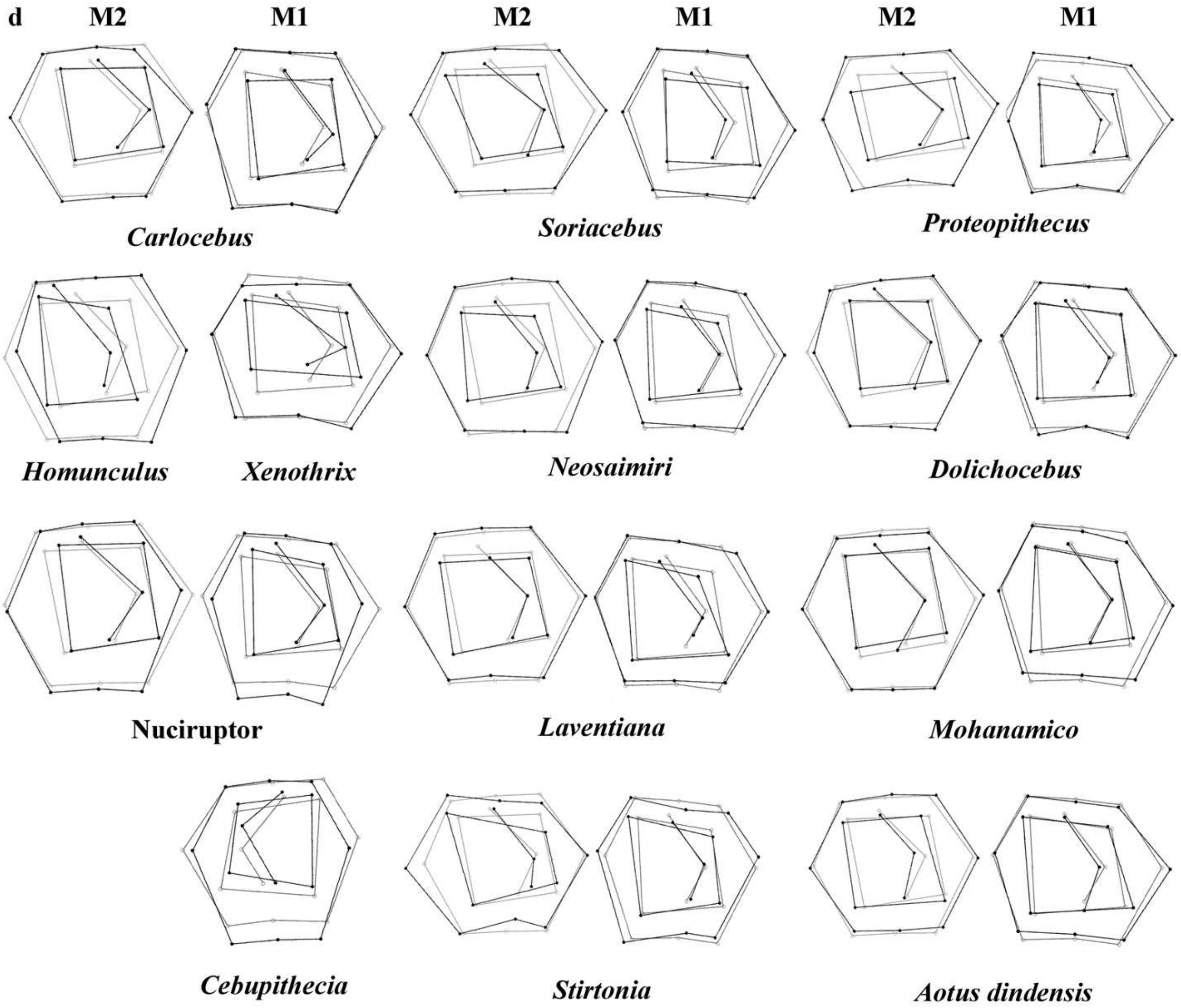

Figure 4. Firts and second molar shapes of the extinct fossil platyrhines used in this study.

DISCUSSION

The positions of the anthropoid form *Proteopithecus sylviae* (F1) in the morphospace and its molar shapes showed pattern resemblance to that of platyrrhines. However, because, many dental and postcranial features of *P. sylviae* are considered to be symplesiomorphic characters of all anthropoids, so it is placed as the stem anthropoid (Kay, 1990, 2014). The recent discovery of *Perupithecus ucayaliensis,* probably from the Late Eocene, suggests that this fossil exhibits similarities with *Proteopithecus,* also with *Talahpithecus* and Oligopithecidae (Bond et al., 2015). The upper molars of *Perupithecus* are slightly resembled to the callitrichines, but its morphology is more similar with *Proteopithecus* and *Talahpithecus* (Bond et al., 2015). *Proteopithecus sylviae* differed from the extant and extinct platyrrhines in having a molar distomesially expanded, marked by a rectangular shape of the occlusal polygon (especially on M_2) (also seen in *Xenothrix*). Thus, if the Fayum form likely was a sister taxon to platyrrhines, the interspecific variation of shape would have shown relatively little change. This could mean that the main traits of molars shapes in platyrrhines represent retention of a primitive ancestral form. Moreover, the LDA showed a high probability of *P. sylviae* belonging to the Cebidae clade, suggesting that the molar of the earliest ancestors of platyrrhines must have exhibited close similarity to *Saimiri-Callimico.* This resemblance matches with the description of an Oligocene primate fossil found in South America, *Branisella* (Rosenberger, 2002; Rosenberger et al., 2009), whose morphology indicates that the structural characteristics of M_2 may have been *Saimiri*-like, and the upper P^2 a *Callimico*-like (Rosenberger, 1980). However, both molar shapes of *P. sylviae* were more closely resembles to *Callimico* than *Saimiri*. Furthermore, the subtriangular upper molars of *Perupithecus,* show relative similarity with *Callimico* (Bond et al., 2015). Thus, if *P. sylviae* was a sister taxon of platirrhines, is likely that the hypothetical ancestral molar shape of pre-platyrrhine would have been similar to a molar of *Callimico*. By contrast, if *P. sylviae* was a stem species, *Callimico* would show retention of primitive pre-anthropoid platyrrhine molar shape.

Early Miocene platyrrhines from Patagonia

The fossils recovered from Early Miocene strata have been highly debated by Kay (1990, 2010, 2014), who argued that most of the traits used to identify phylogenetic affinities show high levels of homoplasy. The present work alone cannot reject the successive radiations or the long lineages hypotheses, nor can confirm which of both is correct. However, studying phenotypic similarities and differences of molar shapes, allowed us to explore morphological patterns between extinct and extant taxa. For example, the PCA indicated that the two PCs did not have a large variance, however can observe differences to subfamily levels (Fig. 2 and 3). Also, although fossils were not very spread out in the morphospace, many of them were located mainly into Callicebinae and Callitrichinae range (except to *Homunculus* for M_2). This means that the main traits observed in fossil platyrrines are related to affinities for both subfamilies

The Early Miocene fossils were mainly assigned to two taxa by the LDA; a *Callicebus*-shaped and a *Sagunus*- shaped. For example, *Dolichocebus* (F3) were classified as a pitheciid, mainly by having a square occlusal polygon (Table 4). However, although the PCA for M_1 placed this specimen in the Callicebinae range, a morphological similarity with Saimiriinae was seen for M_2 (Fig. 3a). In contrast, *Soriacebus* (F2) was related mainly to the callitrichine clade, but for M_2 the probability of belonging to this group was small (Table 4). Because, *Soriacebus* showed a rectangular occlusal polygon on M_2 and the ectoconid was inclined distolingually. Regarding callitrichines, although *Soriacebus* also showed differences in cusp configuration, the callitrichines and *Soriacebu* share a C-shaped distal side and a somewhat straight lingual-side contour (mostly seen in *Saguinus*). Kay (1990) reported that many dental features of marmosets and *Soriacebus* were convergent. In contrast, Rosenberger et al. (1990b) suggested that there are some similarities with callitrichines (development of hypoconids and entoconids in the talonid). However, based on the anterior teeth, they concluded that *Soriacebus* represents the first branch of pitheciines. Although marmosets are considered derived linajes (e.g. Chatterjee et., 2009; Perelman et al., 2009; Jameson Kiesling et al., 2014), it is likely that the relation with *Soriacebus* may be due to the fact that callitrichines exhibit primitive traits on their molars, which means that both taxa share a retention of rectangular contour and occlusal polygon shape. In the case of *Carlocebus* (F5), it was classified as a Callitrichinae in the DFA. However, it has been shown to be more similar with *Callicebus* than marmosets, such as the shape contour and quadrate alignment of cusps in both molars. *Homunculus* (F4), was placed outside the range of Patagonian forms in the PCA (Fig. 2a), whereas the LDA indicated a high probability of belonging to Pitheciidae (ca. 91–99%; Table 4), and especially to *Calliecebus*. Nonetheless, *Homunculus* molar showed an asymmetrical shape compared to pitheciid forms. Furthermore, unlike pitheciids, *Homunculus* cusps were predominantly inclined toward the distal side and the trigonid was almost as broad as the basin-like talonid, which means that although sharing some traits with pitheciids, its position is highly uncertain.

Middle Miocene platyrrhines from Colombia and the Caribbean Xenothrix

Many of these fossils were mostly catalogued as callitrichines, specifically into the *Saguinus* clade, except *Nuciruptor*, *Cebupithecia*, *Aotus dindensis*, and *Stirtonia*. One of the major differences between these primates and the extant forms (excepting *Alouatta* and *Brachyteles*) was the rectangular-shaped molar (see *Xenothrix* below). This phenetic similarity among phyletically distinct groups of extinct primates indicates that a rectangular-shaped molar almost certainly represents a plesiomorphy in the Patagonian fossils. Thus, the trend toward ovoid molar shape might be a derived feature in many living forms. *Laventania* (F7) exhibited distally oriented cusps on M_1, showing considerable resemblance with some atelid groups, which provided a confusing classification between atelids and *Callicebus* in the LDA (Table 5). Thus, the trend to rectangular shape for M_1 in *Laventania* differs notably from the phylogenetic relationship with Cebinae and Saimiriinae. Nonetheless, when M_2 was analyzed, the fossil was classified as member of the Callitrichinae clade. As with *Laventania*, some neotypes of *Neosaimiri* (F6) were classified in completely distant taxonomic groups (Table 4). However, despite these results, *Neosaimiri* was principally associated to the Cebidae family, although the molar shape was found to have more affinities with callitrichines than *Saimiri.* On the other hand, *Mohanamico* (F8) and *Aotus dindensis* (F9) have been considered by Kay and collaborators (Meldrum and Kay, 1997; Kay 2014) to belong to the same genus, despite Takai et al. (2009) suggested that *A. dindensis* should be assigned to distinct genus. According to their molar shape, *Mohanamico* and *A. dindensis* may be classified into different species. Both fossils showed a relative rectangular shape of the outline, as well as in the occlusal polygon, although M_2 in both species were slightly square shaped. In fact, PCA for M_1 (Fig. 2a) showed that the two forms were placed closer to each other. Thus, similar molar shape might be due to the fact that the two forms must have shared relatively similar ecological niches, likely because *Mohanamico* and *A. dindensis* were found in the same locality and at the same stratigraphic level (Kay, 1990). However, the LDA indicated that the probability of classification was different for both groups. *Aotus dindensis* was mainly related to *Aotus/Callicebus*, whereas *Mohanamico* was assigned to Callitrichinae (Table 4). In the case of *Nuciruptor* (F11) and *Cebupithecia* (F12), the occlusal views in both species were relatively rounded, with a slightly rectangular alignment of cusps, and buccally oriented, which resembles the condition in most extant Pitheciinae.

Moreover, the LDA indicated that *Cebupithecia* and *Nuciruptor* had a close affinity with the Pitheciidae clade (Table 4). However, despite the two neotypes clustered close to the pitheciids, they were not placed into the extant species range (except *Nuciruptor* on M_2) (Fig. 2a). Several studies have suggested that, although there are important characteristics that have been associated with the living taxa, both fossils should be considered stem pitheciines (Meldrum and Kay, 1997; Kay et al., 2013; Kay, 2014).

The sister relationship between *Stirtonia* and *Alouatta* was classified in the LDA with a 99.9% probability for M_1 and 94.0% for M_2. Likewise, the PCA showed that *Stirtonia* was placed close to howler monkeys (Figs. 2a and 3a). However, differences between *Stirtonia* and *Alouatta* were mainly seen in the occlusal polygon of M_2. The metaconid of *Stirtonia* was located near the protoconid and the ectoconid was distolingually inclined, somewhat similar to the *Cebuella* configuration. This relationship was reflected in the high percentage of probability at the subfamily level, Callitrichinae (Table 5).

Finally, *Xenothrix* (F13), the Caribbean platyrrhine form, has been allied with pitheciids (Rosenberger, 2002; Horovitz and MacPhee, 1999). In the LDA, *Xenothrix* was mainly attributed to pitheciids, but at the genus level, it was assigned to *Callithrix* (Table 4). Thus, some resemblance with marmosets could be interpreted as convergent evolution. However, the relationship between *Xenothrix* and pitheciids was highly uncertain, given that its molar morphology (especially the occlusal configuration) differs from that of the pitheciids. It is likely that *Xenothrix* could be a single branch that evolved independent of crown platyrrhines, as was suggested by some investigations that proposed an early Antillen arrival (Iturralde-Vinent and MacPhee, 1999; MacPhee and Iturralde-Vinent, 1995; MacPhee and Horovitz, 2004; Kay et al., 2011; Kay, 2014).

The slow rate of phenotypic changes on molar shapes suggests that morphological stasis (different concept to long lineages hypothesis) explains the low interspecific variation between extinct and extant linages and between Early Miocene platyrrhines (including *P. sylviae*) and forms from La Venta, in comparison to extinct and extanct catarrhines (Nova Delgado et al., 2015a; Gamarra et al., 2016). This small phenotypic variation could be due to development and functional constraints, given the role in occlusion and masticarion (Gómez-Robles and Polly 2012). Further, due to the relative low diversification in diet of platyrrhines (for example compared with carnivores). This ecological constraint may be related to the fact that the phenotypic adaptation of main platyrrhine families could have happened in Amazon rainforest (Jameson Kiesling et al. 2014). Following an African origin scenario, and taking into account the phenotypic similarity of the most recent discovered and oldest fossil found in Peru, *Perupithecus* (Bond et al., 2015), it is likely that the ancestor of extant platyrrhines could have exhibited a *Callimico*-like molar shape, We also observed that *Saguinus* and *Callicebus* were the main assigned groups for Patagonian fossils by LDA, also in the PCA. It could mean that: there were a *Callicebus*-like and *Saguinus*-like morphology in early stem platyrrhines, or that both taxa represent the earliest offshoot Patagonian molar shapes. Currently, *Callicebus* and *Saguinus* present relatively high diversity of species and geographic range (Rylands and Mittermeier 2009). The *Callicebus* and *Saguinus* species richness probably are related to expansion and diversification of both clades in the Amazon basin, during the period of platyrrhine evolution (Ayres and Clutton-Brock, 1992; Boubli et al., 2015). Thus, it is feasible that *Callicebus*, as well as *Saguinus*, molar shape would be an ancestral precursor for the existing forms. Moreover, the Middle Miocene platyrrhines indicate continuity in molar shape pattern with the early fossils, incorporating also new molar shapes not observed in the Patagonian forms: the *Alouatta*-like and the Pitheciinae-like forms.

CONCLUSIONS

This study develops a dental model based on molar shapes of M_1 and M_2 to explore phenotypic variation in extinct and extant platyrrhines. Our results showed that morphological stasis explains the low phenotypic changes in extinct and exctant platyrrhine, probably due to the ecological constraint, causing by phenotypic adaptation of platyrrhine in a relative narrow ecological niche. Early and Middle Miocene platyrrhines shared a relative similar shape pattern, while other patterns as *Alouatta*-like and Pitheciinae-like were incorpored in the Colombian fossils. The relation between both fossil samples could be due to: 1. All platyrrhine molar shapes share a primitive retention of the ancestral state. 2. An early divergence between two parallel shapes; a *Callicebus*-like and a *Saguinus*-like, which would be the ancestral precursors to all other forms. 3. A *Callicebu*s-like and *Saguinus*-like morphology have also been seen in the early stem platyrrhines.

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Table 1: List of fossils used in the study.

Fossils	**Location**	**Age (Ma)**	**Phylogenetic position**	**Specimen number and reference**
F1 *Proteopithecus sylviae*	Fayum, Egypt	33.9 -28.4[a]	stem anthropoid[b]	CGM 42209; Miller and Simons (1997)
F2 *Soriacebus* spp.	Pinturas Formation, Santa Cruz Province, Argentina	17[c]	stem platyrrhine[d]/ Pitheciidae[e]	MACN-SC 2[1], MACN-SC 5[2] MPM-PV 36[3]; Tejedor (2005)
F3 *Dolichocebus gaimanesis*	Gaiman, Chubut Province, Argentina	20[f]	stem platyrhine/ sister to *Saimiri*[g]	MPEF 5146; Kay et al. (2008)
F4 *Homunculus* spp.	Santa Cruz Formation, Santa Cruz Province, Argentina	16.5[h]	stem platyrrhine/ Pitheciidae	MACN-A5969; Tejedor and Rosemberger (2008)
F5 *Carlocebus* spp.	Pinturas Formation, Santa Cruz Province, Argentina	18-19[i]	stem platyrrhine/ Pitheciidae	MACN-SC 266; Fleagle (1990)
F6 *Neosaimiri fieldsi*	La Venta, Huila, Colombia	13.5 -11.8[j]	sister to *Saimiri*[k]	IGM-KU 89029[4], IGM-KU 89019[5], UCMP 39205[6], IGM-KU 89002[7], IGM-KU 39034[8], IGM-KU 89053[9], IGM-KU 89130[10]; Takai (1994)
F7 *Laventiana annectens*	La Venta, Huila,	13.5 -11.8	sister to *Saimiri/*	IGM-KU 880; Rosemberger et al.,

	Colombia		synonymy with *Neosaimiri*[l]	(1991b)
F8 *Mohanamico hershkouitzi*	La Venta, Huila, Colombia	13.5 -11.8	sister to *Callimico*[m]	IGM 181500; Kay (1990)
F9 *Aotus dindensis*	La Venta, Huila, Colombia	13.5 -11.8	sister to *Aotus*[n]/ coespecific with *Mohanamico*[o]	IGM-KU 8601; Kay (1990)
F10 *Stirtonia* spp.	La Venta, Huila, Colombia	13.5 -11.8	sister to *Alouatta*[p]	UCPM 38989; Kay et al. (1987)
F11 *Nuciruptor rubricae* (1997)	La Venta, Huila, Colombia	13.5 -11.8	Pitheciidae[q]/ stem Pitheciinae[r]	IGM 251074; Meldrum and Kay
F12 *Cebupithecia sarmientoni* (1997)	La Venta, Huila, Colombia	13.5 -11.8	Pitheciidae/ stem Pitheciinae	UCMP 38762; Meldrum and Kay
F13 *Xenothrix macgregori*	Jamaica	Holocene[s]	stem platyrhine/ retaded to *Callicebus*[t]	AMNHM 148198; MacPhee and Horovitz (2004)

References used in the table: Miller and Simons 1997[a]; Kay 1990[b]; Fleagle et al., 1987[c]; (Kay, 2010; 2014[r]; Kay and Fleagle, 2010; Kay et al., 2008[f])[d]; (Rosenberger, 1979[g]; Tejedor 2000[g]; Tejedor and Rosenberger, 2008[h])[e]; Rosenberger, 1979[g]; Fleagle 1990[i]; Flynn et al., 1997[j]; Rosenberger et al., 1991b[k]; (Takai, 1994; Meldrum y Kay 1997)[l]; Rosenberger et al., 1990b[m]; (Setoguchi and

Rosenberger, 1987; Takai et al., 2009)[n]; Meldrum y Kay, 1997[o,q]; (e g., Hershkovitz P 1970; Kay et al., 1987)[p]; Cooke et al., 2011[s]; MacPhee and Horovitz 2004[t]

Institutional abbreviations: CGM: Cairo Geological Museum; MPM-PV: Museo Regional Provincial Padre Manuel Jesús Molina, Río Gallegos, Argentina; MPEF: Museo Paleontológico E. Feruglio, Trelew, Chubut Province, Argentina; MACN, MACN-SC/A: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; SC/A denotes locality; IGM, IGM-KU: Museo Geologico del Instituto Nacional de Investigaciones Geológico-Mineras, Bogota, Colombia; KU denotes Kyoto University; UCPM: University of California Museum of Paleontology, Berkeley, California; AMNHM: Division of Vertebrate Zoology Mammalogy, American Museum of Natural History.

Table 2 List of the specimens included in this analysis of M_1 and M_2. The Subfamily-level classification was proposed by Groves (2005).

Genus / species	**M_{1-2}**	**Collection**[a]
Subfamily: Cebinae		
Cebus (gracile capuchins)		
1 *C. albifrons*	9	MZUSP, MNRJ
2 *C. olivaceus*	6	MNRJ
Sapajus (robust capuchins)		
3 *S. apella*	14	MZUSP
4 *S. libidinosus*	15	MNRJ
5 *S. nigritus*	15	MNRJ
6 *S. robustus*	15	MNRJ
7 *S. xanthosternos*	7	MNRJ
Subfamily: Samiriinae		
Saimiri (squirrel monkeys)		
8 *S. boliviensis*	17	MZUSP, MNRJ
9 *S. sciureus*	25	MZUSP, MNRJ
10 *S. ustus*	18	MZUSP, MNRJ
11 *S. vanzolinii*	8	MNRJ
Subfamily: Callitrichinae		
Callithrix (marmosets from Atlantic Forest)		
12 *C. aurita*	11	MNRJ
13 *C. geoffroyi*	15	MNRJ

14 *C. jacchus*	21	MZUSP
15 *C. kuhlii*	20	MNRJ
16 *C. penicillata*	14	MNRJ
Mico (marmosets from Amazon)		
17 *M. argentata*	21	MZUSP, MNRJ
18 *M. chrysoleuca*	16	MZUSP, MNRJ
19 *M. emiliae*	6	MZUSP
20 *M. humeralifer*	16	MZUSP
21 *M. melanurus*	8	MZUSP, MNRJ
Cebuella (pygmy marmoset)		
22 *C. pygmaea*	7	MZUSP
Callimico (goeldi's marmoset)		
23 *C. goeldii*	4	MZUSP
Leontopithecus (lion tamarins)		
24 *L. chrysomelas*	5	MZUSP, MNRJ
25 *L. rosalia*	17	MZUSP, MNRJ
Saguinus (tamarins)		
26 *S. fuscicollis*	13	MZUSP
27 *S. imperator*	10	MZUSP
28 *S. labiatus*	9	MZUSP, MNRJ
29 *S. midas*	22	MZUSP, MNRJ
30 *S. mystax*	13	MZUSP, MNRJ
31 *S. niger*	14	M2NRJ

Subfamily: Aotinae		
Aotus (owl or night monkeys)		
31 *A. azarae*	4	MZUSP, MNRJ
32 *A. nigriceps*	9	MZUSP, MNRJ
33 *A. trivirgatus*	21	MZUSP
Subfamily: Callicebinae		
Callicebus (titi monkeys)		
34 *C. bernhardi*	5	MNRJ
35 *C. cupreus*	14	MZUSP, MNRJ
36 *C. hoffmannsi*	12	MNRJ
37 *C. moloch*	16	MZUSP, MNRJ
38 *C. nigrifrons*	8	MNRJ
39 *C. personatus*	16	MZUSP, MNRJ
Subfamily: Pitheciinae		
Cacajao (uakaris)		
40 *C. calvus*	14	MZUSP, MNRJ
41 *C. melanocephalus*	9	MZUSP, MNRJ
Chiropotes (bearded sakis)		
42 *C. albinasus*	18	MZUSP, MNRJ
43 *C. satanas*	15	MZUSP, MNRJ
Pithecia (sakis)		
44 *P. irrorata*	17	MZUSP, MNRJ
45 *P. monachus*	7	MZUSP, MNRJ

46 *P. pithecia*	16	MZUSP, MNRJ
Subfamily: Atelinae		
Lagothrix (woolly monkeys)		
47 *L. cana*	7	MNRJ
48 *L. lagotricha*	8	MZUSP
Brachyteles (muriquis)		
49 *B. arachoides*	16	MZUSP, MNRJ
50 *B. hypoxanthus*	5	MNRJ
Ateles (spider monkeys)		
51 *A. belzebuth*	2	RBINS
52 *A. chamek*	15	MNRJ
53 *A. marginatus*	20	MZUSP
Subfamily: Alouatinae		
Alouatta (howler monkeys)		
54 *A. belzebul*	15	MZUSP
55 *A. caraya*	15	MZUSP, MNRJ
56 *A. discolor*	10	MNRJ
57 *A. guariba*	5	MZUSP, MNRJ
58 *A. g. clamitas*†	15	MNRJ
59 *A. nigerrima*	10	MNRJ
60 *A. palliata*	15	HLP
61 *A. seniculus*	15	MZUSP

62 *A. ululata*	7	MNRJ

† Subspecies of *Alouatta guariba*

[a] Institutional abbreviations: MZUSP: Museu de Zoologia Universidade de São Paulo (Brazil); MNRJ: Museu Nacional do Rio de Janeiro (Brazil); HLP: Hacienda La Pacífica.

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Table 3. Landmarks considered for the geometric morphometrics analysis of dental crown shape.

Landmark	Type	Definition
1	2	Tip of the distolingual cusp (entoconid)
2	2	Tip of the mesiolingual cusp (metaconid)
3	2	Tip of the mesiobuccal cusp (protoconid)
4	2	Tip of the distobuccal cusp (hypoconid)
5	3	Most distal point of the mid mesiodistal line on the crown outline
6	2	Point of maximum curvature directly below the entoconid*
7	3	Point on the dental crown outline at the lingual groove
8	2	Point of maximum curvature directly below the metaconid*
9	3	Most mesial point of the mid mesiodistal line on the crown outline
10	2	Point of maximum curvature directly below the protoconid*
11	3	Point on the dental crown outline at the mesial groove
12	2	Point of maximum curvature directly below the hypoconid*
13	2	Midpoint between the preentocristid and postmetacristid*
14	2	Lowest point on the protocristid*
15	2	Lowest point on the crista oblique*

* Landmarks follow definitions by Cooke (2011)

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Table 4. A comparison of platyrrhines at the subfamily level classifications

Genus	**Subfamily by Groves (2005)**	**Subfamily by Rosenberger (2011)**
Cebus	Cebinae	Cebinae
Sapajus		
Saimiri	Saimiriinae	
Callithrix	Callitrichinae	Callitrichinae
Mico		
Cebuella		
Callimico		
Leontopithecus		
Saguinus		
Aotus	Aotinae	Homunculinae
Callicebus	Callicebinae	
Cacajao	Pitheciinae	Pitheciinae
Chiropotes		
Pithecia		
Lagothrix	Atelinae	Atelinae
Brachyteles		
Ateles		
Alouatta	Alouattinae	

Table 5. Summary of the LDA, including the percentage of variance for the two discriminant function (DF1 and DF2), the percentage of original grouped cases correctly classified and the percentage of cross-validated. Further, the percentage of probability that each case (fossil) belongs to the predicted group. Family: Pitheciidae, Cebidae, Atelidae; subfamily by Groves (2005) (Subfamily by G): Aotinae, Cebinae, Saimiriinae, Callitrichinae, Pitheciinae, Callicebinae, Atelinae, Alouattinae; subfamily by Rosenberger (2011) (Subfamily by R): Cebinae, Callitrichinae, Pitheciinae, Homunculinae, Atelinae; Genus: The names are listed in Table 2. *Soriacebus*[1, 2,3] and *Neosaimiri*[4, 5, 6, 7, 8, 9, 10] corresponding to the holotypes numbered on Table 1.

a) M_1

	Family%	**Subfamily by G %**	**Subfamily by R %**	**Genus %**
DF1	56.0	50.5	42.4	49.0
DF2	44.0	19.1	29.1	14.2
Classification	88.7	91.3	88.2	91.0
Cross-validation	87.4	88.0	85.7	86.3

(M_1)	**Family**	**%**	**Subfamily by G%**		**Subfamily by R%**		**Genus**	**%**
Proteopithecus	Cebidae	99.6	Saimiriinae	99.2	Cebinae	99.9	*Saimiri*	99.3
Soriacebus [1]	Cebidae	99.9	Callitrichinae	99.9	Callitrichinae	99.8	*Saguinus*	89.6
Soriacebus [2]	Cebidae	99.1	Callitrichinae	76.6	Callitrichinae	94.0	*Callithrix*	69.1
Dolichocebus	Cebidae	86.5	Callicebinae	77.9	Homunculinae	67.4	*Callicebus*	86.4

Carlocebus	Cebidae	97.0	Callitrichinae	94.2	Callitrichinae	83.7	*Callithrix*	87.1
Neosaimiri [4]	Pitheciidae	48.5	Atelinae	48.8	Callitrichinae	52.2	*Saguinus*	78.7
Neosaimiri [5]	Cebidae	98.4	Callitrichinae	97.5	Callitrichinae	97.3	*Saguinus*	99.6
Neosaimiri [6]	Cebidae	97.0	Callitrichinae	76.5	Callitrichinae	94.6	*Saguinus*	72.2
Laventiana	Atelidae	94.6	Atelinae	44.5	Atelinae	94.9	*Callicebus*	53.0
Mohanamico	Cebidae	96.2	Callitrichinae	87.3	Callitrichinae	70.3	*Leontopithecus*	65.4
Aotus dindensis	Pitheciidae	59.0	Aotinae	99.7	Homunculinae	97.4	*Aotus*	98.7
Stirtonia	Atelidae	98.9	Alouattinae	99.9	Atelinae	98.2	*Alouatta*	99.9
Nuciruptor	Pitheciidae	99.7	Callicebinae	99.5	Homunculinae	83.6	*Callicebus*	63.3
Cebupithecia	Pitheciidae	96.5	Pitheciinae	92.1	Pitheciinae	65.3	*Chiropotes*	59.2
Xenothrix	Pitheciidae	75.8	Callicebinae	30.5	Homunculinae	61.9	*Callithrix*	90.7

b) M$_2$

	Family%	Subfamily by G %	Subfamily by R %	Genus %
DF1	68.3	45.6	47.6	43.5
DF2	31.7	29.0	32.8	22.6
Classification	89.5	93.3	90.3	88.7
Cross-validation	88.2	90.6	89.0	84.7

(M_2)	**Family**	**%**	**Subfamily by G**	**%**	**Subfamily by R**	**%**	**Genus**	**%**
Proteopithecus	Cebidae	99.4	Callitrichinae	82.3	Callitrichinae	80.3	*Callimico*	86.7
Soriacebus[1]	Cebidae	65.6	Callicebinae	81.6	Homunculinae	58.4	*Saguinus*	74.6
Soriacebus[3]	Atelidae	77.1	Callitrichinae	96.7	Callitrichinae	98.0	*Saguinus*	65.6
Dolichocebus	Cebidae	50.7	Callicebinae	92.6	Homunculinae	90.1	*Callicebus*	92.6
Homunculus	Pitheciidae	91.4	Callicebinae	93.7	Homunculinae	97.3	*Callicebus*	99.9
Carlocebus	Cebidae	55.6	Callitrichinae	58.8	Callitrichinae	50.4	*Mico*	72.5
Neosaimiri[7]	Cebidae	98.3	Callicebinae	92.9	Cebinae	35.8	*Callicebus*	67.2
Neosaimiri[8]	Cebidae	64.9	Callicebinae	61.2	Homunculinae	93.7	*Saguinus*	65.1
Neosaimiri[9]	Cebidae	99.5	Callitrichinae	61.3	Callitrichinae	51.7	*Saguinus*	92.3
Neosaimiri[10]	Cebidae	98.9	Callicebinae	84.6	Callitrichinae	71.9	*Saguinus*	98.3
Laventiana	Cebidae	99.9	Callitrichinae	99.8	Callitrichinae	99.7	*Saguinus*	40.8

Mohanamico	Cebidae	97.7	Callitrichinae	94.9	Callitrichinae	94.6	*Saguinus*	99.9
Aotus dindensis	Cebidae	84.4	Callicebinae	88.9	Homunculinae	76.1	*Callicebus*	96.5
Nuciruptor	Pithecidae	89.7	Pitheciinae	89.7	Pitheciinae	73.0	*Pithecia*	49.4
Stirtonia	Atelidae	81.8	Alouattinae	86.0	Callitrichinae	92.1	*Alouatta*	94.0