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Mónica Nova Delgado, Jordi Galbany, Alejandro Pérez-Pérez

The phylogenetic position of fossil platyrrhines with respect to extant ones is not clear yet. 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 lineages* hypothesis argues for an evolutionary continuity of all platyrrhine lineages. Despite dental morphology may reflect a certain degree of homoplasia, a significant genetic signal has been detected, reflecting phylogenetic relationships among extant taxa. A geometric morphometric analysis of a 15 landmark-based configuration was applied to a sample of 802 platyrrhines' first and second lower molars representing all living families and subfamilies (62 species). A Linea Discriminant Analysis was applied to derive the *post-hoc* probability of classification of 11 fossil Platyrhins and 1 fossil anthrpoid from El Fayum within the extant comparative collection. The phenipic affinities within the fossil specimens and with the extant groups were used to test hypotheses of Platyrhine diversification and evolution. The reduced geometric morphometric molar shape variation observed within both the fossil and living taxa suggest that morphological stasis, a slow rate of phenotypic change, may explain the great similarities between both groups. 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. Phenotypic diversification of molar shaped was already settled during the Middle Miocene, which may reflect either that platyrrhines share a retention of a primitive molar shape or that an early divergence between two parallels shapes, *Callicebus*-like and *Saguinus*-like, would be the ancestral precursors to all other forms, with *Callicebus*-like and *Saguinus*-like morphologies already present in the early stem platyrrhines.

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

Mónica Nova Delgado,[a] Jordi Galbany,[a–b] and Alejandro Pérez-Pérez[a]

[a] Secció d'Antropologia, Departament de Biologia Animal, Universitat de Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain.

[b] Center for the Advanced Study of Human Paleobiology, Department of Anthropology, George Washington University, 800 22nd Street NW, Ste 6000, Washington DC 20052, USA.

***Corresponding author:**

Dr. Alejandro Pérez-Pérez

martinez.perez.perez@ub.edu

Tf. +34-934021460

Dept. Animal Biology (Anthropology). Av. Diagonal 645, 08028 Barcelona – Spain.

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ABSTRACT

The phylogenetic position of fossil platyrrhines with respect to extant ones is not clear yet. 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 lineages* hypothesis argues for an evolutionary continuity of all platyrrhine lineages. Despite dental morphology may reflect a certain degree of homoplasia, a significant genetic signal has been detected, reflecting phylogenetic relationships among extant taxa. A geometric morphometric analysis of a 15 landmark-based configuration was applied to a sample of 802 platyrrhines' first and second lower molars representing all living families and subfamilies (62 species). A Linea Discriminant Analysis was applied to derive the *post-hoc* probability of classification of 11 fossil Platyrhins and 1 fossil anthrpoid from El Fayum within the extant comparative collection. The phenipic affinities within the fossil specimens and with the extant groups were used to test hypotheses of Platyrhine diversification and evolution. The reduced geometric morphometric molar shape variation observed within both the fossil and living taxa suggest that morphological stasis, a slow rate of phenotypic change, may explain the great similarities between both groups. 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. Phenotypic diversification of molar shaped was already settled during the Middle Miocene, which may reflect either that platyrrhines share a retention of a primitive

molar shape or that an early divergence between two parallels shapes, *Callicebus*-like and *Saguinus*-like, would be the ancestral precursors to all other forms, with *Callicebu*s-like and *Saguinus*-like morphologies already present in the early stem platyrrhines.

INTRODUCTION

Platyrrhine evolution is controversial. Despite 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), the phylogenetic position of some living taxa and the affinities of fossil specimens ~~are~~ still uncertain. Currently, two different viewpoints have been proposed about 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, phylogenetically unrelated to the crown platyrrhines, that went extinct (along with some Antillean species) lacking modern descendants (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, is indicative 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, the datings of the fossil specimens and the 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 analyses of both extinct and extant forms may be a useful tool to gain further insight into this debate on evolutionary continuity (Cardini and Elton, 2008; Klingenberg and Gidaszewski, 2010), since tooth development is under strong genetic control (Jernvall and Jung, 2000). Indeed, dental 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). We have recently reported a significant phylogenetic signal of molar morphology in some Platyrrine taxa (Nova Delgado et al., 2015), with closely related species exhibiting common phenotypic traits.

Affinities of the fossil platyrrhine primates

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 *Dolichochebus* (Chubut Province, Argentina) have been included within the Cebinae (Rosenberger, 2011), whereas *Neosaimiri* has been considered a direct ancestor of the extant *Saimiri*, ~~with~~ which shares a symmetric molar shape pattern (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 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. *Aotus dindensis* was first described as a sister taxon of *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) and *Callicebus* has been classified within the Homunculinae, along with *Aotus* and some Argentinian and Caribbean fossil primates (Rosenberg, 1981, 2002, 2011). Tejedor and Rosenberger (2008) proposed that *Homunculus* is likely the ancestral pitheciine 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).

Soriacebus, another fossil included in the same monophyletic clade, would represent the earliest Pitheciinae taxon (Perez et al 2013), which it shares anatomical traits on the anterior dentition and the mandibular shape (Fleagle et al., 1987; Fleagle, 1990; Fleagle and Tejedor, 2002; Tejedor, 2005). Some dental traits of *Soriacebus* (premolars-molars size, lower molar trigonid, and reduction hypocone) may suggest a link with the Callitrhichines, but Kay (1990) has considered them to be homoplasies and has placed *Soriacebus* as stem platyrrhine. *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*, a Caribbean primate. Rosenberger (2002) argued that *Xenothrix* is closely related to *Aotus* and *Tremacebus* by the enlargement of the orbits and the central incisor~~s~~ enlargment, 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 (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*, it was interpreted by Meldrum and Kay (1997) as 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*; both 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; Nova Delgado et al., 2015; Singleton et al. 2011; White 2009). However, in Platyrrhini 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., 2014). The aim of the present study was to use the two-dimensional (2D) GM variability of occlusal shapes 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 estimat~~ing~~ 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 holotype fossil platyrrhine specimens and one fossil from Fayum (*Proteopithecus sylviae*), used as an outgroup, were obtained from the literature. 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 35 Ma (Table 1).

The extant comparative samples (Table 2) consisted in 802 adult individuals representing all recognized platyrrhine groups (3 families, 18 genera, 61 species, one subspecies), whose 2D and 3D morphometric variability of lower molars has ~~partially been~~ analysed (Nova Delgado et al., 2015). Dental casts were obtained from original specimens housed at various institutions: 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. Only unworn teeth were studied. 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., 2014). The images of the dental crowns of the fossil specimens, obtained from the literature, were imported into Adobe Photoshop and scaled to the same resolution (400 dpi) than those of the extant specimens. In both cases, the images were 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 was adapted from

Cooke (2011) and consisted of 15 landmarks (Table 3). The tips of the four main cusps (protoconid, metaconid, hypoconid and entoconid) defined the molar occlusal polygon. 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 the crests (Fig. 1). 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, 1999; Rohlf and Slice, 1990; Rohlf and Marcus 1993; Goodall, 1991; 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).

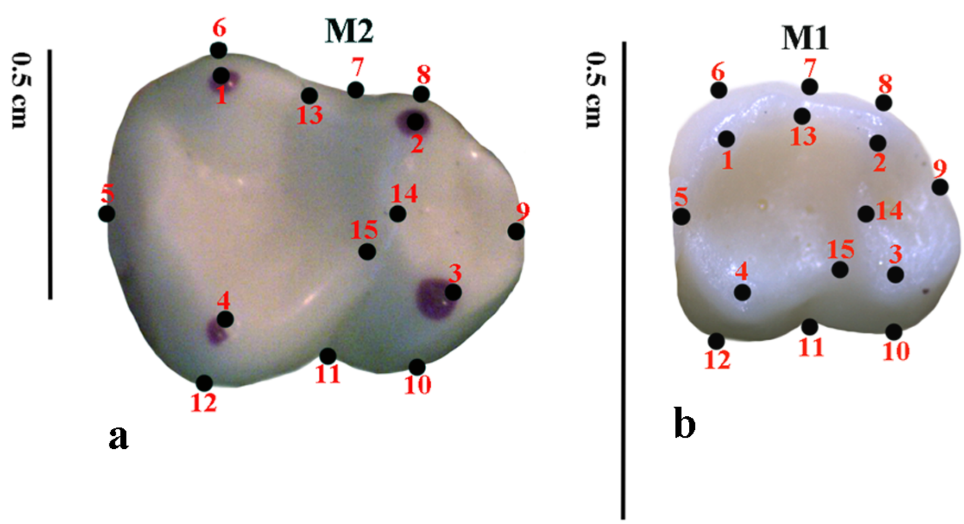

Figure 1. Set of landmarks used in the geometric morphometrics analyses. a) M_2; *Alouatta guariba* 23177 MNRJ; b) M_1: *Sapajus libidinosus* 23246 MNRJ.

The PCAs of M_1 and M_2 morphometric variability of the extant species was used to explore dental affinities of the fossil specimens with the extant comparative platyrrhine sample. *One-way* ANOVA comparison was carried out to evaluate statistically significant between subfamilies. The procrustes coordinates of the extant samples were used to make a Linear Discriminant Function analyses (LDA) to classify the ungrouped fossil specimens (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), and 4) a genus level (*Cebus*, *Sapajus*, *Saimiri*, *Callithrix*, *Mico*, *Cebuella*, *Callimico*, *Leontopithecus*, *Saguinus*, *Aotus*, *Callicebus*, *Cacajao*, *Chiropotes*, *Pithecis*, *Lagothrix*, *Brchyteles*, *Atelles*, *Allouatta*). The LDF and *One-way* ANOVA 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) explained 42.06 % of total shape variance (PC1 30.60%; PC2 11.46%). Positive scores on PC1 corresponded to molars with a broad occlusal polygon~~s~~ and a mesiodistally rectangular outline; whereas a negative PC1 score was indicative of a relatively quadrangular outline and slight buccolingually rectangular occlusal polygon, characterized by a mesio-lingual displacement of the distal cusps (entoconid and hypoconid) and a disto-lingual one of the mesial cusps (metaconid and protoconid). Positive scores on PC2 indicateed a rectangular occlusal polygon and a mesiodistally rectangular outline, whereas negative score on PC2 reflected molars with relatively quadrangular outline and a slightly rectangular occlusal polygon, wider on the buccal side.

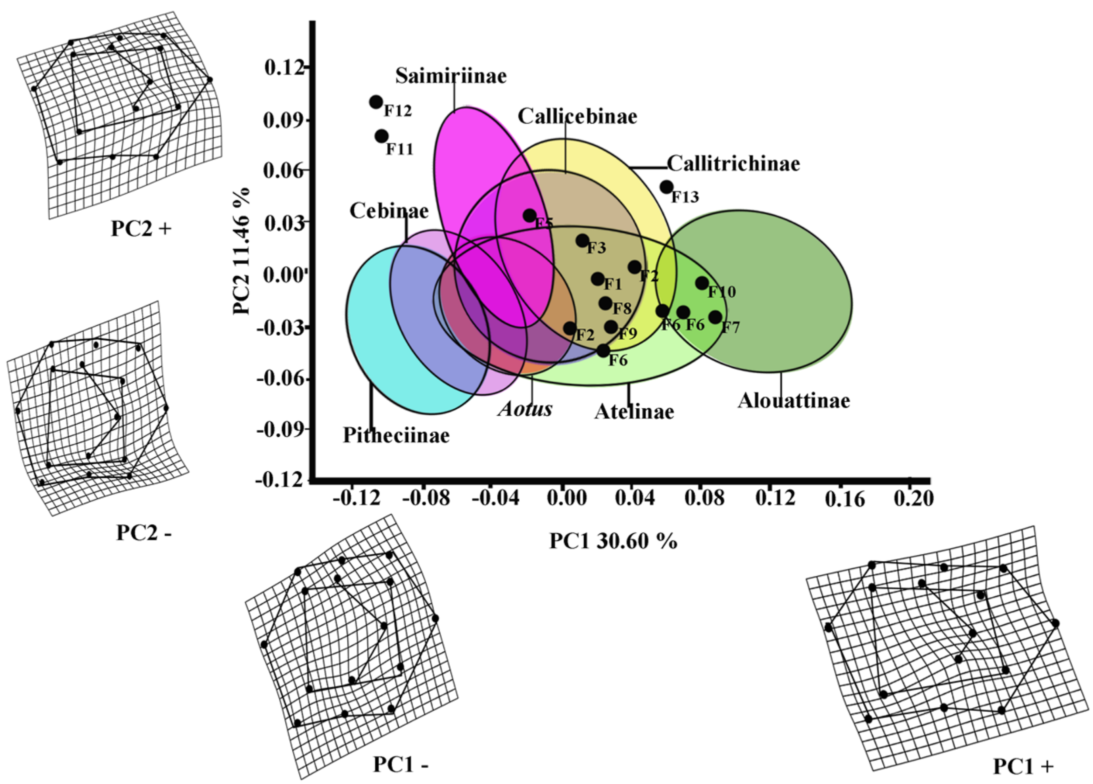

Figure 2. Scatterplot of the first two principal components (PCs) derived from the PCA of M_1 shape variability of Platyrrhini. Grids indicate the deformations associated with the extreme values of each principal component.

In the PC1 *versus* PC2 plot (Fig. 2) the 95% confidence ellipses of the subfamily groups greatly overlapped. However, the *One-way* ANOVA analyses detected statistically significant differences between the groups (PC1: F= 361.0 P < 0.0001; PC2: F= 39.7 P < 0.0001). Alouattinae clearly clustered on the positive scores of PC1, whereas Pithecinae and Cebinae greatly overlapped on the most negative scores of PC1. The rest of the groups (Saimirinae, Callicebinae, Callitrichidae, Atellidae and *Aotinae*) showed intermediate values for PC1. For the function (PC2), all groups greatly overlapped, though Saimirinae, Callitrichinae and Callicebinae showed somewhat ~~hiegher~~ 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) and *Nuciruptor* and *Cebupithecia*.

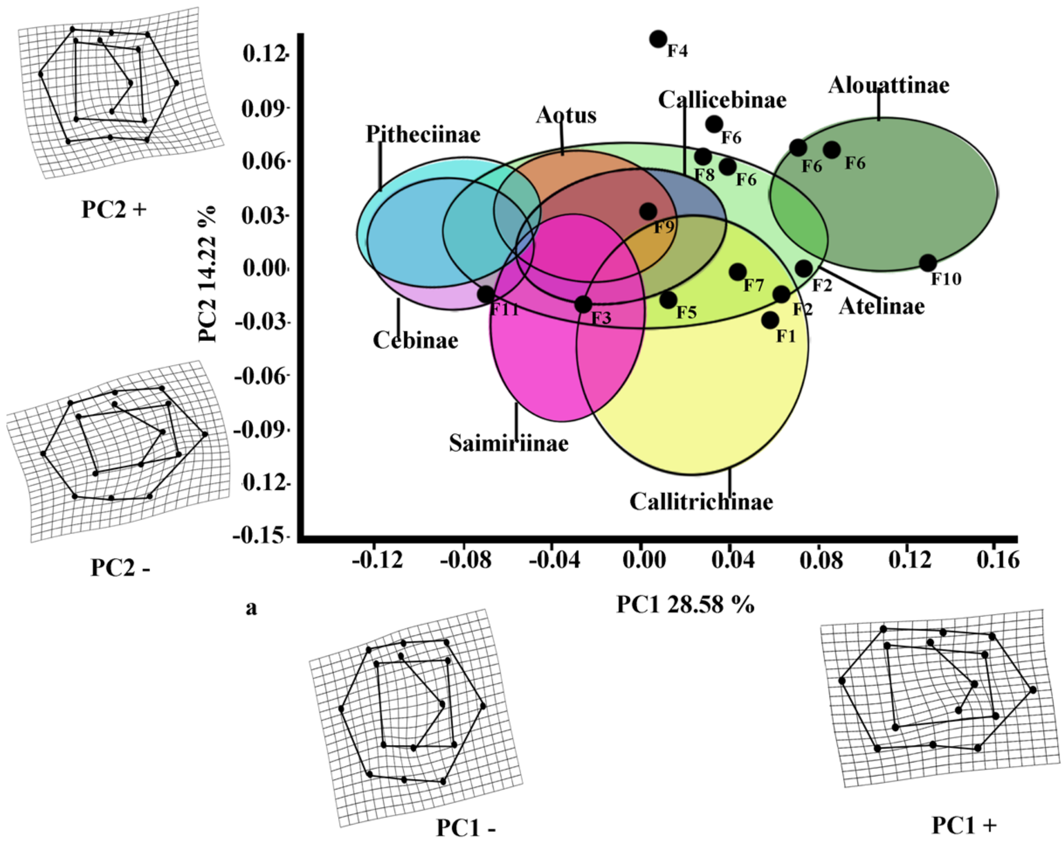

Figure 3. Scatterplot of the first two principal components (PCs) derived from the PCA of M_2 shape variability of Platyrrhini. Grids indicate the deformations associated with the extreme values of each principal component**.**

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 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. Further, a *One-Way* ANOVA of the two first PC scores showed that dental shapes among subfamilies were statistically distinct (M_2; PC1: F= 455.8 P < 0.0001; PC2: F= 102.6 P < 0.0001). 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 Atellinae, Callitrichinae and Atellinae, although *Stirtonia* (F10), *Dolichocebus* (F3) and *Nuciruptor* (F11) clearly fell within the Alouattinae clade, and *Nuciruptor* (F11) was closer to Cebinae and Pitheciinae on the negative scores of PC1. *Homunculus* (F4) did not fall at all within any extant taxa, showing highly possitive PC2 scores.

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 Grooves' (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 4). 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 adn 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 4; Fig. 4, showing 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/Homonculinae for M_2. *Cebupithecia* (M_2 not available) and *Nuciruptor* neotypes showed a high probability of belonging to the pitheciid clade. In contrast, *Xenothrix* (M_2 not available) likely belonged to *Callithrix*, despite in the PCA this fossil specimen did not fall within the 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 the callitrichids 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 to *Saimiri* for M_1, but to *Callimico* for M_2.

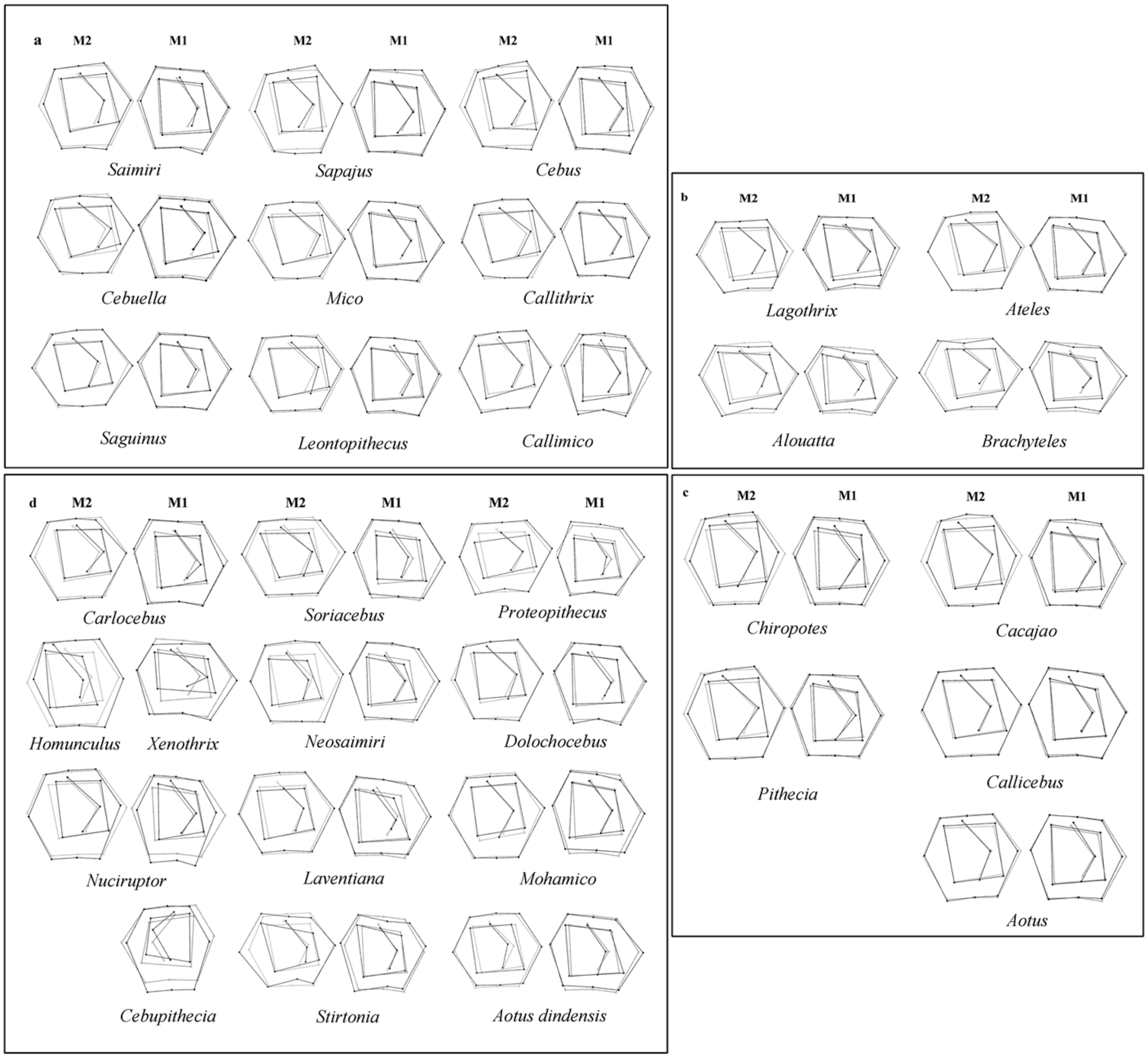

Figure 4. Firts and second molar shapes of the extinct fossil platyrhines used in this study.

DISCUSSION

Proteopithecus sylviae (F1) showed molar shape resemblances with the platyrrhines. Although many dental and postcranial features of *P. sylviae* are considered to be symplesiomorphic traits of all anthropoids, it is considered a stem anthropoid (Kay, 1990, 2014). However, the recently discovered *Perupithecus ucayaliensis,* from the Late Eocene, exhibits similarities with *Proteopithecus,* as well as with *Talahpithecus* and *Oligopithecidae* (Bond et al., 2015). The upper molars of *Perupithecus* are similar to those of the calitrichines, but their morphology more closely resemble that of *Proteopithecus* and *Talahpithecus* (Bond et al., 2015). *Proteopithecus sylviae* differes from extant and extinct platyrrhines in having a distomesially expanded molar and a rectangular occlusal polygon (especially M_2) (also described in *Xenothrix*). If the Fayum fossil is a sister taxon to platirrhines, the interspecific variation of molar shape would have shown relatively little change through time molars shapes in platyrrhines would represent a retention of the primitive ancestral form. The LDA showed a high probability of *P. sylviae* belonging to the Cebidae clade, suggesting that the molar of the earliest ancestors of platyrrhines might have exhibited close similarities to *Saimiri-Callimico.* This resemblance matches with the description of *Branisella* − a South American Oligocene fossil primate (Rosenberger, 2002; Rosenberger et al., 2009) − that shows a *Saimiri*-like M_2 morphology and a *Callimico*-like upper P^2 (Rosenberger, 1980). However, the shapes of both molars of *P. sylviae* more closely resembled those of *Callimico* than of *Saimiri*. In addition, its subtriangular upper molars also show similarities with *Callimico* (Bond et al., 2015). If *P. sylviae* was a sister taxon to platirrhines, it is likely that the ancestral molar shape of pre-platyrrhines would have been similar to the molar shape of *Callimico*. By contrast, if *P. sylviae* was a stem species, *Callimico* dental anatomy would represent a retention of the primitive pre-anthropoid molar shape.

Early Miocene platyrrhines from Patagonia

The Early Miocene fossils were mainly assigned to either *Callicebus* or *Sagunus* in the LDA. *Dolichocebus* (F3) was classified as a pitheciid, mainly by having a square occlusal polygon, but while 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 callitrichid clade, but for M_2 the probability of belonging to this group was small (Table 4). *Soriacebus* showed a rectangular occlusal polygon on $M_{2,}$ and its ectoconid was inclined distolingually. Regarding callitricids, although *Soriacebus* also showed differences in cusp configuration, the callitricids 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, *Soriacebus* ~~r~~may epresent the first branching of pitheciids. Although marmosets are considered a derived clade (e.g. Chatterjee et., 2009; Perelman et al., 2009; Jameson Kiesling et al., 2014), it is likely that their relationship with *Soriacebus* may be due to the fact that callitrichines exhibit primitive traits on their molars, which might indicate that both taxa share the retention of a rectangular contour of the occlusal polygon. *Carlocebus* (F5) was classified as a callitrichinae by the LDA but it more closely resemble *Callicebus* than marmosets in the shape contour and square alignment of cusps in both molars. *Homunculus* (F4) was placed outside the range of Patagonian forms (Fig. 2a), but 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 the pitheciids and, unlike pitheciids, *Homunculus* cusps were more distally place and the trigonid was almost as broad as the basin-like talonid, which indicates that although sharing some traits with pitheciids, its position is still highly uncertain. It is likely that some Patagonian lineages became extinct without direct descendants, but other taxa could have significantly diversified after migrating north in South American.

Middle Miocene platyrrhines from Colombia and the Caribbean

Most Miocene fossils were catalogued as callitrichines, specifically into the *Saguinus* clade, except *Nuciruptor*, *Cebupithecia*, *Aotus dindensis*, and *Stirtonia*. The fossil specimens mainly differred from the extant forms (excepting *Alouatta* and *Brachyteles*) in their rectangular-shaped molar, which indicates that a rectangular-shaped molar may represents a plesiomorphy retention in the Patagonian fossils. Thus, the trend toward ovoid molar shape might be a derived feature in many living forms. *Laventania* (F7) exhibits distally oriented cusps on M_1, showing considerable resemblances with some atelid groups, which results in a confusing classification between atelids and *Callicebus* in the LDA (Table 4). The trend to rectangular shape for M_1 in *Laventania* differs notably from the phylogenetic relationship between Cebinae and Saimiriinae. Nonetheless, when M_2 was analyzed, the fossil was classified as a member of the Callitrichinae clade. As with *Laventania*, some neotypes of *Neosaimiri* (F6) were classified in distinct taxonomic groups (Table 4). Despite this, *Neosaimiri* was associated to the Cebidae family, although the molar shape was found to have more affinities with callitrichines than *Saimiri. 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 a distinct genus. According to their molar shape, *Mohanamico* and *A. dindensis* may be classified into different species. Both fossils showed a relatively rectangular molar outline, although M_2 in both species were slightly square shaped. In fact, the LDA for M_1 (Fig. 2a) placed the two forms close to each other, likely because the two forms might have shared ecological niches; *Mohanamico* and *A. dindensis* were found in the same locality and at the same stratigraphic level (Kay, 1990). However, the LDA classification probabilitis different in the two taxa: *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 the cusps that were buccally oriented, which resembles the condition in most extant pitheciinae. *Cebupithecia* and *Nuciruptor* had close affinities with the Pitheciidae clade (Table 4), although they were not placed within 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 pitheciids (Meldrum and Kay, 1997; Kay et al., 2013; Kay, 2014).

The sister relationship between *Stirtonia* and *Alouatta* was classified was shown both LDA analyses (99.9% probability for M_1 and 94.0% for M_2). Likewise, the PCA showed that *Stirtonia* was placed close to the 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, similar to the *Cebuella* configuration.

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

As a whole, the reduced morphological variability observed in platyrhin molars shape suggests a slow rate of phenotypic change. A morphological stasis (a different concept to the *long lineages hypothesis*) would explain the low interspecific variation seen between extinct and extant linages and between Early Miocene platyrrhines (including *P. sylviae*) and forms from La Venta. This small phenotypic variation − as well as the reduced dietary diversification in platyrrhines compared to carnivores − could be due to developmental and functional constraints, given the significant role of dental occlusion during masticarion (Gómez-Robles and Polly 2012).). This ecological constraint might derive from a phenotypic adaptation of the main platyrrhine families in the Amazon rainforest (Jameson Kiesling et al. 2014). Following an African origin scenario, and taking into account the oldest fossil found in Peru, *Perupithecus* (Bond et al., 2015), it is likely that the ancestor of the extant platyrrhines could have exhibited a *Callimico*-like molar shape. *Saguinus* and *Callicebus* were the main assigned groups for the Patagonian fossils in the LDA and, thus, both *Callicebu*s-like and *Saguinus*-like morphologies might have beeb presented in the stem platyrrhines. At present both *Callicebus* and *Saguinus* show a high species diversity and geographic dispersion (Rylands and Mittermeier 2009), which might have diversifyed in the Amazon basin during platyrrhine evolution (Ayres and Clutton-Brock, 1992; Boubli et al., 2015). It is feasible that *Callicebus* and *Saguinus* molar shape would be an ancestral precursor for all extant forms and, thus, Middle Miocene platyrrhines molar shape would represent evolutionary continuity in molar shape pattern from earlier fossils along with new molar pattern, such as *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 explorer phenotypic variation in extinct platyrrhine specimens. The results show that morphological stasis explains the low phenotypic changes in both extinct and ex~~e~~tant platyrrhines, probably due to the ecological constraint, caus~~ing~~ by phenotypic adaptation of platyrrhine in a relative narrow ecological niche. Early and Middle Miocene platyrrhines show similar molar shape pattern, while *Alouatta*-like and Pitheciinae-like molar patterns were incorpored in the Colombian fossils. The similarities among all the fossil samples studied could be due to: 1) all platyrrhine molar shapes share a primitive retention of the ancestral state; 2) an early divergence between two parallels shapes, *Callicebus*-like and *Saguinus*-like, would be the ancestral precursors to all other forms; and 3) *Callicebu*s-like and *Saguinus*-like morphologies could have been present 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*	La Venta, Huila, Colombia	13.5 -11.8	Pitheciidae[q]/ stem Pitheciinae[r]	IGM 251074; Meldrum and Kay (1997)
F12 *Cebupithecia sarmientoni*	La Venta, Huila, Colombia	13.5 -11.8	Pitheciidae/ stem Pitheciinae	UCMP 38762; Meldrum and Kay (1997)
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. Comparative sample of extant Platyrhini specimens included in the analysis of the fossils specimens. The total number of M_1 and M_2 teeth studied (N) and the provenance (Collection) are indicated.

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

C. geoffroyi	15	MNRJ
C. jacchus	21	MZUSP
C. kuhli	20	MNRJ
C. penicillata	14	MNRJ
Mico (marmosets from Amazon)		
M. argentata	21	MZUSP, MNRJ
M. chrysoleuca	16	MZUSP, MNRJ
M. emiliae	6	MZUSP
M. humeralifer	16	MZUSP
M. melanura	8	MZUSP, MNRJ
Cebuella (pygmy marmoset)		
C. pygmaea	7	MZUSP
Callimico (goeldi's marmoset)		
C. goeldi	4	MZUSP
Leontopithecus (lion tamarins)		
L. chrysomelas	5	MZUSP, MNRJ
L. rosalia	17	MZUSP, MNRJ
Saguinus (tamarins)		
S. fuscicollis	13	MZUSP
S. imperator	10	MZUSP
S. labiatus	9	MZUSP, MNRJ
S. midas	22	MZUSP, MNRJ
S. mystax	13	MZUSP, MNRJ

S. niger	14	M$_2$NRJ
Subfamily: Aotinae		
Aotus (owl or night monkeys)		
A. azarae	4	MZUSP, MNRJ
A. nigriceps	9	MZUSP, MNRJ
A. trivirgatus	21	MZUSP
Subfamily: Callicebinae		
Callicebus (titi monkeys)		
C. bernhardi	5	MNRJ
C. cupreus	14	MZUSP, MNRJ
C. hoffmanni	12	MNRJ
C. moloch	16	MZUSP, MNRJ
C. nigrifrons	8	MNRJ
C. personatus	16	MZUSP, MNRJ
Subfamily: Pitheciinae		
Cacajao (uakaris)		
C. calvus	14	MZUSP, MNRJ
C. melanocephalus	9	MZUSP, MNRJ
Chiropotes (bearded sakis)		
C. albinasus	18	MZUSP, MNRJ
C. satanas	15	MZUSP, MNRJ
Pithecia (sakis)		
P. irrorata	17	MZUSP, MNRJ

P. monachus	7	MZUSP, MNRJ
P. pithecia	16	MZUSP, MNRJ
Subfamily: Atelinae		
Lagothrix (woolly monkeys)		
L. cana	7	MNRJ
L. lagotricha	8	MZUSP
Brachyteles (muriquis)		
B. arachoides	16	MZUSP, MNRJ
B. hypoxanthus	5	MNRJ
Ateles (spider monkeys)		
A. belzebuth	2	RBINS
A. chamek	15	MNRJ
A. marginatus	20	MZUSP
Subfamily: Alouatinae		
Alouatta (howler monkeys)		
A. belzebul	15	MZUSP
A. caraya	15	MZUSP, MNRJ
A. discolor	10	MNRJ
A. guariba	5	MZUSP, MNRJ
A. g. clamitas†	15	MNRJ
A. nigerrima	10	MNRJ
A. paliatta	15	HLP
A. seniculus	15	MZUSP

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.

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)

Table 4. Summary of the DFA, 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. *Soriacebus*[1, 2,3] and *Neosaimiri*[4, 5, 6, 7, 8, 9, 10] corresponding to the holotypes numbered on Table 1b.

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.