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

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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 throughout 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 displayed new, derived molar patterns, *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.

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

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17 **ABSTRACT**

18       The phylogenetic position of many fossil platyrrhines with respect to extant ones is not yet  
19 clear. Two main hypotheses have been proposed: the *layered* or *successive radiations* hypothesis  
20 suggests that Patagonian fossils are Middle Miocene stem platyrrhines lacking modern  
21 descendants, whereas the *long lineage* hypothesis argues for an evolutionary continuity of all  
22 fossil platyrrhines with the extant ones. Our geometric morphometric analysis of a 15 landmark-  
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25 might be a primitive retention of the ancestral state affected by strong ecological constraints  
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27 two distinct morphological patterns of lower molars, *Callicebus*-like and *Saguinus*-like, which  
28 might be the precursors of the extant forms, whereas the Middle Miocene specimens, though  
29 showing morphological resemblances with the Patagonian fossils, also displayed new, derived  
30 molar patterns, *Alouatta*-like and *Pitheciinae*-like, thereby suggesting that despite the overall  
31 morphological stasis of molars, phenotypic diversification of molar shape was already settled  
32 during the Middle Miocene.

## 34 INTRODUCTION

35         Platyrrhine evolution is controversial. However, most researchers agree that they most  
36 likely constitute a monophyletic clade derived from African ancestors (Fleagle and Kay, 1997;  
37 Takai et al., 2000; Kay et al., 2004; Oliveira et al., 2009; Bond et al., 2015), although the  
38 phylogenetic position of some living taxa and the affinities of some fossil specimens are still  
39 uncertain. Currently, two different viewpoints have been proposed regarding the evolutionary  
40 history of the earliest platyrrhines and their overall relationships with extant forms. The “long  
41 lineages” hypothesis argues that the oldest known Patagonian fossils (16–20 Ma) are to be  
42 included within the extant Platyrrhines (Rosenberger, 1979, 1980, 1981, 1984; Rosenberger et  
43 al., 2009; Tejedor, 2013), whereas the “layered or successive radiations” hypothesis suggests that  
44 these fossils constitute a geographically isolated stem group, phylogenetically unrelated to the  
45 crown platyrrhines, that went extinct (along with some Antillean species) (Kay, 2010; 2014; Kay  
46 and Fleagle, 2010; Kay et al., 2008). According to Kay (2014), the divergence of modern  
47 lineages occurred in the tropics. The Late Oligocene and Early Miocene platyrrhines would have  
48 branched off from the ancestral lineage when climatic conditions in Patagonia became  
49 unfavorable and the Andean uplift was a potential barrier to their dispersal. However, Tejedor  
50 (2013) has suggested that *Chilecebus* (20 Ma), a fossil specimen (Tejedor, 2003) from the  
51 western Andean cordillera, south of Santiago de Chile, indicates that the Andean mountains did  
52 not constitute a biogeographic barrier. Tejedor (2013) argued that a paleobiogeographic corridor  
53 throughout western South America would have allowed for a continental connectivity between  
54 the north and the southernmost fossil platyrrhines. Unfortunately, dating of the fossil specimens  
55 and fossil-based approaches for calibrating the molecular phylogeny support both models. Perez  
56 et al. (2013) have estimated a crown platyrrhine origin at around 29 Ma (27–31), which allows

57 for the inclusion of the fossil Patagonian primates into a crown Platyrrhini lineage showing  
58 evolutionary continuity with the Middle Miocene lineages. In contrast, Hodgson et al. (2009)  
59 have dated their origin between 16.8 and 23.4 Ma, suggesting an unlikely relationship of the  
60 early Miocene fossils with the crown platyrrhine clade (but see different temporal models in  
61 Goodman et al., 1998; Opazo et al., 2006; Chatterjee et al. 2009; Perelman et al. 2011; Wilkinson  
62 et al. 2011; Jameson Kiesling et al. 2014).

63 Molar morphology has been widely used to determine the phylogenetic positions of extinct  
64 specimens with respect to living forms (e.g., Kay, 1990; Rosenberger et al., 1991a, b; Benefit,  
65 1993; Meldrum and Kay, 1997; Miller and Simons, 1997; Horovitz and MacPhee, 1999; Kay and  
66 Cozzuol, 2006; Kay et al., 2008), since tooth development is under strong genetic control  
67 (Jernvall and Jung, 2000). Recent studies have reported that molar shapes carries strong  
68 phylogenetic signals, and can be useful tool for establishing taxonomic affinities between extant  
69 and extinct catarrhine primates (Nova Delgado et al., 2015a; Gamarra et al., 2016), and also in  
70 some Platyrrhine taxa (Nova Delgado et al., 2015b), with closely related species exhibiting  
71 common phenotypic traits.

72

### 73 **Affinities of the fossil platyrrhine primates based on dental morphology**

74 Until now, a total of 31 Early Miocene Platyrrhini fossil genera have been so far reported in  
75 the South American continent and the Caribbean: 11 in La Venta (Colombia), 8 in the Argentinian  
76 Patagonia, 4 in the Greater Antilles, 5 in Brazil, and 1 each in Chile, Bolivia and Peru (Tejedor,  
77 2013; Bond et al., 2015). *Neosaimiri*, *Laventiana* (La Venta, Colombia) and *Dolichocebus*  
78 (Chubut Province, Argentina) have been included in Cebinae (Rosenberger, 2011). *Neosaimiri* is  
79 considered a direct ancestor of the extant *Saimiri* due to its similar molar shape (Rosenberger et

80 al., 1990a; 1991a). Its molars exhibit sharp cusps, well-developed distal cusps, buccal cingulum,  
81 a strong buccal flare, and a distinct post-entoconid notch on molars only found in *Saimiri* and  
82 *Laventiana* (Rosenberger et al., 1991a, 1991b; Takai, 1994; Tejedor, 2008). *Laventiana* is  
83 sometimes considered a synonym of *Neosaimiri* (Takai, 1994; Meldrum and Kay, 1997),  
84 although it has been suggested to be more primitive than *Neosaimiri* (Rosenberger et al., 1991b).  
85 *Laventiana*'s teeth closely resemble those of *Saimiri* and *Cebus-Sapajus*; it shows thick-enamel  
86 bunodont molars exhibiting a small buccal cingulum and an angular cristid obliqua, lacking  
87 buccal flare (Rosenberger et al., 1991b). *Dolichocebus* has been suggested to be a member of the  
88 *Saimiri* lineage, mainly for its interorbital fenestra considered a derived feature in squirrel  
89 monkeys (Tejedor, 2008; Rosenberger et al., 2009; Rosenberger, 2010). However, Kay and  
90 colleagues (Kay et al., 2008; Kay and Fleagle, 2010) argued that *Dolichocebus* is a stem  
91 platyrrhine and that the description of the orbital region was probably affected by postmortem  
92 damage.

93 On the other hand, *Aotus dindensis* was first described as a sister taxon of extant *Aotus*  
94 (Setoguchi and Rosenberger, 1987), although Kay (1990) has suggested that it is probably  
95 conspecific with *Mohanamico hershkovitzi*, which may be closely related to the callitrichines,  
96 especially *Callimico*, due to their morphological similarities in the canine and the second  
97 premolar. *Aotus dindensis* is included into the Pitheciidae (Rosenberger et al., 1990a) within the  
98 Homunculinae subfamily, along with *Aotus*, *Callicebus* and some Argentinian and Caribbean  
99 fossil primates (Rosenberger, 1981, 2002, 2011). However, molecular phylogenetic analyses  
100 have repeatedly rejected a link between *Aotus* and Pitheciids (e.g Hodgson et al., 2009;  
101 Osterholz et al., 2009; Wildman et al., 2009), placing it as a basal cebid. Tejedor and  
102 Rosenberger (2008) proposed that *Homunculus* is likely an ancestral pitheciid because although

103 it shows a primitive dental morphology, it notably resembles that of *Callicebus*. The two taxa  
104 show rectangular-shaped molars, small incisors and non-projecting canines, a trait shared with  
105 *Carlocebus* (Fleagle, 1990). Nonetheless, unlike *Callicebus*, the molars of *Homunculus* exhibit  
106 well-marked crests and prominent cusps (Tejedor, 2013), and an unusual paraconid on the lower  
107 first molar (also found in *Dolichocebus*; Kay et al., 2008). Another fossil from the early Miocene  
108 known as *Soriacebus* was initially included by Rosenberger (1990) as an early pitheciinae, due to  
109 its resemblance on the anterior dentition (Fleagle et al., 1987; Fleagle, 1990; Fleagle and  
110 Tejedor, 2002; Tejedor, 2005). However, some dental traits of *Soriacebus* (premolars-molars  
111 size, lower molar trigonid, and reduction hypocone) bear resemblance also with the  
112 callitrichines. Indeed, Kay (1990) argues that such similarities traits found between *Soriacebus*  
113 and pitheciins or with callitrichines are due to homoplasy, rather than phylogenetic relationships  
114 among such lineages (Kay, 1990). According to Kay (1990) *Soriacebus*, *Carlocebus*,  
115 *Homunculus* as all Patagonian fossils should be considered stem platyrrhines.

116 *Xenothrix* is a Late Pleistocene Caribbean fossil from Jamaica that shows a callitrichine-like  
117 dental formula (2132; MacPhee and Horovitz, 2004), low relief molars and a narrowing of  
118 intercuspal distance and augmentation of the mesial and distal crown breadths (Cooke et al.,  
119 2011), a feature also seen in *Insulacebus toussaintiana*, another Caribbean primate. Rosenberger  
120 (2002) argued that *Xenothrix* is closely related to *Aotus* and *Tremacebus* by the enlargement of  
121 the orbits and the central incisors, while MacPhee and Horovitz (2004) suggested a possible  
122 Pitheciidae affinity, due to its low relief molar pattern. Nonetheless, the puffed cusps and the  
123 lack of crenulation on the molar crown discriminate the Jamaican fossil from the Pitheciidae,  
124 suggesting that is likely that *Xenothrix* does not belong to crown platyrrhine group (Kay, 1990;  
125 Kinzey, 1992).



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

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

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

148

149 **MATERIAL AND METHODS**

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

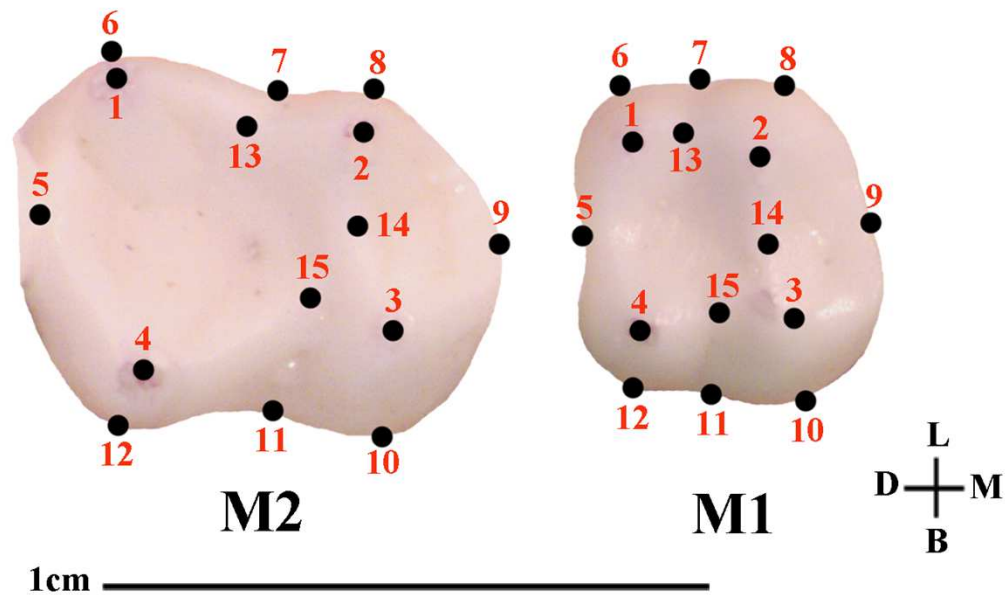
156 The extant comparative samples consisted in 802 adult individuals representing all  
157 recognized platyrrhine groups (3 families, 18 genera, 61 species,; Table 2), whose 2D and 3D  
158 morphometric variability of lower molars has already been analysed in some platyrrhine species  
159 (Nova Delgado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

172

173 **Geometric morphometric analysis**

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

195



196

197 **Figure 1.** Set of landmarks used in the geometric morphometrics analyses. a) M<sub>2</sub>; *Alouatta*  
 198 *guariba* 23177 MNRJ; b) M<sub>1</sub>; *Sapajus libidinosus* 23246 MNRJ.

199

200 The PCA of M<sub>1</sub> and M<sub>2</sub> morphometric variability of the extant species were used to explore  
 201 dental affinities of fossil specimens within the extant comparative platyrrhine sample. The  
 202 resulting PCs were used to conduct Linear Discriminant Function analysis (LDA). Because PCA  
 203 transforms original high-dimensional data, and removes the irrelevant and redundant dimensions  
 204 (Zelditch et al., 2004). LDA maximizes differences between groups but allows classifying  
 205 isolated cases based on their distances to the group centroids of the extant taxa. The probability  
 206 that a case belongs to a particular group is proportional to the distance to the group centroid  
 207 (Kovarovic et al., 2011). The reliability of the classification was estimated from the *post-hoc*  
 208 correct classification probability after cross-validation (*pcc*), and the *a posteriori* probability  
 209 score was used as the probability that a fossil belongs to a particular group. Several LDAs were

210 made considering different discriminant factors: 1) family (Cebidae, Atelidae, Pitheciidae), 2)  
211 the subfamily-level classification proposed by Groves (2005) (Subfamily G) (Cebinae,  
212 Saimiriinae, Callitrichinae, Pitheciinae, Callicebinae, Aotinae, Atelinae, Alouattinae), 3) the  
213 subfamily classification by Rosenberger (2011) (Subfamily R) (Cebinae, Callitrichinae,  
214 Pitheciinae, Homunculinae, Atelinae) (Table 4), and 4) a genus level (*Cebus*, *Sapajus*, *Saimiri*,  
215 *Callithrix*, *Mico*, *Cebuella*, *Callimico*, *Leontopithecus*, *Saguinus*, *Aotus*, *Callicebus*, *Cacajao*,  
216 *Chiropotes*, *Pithecis*, *Lagothrix*, *Brachyteles*, *Atelles*, *Allouatta*). The LDA analyses were carried  
217 out with SPSS v.15 (SPSS, Inc. 2006).

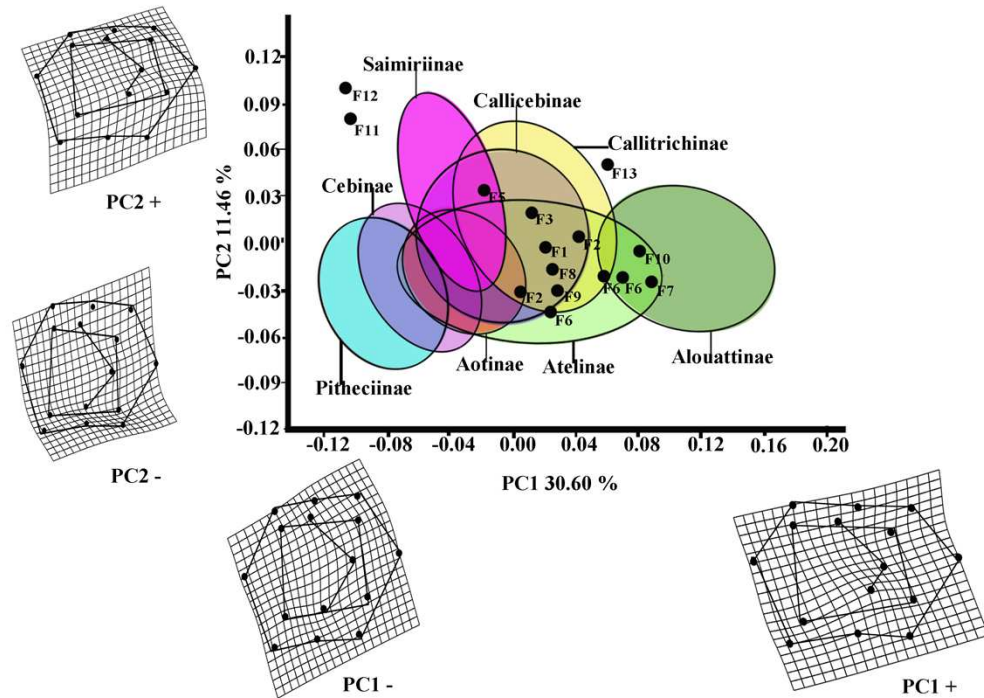
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## 219 RESULTS

### 220 Principal components analyses

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

230



231

232

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

238

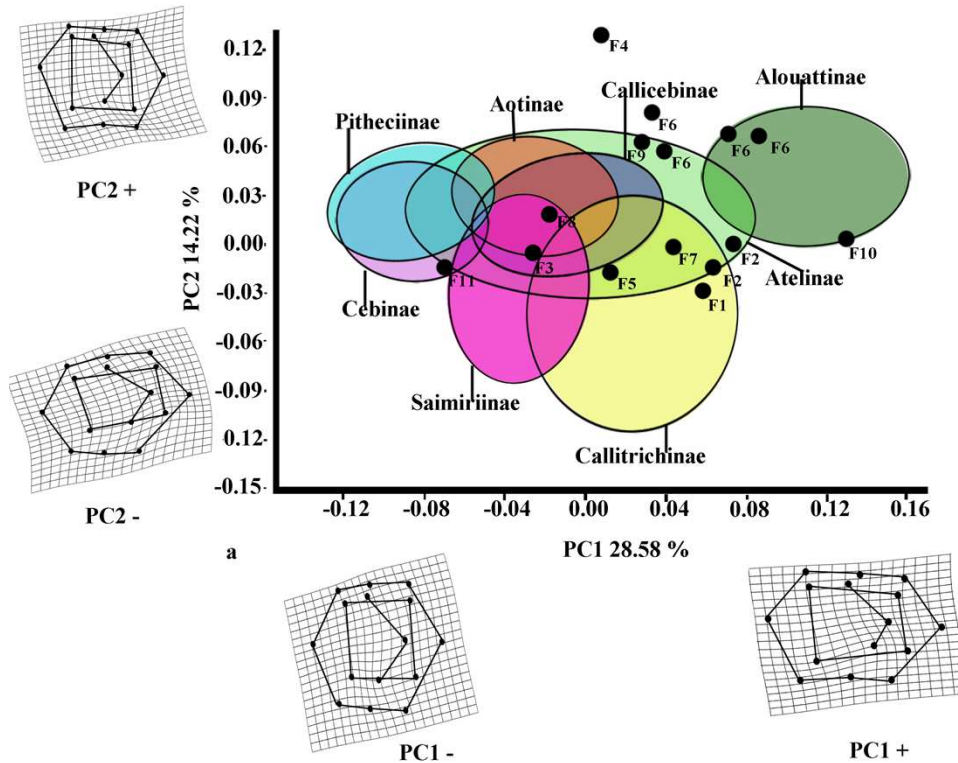
239 Despite the PCA does not discriminate groups, the plot of PC1 *versus* PC2 (Fig. 2,  
 240 including 95% confidence ellipses of the subfamily groups) shows differences between  
 241 subfamilies. Alouattinae clearly cluster on the positive scores of PC1, whereas contrast Pitheciinae  
 242 and Cebinae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

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

250 The first two PCs for M<sub>2</sub> (Fig. 3) accounted for 42.80% of the total variance (PC1: 28.58%;  
251 PC2: 14.22%). The molar shape changes for positive and negative PC1 scores for M<sub>2</sub> were  
252 relatively similar to those observed for M<sub>1</sub>, whereas positive PC2 scores for M<sub>2</sub> corresponded to  
253 the negative ones on PC2 for M<sub>1</sub>, and negative ones on PC2 for M<sub>2</sub> were equivalent to the  
254 positive score of PC2 for M<sub>1</sub>. The PC1 *versus* PC2 plot (Fig. 3) showed similar distributions of  
255 the subfamilies to those for M<sub>1</sub>, although greater separations between groups were observed.  
256 Alouattinae showed the largest, positive scores for PC1, and Pitheciinae and Cebinae the most  
257 negative scores, with the other groups showing again intermediate values. Callitrichinae and  
258 Saimiriinae were placed mainly on the negative score of the PC2 axis, although overlapped  
259 somewhat with the other groups. Most fossil specimens again clustered on positive scores for  
260 PC1 and PC2, mainly within the dispersion of Callitrichinae, although *Stirtonia* (F10), and some  
261 specimens of *Neosaimiri* clearly fell within the Alouattinae clade, *Dolichocebus* (F3) within  
262 Saimiriinae, and *Nuciruptor* (F11) was closer to Cebinae and Pitheciinae on the negative scores  
263 of PC1. *Homunculus* (F4) did not fall at all within any extant taxa, showing highly positive PC2  
264 scores.

265





266

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

### 272 Discriminant analyses of the fossil specimens

273 The *post-hoc* percentages of correct classification after cross-validation (*pcc*) were high both  
 274 for  $M_1$  (Table 4a, range = [85.7–88.0%]) and  $M_2$  (Table 4b, range = [84.7–90.6%]). In both  
 275 cases the highest *pcc* value was obtained when Groves' *subfamily* factor was discriminated. The  
 276 range of differences between *pcc* values before and after cross-validation was [1.3–4.7] and in  
 277 both teeth the *genus* discriminant factor showed the highest decrease in *pcc*. The difference in *pcc*  
 278 values between Groves' (Cebinae, Saimiriinae, Callitrichinae, Pitheciinae, Callicebinae, Aotinae,

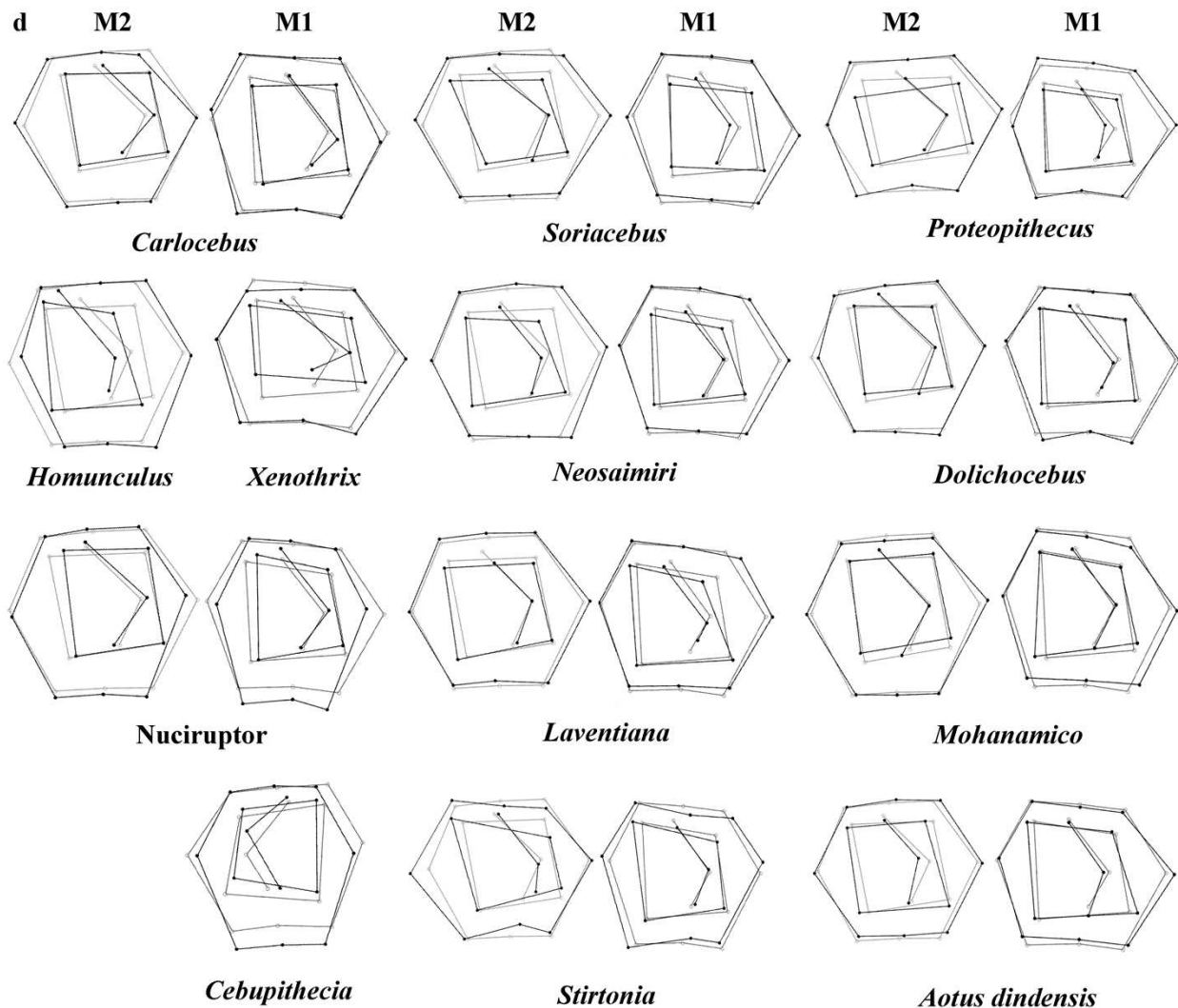


279 Atelinae, Alouattinae) and Rosenberger's (Cebinae, Callitrichinae, Pitheciinae, Homunculinae,  
280 Atelinae) *pcc* values were 2.3% for M<sub>1</sub> and 1.6% for M<sub>2</sub> (Table 5). The percentage of total  
281 variance explained by the first two discriminant functions (DF1, DF2; Table 4) for all discriminat  
282 factors ranged from 63.3% (*genus*) to 100% (*family*) for M<sub>1</sub>, and from 66.1% (*genus*) to 100%  
283 (*family*) for M<sub>2</sub>. The highest percentage of total variance explained by DF1 was 56.0% (*family*)  
284 for M<sub>1</sub> and 68.3% (*family*) for M<sub>2</sub>, and the highest one for DF2 was 44.0% (*family*) for M<sub>1</sub> and  
285 32.8% (*subfamily R*) for M<sub>2</sub>.

286 Regarding the classification of the fossils specimens, the ranges of the *a priori* classification  
287 probabilities varied depending on the discriminant factor used (Table 5; Fig. 4 shows the  
288 landmark configurations of the fossil specimens analysed). *Mohanamico* showed a high  
289 probability of belonging to the callitrichines clade, as well as *Carlocebus*, although the  
290 probability was smaller for M<sub>2</sub>. Both *Neosaimiri* and *Soriacebus* showed high probabilities of  
291 belonging to the callitrichines for M<sub>1</sub>, though to Callicebinae/ Homunculinae for M<sub>2</sub>.  
292 *Cebupithecia* (M<sub>2</sub> not available) and *Nuciruptor* neotypes showed a high probability of  
293 belonging to the pitheciid clade in LDAs. In contrast, *Xenothrix* (M<sub>2</sub> not available) likely  
294 belonged to *Callithrix*, despite in the PCA this fossil specimen did not fall within Callitrichinae  
295 range. *Stirtonia* was assigned to the Atelidae clade, and to *Alouatta* at the genus level, except for  
296 Rosenberger' *subfamily* factor for M<sub>2</sub>. *Laventiana* was also classified into the atelids for M<sub>1</sub>, but  
297 was more closely related to callitrichines for M<sub>2</sub>. *Aotus dindensis* showed a high probability of  
298 belonging to *Aotus* taxa for M<sub>1</sub>, but *Callicebus* was the group with the greatest affinity for M<sub>2</sub>.  
299 Finally, *Proteopithecus* showed a high resemblance with *Saimiri* for M<sub>1</sub>, but with *Callimico* for  
300 M<sub>2</sub>.

301

302



303

304

305 **Figure 4.** First and second molar shapes of the extinct fossil platyrrhines used in this study.

306

307

## 308 DISCUSSION

309 The positions of the anthropoid form *Proteopithecus sylviae* (F1) in the morphospace and its  
 310 molar shapes showed pattern resemblance to that of platyrrhines. However, because, many dental

311 and postcranial features of *P. sylviae* are considered to be symplesiomorphic characters of all  
312 anthropoids, so it is placed as the stem anthropoid (Kay, 1990, 2014). The recent discovery of  
313 *Perupithecus ucayaliensis*, probably from the Late Eocene, suggests that this fossil exhibits  
314 similarities with *Proteopithecus*, also with *Talahpithecus* and Oligopithecidae (Bond et al.,  
315 2015). The upper molars of *Perupithecus* are slightly resembled to the callitrichines, but its  
316 morphology is more similar with *Proteopithecus* and *Talahpithecus* (Bond et al., 2015).  
317 *Proteopithecus sylviae* differed from the extant and extinct platyrrhines in having a molar  
318 distomesially expanded, marked by a rectangular shape of the occlusal polygon (especially on  
319 M<sub>2</sub>) (also seen in *Xenothrix*). Thus, if the Fayum form likely was a sister taxon to platyrrhines,  
320 the interspecific variation of shape would have shown relatively little change. This could mean  
321 that the main traits of molars shapes in platyrrhines represent retention of a primitive ancestral  
322 form. Moreover, the LDA showed a high probability of *P. sylviae* belonging to the Cebidae  
323 clade, suggesting that the molar of the earliest ancestors of platyrrhines must have exhibited  
324 close similarity to *Saimiri-Callimico*. This resemblance matches with the description of an  
325 Oligocene primate fossil found in South America, *Branisella* (Rosenberger, 2002; Rosenberger  
326 et al., 2009), whose morphology indicates that the structural characteristics of M<sub>2</sub> may have been  
327 *Saimiri*-like, and the upper P<sup>2</sup> a *Callimico*-like (Rosenberger, 1980). However, both molar shapes  
328 of *P. sylviae* were more closely resembles to *Callimico* than *Saimiri*. Furthermore, the  
329 subtriangular upper molars of *Perupithecus*, show relative similarity with *Callimico* (Bond et al.,  
330 2015). Thus, if *P. sylviae* was a sister taxon of platyrrhines, is likely that the hypothetical  
331 ancestral molar shape of pre-platyrrhine would have been similar to a molar of *Callimico*. By  
332 contrast, if *P. sylviae* was a stem species, *Callimico* would show retention of primitive pre-  
333 anthropoid platyrrhine molar shape.

334

335 ***Early Miocene platyrrhines from Patagonia***

336 The fossils recovered from Early Miocene strata have been highly debated by Kay (1990,  
337 2010, 2014), who argued that most of the traits used to identify phylogenetic affinities show high  
338 levels of homoplasy. The present work alone cannot reject the successive radiations or the long  
339 lineages hypotheses, nor can confirm which of both is correct. However, studying phenotypic  
340 similarities and differences of molar shapes, allowed us to explore morphological patterns  
341 between extinct and extant taxa. For example, the PCA indicated that the two PCs did not have a  
342 large variance, however can observe differences to subfamily levels (Fig. 2 and 3). Also,  
343 although fossils were not very spread out in the morphospace, many of them were located mainly  
344 into Callicebinae and Callitrichinae range (except to *Homunculus* for M<sub>2</sub>). This means that the  
345 main traits observed in fossil platyrrhines are related to affinities for both subfamilies

346 The Early Miocene fossils were mainly assigned to two taxa by the LDA; a *Callicebus*-  
347 shaped and a *Saguinus*- shaped. For example, *Dolichocebus* (F3) were classified as a pitheciid,  
348 mainly by having a square occlusal polygon (Table 4). However, although the PCA for M<sub>1</sub>  
349 placed this specimen in the Callicebinae range, a morphological similarity with Saimiriinae was  
350 seen for M<sub>2</sub> (Fig. 3a). In contrast, *Soriacebus* (F2) was related mainly to the callitrichine clade,  
351 but for M<sub>2</sub> the probability of belonging to this group was small (Table 4). Because, *Soriacebus*  
352 showed a rectangular occlusal polygon on M<sub>2</sub> and the ectoconid was inclined distolingually.  
353 Regarding callitrichines, although *Soriacebus* also showed differences in cusp configuration, the  
354 callitrichines and *Soriacebu* share a C-shaped distal side and a somewhat straight lingual-side  
355 contour (mostly seen in *Saguinus*). Kay (1990) reported that many dental features of marmosets  
356 and *Soriacebus* were convergent. In contrast, Rosenberger et al. (1990b) suggested that there are

357 some similarities with callitrichines (development of hypoconids and entoconids in the talonid).  
358 However, based on the anterior teeth, they concluded that *Soriacebus* represents the first branch  
359 of pitheciines. Although marmosets are considered derived linajes (e.g. Chatterjee et., 2009;  
360 Perelman et al., 2009; Jameson Kiesling et al., 2014), it is likely that the relation with *Soriacebus*  
361 may be due to the fact that callitrichines exhibit primitive traits on their molars, which means  
362 that both taxa share a retention of rectangular contour and occlusal polygon shape. In the case of  
363 *Carlocebus* (F5), it was classified as a Callitrichinae in the DFA. However, it has been shown to  
364 be more similar with *Callicebus* than marmosets, such as the shape contour and quadrate  
365 alignment of cusps in both molars. *Homunculus* (F4), was placed outside the range of Patagonian  
366 forms in the PCA (Fig. 2a), whereas the LDA indicated a high probability of belonging to  
367 Pitheciidae (ca. 91–99%; Table 4), and especially to *Calliecebus*. Nonetheless, *Homunculus*  
368 molar showed an asymmetrical shape compared to pitheciid forms. Furthermore, unlike  
369 pitheciids, *Homunculus* cusps were predominantly inclined toward the distal side and the  
370 trigonid was almost as broad as the basin-like talonid, which means that although sharing some  
371 traits with pitheciids, its position is highly uncertain.

372

### 373 ***Middle Miocene platyrrhines from Colombia and the Caribbean Xenothrix***

374 Many of these fossils were mostly catalogued as callitrichines, specifically into the *Saguinus*  
375 clade, except *Nuciruptor*, *Cebupithecia*, *Aotus dindensis*, and *Stirtonia*. One of the major  
376 differences between these primates and the extant forms (excepting *Alouatta* and *Brachyteles*)  
377 was the rectangular-shaped molar (see *Xenothrix* below). This phenetic similarity among  
378 phylogenetically distinct groups of extinct primates indicates that a rectangular-shaped molar almost  
379 certainly represents a plesiomorphy in the Patagonian fossils. Thus, the trend toward ovoid molar

380 shape might be a derived feature in many living forms. *Laventania* (F7) exhibited distally  
381 oriented cusps on  $M_1$ , showing considerable resemblance with some atelid groups, which  
382 provided a confusing classification between atelids and *Callicebus* in the LDA (Table 5). Thus,  
383 the trend to rectangular shape for  $M_1$  in *Laventania* differs notably from the phylogenetic  
384 relationship with Cebinae and Saimiriinae. Nonetheless, when  $M_2$  was analyzed, the fossil was  
385 classified as member of the Callitrichinae clade. As with *Laventania*, some neotypes of  
386 *Neosaimiri* (F6) were classified in completely distant taxonomic groups (Table 4). However,  
387 despite these results, *Neosaimiri* was principally associated to the Cebidae family, although the  
388 molar shape was found to have more affinities with callitrichines than *Saimiri*. On the other  
389 hand, *Mohanamico* (F8) and *Aotus dindensis* (F9) have been considered by Kay and  
390 collaborators (Meldrum and Kay, 1997; Kay 2014) to belong to the same genus, despite Takai et  
391 al. (2009) suggested that *A. dindensis* should be assigned to distinct genus. According to their  
392 molar shape, *Mohanamico* and *A. dindensis* may be classified into different species. Both fossils  
393 showed a relative rectangular shape of the outline, as well as in the occlusal polygon, although  
394  $M_2$  in both species were slightly square shaped. In fact, PCA for  $M_1$  (Fig. 2a) showed that the  
395 two forms were placed closer to each other. Thus, similar molar shape might be due to the fact  
396 that the two forms must have shared relatively similar ecological niches, likely because  
397 *Mohanamico* and *A. dindensis* were found in the same locality and at the same stratigraphic level  
398 (Kay, 1990). However, the LDA indicated that the probability of classification was different for  
399 both groups. *Aotus dindensis* was mainly related to *Aotus/Callicebus*, whereas *Mohanamico* was  
400 assigned to Callitrichinae (Table 4). In the case of *Nuciruptor* (F11) and *Cebupithecia* (F12), the  
401 occlusal views in both species were relatively rounded, with a slightly rectangular alignment of  
402 cusps, and buccally oriented, which resembles the condition in most extant Pitheciinae.



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

409 The sister relationship between *Stirtonia* and *Alouatta* was classified in the LDA with a  
410 99.9% probability for M<sub>1</sub> and 94.0% for M<sub>2</sub>. Likewise, the PCA showed that *Stirtonia* was placed  
411 close to howler monkeys (Figs. 2a and 3a). However, differences between *Stirtonia* and *Alouatta*  
412 were mainly seen in the occlusal polygon of M<sub>2</sub>. The metaconid of *Stirtonia* was located near the  
413 protoconid and the ectoconid was distolingually inclined, somewhat similar to the *Cebuella*  
414 configuration. This relationship was reflected in the high percentage of probability at the  
415 subfamily level, Callitrichinae (Table 5).

416 Finally, *Xenothrix* (F13), the Caribbean platyrrhine form, has been allied with pitheciids  
417 (Rosenberger, 2002; Horovitz and MacPhee, 1999). In the LDA, *Xenothrix* was mainly attributed  
418 to pitheciids, but at the genus level, it was assigned to *Callithrix* (Table 4). Thus, some  
419 resemblance with marmosets could be interpreted as convergent evolution. However, the  
420 relationship between *Xenothrix* and pitheciids was highly uncertain, given that its molar  
421 morphology (especially the occlusal configuration) differs from that of the pitheciids. It is likely  
422 that *Xenothrix* could be a single branch that evolved independent of crown platyrrhines, as was  
423 suggested by some investigations that proposed an early Antillen arrival (Iturralde-Vinent and  
424 MacPhee, 1999; MacPhee and Iturralde-Vinent, 1995; MacPhee and Horovitz, 2004; Kay et al.,  
425 2011; Kay, 2014).

426           The slow rate of phenotypic changes on molar shapes suggests that morphological stasis  
427 (different concept to long lineages hypothesis) explains the low interspecific variation between  
428 extinct and extant lineages and between Early Miocene platyrrhines (including *P. sylviae*) and  
429 forms from La Venta, in comparison to extinct and extant catarrhines (Nova Delgado et al.,  
430 2015a; Gamarra et al., 2016). This small phenotypic variation could be due to development and  
431 functional constraints, given the role in occlusion and mastication (Gómez-Robles and Polly  
432 2012). Further, due to the relative low diversification in diet of platyrrhines (for example  
433 compared with carnivores). This ecological constraint may be related to the fact that the  
434 phenotypic adaptation of main platyrrhine families could have happened in Amazon rainforest  
435 (Jameson Kiesling et al. 2014). Following an African origin scenario, and taking into account  
436 the phenotypic similarity of the most recent discovered and oldest fossil found in Peru,  
437 *Perupithecus* (Bond et al., 2015), it is likely that the ancestor of extant platyrrhines could have  
438 exhibited a *Callimico*-like molar shape, We also observed that *Saguinus* and *Callicebus* were the  
439 main assigned groups for Patagonian fossils by LDA, also in the PCA. It could mean that: there  
440 were a *Callicebus*-like and *Saguinus*-like morphology in early stem platyrrhines, or that both  
441 taxa represent the earliest offshoot Patagonian molar shapes. Currently, *Callicebus* and *Saguinus*  
442 present relatively high diversity of species and geographic range (Rylands and Mittermeier  
443 2009). The *Callicebus* and *Saguinus* species richness probably are related to expansion and  
444 diversification of both clades in the Amazon basin, during the period of platyrrhine evolution  
445 (Ayres and Clutton-Brock, 1992; Boubli et al., 2015). Thus, it is feasible that *Callicebus*, as well  
446 as *Saguinus*, molar shape would be an ancestral precursor for the existing forms. Moreover, the  
447 Middle Miocene platyrrhines indicate continuity in molar shape pattern with the early fossils,



448 incorporating also new molar shapes not observed in the Patagonian forms: the *Alouatta*-like and  
449 the Pitheciinae-like forms.

450

451

## 452 CONCLUSIONS

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

464

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711 **Table 1:** List of fossils used in the study.

712	<b>Fossils</b>	<b>Location</b>	<b>Age (Ma)</b>	<b>Phylogenetic position</b>	<b>Specimen number and</b>
713	<b>reference</b>				
714	<b>F1</b> <i>Proteopithecus sylviae</i>	Fayum, Egypt	33.9 -28.4 <sup>a</sup>	stem anthropoid <sup>b</sup>	CGM 42209; Miller and Simons
715	(1997)				
716	<b>F2</b> <i>Soriacebus</i> spp.	Pinturas Formation,	17 <sup>c</sup>	stem platyrrhine <sup>d</sup> / Pitheciidae <sup>e</sup>	MACN-SC 2 <sup>1</sup> , MACN-SC 5 <sup>2</sup> MPM-PV 36 <sup>3</sup> ; Tejedor (2005)
717		Santa Cruz Province,			
718		Argentina			
719					
720	<b>F3</b> <i>Dolichocebus gaimanesis</i>	Gaiman,	20 <sup>f</sup>	stem platyrrhine/ sister to <i>Saimiri</i> <sup>g</sup>	MPEF 5146; Kay et al. (2008)
721		Chubut Province,			
722		Argentina			
723					
724	<b>F4</b> <i>Homunculus</i> spp.	Santa Cruz Formation,	16.5 <sup>h</sup>	stem platyrrhine/ Pitheciidae	MACN-A5969; Tejedor and (2008)
725	Rosemberger	Santa Cruz Province,			
726		Argentina			
727					
728					
729	<b>F5</b> <i>Carlocebus</i> spp.	Pinturas Formation,	18-19 <sup>i</sup>	stem platyrrhine/ Pitheciidae	MACN-SC 266; Fleagle (1990)
730		Santa Cruz Province,			
731		Argentina			
732					
733	<b>F6</b> <i>Neosaimiri fieldsi</i>	La Venta, Huila,	13.5 -11.8 <sup>j</sup>	sister to <i>Saimiri</i> <sup>k</sup>	IGM-KU 89029 <sup>4</sup> , IGM-KU 89019 <sup>5</sup> , UCMP 39205 <sup>6</sup> , IGM-KU 89002 <sup>7</sup> , IGM-KU 39034 <sup>8</sup> , IGM-KU 89053 <sup>9</sup> , IGM-KU 89130 <sup>10</sup> ; Takai (1994)
734		Colombia			
735					
736					
737					
738	<b>F7</b> <i>Laventiana annectens</i>	La Venta, Huila,	13.5 -11.8	sister to <i>Saimiri</i> / Pitheciidae	IGM-KU 880; Rosemberger et al.,

739		Colombia		synonymy with	(1991b)
740				<i>Neosaimiri</i> <sup>l</sup>	
741					
742	<b>F8</b>	<i>Mohanamico hershkouitzi</i>	La Venta, Huila, Colombia	13.5 -11.8 sister to <i>Callimico</i> <sup>m</sup>	IGM 181500; Kay (1990)
743					
744					
745	<b>F9</b>	<i>Aotus dindensis</i>	La Venta, Huila, Colombia	13.5 -11.8 sister to <i>Aotus</i> <sup>n</sup> / coespecific with <i>Mohanamico</i> <sup>o</sup>	IGM-KU 8601; Kay (1990)
746					
747					
748					
749					
750	<b>F10</b>	<i>Stirtonia</i> spp.	La Venta, Huila, Colombia	13.5 -11.8 sister to <i>Alouatta</i> <sup>p</sup>	UCPM 38989; Kay et al. (1987)
751					
752					
753	<b>F11</b>	<i>Nuciruptor rubricae</i>	La Venta, Huila, Colombia	13.5 -11.8 Pitheciidae <sup>q</sup> / stem Pitheciinae <sup>r</sup>	IGM 251074; Meldrum and Kay
754	(1997)				
755					
756					
757	<b>F12</b>	<i>Cebupithecia sarmientoni</i>	La Venta, Huila, Colombia	13.5 -11.8 Pitheciidae/ stem Pitheciinae	UCMP 38762; Meldrum and Kay
758	(1997)				
759					
760					
761	<b>F13</b>	<i>Xenothrix macgregori</i>	Jamaica	Holocene <sup>s</sup> stem platyrrhine/ retaded to <i>Callicebus</i> <sup>t</sup>	AMNHM 148198; MacPhee and Horovitz (2004)
762					

763

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

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

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

775 **Table 2** List of the specimens included in this analysis of M<sub>1</sub> and M<sub>2</sub>. The Subfamily-level  
 776 classification was proposed by Groves (2005).

777	<b>Genus / species</b>	<b>M<sub>1-2</sub></b>	<b>Collection<sup>a</sup></b>
778	<b>Subfamily: Cebinae</b>		
779	<i>Cebus</i> (gracile capuchins)		
780	<b>1</b> <i>C. albifrons</i>	9	MZUSP, MNRJ
781	<b>2</b> <i>C. olivaceus</i>	6	MNRJ
782	<i>Sapajus</i> (robust capuchins)		
783	<b>3</b> <i>S. apella</i>	14	MZUSP
784	<b>4</b> <i>S. libidinosus</i>	15	MNRJ
785	<b>5</b> <i>S. nigritus</i>	15	MNRJ
786	<b>6</b> <i>S. robustus</i>	15	MNRJ
787	<b>7</b> <i>S. xanthosternos</i>	7	MNRJ
788	<b>Subfamily: Samiriinae</b>		
789	<i>Saimiri</i> (squirrel monkeys)		
790	<b>8</b> <i>S. boliviensis</i>	17	MZUSP, MNRJ
791	<b>9</b> <i>S. sciureus</i>	25	MZUSP, MNRJ
792	<b>10</b> <i>S. ustus</i>	18	MZUSP, MNRJ
793	<b>11</b> <i>S. vanzolinii</i>	8	MNRJ
794	<b>Subfamily: Callitrichinae</b>		
795	<i>Callithrix</i> (marmosets from Atlantic Forest)		
796	<b>12</b> <i>C. aurita</i>	11	MNRJ
797	<b>13</b> <i>C. geoffroyi</i>	15	MNRJ



798	<b>14</b> <i>C. jacchus</i>	21	MZUSP
799	<b>15</b> <i>C. kuhlii</i>	20	MNRJ
800	<b>16</b> <i>C. penicillata</i>	14	MNRJ
801	<b><i>Mico</i></b> (marmosets from Amazon)		
802	<b>17</b> <i>M. argentata</i>	21	MZUSP, MNRJ
803	<b>18</b> <i>M. chrysoleuca</i>	16	MZUSP, MNRJ
804	<b>19</b> <i>M. emiliae</i>	6	MZUSP
805	<b>20</b> <i>M. humeralifer</i>	16	MZUSP
806	<b>21</b> <i>M. melanurus</i>	8	MZUSP, MNRJ
807	<b><i>Cebuella</i></b> (pygmy marmoset)		
808	<b>22</b> <i>C. pygmaea</i>	7	MZUSP
809	<b><i>Callimico</i></b> (goeldi's marmoset)		
810	<b>23</b> <i>C. goeldii</i>	4	MZUSP
811	<b><i>Leontopithecus</i></b> (lion tamarins)		
812	<b>24</b> <i>L. chrysomelas</i>	5	MZUSP, MNRJ
813	<b>25</b> <i>L. rosalia</i>	17	MZUSP, MNRJ
814	<b><i>Saguinus</i></b> (tamarins)		
815	<b>26</b> <i>S. fuscicollis</i>	13	MZUSP
816	<b>27</b> <i>S. imperator</i>	10	MZUSP
817	<b>28</b> <i>S. labiatus</i>	9	MZUSP, MNRJ
818	<b>29</b> <i>S. midas</i>	22	MZUSP, MNRJ
819	<b>30</b> <i>S. mystax</i>	13	MZUSP, MNRJ
820	<b>31</b> <i>S. niger</i>	14	MNRJ

821	<b>Subfamily: Aotinae</b>		
822	<i>Aotus</i> (owl or night monkeys)		
823	<b>31</b> <i>A. azarae</i>	4	MZUSP, MNRJ
824	<b>32</b> <i>A. nigriceps</i>	9	MZUSP, MNRJ
825	<b>33</b> <i>A. trivirgatus</i>	21	MZUSP
826	<b>Subfamily: Callicebinae</b>		
827	<i>Callicebus</i> (titi monkeys)		
828	<b>34</b> <i>C. bernhardi</i>	5	MNRJ
829	<b>35</b> <i>C. cupreus</i>	14	MZUSP, MNRJ
830	<b>36</b> <i>C. hoffmannsi</i>	12	MNRJ
831	<b>37</b> <i>C. moloch</i>	16	MZUSP, MNRJ
832	<b>38</b> <i>C. nigrifrons</i>	8	MNRJ
833	<b>39</b> <i>C. personatus</i>	16	MZUSP, MNRJ
834	<b>Subfamily: Pitheciinae</b>		
835	<i>Cacajao</i> (uakaris)		
836	<b>40</b> <i>C. calvus</i>	14	MZUSP, MNRJ
837	<b>41</b> <i>C. melanocephalus</i>	9	MZUSP, MNRJ
838	<i>Chiropotes</i> (bearded sakis)		
839	<b>42</b> <i>C. albinasus</i>	18	MZUSP, MNRJ
840	<b>43</b> <i>C. satanas</i>	15	MZUSP, MNRJ
841	<i>Pithecia</i> (sakis)		
842	<b>44</b> <i>P. irrorata</i>	17	MZUSP, MNRJ
843	<b>45</b> <i>P. monachus</i>	7	MZUSP, MNRJ

844	<b>46</b> <i>P. pithecia</i>	16	MZUSP, MNRJ
845			
846	<b>Subfamily: Atelinae</b>		
847	<i>Lagothrix</i> (woolly monkeys)		
848	<b>47</b> <i>L. cana</i>	7	MNRJ
849	<b>48</b> <i>L. lagotricha</i>	8	MZUSP
850	<i>Brachyteles</i> (muriquis)		
851	<b>49</b> <i>B. arachoides</i>	16	MZUSP, MNRJ
852	<b>50</b> <i>B. hypoxanthus</i>	5	MNRJ
853	<i>Ateles</i> (spider monkeys)		
854	<b>51</b> <i>A. belzebuth</i>	2	RBINS
855	<b>52</b> <i>A. chamek</i>	15	MNRJ
856	<b>53</b> <i>A. marginatus</i>	20	MZUSP
857	<b>Subfamily: Alouatinae</b>		
858	<i>Alouatta</i> (howler monkeys)		
859	<b>54</b> <i>A. belzebul</i>	15	MZUSP
860	<b>55</b> <i>A. caraya</i>	15	MZUSP, MNRJ
861	<b>56</b> <i>A. discolor</i>	10	MNRJ
862	<b>57</b> <i>A. guariba</i>	5	MZUSP, MNRJ
863	<b>58</b> <i>A. g. clamitas</i> †	15	MNRJ
864	<b>59</b> <i>A. nigerrima</i>	10	MNRJ
865	<b>60</b> <i>A. palliata</i>	15	HLP
866	<b>61</b> <i>A. seniculus</i>	15	MZUSP

867 **62** *A. ululata* 7 MNRJ

868 † Subspecies of *Alouatta guariba*

869 <sup>a</sup> Institutional abbreviations: MZUSP: Museu de Zoologia Universidade de São Paulo (Brazil);

870 MNRJ: Museu Nacional do Rio de Janeiro (Brazil); HLP: Hacienda La Pacífica.

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

872

873	Landmark	Type	Definition
874	1	2	Tip of the distolingual cusp (entoconid)
875	2	2	Tip of the mesiolingual cusp (metaconid)
876	3	2	Tip of the mesiobuccal cusp (protoconid)
877	4	2	Tip of the distobuccal cusp (hypoconid)
878	5	3	Most distal point of the mid mesiodistal line on the crown outline
879	6	2	Point of maximum curvature directly below the entoconid*
880	7	3	Point on the dental crown outline at the lingual groove
881	8	2	Point of maximum curvature directly below the metaconid*
882	9	3	Most mesial point of the mid mesiodistal line on the crown outline
883	10	2	Point of maximum curvature directly below the protoconid*
884	11	3	Point on the dental crown outline at the mesial groove
885	12	2	Point of maximum curvature directly below the hypoconid*
886	13	2	Midpoint between the preentocristid and postmetacristid*
887	14	2	Lowest point on the protocristid*
888	15	2	Lowest point on the crista oblique*

889 \* Landmarks follow definitions by Cooke (2011)

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

891

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

892

893

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

900 **a) M<sub>1</sub>**

		Family%		Subfamily by G %		Subfamily by R %		Genus %	
902	<b>DF1</b>	56.0		50.5		42.4		49.0	
903	<b>DF2</b>	44.0		19.1		29.1		14.2	
904	<b>Classification</b>	88.7		91.3		88.2		91.0	
905	<b>Cross-validation</b>	87.4		88.0		85.7		86.3	
906	<b>(M<sub>1</sub>)</b>	<b>Family</b>	<b>%</b>	<b>Subfamily by G%</b>	<b>Subfamily by R%</b>	<b>Genus</b>	<b>%</b>		
907	<i>Proteopithecus</i>	Cebidae	99.6	Saimiriinae	99.2	Cebinae	99.9	<i>Saimiri</i>	99.3
908	<i>Soriacebus</i> <sup>1</sup>	Cebidae	99.9	Callitrichinae	99.9	Callitrichinae	99.8	<i>Saguinus</i>	89.6
909	<i>Soriacebus</i> <sup>2</sup>	Cebidae	99.1	Callitrichinae	76.6	Callitrichinae	94.0	<i>Callithrix</i>	69.1
910	<i>Dolichocebus</i>	Cebidae	86.5	Callicebinae	77.9	Homunculinae	67.4	<i>Callicebus</i>	86.4

911	<i>Carlocebus</i>	Cebidae	97.0	Callitrichinae	94.2	Callitrichinae	83.7	<i>Callithrix</i>	87.1
912	<i>Neosaimiri</i> <sup>4</sup>	Pitheciidae	48.5	Atelinae	48.8	Callitrichinae	52.2	<i>Saguinus</i>	78.7
913	<i>Neosaimiri</i> <sup>5</sup>	Cebidae	98.4	Callitrichinae	97.5	Callitrichinae	97.3	<i>Saguinus</i>	99.6
914	<i>Neosaimiri</i> <sup>6</sup>	Cebidae	97.0	Callitrichinae	76.5	Callitrichinae	94.6	<i>Saguinus</i>	72.2
915	<i>Laventiana</i>	Atelidae	94.6	Atelinae	44.5	Atelinae	94.9	<i>Callicebus</i>	53.0
916	<i>Mohanamico</i>	Cebidae	96.2	Callitrichinae	87.3	Callitrichinae	70.3	<i>Leontopithecus</i>	65.4
917	<i>Aotus dindensis</i>	Pitheciidae	59.0	Aotinae	99.7	Homunculinae	97.4	<i>Aotus</i>	98.7
918	<i>Stirtonia</i>	Atelidae	98.9	Alouattinae	99.9	Atelinae	98.2	<i>Alouatta</i>	99.9
919	<i>Nuciruptor</i>	Pitheciidae	99.7	Callicebinae	99.5	Homunculinae	83.6	<i>Callicebus</i>	63.3
920	<i>Cebupithecia</i>	Pitheciidae	96.5	Pitheciinae	92.1	Pitheciinae	65.3	<i>Chiropotes</i>	59.2
921	<i>Xenothrix</i>	Pitheciidae	75.8	Callicebinae	30.5	Homunculinae	61.9	<i>Callithrix</i>	90.7

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926 **b) M<sub>2</sub>**



927		<b>Family%</b>		<b>Subfamily by G %</b>		<b>Subfamily by R %</b>		<b>Genus %</b>	
928	<b>DF1</b>		68.3		45.6		47.6		43.5
929	<b>DF2</b>		31.7		29.0		32.8		22.6
930	<b>Classification</b>		89.5		93.3		90.3		88.7
931	<b>Cross-validation</b>		88.2		90.6		89.0		84.7
932	<b>(M<sub>2</sub>)</b>	<b>Family</b>	<b>%</b>	<b>Subfamily by G %</b>	<b>Subfamily by R%</b>	<b>Genus</b>	<b>%</b>		
933	<i>Proteopithecus</i>	Cebidae	99.4	Callitrichinae 82.3	Callitrichinae 80.3	<i>Callimico</i>	86.7		
934	<i>Soriacebus</i> <sup>1</sup>	Cebidae	65.6	Callicebinae 81.6	Homunculinae 58.4	<i>Saguinus</i>	74.6		
935	<i>Soriacebus</i> <sup>3</sup>	Atelidae	77.1	Callitrichinae 96.7	Callitrichinae 98.0	<i>Saguinus</i>	65.6		
936	<i>Dolichocebus</i>	Cebidae	50.7	Callicebinae 92.6	Homunculinae 90.1	<i>Callicebus</i>	92.6		
937	<i>Homunculus</i>	Pitheciidae	91.4	Callicebinae 93.7	Homunculinae 97.3	<i>Callicebus</i>	99.9		
938	<i>Carlocebus</i>	Cebidae	55.6	Callitrichinae 58.8	Callitrichinae 50.4	<i>Mico</i>	72.5		
939	<i>Neosaimiri</i> <sup>7</sup>	Cebidae	98.3	Callicebinae 92.9	Cebinae 35.8	<i>Callicebus</i>	67.2		
940	<i>Neosaimiri</i> <sup>8</sup>	Cebidae	64.9	Callicebinae 61.2	Homunculinae 93.7	<i>Saguinus</i>	65.1		
941	<i>Neosaimiri</i> <sup>9</sup>	Cebidae	99.5	Callitrichinae 61.3	Callitrichinae 51.7	<i>Saguinus</i>	92.3		
942	<i>Neosaimiri</i> <sup>10</sup>	Cebidae	98.9	Callicebinae 84.6	Callitrichinae 71.9	<i>Saguinus</i>	98.3		
943	<i>Laventiana</i>	Cebidae	99.9	Callitrichinae 99.8	Callitrichinae 99.7	<i>Saguinus</i>	40.8		

944	<i>Mohanamico</i>	Cebidae	97.7	Callitrichinae	94.9	Callitrichinae	94.6	<i>Saguinus</i>	99.9
945	<i>Aotus dindensis</i>	Cebidae	84.4	Callicebinae	88.9	Homunculinae	76.1	<i>Callicebus</i>	96.5
946	<i>Nuciruptor</i>	Pitheciidae	89.7	Pitheciinae	89.7	Pitheciinae	73.0	<i>Pithecia</i>	49.4
947	<i>Stirtonia</i>	Atelidae	81.8	Alouattinae	86.0	Callitrichinae	92.1	<i>Alouatta</i>	94.0

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