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Molar shape variability in platyrrhine primates

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ABSTRACT

Recent phylogenetic analyses suggest that platyrrhines constitute a monophyletic group represented by three families: Cebidae, Atelidae, and Pitheciidae. Morphological variability between and within these three families, however, is widely discussed and debated. The aim of this study was to assess molar shape variability in platyrrhines, to explore patterns of interspecific variation among extant species, and to evaluate how molar shape can be used as a taxonomic indicator. The analyses were conducted using standard multivariate analyses of geometric morphometric data from 802 platyrrhine lower molars. The results indicated that the interspecific variation exhibited a highly homoplastic pattern related to functional adaptation of some taxa. However, phylogeny was also an important factor in shaping molar morphological traits, given that some phenotypic similarities were consistent with current phylogenetic positions. Our results show that the phylogenetic and functional signals of lower molar shape vary depending on the taxa and the tooth considered. Based on molar shape, *Aotus* showed closer similarities to *Callicebus*, as well as to some Cebidae and *Ateles-Lagothrix*, due to convergent evolutionary trends caused by similar dietary habits, or due to fast-evolving branches in the *Aotus* lineage, somewhat similar to the shape of *Callicebus* and Cebidae.

1. Introduction

Molecular-based approaches have supported the division of platyrrhines into three main clades: Atelidae, Pitheciidae, and Cebidae (Wildman et al., 2009; Perelman et al., 2011; Perez et al., 2012; Jameson Kiesling et al., 2015). Further, the divergence times between these families have been extensively estimated (e.g., Goodman et al., 1998; Horovitz et al., 1998; Schneider, 2000; Opazo et al., 2006; Wildman et al., 2009; Perelman et al., 2011; Perez et al., 2012). Jameson Kiesling et al. (2015) have suggested that the Pitheciidae branched off at 25.51 Ma and the divergence between Atelidae/Cebidae occurred at 24.04 Ma (Fig. 1), which is consistent with most recent tree topologies (Osterholz et al., 2009; Wildman et al., 2009; Perelman et al., 2011; Perez et al., 2012). However, the phylogenetic position of *Aotus* is still controversial. Some molecular studies have argued that this genus is the sister taxon of Callithrichinae (Schrago, 2007; Perelman et al., 2011; Springer et al., 2012; Jameson Kiesling et al., 2015), while others have suggested that it lies at the base of cebines (Ray et al., 2005; Opazo et al., 2006; Chatterjee et al., 2009; Hodgson et al., 2009; Osterholz et al., 2009; Wildman et al., 2009). Moreover, Rosenberger's morphological studies (Rosenberger, 1984; Rosenberger et al., 1996, 2009), including fossil taxa, have proposed that *Aotus* is closely related to the pitheciine clade. However, Kay's investigations, also including fossil taxa, suggest that the traits used to identify phylogenetic affinities of *Aotus* with regard to Pitheciidae present high levels of homoplasy (Kay et al., 2004, 2008; Kay, 2015), but molecular analyses argue against such an interpretation (Opazo et al., 2006; Hodgson et al., 2009; Osterholz et al., 2009; Wildman et al., 2009).

1.1. *Lower molar morphology and dietary adaptations in platyrrhine primates*

Primate molar morphology derives from a primitive tribosphenic dental pattern (Simpson, 1936). In the tribosphenic lower molar, three main cusps (protoconid, paraconid, and metaconid) placed in a triangular shape form the trigonid. However, in platyrrhines, the trigonid only shows two cusps (protoconid and metaconid) connected by a protocristid, and the paraconid is absent

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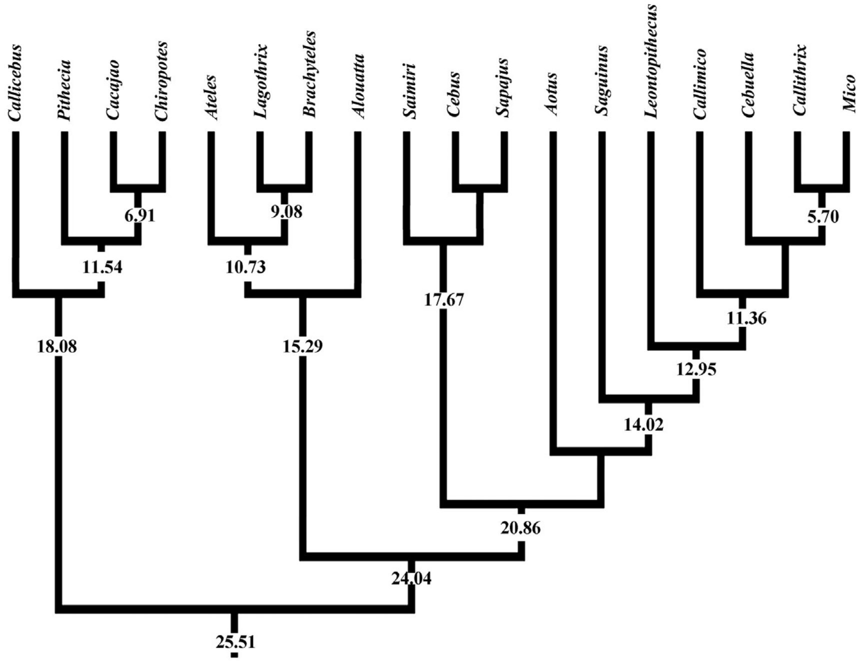

Figure 1. Consensus tree of extant platyrrhines at the genus level based on molecular data (Schrago, 2007; Perelman et al., 2011; Jameson Kiesling et al., 2015). Arrangement of *Callithrix* according to Rylands et al. (2009), who divided marmosets in *Callithrix, Mico*, and *Cebuella* (*Callibella* was not included). Ages at the nodes based on Jameson Kiesling et al. (2015) estimates. Phylogenetic placement of *Aotus* based on Schrago (2007), Perelman et al. (2011), Springer et al. (2012), and Jameson Kiesling et al. (2015).

(Kay, 1980; Swindler, 2002; Hillson, 2005). Retention of the paraconid might be a primitive trait maintained by the earliest platyrrhines (Miller and Simons, 1997; Kay et al., 2008). It is present on the molars of the Fayum anthropoid *Proteopithecus sylviae* (late Eocene), a possible ancestor of platyrrines (Miller and Simons, 1997), as well as in *Homunculus*, a Patagonian taxon dated to the early Miocene (Kay et al., 2008). The height of the trigonid may vary depending on the taxon. In some taxa it is higher than the talonid base (Callitrichinae, *Saimiri, Alouatta*, slightly higher in Cebinae), while in others both have the same height (Rosenberger et al., 1990; Lucas, 2004). Two main cusps (entoconid and hypoconid) form the talonid basin of the platyrrhines, although *Ateles* may also display a small hypoconulid (Hillson, 2005). The entoconid is located on the lingual side and the hypoconid on the buccal side, and the cristid obliqua contacts the trigonid wall at the level of the protoconid (in some taxa it is not fully oblique, as in the Pitheciinae) and runs along the trigonid wall to link with the protoconid (Kay, 1980; Swindler, 2002; Hillson, 2005). This basic anatomy of the lower molar may, however, greatly vary among groups depending on dental function, showing either pointed cusps (Callitrichinae, *Saimiri, Alouatta, Brachyteles*), rounded cusps (*Ateles, Lagothrix, Callicebus, Aotus, Cebus-Sapajus*), poorly developed shearing crests (Pitheciinae), or strong and sharp crests (Rosenberger and Kinzey, 1976; Kay, 1980, 1990; Swindler, 2002; Hillson, 2005).

In Cebidae, both *Cebus* and *Sapajus* exhibit molars with low relief, poorly developed shearing crests, and thickened enamel, features associated with an omnivorous diet, although robust capuchins (*Sapajus*) consume hard seeds and immature fruits more frequently than gracile capuchins (*Cebus*) that are more restricted to ripe fruit (Wright, 2005). *Saimiri*, on the other hand, displays well-developed cusps, sharp crests, and a buccal cingulid (also found in callitrichines, except in *Callimico*; Rosenberger et al., 1990, 1991; Swindler, 2002), features indicative of consumption of tough and stiff insect chitin (Rosenberger and Kinzey, 1976; Lucas, 2004). Lower molars in Callitrichinae show more sharply pointed cusps and more developed shearing crests than *Saimiri*. Nevertheless, the most relevant trait found in this clade is the loss of the third molars (M_3, M^3; Swindler, 2002; Hillson, 2005), except in *Callimico* (although it is reduced; Kay, 1990). Within the Callitrichinae, *Callithrix* and *Cebuella* are gum-feeding specialists. *Mico* consumes exudates, but also eats a high percentage of fruit. These genera use mainly the incisors to gouge holes in the bark of trees to elicit exudate flow (Coimbra-Filho and Mittermeier, 1976, 1977; Taylor et al., 2009). *Saguinus, Leontopithecus*, and *Callimico* lack specialized incisors. They exploit exudate sources by nongouging only during the dry season (Garber, 1984, 1993; Taylor et al., 2009). During the rainy season, these taxa include flowers, arthropods, and small vertebrates (Kinzey, 1997; Norconk et al., 2009). *Callimico* also consumes fungus, showing molars with well-developed shearing crests (Anthony and Kay, 1993; Kinzey, 1997).

Within Pitheciidae, *Callicebus* and Pitheciinae are closely related. However, dental topography reflects differences in morphology and in feeding preferences (Cooke, 2011; Ledogar et al., 2012; Winchester et al., 2014). *Callicebus* molars exhibits low, round, and bunodont cusps, slightly sharpened crests, and a high, restricted molar trigonid relative to the talonid, whereas Pitheciinae display poorly developed cusps and crests, and their trigonid and talonid are approximately equal in breadth (Kay, 1990; Meldrum and Kay, 1997; Cooke, 2011). Functional patterns of molar occlusion (relief, curvature, and shear) and the crenulated surface suggest that pitheciines are adapted to consumption of tough and hard foods (Anapol and Lee, 1994; Martin et al., 2003; Ledogar et al., 2012). By contrast, the pattern in *Callicebus* (also seen in *Aotus*; Wright, 1989) is likely an adaptation to a flexible dietary profile (Kinzey, 1992; Norconk et al., 2009; Cooke, 2011). For example, during the dry season, when fruit is scarce, the consumption of leaves and insects in *Callicebus* increases (Kinzey and Norconk, 1990, 1993; Souza-Alves et al., 2011).

In Atelidae, the two frugivorous taxa (Di Fiore, 2004; Cooke, 2011) *Ateles* and *Lagothrix* show molars characterized by having narrow and relatively lower cusp relief than *Alouatta* and *Brachyteles* (Hillson, 2005; Allen et al., 2015), although *Lagothrix* has