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

Guido Rocatti [a], Leandro Aristide [a], Alfred L. Rosenberger [b], S. Ivan Perez [a, *]

[a] División Antropología, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, CONICET. 122 y 60, 1900, La Plata, Argentina
[b] Department of Anthropology and Archaeology, Brooklyn College, CUNY, 2900 Bedford Ave., Brooklyn, NY, USA

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ABSTRACT

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

1. Introduction

New World monkeys, or platyrrhines, are one of the main clades of the order Primates and an example of a major mammalian evolutionary radiation in the Americas. The clade is considered to be monophyletic and has a relatively long evolutionary history of nearly 30 million years (Ma) spanning South and Central America, and the Caribbean (e.g., Rosenberger et al., 2009; Perez et al., 2013; Opazo et al., 2006). The fossil record of platyrrhines is contentious, but there is well supported paleontological evidence of their presence in the late Oligocene (ca. 26 Ma; Fleagle and Tejedor, 2002) or even in the late Eocene (>35 Ma; Bond et al., 2015). Therefore, the clade's earliest representatives probably invaded the continent by the Eocene–Oligocene transition, ~35 Ma, and evolved in isolation from the Old World primates from then on (e.g., Rosenberger, 2002; Tejedor and Rosenberger, 2008; Fleagle, 2013; Perez et al., 2013). While taxonomic interpretations differ, a picture of their diversity depicts a radiation within the Americas that evolved into several lineages that comprise approximately 125 extant species in 16 or 17 genera and five main clades (i.e., families or subfamilies; Wilson and Reeder, 2005; Perelman et al., 2011; Aristide et al., 2015a).

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

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* Corresponding author.
E-mail addresses: iperez@fcnym.unlp.edu.ar, ivanperezmorea@gmail.com (S.I. Perez).

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

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

Here, we analyze the mandible to test the above proposals. Rosenberger (1980, 1992) suggested that during the initial differentiation of platyrrhines, two fundamental patterns of jaw morphology arose (Fig. 1). As now seen among the extant forms, in the cebid clade (excluding *Aotus*, a genus now often classified as a cebid but then considered what modern classifications call a pitheciid), the lower border of the corpus is approximately horizontal, paralleling the occlusal plane, and the angular region forms a right angle (Fig. 1b). In atelids and pitheciids, and specifically in *Aotus*, the profile is different. The jaw deepens posteriorly and tends to become wider in the anteroposterior direction in the region of the mandibular angle (Fig. 1a). In extreme variations, as in pitheciids such as *Callicebus* (and occasionally *Aotus*), and in the atelid *Alouatta*, the mandible is greatly deepened below the molars and the gonial region is widened in depth and anteroposterior length. These two patterns may be the ancestral conditions of the major clades (Rosenberger, 1980, 1992), as they predominate among the genera included in these clades. However, there are also exceptions in both mandibular morphologies that appear to converge on the alternative condition. For example, the cebid *Leontopithecus* presents a jaw profile that tends to deepen posteriorly, while *Chiropotes* and *Cacajao* tend to display the opposite silhouette; *Aotus*, if considered to be a cebid, would also be an example, having a more pitheciid-like morphology. There are alternative explanations for the evolution of patterns of mandibular morphology in platyrrhines. It is well established that the lower jaw is biomechanically and adaptively important, and presumed to reflect diet to certain degree (e.g., Hylander, 1979, 1985; Anapol and Lee, 1994; Ravosa, 1996; Ross et al., 2012; Meloro et al., 2015). Specifically for platyrrhines, Rosenberger (1980, 1992) pointed out the correspondence between mandible morphology and diet. The extant cebids have frugivorous and insectivorous feeding habits and have a lightweight feeding mechanism, while atelids have frugivorous-folivorous habits and show a heavy-duty masticatory system (Rosenberger, 1980). This suggests that the evolutionary pattern of the mandible does not correspond with a neutral (Brownian motion) expectation. Alternatively, previous work based largely on the living species pointed out that patterns of mandibular morphology track the phylogenetic history of platyrrhines (e.g., Rosenberger, 1977, 1992; Meloro et al., 2015; Terhune et al., 2015), suggesting that its diversification might not depend mainly on diet or biomechanical factors. This suggests that platyrrhine mandible evolution was a deeply complex process.

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

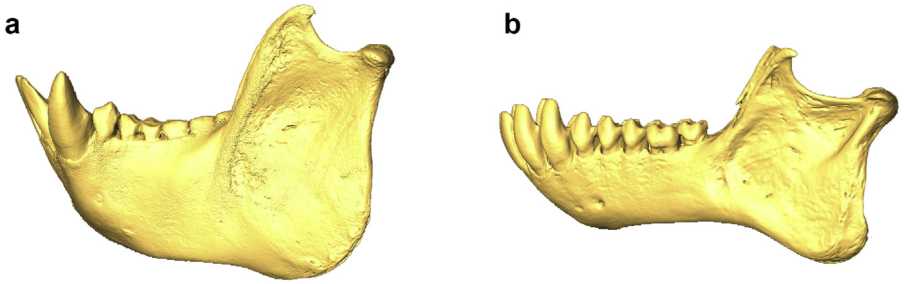

Figure 1. Image showing the two mandible shape patterns proposed by Rosenberger (1980, 1992) in lateral view. (a) An example of the atelid and pitheciid pattern represented by a *Cacajao calvus* mandible specimen. (b) An example of the cebid pattern represented by a *Callithrix penicillata* mandible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