



The evolution of the platyrrhine talus: A comparative analysis of the phenetic affinities of the Miocene platyrrhines with their modern relatives



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ABSTRACT

Platyrrhines are a diverse group of primates that presently occupy a broad range of tropical-equatorial environments in the Americas. However, most of the fossil platyrrhine species of the early Miocene have been found at middle and high latitudes. Although the fossil record of New World monkeys has improved considerably over the past several years, it is still difficult to trace the origin of major modern clades. One of the most commonly preserved anatomical structures of early platyrrhines is the talus. This work provides an analysis of the phenetic affinities of extant platyrrhine tali and their Miocene counterparts through geometric morphometrics and a series of phylogenetic comparative analyses. Geometric morphometrics was used to quantify talar shape affinities, while locomotor mode percentages (LMPs) were used to test if talar shape is associated with locomotion. Comparative analyses were used to test if there was convergence in talar morphology, as well as different models that could explain the evolution of talar shape and size in platyrrhines. Body mass predictions for the fossil sample were also computed using the available articular surfaces. The results showed that most analyzed fossils exhibit a generalized morphology that is similar to some 'generalist' modern species. It was found that talar shape covaries with LMPs, thus allowing the inference of locomotion from talar morphology. The results further suggest that talar shape diversification can be explained by invoking a model of shifts in adaptive peak to three optima representing a phylogenetic hypothesis in which each platyrrhine family occupied a separate adaptive peak. The analyses indicate that platyrrhine talar centroid size diversification was characterized by an early differentiation related to a multidimensional niche model. Finally, the ancestral platyrrhine condition was reconstructed as a medium-sized, generalized, arboreal, quadruped.

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1. Introduction

Modern New World monkeys (NWM) occupy a diverse array of habitats, ranging from the Amazonian Basin, the semi-deciduous Atlantic Forest, to the fringes of great forests such as in the Venezuelan plains (Rylands and Mittermeier, 2009; Fleagle, 2013). The occupation of these diverse environments has been accompanied by distinct behavioral, morphological and ecological adaptations,

which are broadly correlated with specific phylogenetic groups (Ford and Davis, 1992; Rosenberger, 1992; Fleagle and Reed, 1996; Fleagle et al., 1999; Rosenberger, 2002; Youlatos, 2004; Rosenberger et al., 2009). Whilst the modern day success of the group is clear, the evolutionary history of these lineages is still highly debated (Youlatos and Meldrum, 2011). Currently one of the main difficulties in platyrrhine paleontology is the scarcity of data available from the Eocene and Oligocene, because most platyrrhine fossils have been dated to the Miocene or the Pleistocene of South America and the Caribbean (Rímoli, 1977; MacPhee and Woods, 1982; MacPhee et al., 2003; Kay and Cozzuol, 2006; Tejedor et al., 2006; Fleagle et al., 2012; Perkins et al., 2012), although there are

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notable exceptions from Bolivia and Peru (Hoffstetter, 1969; Rosenberger, 1981; Wolff, 1984; Rosenberger et al., 1991; Takai and Anaya, 1996; Takai et al., 2000; Kay et al., 2002; Bond et al., 2015). Most of these fossils are composed of fragmentary dental remains, with several species, such as *Branisella boliviana* (Hoffstetter, 1969), *Mohanimico hershkovitzi* (Luchterhand et al., 1986), *Szalatavus attricuspis* (Rosenberger et al., 1991), *Solimoea acrensis* (Kay and Cozzuol, 2006), *Insulacebus toussainatiana* (Cooke et al., 2011), *Perupithecus ucayaliensis* (Bond et al., 2015), *Panamacebus transitus* (Bloch et al., 2016) and *Canaanimico amazonensis* (Marivaux et al., 2016a), being classified based on limited dental traits.

Interestingly, most of the fossil platyrrhine species of the early Miocene have been found at middle and high latitudes (i.e., central Chile and Patagonia), which are areas that are nowadays uninhabited by non-human primates (Bordas, 1942; Fleagle and Bown, 1983; Fleagle et al., 1987; Fleagle and Kay, 1989; Fleagle, 1990; Meldrum, 1990; Flynn et al., 1995; Tejedor, 2002, 2003, 2005a,b), as well as one from a tropical-equatorial area (i.e., Peruvian Amazonia) (Marivaux et al., 2012) and one from Panama (Bloch et al., 2016). Even though the NWM fossil record has improved considerably over the past several years (Tejedor, 2008; Bond et al., 2015; Kay, 2015a; Bloch et al., 2016; Marivaux et al., 2016a,b), it is still difficult to trace the origin of major modern clades (i.e., Atelidae, Pitheciidae and Cebidae), especially considering that some of the earliest fossil taxa may fall outside the crown radiation (Kay et al., 2008; Hodgson et al., 2009; Kay and Fleagle, 2010; Youlatos and Meldrum, 2011; but for a different opinion see Schrago, 2007; Rosenberger, 2010). There are two diverging positions regarding the relationship between the early platyrrhine fossils and the modern species that have been proposed: the long lineage hypothesis (LLH) and the stem platyrrhine hypothesis (SPH) (Kay et al., 2008). The LLH states that modern platyrrhines are defined by a number of long-lived clades and that most of the known fossil taxa belong to these lineages (Rosenberger et al., 2009). This position is supported by some divergence date estimates based on molecular clock data (Schneider et al., 2001; Opazo et al., 2006; Schrago, 2007). The SPH proposes that most of the early Patagonian fossil taxa are not ancestral to the modern clades (Kay et al., 2008; Kay and Fleagle, 2010). Instead they represent a sister group of all living platyrrhines that occupied niches analogous to those filled by modern NWM (Kay et al., 2008; Hodgson et al., 2009; Kay and Fleagle, 2010). Kay and Fleagle (2010) indicate that dissimilar methods can produce varying results starting from the same data and that alternate divergence times lend support to the SPH. Nonetheless, it is important to consider that a phylogenetic meta-analysis carried out by Perez and Rosenberger (2014) comparing the topologies of the 31 major neontological phylogenies concluded that major disparities are rather common among the hypotheses concerning higher level relationships of platyrrhines (e.g., the position of *Aotus*). Additionally, they also found that the correspondence among phylogenetic trees seems to depend on the type of dataset analyzed (i.e., nuclear DNA, mtDNA, Alu sequences, morphology or mixed data), which implies that the biological characteristics emphasized in different datasets intrinsically influence the likelihood of producing similar reconstructions (Perez and Rosenberger, 2014).

One of the most commonly preserved anatomical elements in the platyrrhine fossil record is the talus (Tejedor, 2008). Many Argentinian platyrrhine taxa exhibit at least one preserved talus (i.e., *Carlocebus carmenensis*, *Soriacebus ameghinorum*, *Dolichocebus gaimanensis*, *Proteropithecina neuquenensis*), while in Chile (Río Cisnes) and Peru (Madre de Dios) the post-cranial fossil record is represented by tali (Bordas, 1942; Fleagle and Bown, 1983; Fleagle

et al., 1987; Fleagle and Kay, 1989; Fleagle, 1990; Meldrum, 1990; Flynn et al., 1995; Tejedor, 2002, 2003, 2005a,b; Marivaux et al., 2012). Many of the Colombian fossils from La Venta also have preserved tali (i.e., *Neosamiri fieldsi*, *Aotus dindensis*, *Cebupithecina sarmientoi*) and the Miocene Caribbean fossil of *Paralouatta marianae* is represented only by one talus (MacPhee et al., 2003). Furthermore, the talus is important because it has been suggested that its morphology could reflect postural adaptations, based on its central position in the foot as well as its functional relationship with other foot bones (Lisowski et al., 1974; Boyer et al., 2010, 2015; Yapuncich and Boyer, 2014; Yapuncich et al., 2015). The talus is the principal mechanical link between the leg and the foot, hence it is responsible for transmitting forces derived from an animal's body mass, as well as allowing mobility and providing stability during most postural and locomotor behaviors (Boyer et al., 2015). Consequently, it has been argued that the talus is a useful element for both functional and phylogenetic analyses based on its high prevalence and good preservation in the fossil record, and also because its intricate morphology coupled with a relatively straightforward functional role in the ankle joint allow postural and locomotor inferences (Gebo, 1986, 1988, 2011; Boyer and Seiffert, 2013). Even though some platyrrhine fossil tali have been analyzed using linear morphometrics (Meldrum, 1990), there is an absence of current morphometric and comparative analyses that could provide important information regarding the evolution of this anatomical structure.

In this study we analyze Miocene fossil platyrrhine talar shape and size in the context of a broad comparative sample representing all extant platyrrhine families. Modern NWM are represented by three families that are well-defined based on congruent morphological and molecular data (Aristide et al., 2015; Kay, 2015b), except for the still debated position of *Aotus*, which has been classified either as a member of the cebines, as a sister group of the callitrichines or as a pithecid (Kay, 1990; Rosenberger et al., 1990; Rosenberger, 2002; Wildman et al., 2009). These clades show remarkable adaptations to different environments, occupying very distinct habitats and climates. Consequently their ecomorphological adaptations and body sizes are variable, ranging in the modern platyrrhine clade from 100 g to more than 10,000 g (Ford and Davis, 1992). Thus, this research has four objectives. First, to examine morphological affinities, and identify the phenetic affinities between fossil and living NWM tali. Second, to analyze locomotor mode percentages to understand the relationship between locomotion and talar shape and reconstruct the ancestral locomotor condition of the NWM. Third, to undertake evolutionary modeling to test if there is morphological convergence among NWMs and model the possible evolutionary processes explaining observed diversity in talar shape and size. Fourth, to predict body mass for the fossil sample.

2. Material and methods

2.1. Sample

The comparative sample included platyrrhines from nearly every extant genus in order to capture the full morphological diversity of the extant crown group ($n = 203$; 40 species; Table 1). The fossil sample included most of the available Miocene platyrrhine tali ($n = 15$; eight species plus two specimens that have not been taxonomically assigned; Table 2). A total of 34 three-dimensional (3D) tali scans were downloaded from Morphosource (<http://morphosource.org/>) – an online repository of 3D scan data (Copes et al., 2016) – as ply surface models, while the rest were

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