

New primate locality from the early Miocene of Patagonia, Argentina

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Abstract

Objectives: The purpose of this work is to present a new primate locality with evidence that increases the knowledge on the radiation of the extinct platyrrhine primates.

Materials and methods: We studied the new specimen and compared it to specimens identified as *Mazzonicebus almendrae*.

Results: The new first and second molars were comparable to *Mazzonicebus almendrae* in all morphological details, allowing us to allocate the new specimen to *M. almendrae* and add comments on morphological variation in this species regarding the orientation of the labial cristae and development of the anterolingual cingulum. This new maxilla also present the first known M3 for the species.

Discussion: The new specimen increases our knowledge of the extinct platyrrhines from Patagonia. Their age and geographical distribution ranges from early to middle Miocene in an area between 40° to 47° of southern latitude.

KEYWORDS

early Miocene, fossil platyrrhines, Patagonia

1 | INTRODUCTION

More than 30 extinct platyrrhine genera have been recorded in Central and South America and the Caribbean islands, including fossil from the Amazon region of Peru (late Eocene through early Miocene), western Bolivia (late Oligocene), Patagonia and Chile (early through middle Miocene), central Colombia (middle Miocene), Brazil (late Miocene and Pleistocene), Panama (early Miocene), and the Greater Antilles (early Miocene and late Cenozoic) (Bloch et al., 2016; Bond et al., 2015; Fleagle & Tejedor, 2002; Kay, 2015; Marivaux et al., 2016).

Eight genera and 10 species of fossil platyrrhines have been discovered in Patagonia, Argentina (Tejedor & Novo, 2017, in press). Among the oldest Patagonian taxa, *Mazzonicebus almendrae* has been recorded in early Miocene levels at Gran Barranca, south-central Chubut Province, and assigned to the Colhuehuapian South American Land Mammal Age (SALMA) (Kay, 2010). The bed bearing *Mazzonicebus* was constrained by ⁴⁰Ar/³⁹Ar dating to the interval 21.30–19.12 Ma (Ré et al., 2010), thus indicating a Colhuehuapian SALMA occurring between about 21.0 and 20.5 Ma (Dunn et al., 2013). *Mazzonicebus almendrae* is represented by about 30 dental specimens.

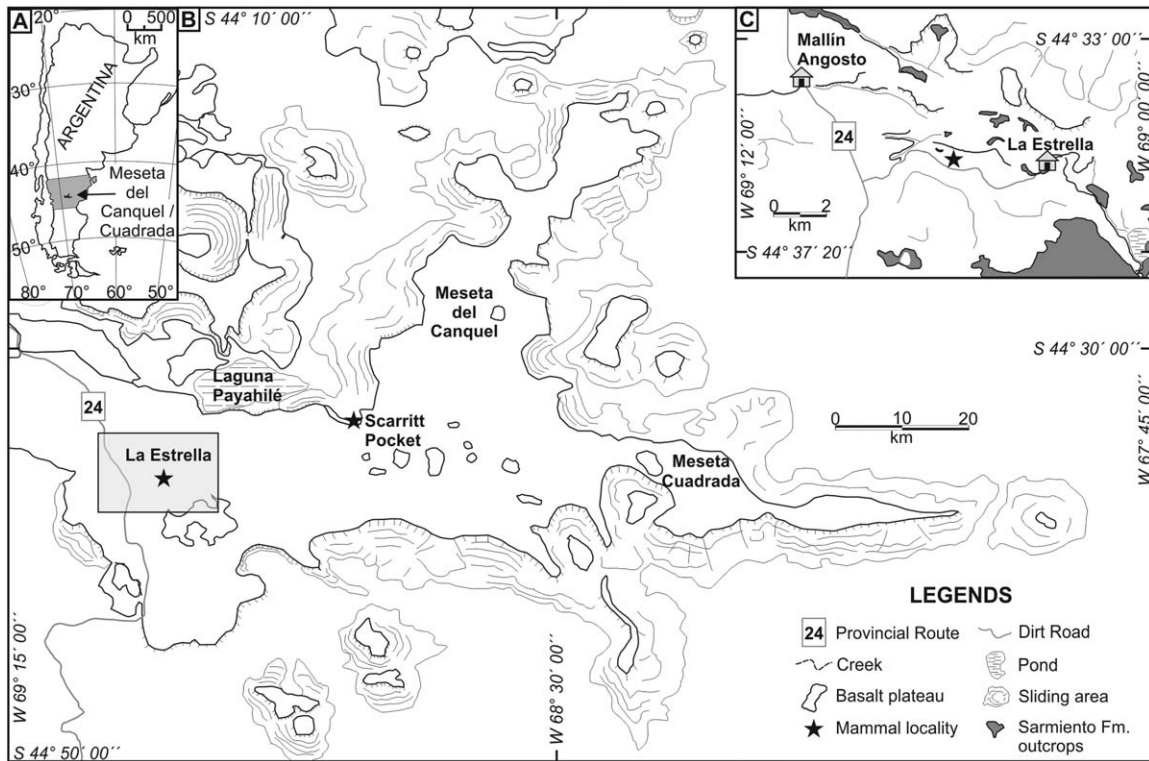


FIGURE 1 (A) Map of Argentina showing Chubut Province (gray) and location of Meseta del Canquel and Cuadrada (black). (B) Morphological scheme of Meseta del Canquel and Cuadrada, displaying location of La Estrella (black star in western area) and Scarritt Pocket (middle area). (C) Detailed map for the location of La Estrella locality (black star), displaying roads and closer ranches

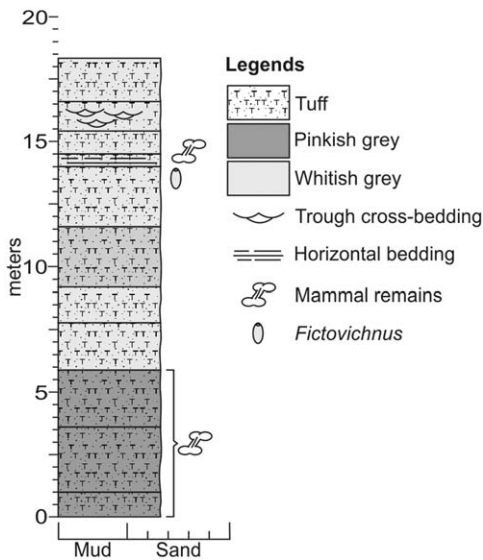


FIGURE 2 Sedimentary section at La Estrella

The specimen here reported was collected during a field expedition organized by two of the authors (MEP and JMK) along with Pablo Puerta from the Museo Paleontológico Egidio Feruglio (MEF, Trelew, Argentina) in 2016. It is a partial maxilla attributed to *M. almendrae* coming from a new primate locality at about 75 km N-NW of the Colhue-Huapi lake, and it contributes additional information on the morphological variation and geographical distribution of *Mazzonicebus*.

2 | MATERIALS AND METHODS

We studied the new specimen in comparison with *Mazzonicebus almendrae* material deposited at the Museo Paleontológico Egidio Feruglio, Paleontology Collection (MPEF-PV), Trelew, Argentina. The teeth were compared in all morphological details with those described by Kay (2010).

3 | RESULTS

3.1 | Geological setting and mammalian assemblage

The fossiliferous locality, here named “La Estrella” (S 44°35'36.60”; W 69° 5'47.90”) due to its proximity (around 3 km in west-east direction) to the homonymous ranch, is located in the western part of the Meseta del Canquel, central Chubut Province, Argentina (Figure 1). It consists of an isolated outcrop of the Sarmiento Formation, with both base and top unexposed. The section is ~18 m thick and characterized by a monotonous succession of mostly massive, fine tuffs (Figure 2). The lowermost 6 m are pinkish gray in color, and contain floated medium-size mammal remains. The upper part displays whitish and light greenish grey tuffs, and displays insect pupation chambers (*Fictovichnus* sp.) and small-sized mammal remains in place, including the material herein reported. This and other outcrops fill small depressions or directly lie above the basaltic plateau conforming the Meseta del Canquel, and are close to the classical vertebrate locality “Scarritt Pocket”, located at

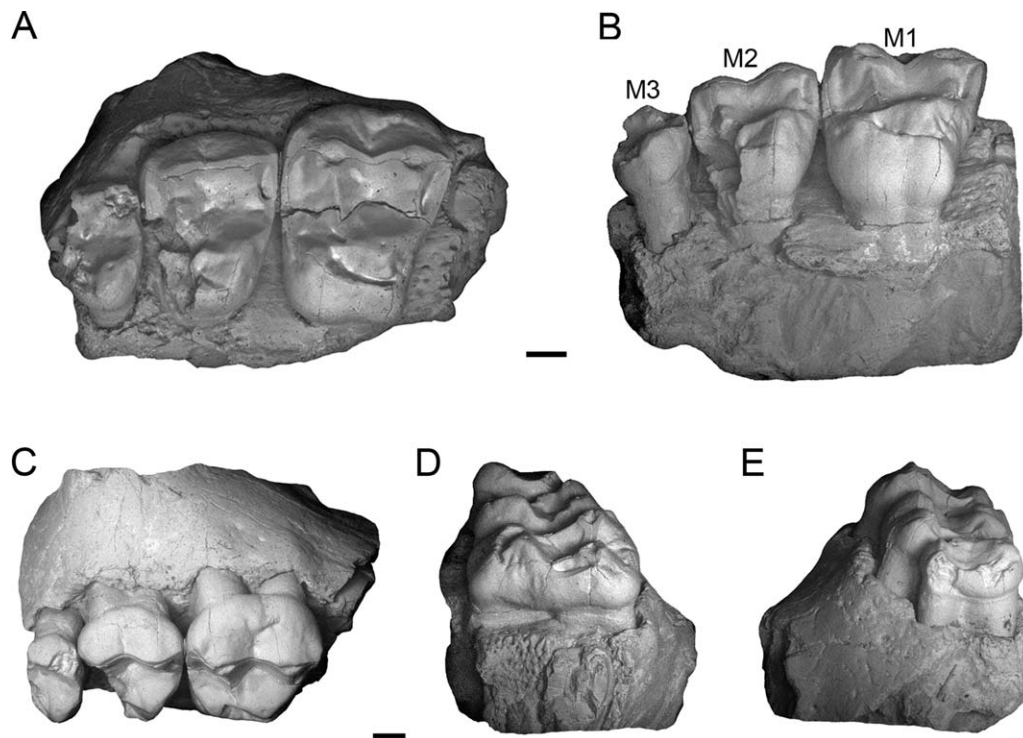


FIGURE 3 MPEF-PV 10970, left maxillary fragment with M1–3 in occlusal (A), $3/4$ lingual (B), $3/4$ labial (C), mesial (D), and distal (E) views. Scale bar = 1 mm.

approximately 25 km to the east (Marshall, Cifelli, Drake, & Curtis, 1986) (Figure 1). The fossil-bearing bed is around 15 m below a flow basalt, herein correlated with the uppermost flow basalt recorded in the Scarritt Pocket section.

Geochronologic, stratigraphic, and paleontological evidence from Gran Barranca and Scarritt Pocket support the correlation of La Estrella section to the lower Colhue-Huapi Member, as follows:

(1) The stratigraphic position of the bed bearing *M. almendrae*, along with the U-Pb LA-ICPMS date for a tuff from the lower-middle Scarritt Pocket section (27.17 ± 0.54 Ma; Vucetich et al., 2014), and ^{40}K - ^{40}Ar age for the uppermost basalt flows in that section (~ 20 Ma; Marshall et al., 1986), indicate a relative age younger than Deseadan. (2) The Colhue-Huapi Member at Gran Barranca is a monotonous succession of fine tuffaceous material, ranging in color from pink in the lower section, to pinkish grey upward the section (Spalletti & Mazzoni, 1979: p. 276). (3) The paleontological record includes an expected fauna according to the lithostratigraphic interpretation. Associated with *M. almendrae*, the following taxa are represented at La Estrella, and depending on the preservation and quality of the specimens, some were only identified provisionally as higher taxa: Marsupialia: Paucituberculata, Sparassodonta; Caviomorpha: *Perimys*, *Banderomys*, *Eosteiomys*; Xenarthra: Dasypodinae, Glyptodontidae; Notungulata: Hegetotheriidae, and Interatheriidae. Thus far, *Banderomys* was exclusive to the Cerro Bandera locality (Neuquén Province), considered early Miocene in age (Colhuehuapian SALMA) by Kramarz (2005). However, Kramarz, Bond, & Arnal (2015) and Kramarz, Tejedor, Forasiepi, and Garrido, (2012), questioned the age of Cerro Banderas following the discovery of additional taxa that are present in older, Deseadan levels

(e.g., Rodentia, Caviomorpha: *Leucokephalos*, *Cephalomys*). The presence of *Perimys* and *Eosteiomys* in La Estrella, along with the absence of typical Deseadan taxa, suggests an age not older than the Colhuehuapian. The Colhue-Huapi Member at Gran Barranca bears a lower zone with records of Colhuehuapian mammals, as well as an upper zone with a younger, "Pinturan" mammal assemblage (e.g., Bellosi, 2010). According to the above described mammal assemblages, we correlate the La Estrella section with the lower Colhue-Huapi Member.

3.2 | Description and comparisons

MPEF-PV 10970 (Figure 3) is a right maxillary fragment preserving M1–3, moderately worn. Table 1 shows the measurements of the new specimen compared with other Patagonian fossil primates. M1 is complete, M2 is broken distolingually, and M3 is somewhat damaged distally. M1 is a three-rooted tooth with trapezoidal occlusal outline, being lingually narrower. The four main cusps are well developed, including a moderate hypocone connected to the short, distally oriented postprotocrista by a prehypocrista. The prehypocrista is oriented more mesiodistally compared with M1 in MPEF-PV 5347a (see Figure 4C), where it runs slightly more lingual. The M1 has a very weak labial cingulum, absent in MPEF-PV 7195 and MPEF-PV 5347a (Figure 4B,C). There is a moderate lingual cingulum which is not expanded as a precingulum. The mesial fovea is present and deeper than in MPEF-PV 7195 and 5347a, and it is delimited by well developed hypoparacrista descending from the paracone and reaching the preprotocrista at about the anteromedial part of the tooth. The M1 preprotocrista of MPEF-PV 10970 is shorter than in MPEF-PV 7195

TABLE 1 Comparative measurements of the upper molars of MPEF-PV 10970 and other Patagonian platyrrhines

	M1		M2		M3	
	MD	BL	MD	BL	MD	BL
MPEF-PV 10970 New specimen	4.13	5.32	3.52	4.4	2.08	3.26
MPEF-PV 7195 <i>Mazzonicebus almendrae</i>	4.01	5.41				
MPEF-PV 5347a <i>M. almendrae</i>	4.1	5.38				
MPEF-PV 7063 <i>M. almendrae</i>	3.93	5.32				
MPEF-PV 5347b <i>M. almendrae</i>			3.92	4.83		
MPEF-PV 5699 <i>M. almendrae</i>			3.92	4.88		
MPEF-PV 5467 <i>M. almendrae</i>			3.55	5.1		
MPEF-PV 5342 <i>M. almendrae</i>			3.64	4.83		
MACN Pv-SC 90 <i>Carlocebus carmenensis</i>			4.51	6.65		
MACN Pv-SC 98 <i>C. carmenensis</i>	4.61	6.39				
MACN Pv-SC 230 <i>C. carmenensis</i>	4.67	6.61				
MACN Pv-SC 45 <i>C. carmenensis</i>					3.7	5.92
MACN Pv-SC 334 <i>Homunculus patagonicus</i>	3.96	5.28				
MACN Pv-SC 274 <i>H. patagonicus</i>					3.03	4.7
MPM-PV 5000 <i>Killikaika blakei</i>	4.06		3.69	4.98	2.93	4.55
MPM-PV 1607 <i>K. blakei</i>	4.26	5.42	4.2	5.17	3.18	4.69
MACN Pv-CH 357 <i>Dolichocebus gaimanensis</i>					2.94	4.39
MACN Pv-CH 356 <i>D. gaimanensis</i>	4.19	5.5				
MACN Pv-SC-47 <i>Soriacebus ameghinorum</i>					2.81	3.99
MACN Pv-SC-39 <i>S. ameghinorum</i>					2.73	3.78
MACN Pv-SC-67 <i>S. ameghinorum</i>	3.79	4.96	3.6	4.55		

and 5347a, and the mesial fovea is larger. The talon is expanded distally but not as much as in *Soriacebus*, and even more in *Cebupithecia* [see Section 4 for similarities in this trait of *Soriacebus* and *Cebupithecia* cited by Tejedor (2005)].

Parastyle and metastyle are slightly developed. The postmetacrista is oriented more labially, ending in the metastyle, as is the preparacrista, both differing from MPEF-PV 5347a and 7195, where both cristae are straighter. The hypometacrista is also present and strong as in MPEF-PV 7195 and 5347a, reaching the short postprotocrista.

In general aspect, the M1 of MPEF-PV 10970 is indistinguishable from the M1 of MPEF-PV 5347a, but slightly differs from MPEF-PV 7195 (Figure 4B), in that the latter is mesiodistally narrower with the hypocone less expanded lingually. Also, the distal crown margin of M1 in MPEF-PV 10970 appears buccolingually straight, whereas it is more rounded in other specimens attributed to *Mazzonicebus*.

M2 of MPEF-PV 10970 is three-rooted, approximately three quarter the size of M1, but it is broken in the region of the hypocone and talon. It preserves a smaller mesial fovea. There is no mesiolingual cingulum but part of the lingual cingulum is preserved, and seems well developed. This M2 is also indistinguishable from those assigned to *Mazzonicebus*, such as MPEF-PV 5699 (although published as an M1, this is certainly an M2),

MPEF-PV 5342 (Figure 4E), and MPEF-PV 5347b (Figure 3F), only differing in the absence of a mesiolingual cingulum.

M3 in MPEF-PV 10970 is approximately one half the size of M2; it is distally damaged, broken at the metacone area. Most of the hypocone and talon are lost, as well as the tip of the paracone. However, in the middle of the distal side the enamel is complete and shows that the tooth was mesiodistally narrow, somewhat oval in shape. There is no lingual cingulum around the protocone, from which a very short and rounded prehypocrista runs distolingually. Other aspects of this M3 are difficult to describe due to its damage. This is the first M3 recorded for *Mazzonicebus*.

MPEF-PV 10970 also preserves the labial root of P4, and the base of the zygomatic arch that was apparently robust.

4 | DISCUSSION

This specimen expands the geographical distribution of *Mazzonicebus*, thus the related extinct pitheciines, and adds a new primate locality to the widespread latitudinal radiation of the Patagonian platyrrhines. There has been a long controversy regarding the phylogenetic affinities of the Patagonian platyrrhines, which influences interpretations when

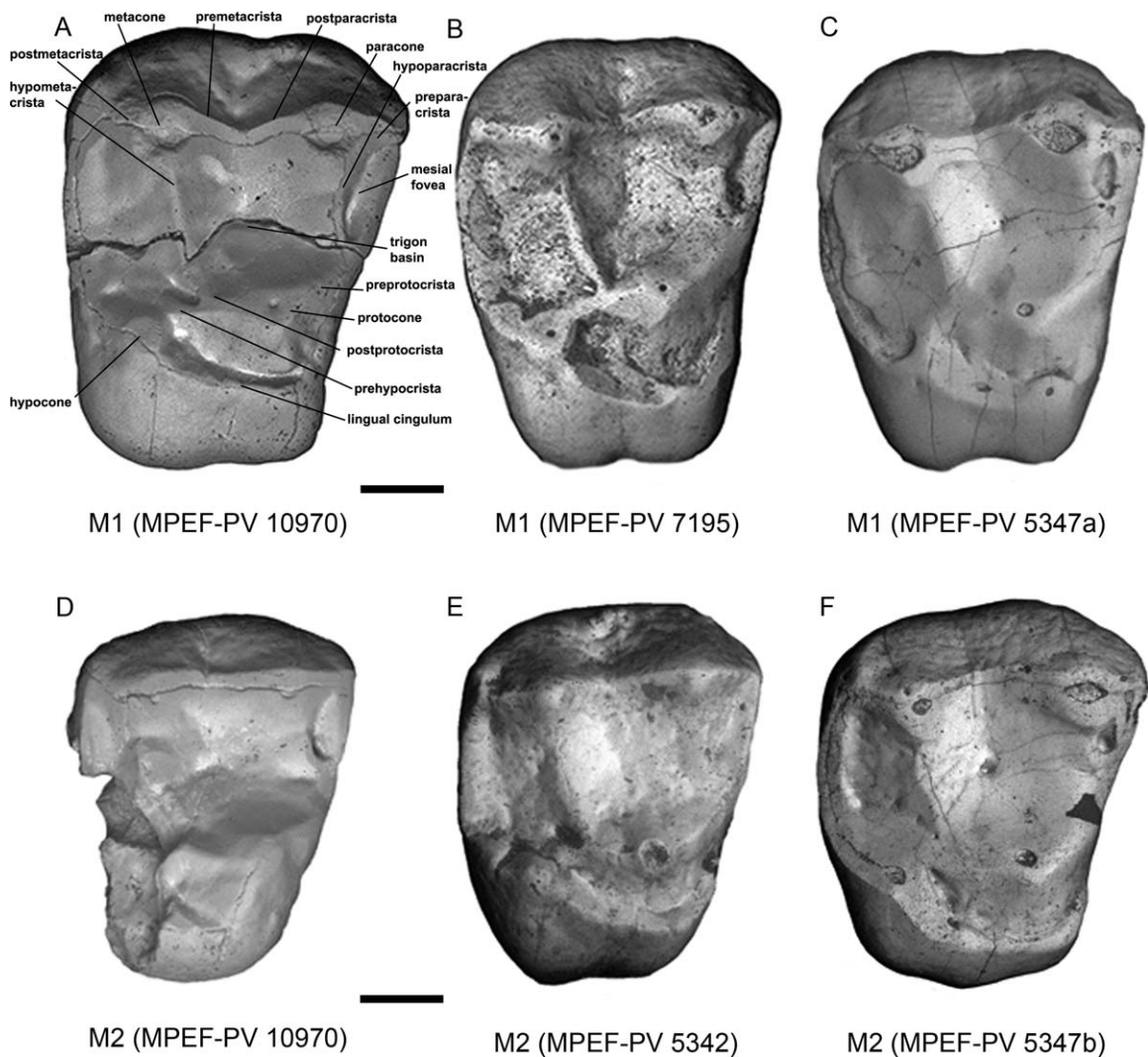


FIGURE 4 Comparison between MPEF-PV 10970 (A) and other upper molars assigned to *Mazzonicebus almendrae* by Kay (2010) (see comments in the text). Scale bar = 1mm.

they are compared to the northern Neotropical forms. One proposal, followed here (see below), suggests that they are part of an ancient radiation of crown platyrrhines, in keeping with the Long Lineage Hypothesis (LLH; see Rosenberger, 2010; Rosenberger & Tejedor, 2013, and references therein). The second proposal suggests successive radiations indicating that the Patagonian primates are stem Platyrrhini, the Successive Radiations Hypothesis (Hodgson et al., 2009; SRH; Kay et al., 2008 et seq). Considering the SRH, Kay (2010) suggested that *Mazzonicebus* shows affinities with *Soriacebus* and integrated both into a subfamily “Soriacebinae”, as part of his stem family “Homunculidae” that would include all the Patagonian primates, excepting *Proteropithecina*. However, the family “Homunculidae” as employed by Kay has been not diagnosed up to now, thus, the SRH lacks the basis determining what characters define the alleged “homunculid” radiation. In Kay’s view, “soriacebines” shared convergent adaptations with living pitheciines and the extinct *Proteropithecina*, but Kay and co-workers did not discuss the paleobiological arguments explaining how *Proteropithecina* became the only crown platyrrhine taxon

coexisting in the region during a time range of about 5 million years while all the other primates are considered a stem group. Due to the above discussed arguments, we maintain the position that the characters of *Mazzonicebus* and *Soriacebus*, as in *Proteropithecina*, are homologous with the living pitheciines.

The stem hypothesis discussed by Kay (2010) was constructed on the basis of morphological characters supported by molecular studies for divergence times, especially that of Barroso et al. (1997). Considering only the pitheciines for the present work, Barroso et al. (1997) placed the split between *Callicebus* and pitheciines between 13.5 and 16.7 Ma, thus, he argues, *Mazzonicebus* and *Soriacebus* could not be pitheciines due to their older age (about 20 and 17 Ma, respectively). Subsequently, Kay (2015) argued that the crown platyrrhine clade did not originate before about 20–24 Ma, following his phylogenetic analysis of fossil taxa as well as the molecular clock estimates of Hodgson et al. (2009), that placed the origin of crown platyrrhines between 16.8 and 23.4 Ma, and also based on Perez, Tejedor, Novo, and Aristide, (2013, “second hypothesis”) with a range of 21.2–27.9. In both cases,

however, the age of the Patagonian fossils fell within the time range for the origin of the crown platyrrhines.

Other studies giving older divergence times for crown platyrrhines have been published. As examples, Opazo, Wildman, Prychitko, Johnson, and Goodman, (2006) placed the split of *Callicebus* at about 20.3 Ma, and it was not mentioned by Kay in 2010, as well as Perelman et al. (2011) and Springer et al. (2012), with dates of 20.24 and 19.84 Ma, respectively, for the last common ancestor of *Callicebus* and pitheciines. In a phylogenetic analysis using mitochondrial DNA sequence, Finstermeier et al. (2013) estimated the divergence of the Pitheciidae at about 22 Ma, and *Callicebus* at 18 Ma. Wilkinson et al. (2011) studied the divergence times among primates and found a proportional discrepancy of 57% for the crown platyrrhines divergence following the stem hypothesis (by eliminating the Patagonian taxa from the analysis); when they added the Patagonian taxa the discrepancy was reduced to 26%. More recently, Perez et al. (2013) suggested two possible divergence times for the last common ancestor of the crown Platyrrhini: about 29 Ma using Bayesian estimates, and 21–29 using substitution rates corrected by generation time and body size.

The empirical evidence presents several morphological characteristics shared by *Soriacebus*, *Mazzonicebus*, and the living pitheciines, as described above, and the most updated phylogeny was presented by Bond et al. (2015) including the oldest records of New World monkeys up to now. That study finds the Patagonian fossils are nested within the crown Platyrrhini, and it supports the monophyly of *Soriacebus*, *Mazzonicebus*, *Proteropithecina*, *Nuciraptor*, *Cebupithecina*, and the living pitheciines. This clade was recovered in all of the most parsimonious trees, and supports the phylogenetic inferences presented by Rosenberger, Setoguchi, and Shigehara, (1990), Tejedor (2000 *et seq.*), and Rosenberger (2010).

These joint evidence strongly support the LLH and, by inference, the view that the morphology of the anterior dentition of the living pitheciines, which is one of the most unusual dental patterns exhibited among living primates, has their homologous counterparts in Patagonia, in more primitive taxa such as *Mazzonicebus* and *Soriacebus*, as well as the slightly more advanced *Proteropithecina*. The ecomorphology of the anterior teeth of these fossils is well established as adaptations for sclerocarpic harvesting in an exclusive niche typical of the living pitheciines as well, and differing from all other platyrrhines. Incisors are positioned procumbently, with tall, compressed and styliform crowns, while canines are robust, subtriangular in outline, and everted. The latter canine characters are completely developed in the living pitheciines but incipient in the Patagonian *Soriacebus*, *Mazzonicebus*, *Proteropithecina*, and the Laventan *Nuciraptor*. Notably, even though it is also an exception in lacking the modern pitheciin canine orientation, all agree *Nuciraptor* is clearly a crown pitheciine. With respect to *Proteropithecina*, it is noted that Kay and coworkers accepts that it is a pitheciine as well. Ostensibly, and its more advanced molars may be the only reason they include it among crown Pitheciinae, because all the other characters in the remaining teeth present no fundamental differences of systematic importance with respect to *Soriacebus* and *Mazzonicebus*. Beyond the mentioned synapomorphies in the anterior dentition, Tejedor (2005)

also noted some similarities between the upper molars of *Soriacebus* and *Cebupithecina*, a *bona fide* crown pitheciine from La Venta, in the position of the hypocone close to the protocone, and a lingual cingulum expanding mesially, while the talon is expanded distally due to a distally long posthypocrista, which is more developed in *Cebupithecina* and gives the upper molars its quadrangular aspect. That is typical for *Soriacebus*, *Cebupithecina* and *Mazzonicebus*.

In sum, the LLH is the most parsimonious hypothesis for interpreting the relationships of the Patagonian primates with respect to the living forms from an ecophylogenetic point of view (see Rosenberger, Tejedor, Cooke, & Pekar, 2009), as well as based on the most recent phylogenetic analysis (Bond et al., 2015).

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