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THE EVOLUTIONARY HISTORY OF PLATYRRHINES: OLD CONTROVERSIES AND NEW INTERPRETATIONS

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The living New World monkeys, Infraorder Platyrrhini, are represented by sixteen genera in subfamilies and families which even today are disputed (Cabrera, 1958; Hershkovitz, 1977; Rosenberger, 1981; Thorington and Anderson, 1984; Ford, 1986; Schneider *et al.*, 1995; Tejedor, 1996a). Their interrelationships have been the subject of considerable debate mainly because of the morphological diversity and the scarcity and fragmentary nature of the fossil record, that should otherwise contribute to constructing phylogenies. However, in recent years, new fossil discoveries and intensive studies of the existing evidence has led to considerable advances in our understanding of the platyrrhine radiation. South American fossil platyrrhines are known from several localities of the late Oligocene through Recent, at sites in Argentina, Bolivia, Chile, Colombia, Brazil, Cuba, Jamaica and Hispaniola. There are considerable gaps in the record between the middle Miocene (Colloncuran Land Mammal Age - LMA) and late Miocene (Huayquerian LMA), but subsequently the absence of fossil platyrrhines is notable until the Pleistocene of Brazil and the Caribbean islands. Although we now know more about the diversity of platyrrhines in the past, the record still consists of a limited number of specimens representing more than 20 extinct genera during the last 26 million years. Table 1 shows the temporal and geographic relationships between the known fossil species as well as the available sources.

The phyletic and geographic sources of platyrrhines are still a matter of speculation, but the oldest "pre-catarrhine" and "pre-platyrrhine" anthropoids are known from Africa and Asia. Therefore, platyrrhines, as anthropoids, should find their ancestral stock in Africa or Asia based on the current evidence. Dental evidence from these potential ancestors strongly favor the morphology found in the Santacrucian genera *Carlocebus* and *Homunculus* and in the living *Callicebus* as closest to the ancestral morphotype for the infraorder, for several reasons exposed elsewhere (Hartwig, 1993; Tejedor, 1997). Controversy persists because the oldest South American records, *Szalatavus* and *Branisella,* came from Bolivia and differ considerably from *Callicebus, Homunculus* and *Carlocebus,* being probably ancient representatives of the Callitrichinae (see Takai and Anaya, 1996). On other other hand, the subsequent *Chilecebus*, from the Chilean Andes (late Deseadan-Colhuehuapian LMA), shows several primitive characters not easily comparable to other fossil forms. Of course, this means that the earliest platyrrhines should have been considerably younger than the oldest Deseadan records of 26 Ma (million years ago) in Bolivia (Kay *et al.*, 1995). The absence of significant derived characters as compelling evidence for assessing early platyrrhine relationships is another unresolved problem. The similarities between *Callicebus, Homunculus* and *Carlocebus* are based largely on superficial resemblances and shared primitive characters (Tejedor, 1996b) which do not justify a phylogenetic link. But these symplesiomorphies strengthen the arguments in favor of a close common origin for the three latter genera. This would not appear to be a convincing solution, but it is also unusual to find several primitive characters shared by three genera of fossil platyrrhines together.

Soriacebus is, to date, the earliest relative of the Pitheciinae (Rosenberger *et al.*, 1990, but see Kay, 1990 for an alternative view). It is possible to argue that the lower molar structure of *Soriacebus* does not characterize the living pitheciines, but the lower premolar structures of *Cebupithecia* and *Nuciruptor* also differ from that of extant pitheciines (Meldrum and Kay, 1997), even though they are undoubtedly pitheciines. In this case, it is interesting to remember that specializations of the anterior dentition in the Pitheciinae possibly preceded those of premolars and molars, being, as Kinzey (1992) suggested, an adaptive response for sclerocarpic foraging. The shared features of the anterior dentition of *Soriacebus*, *Cebupithecia* and *Nuciruptor* are certainly homologous with those of *Pithecia*, *Chiropotes* and *Cacajao*. The fact that *Callicebus* could be closest to the living pitheciines has been proposed by Rosenberger (1981a) and was reinforced by recent molecular studies (Meldrum, 1995; Schneider *et al.*, 1995), but meaningful comparisons could probably only be made in the incisal morphology. It is possible that procumbent, high-crowned and mesiodistally compressed incisors are primitive for all platyrrhines, and the Pitheciinae has evolved further these traits, demonstrating an early divergence from the remaining clades.

It is interesting to note that there are several specimens of Colloncuran platyrrhines from Patagonia (Pardiñas, 1991; Kay and Johnson, 1996) which are still undescribed, and certainly represent a new taxon.

There is no question concerning the phylogenetic relationships between *Stirtonia* and *Alouatta*, as well as between *Saimiri, Neosaimiri* and *Laventiana*. Although Rosenberger *et al.* (1991a) suggested that *Laventiana* is generically distinct, some authors have argued that it should be allocated to *Neosaimiri* (Takai, 1994; Meldrum and Kay, 1997). Each of these points of view has the same phylogenetic implications in relating *Neosaimiri* and *Laventiana* with the living *Saimiri*. The Patagonian *Dolichocebus* shares important cranial synapomorphies also with *Saimiri* (Rosenberger, 1979). There are several reported occurrences of callitrichines in Colombia. The poorly known *Micodon,* the surprising *Lagonimico*, and more recently *Patasola* have confirmed that the Callitrichinae have been differentiated certainly since the middle Miocene (Laventan stage-age), and probably since the Deseadan of Bolivia, as mentioned above. However, *Lagonimico* is a particular case (Kay, 1994). The conclusion about the phyletic position and adaptations of *Lagonimico* does not agree with the hypothesis of "phyletic dwarfing" (Ford, 1980) proposed to explain many distinctive morphological features of the living callitrichines, especially those associated with body size reduction. *Lagonimico* was larger than *Callimico*, the largest living callitrichine, and exhibited features previously

Table 1. Temporal and geographic relationships between the described fossil species of platyrrhines. For each case, the available sources and possible affinities with extant forms is detailed.

Species	Locality	Age	Sources	Living related species
Branisella boliviana	Salla Luribay, Bolivia	Desdeadan (late Oligocene)	Holffstetter (1969) Rosenberger (1981b), Wolff (1984)	Callitrichinae?
Szalatavus attricuspis	Salla Luribay, Bolivia	Deseadan (late Oligocene)	Rosenberger *et al.* (1991b)	Callitrichinae?
Chilecebus carrascoensis	Río Las Leñas, Chile	Late Deseadan-Colhuehuapian (early Miocene)	Flynn *et al.* (1995)	?
Tremacebus harringtoni	Sacanana, Argentina	Colhuehuapian (early Miocene)	Rusconi (1935), Hershkovitz (1974)	*Aotus*
Dolichocebus gaimanensis	Gaiman, Argentina	Colhuehuapian (early Miocene) Fleagle & Bown (1983)	Bordas (1942), Kraglievich (1951),	*Saimiri*
Soriacebus ameghinorum & *Soriacebus adrianae*	Río Pinturas, Argentina	Santacrucian (early Miocene)	Fleagle *et al.* (1987), Fleagle (1990)	Pitheciinae
Carlocebus carmenensis & *Carlocebus intermedius*	Río Pinturas, Argentina	Santacrucian (early Miocene)	Fleagle (1990)	*Callicebus*
Homunculus patagonicus	Santa Cruz Formation (several localities), Argentina	Santacrucian (early Miocene) Fleagle *et al.* (1988), Tauber (1991)	Ameghino (1891, 1906),	*Callicebus*
Cebupithecia sarmientoi	La Venta, Colombia	Laventan (middle Miocene)	Stirton (1951)	Pitheciinae
Nuciruptor rubricae	La Venta, Colombia	Laventan (middle Miocene)	Meldrum & Kay (1997)	Pitheciinae
Mohanamico hershkovitzi	La Venta, Colombia	Laventan (middle Miocene)	Luchterhand *et al.* (1986)	?
Aotus dindensis	La Venta, Colombia	Laventan (middle Miocene)	Setoguchi & Rosenberger (1987)	*Aotus*
Micodon kiotensis	La Venta, Colombia	Laventan (middle Miocene)	Setoguchi & Rosenberger (1985)	Callitrichinae
Lagonimico conclucatus	La Venta, Colombia	Laventan (middle Miocene)	Kay (1994)	Callitrichinae
Patasola magdalenae	La Venta, Colombia	Laventan (middle Miocene)	Kay & Meldrum (1997)	Callitrichinae
Neosaimiri fieldsi	La Venta, Colombia	Laventan (middle Miocene)	Stirton (1951), Takai, 1994	*Saimiri*
Laventiana annectens	La Venta, Colombia	Laventan (middle Miocene)	Rosenberger *et al.* (1991^{a})	*Saimiri*
Stirtonia tatacoensis & *Stirtonia victoriae*	La Venta, Colombia	Laventan (middle Miocene)	Stirton (1951), Hershkovitz (1970), Kay *et al.* (1989)	*Alouatta*
Protopithecus brasiliensis	Toca da Boa Vista, Brazil	Pleistocene	Lund (1840), Hartwig & Cartelle (1996)	*Alouatta* & Atelinae
Caipora bambuiorum	Toca da Boa Vista, Brazil	Pleistocene	Cartelle & Hartwig (1996)	Atelinae
Xenothrix macgregori	Long Mile Cave, Jamaica	Pleistocene	Williams & Koopman (1952), MacPhee & Fleagle (1991)	*Callicebus*?
Antillothrix bernensis	Cueva de Berne, Dominican Rep Caverne Sawo, Haití	Holocene	Rímoli (1977), Mac Phee *et al.* (1995)	?
Paralouatta varonai	Pinar del Río, Cuba	Pleistocene	Rivero & Arredondo (1991)	*Alouatta*
Ateles anthropomorphus	Boca del Purial, Cuba	Recent	Ameghino (1910), Arredondo & Verona (1985)	*Ateles*

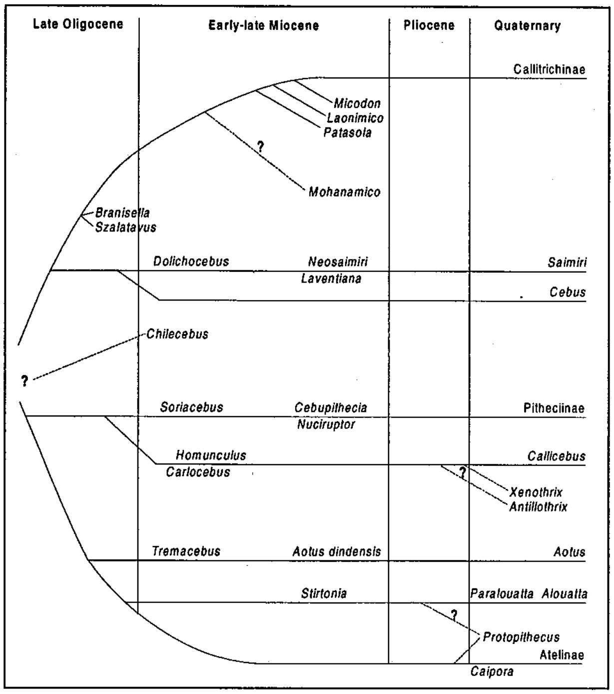

Figure 1. Platyrrhine phylogeny based on current evidence. *Ateles anthropomorphus* is not included because it could pertain to a living species of *Ateles* (see MacPhee and Rivero, 1996).

supposed to be linked with body size reduction such as hypocone loss in the upper molars. Another controversy has arisen with the discoveries of *Aotus dindensis* and *Mohanamico.* While Setoguchi and Rosenberger (1987) found resemblances between. *A. dindensis* and the living owl monkeys, Kay (1990) suggested that it should be congeneric with the previously described *Mohanamico* (Luchterhand *et al.*, 1986), considering the latter as a possible pitheciine (Meldrum and Kay [1997] considered the pitheciine status of *Mohanamico* less probable). On the contrary, Rosenberger *et al.* (1990) hold the view that *Mohanamico* could be related to *Callimico.* All these arguments imply that two extinct taxa (or only one, *sensu* Kay) could be compared with representatives of three different subfamilies: Aotinae, Callitrichinae and Pitheciinae. At present, the affinities of *Mohanamico* are uncertain, and it is convenient to maintain *Aotus dindensis* as a separate genus. Geographically and temporally distant from Colombia, the Colhuehuapian genus *Tremacebus* is also linked with *Aotus* based on shared cranial characters, especially its large orbits (Rosenberger and Fleagle, 1981).

Protopithecus and *Caipora* are larger than any living platyrrhine, being more than 20 kg. in body weight (Hartwig and Cartelle, 1996; Cartelle and Hartwig, 1996). *Caipora* is certainly a giant ateline comparable to *Ateles* and *Brachyteles*, but *Protopithecus* exhibits a mosaic of features with a skull typical of *Alouatta* and a postcranium similar to *Ateles* or *Brachyteles.* They represent the only fossil evidence for the *Ateles-Brachyteles-Lagothrix* clade. Two isolated teeth of another giant platyrrhine were found in the Rio Acre (Huayquerian, LMA), western Amazonia, but the authors found that the morphology is similar to *Cebus* (Kay and Frailey, 1993).

There are no platyrrhines in the Caribbean islands today, but in Pleistocene-Recent times some strange forms inhabited Cuba, Jamaica and Hispaniola. *Xenothrix* is at this moment perhaps the most unusual platyrrhine, without third molars but with extremely bunodont teeth and reduced incisors and canines. Proposals have been made for its affinity with the callitrichines (Williams and Koopman, 1952), *Callicebus* and *Cebus* (Rosenberger, 1977), and with *Callicebus* and the extinct *Paralouatta* and *Antillothrix* (Horovitz *et al.*, 1997). MacPhee and Fleagle (1991) described several postcranial specimens collected in the type locality of *Xenothrix* that were tentatively assigned to this genus. These specimens are morphologically distinct from all living platyrrhines and were reallocated in the monotypic Family Xenotrichidae (after Hershkovitz, 1970). *Antillothrix* (MacPhee *et al.*, 1995), formerly described as "*Saimiri*" *bernensis* by Rímoli (1977), is cladistically considered the sister taxon of *Paralouatta*, *Callicebus* being its closest living relative (MacPhee *et al.*, 1995). However, *Paralouatta* has strong cranial resemblances with the living *Alouatta* (Rivero and Arredondo, 1991). Finally, new data on the exact age of *Ateles anthropomorphus* (Ameghino, 1910; Arredondo and Varona, 1983) concluded that it was introduced in Cuba after the Spanish colonization and probably as recently as the 19th century (MacPhee and Rivero, 1996). One notable exception is an isolated talus from the lower Miocene of Cuba, the only Caribbean record of primates prior to the Pleistocene (MacPhee and Iturralde-Vinent, 1995). The biogeographic implications of the latter discovery are extremely important to explain the supposed endemism of some Caribbean platyrrhines.

As shown above, there are different views on platyrrhine phylogeny and about the phylogenetic relationships of some genera in particular. Although our knowledge of the evolutionary history of platyrrhines is based largely on fragmentary, especially dental, remains it is possible to recognize the generic differences in the majority of the above described extinct forms. Some authors may disagree considerably in their opinions, such as is the case with *Aotus dindensis* and *Mohanamico*, or some hypotheses may still be speculative, such as that of the "phyletic dwarfing" for the callitrichine lineage. An example is *Lagonimico* probably the largest callitrichine ever known, that preserves some characters believed to be associated with body size reduction in the Callitrichinae. There are some problems also in understanding the trends toward increasing body size in the Atelinae, because even though they are among the largest New World monkeys today, the finding of *Protopithecus* and *Caipora* shows that much larger atelines were alive during the Pleistocene. In this case, the size change through time was more complex than has been commonly understood. However, there is clear evidence of the early relatives of *Saimiri* (*Dolichocebus*, *Neosaimiri*, *Laventiana*), *Aotus* (*Tremacebus*, *Aotus dindensis*), *Alouatta* (*Stirtonia*, *Paralouatta*), *Callicebus* (*Homunculus*, *Carlocebus*) and pitheciines (*Soriacebus*, *Cebupithecia*, *Nuciruptor*). Interpretations for the remaining extinct forms require more detailed studies. A scheme representing the living and fossil platyrrhine interrelationships is shown in Figure 1.

It would be possible to find the answers to many of the controversies if we accept a broader radiation of platyrrhines, a greater diversity in the past, and the probability that the history of the infraorder is older than we know from the current evidence. Firstly, it is necessary to reach a consensus regarding the polarity of dental characters for a better understanding of what is primitive or derived, in order to facilitate phylogenetic reconstruction. This is, of course, not only the main problem but the most complicated because of the scarcity of the fossil record. New discoveries from pre-Deseadan sedimentary deposits of South America, especially, would help to explain the complex radiation of these primates.

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PRESENCIA DE *ALOUATTA CARAYA* FUERA DE SU AREA DE DISTRIBUCIÓN NATURAL

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Los monos aulladores (género *Alouatta*) poseen una extensa distribución geográfica desde el nivel del mar hasta los 3200 metros de altura, tanto en pluviselvas como en bosques semideciduos con clima estacional, en selvas de inundación y en ambientes coaccionados por el hombre (Neville, 1972; Glander, 1978; Eisenberg, 1979; Milton, 1980; Mittermeier y Van Roosmalen, 1981; Gaulin y Gaulin, 1982; Wolfheim, 1983; Piantanida *et al.*, 1984; Brown, 1984; Crockett y Eisenberg, 1987; Rumiz, 1990; Hirsch *et al.*, 1991; Redford y Eisenberg, 1992; Zunino *et al.*, 1995). En ciertas regiones de Meso y Sudamérica, *Alouatta* es el único género observado entre los primates neotropicales y en especial *A. caraya* se encuentra en el límite sur de distribución, siendo su localización más austral en Alegrete, Brasil (29°56'S; 55°59'W) (Bicca-Marques, 1990). Todos estos datos reflejarían la capacidad descrita del género a adaptarse a diversas condiciones ecológicas, aún en áreas perturbadas por el hombre (Eisenberg, 1979; Rodríguez-Luna *et al.*, 1996).

Contrastando con la situación presentada en hábitats naturales, *Alouatta* presenta problemas para adaptarse al cautiverio (Crandall, 1964; Dumond, 1967). Trabajos pioneros sobre el mantenimiento de *A. caraya* en estas condiciones dan cuenta de los cuidados que se le debe brindar, aunque no siempre se alcanza el éxito en su supervivencia y reproducción (Benton, 1976; Lindbergh, 1976; Shoemaker, 1978; 1982; Colillas, 1983). En la aclimatación de los aulladores al cautiverio, se han señalado como claves las oportunidades que se les brinde en relación a la complejidad estructural de la jaula, diversidad en la dieta y ambiente social adecuado, aspectos que posibilitan la autorregulación del animal con su ambiente y se mencionan como casos extremos de estas oportunidades, las situaciones de semi-libertad. Al respecto Lindbergh (1976) enfatiza su importancia, aún en climas templados, para la conservación *ex situ* de *A. caraya* y por otra parte menciona que los monos mantenidos en estas condiciones pueden estar mejor preparados, llegado el caso, para liberaciones en hábitat naturales que aquellos monos mantenidos en jaulas de zoológicos.

El objetivo del presente trabajo es informar sobre la presencia de *Alouatta caraya* en un bosque del noreste de la provincia de Buenos Aires, Argentina, detallando el clima, la vegetación del área e historia del grupo y aportando un nuevo caso para la discusión acerca de la adaptabilidad de *A. caraya* en condiciones ambientales extremas.

El área de estudio corresponde a un segmento de bosque de 12 ha incluido en un parque llamado Pereyra-Iraola, localizado 40 km al sur de la ciudad de Buenos Aires (34°51'S, 58°05'W) (Fig. 1). El clima de la región es templado y se sitúa dentro de los límites de la provincia fitogeográfica Pampeana, que ocupa las llanuras del este de Argentina en el rango latitudinal sur 31°-39°. Los datos climáticos que se aportan corresponden a una estación meteorológica situada aproximadamente 20 km al sur del parque (La Plata, aero, 34° 58'S; 57° 54'W). Estos indican que la temperatura media anual es de 15.9 °C, con una amplitud anual de 14.2 °C y la precipitación anual es de 1092.6 mm (Servicio Meteorológico Nacional, período 1981-1990) (Fig. 2). En especial el área citada se caracterizaría originalmente por la presencia de pastizales salpicados por isletas de tala (*Celtis spinosa*) (Cabrera, 1971). Sin embargo la vegetación original del área fue modificada a mediados del siglo XIX introduciéndose

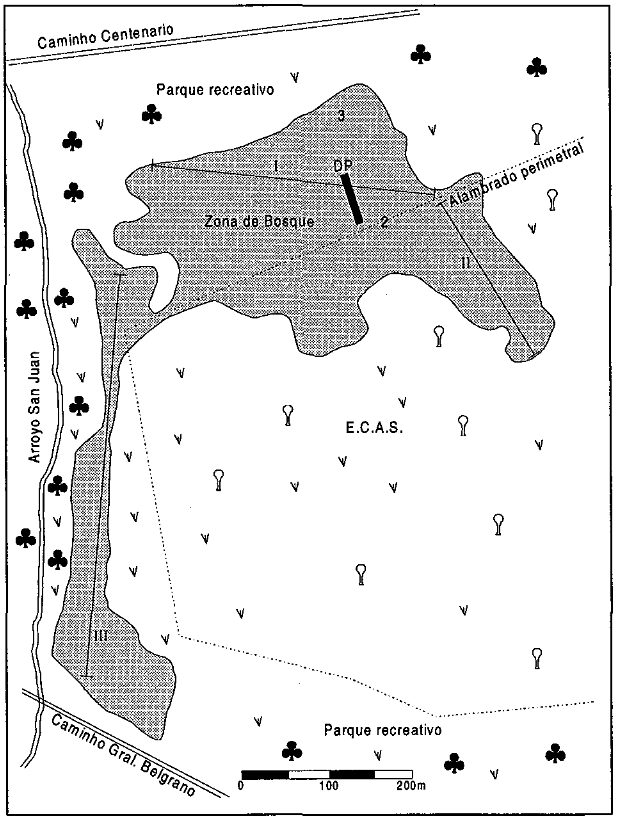

Figura 1. Zona de estudio. Referencias: I, II y III: transectos para análisis de composición florística. DP: franja tomada para representar el diagrama perfil (Figura 3). 1, 2 y 3: corresponden a sitios dentro del bosque en los cuales fueron observados los monos. ♣: árboles exóticos. V : herbáceas. ♀:*Celtis spinosa* y *Phytolacca dioica*