



THE ORIGIN AND EVOLUTION OF NEOTROPICAL PRIMATES ¹

(With 4 figures)

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ABSTRACT: A significant event in the early evolution of Primates is the origin and radiation of anthropoids, with records in North Africa and Asia. The New World Primates, Infraorder Platyrrhini, have probably originated among these earliest anthropoids morphologically and temporally previous to the catarrhine/platyrrhine branching. The platyrrhine fossil record comes from distant regions in the Neotropics. The oldest are from the late Oligocene of Bolivia, with difficult taxonomic attribution. The two richest fossiliferous sites are located in the middle Miocene of La Venta, Colombia, and to the south in early to middle Miocene sites from the Argentine Patagonia and Chile. The absolute ages of these sedimentary deposits are ranging from 12 to 20 Ma, the oldest in Patagonia and Chile. These northern and southern regions have a remarkable taxonomic diversity and several extinct taxa certainly represent living clades. In addition, in younger sediments ranging from late Miocene through Pleistocene, three genera have been described for the Greater Antilles, two genera in eastern Brazil, and at least three forms for Rio Acre. In general, the fossil record of South American primates sheds light on the old radiations of the Pitheciinae, Cebinae, and Atelinae. However, several taxa are still controversial.

Key words: Neotropical Primates. Origin. Evolution.

RESUMO: Origem e evolução dos primatas neotropicais.

Um evento significativo durante o início da evolução dos primatas é a origem e a radiação dos antropóides, com registros no norte da África e da Ásia. Os representantes dos Primates do Novo Mundo, Infraordem Platyrrhini, provavelmente se originaram a partir dos antropóides mais primitivos, morfológica e temporalmente anteriores ao ramo Catarrhini/Platyrrhini. O registro fóssil dos Platyrrhini procede de regiões distantes no Neotrópico. Os mais antigos procedem do Oligoceno Superior da Bolívia, com atribuições taxonômicas difíceis. Os dois sítios fossilíferos mais ricos estão localizados no Mioceno Médio de La Venta, Colômbia, e ao sul, em sítios do Mioceno Inferior à Médio da Patagônia Argentina e Chile. A idade absoluta desses depósitos sedimentares varia de 12 a 20 Ma sendo os mais antigos depósitos os da Patagônia e do Chile. Essas regiões, ao norte e ao sul, tem uma notável diversidade taxonômica e os diversos táxons extintos certamente representam clados viventes. Somado a isto, três gêneros foram descritos para as Grandes Antilhas em sedimentos mais recentes, variando do Mioceno Superior ao Pleistoceno, dois gêneros para o leste do Brasil, e pelo menos três formas para o Rio Acre. Em geral, o registro fóssil dos primatas sul-americanos permite de certa forma esclarecer as antigas radiações dos Pitheciinae, Cebinae e Atelinae. Contudo, vários táxons ainda são controversos.

Palavras-chave: Primatas neotropicais. Origem. Evolução.

INTRODUCTION

The origin and evolution of the Order Primates have been always controversial, but the fossil record has increased considerably especially in the last two decades (HARTWIG, 2002). Currently, the most accepted macro-systematics of Primates is a division between Strepsirrhini and Haplorrhini. The Haplorrhini is a grouping joining Tarsiiformes and Anthropoidea, and the Anthropoidea is the suborder that joins the Infraorders Platyrrhini and Catarrhini. As a native

South American infraorder, finding the closest ancestral stock of the platyrrhines may be a useful tool in reconstructing their phylogeny. As anthropoids, the potential ancestors of the platyrrhines might be found in Africa, where primitive anthropoids that lived before the platyrrhine-catarrhine split have been discovered during the last 100 years (SIMONS, 1995, and references therein). The relevant fossils are mostly of late Eocene and early Oligocene age, and the most popular and rich fossil primate assemblages are located in the Fayum, Egypt.

¹ Submitted on September 14, 2006. Accepted on October 25, 2007.

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The taxa are generally included in the families Propliopithecidae, Parapithecidae, Proteopithecidae, and Oligopithecidae. Traditionally, the Propliopithecidae (*Aegyptopithecus*, *Propliopithecus*) are viewed as morphologically primitive catarrhines, and the Parapithecidae (*Apidium*, *Parapithecus*, *Qatrania*) alternatively as a sister group of platyrrhines plus catarrhines, or as primitive catarrhines (FLEAGLE & KAY, 1987; HARRISON, 1987; KAY *et al.*, 1997). The Oligopithecidae (*Oligopithecus*, *Catopithecus*) are considered either basal catarrhines or basal anthropoids (SIMONS & RASMUSSEN, 1994; KAY *et al.*, 1997). The Proteopithecidae (*Proteopithecus*, *Serapia*) are morphologically primitive anthropoids, and have been linked with platyrrhines dentally (KAY *et al.*, 1997) and also based on postcranial anatomy (SIMONS & SEIFFERT, 1999).

Outside of the Fayum, northern Africa has yielded a small collection of additional primate fossils, some of them possible anthropoids. *Biretia*, from the late Eocene, was largely based on a single lower molar from Algeria originally described as a catarrhine (DE BONIS *et al.*, 1988), but reinterpreted as a parapithecid (RASMUSSEN & SIMONS, 1992; KAY *et al.*, 1997). SEIFFERT *et al.* (2005) reported two new species of *Biretia* from a late Eocene locality of the Fayum, Egypt, suggesting parapithecid relationships. Also from Algeria, but of early Eocene age, *Algeripithecus* (GODINOT & MAHBOUBI, 1992) and *Tabelia* (GODINOT & MAHBOUBI, 1994) are tiny primates with anthropoid affinities. *Djebelemur* came from the early Eocene of Tunisia (HARTENBERGER & MARANDAT, 1992), and was considered as an adapid by its discoverers, but as an anthropoid by GODINOT (1994), as well as *Omanodon* and *Shizarodon* (GHEERBRANT *et al.*, 1993), from the early Oligocene of Oman, in the Arabian Peninsula.

From the late Paleocene of Morocco, *Altiatlasius* was previously known by isolated teeth originally allocated among the Omomyidae, thus being the oldest anatomically modern primate ever discovered. However, recent discoveries of plesiadapiforms shed light on the possible plesiadapiform status of *Altiatlasius* (HOOKER *et al.*, 1999).

Several discoveries from Asia have potentially added information on the anthropoid origin, but the affinities of these forms are highly uncertain. Eosimiidae is a family that includes two species of *Eosimias*, from the middle Eocene of China, considered by some authors as the oldest known anthropoids (BEARD *et al.*, 1994; 1996; GEBBO *et al.*,

2000). However, other authors question its anthropoid status (GODINOT, 1994; SIMONS & RASMUSSEN, 1994). A second genus has also been included among eosimiids, *Bahinia*, found in the late-Middle Eocene of Myanmar (JAEGER *et al.*, 1999; BEARD, 2002).

From the late-Middle Eocene of Myanmar are *Poundangia* and *Amphipithecus*, which were originally described in the 1930s and alternatively considered as adapiforms or anthropoids by different authors (see CIOCHON & HOLROYD, 1994). Along with *Siamopithecus*, from the late Eocene of Thailand (CHAIMANEE *et al.*, 1997), they were recently classified to constitute the family Amphipithecidae (BEARD, 2002).

In sum, these Afro-Arabian and Asian findings reflect a broad radiation of euprimates. Most researchers who have described and evaluated the material regard them as anthropoid or anthropoid-related primates. Several authors also tend to emphasize that this adds new information about an Asian geographic origins of the suborder. For the platyrrhines, their only potential ancestors proposed in this context have been some Fayum forms, as mentioned above (KAY *et al.*, 1997). The fact that some overall similarities are shared between platyrrhines and some parapithecids and proteopithecids is until now speculative, since there was no in depth comparative and phylogenetic studies to sharpen this hypothesis.

MATERIAL AND RESULTS

THE FOSSIL RECORD OF NEOTROPICAL PRIMATES

Since the times of Peter Lund and later Carlos and Florentino Ameghino, fossil primates have been found in South America and the Caribbean. Figure 1 shows the localities of fossil platyrrhines, and table 1 is a detailed taxonomic and temporal scheme for the platyrrhine fossil record.

BOLIVIA

The oldest records in South America, *Branisella boliviana* and *Szalatavus attricuspis*, come from the locality of Salla, Bolivia (HOFFSTETTER, 1969; ROSENBERGER *et al.*, 1991a; WOLFF, 1984; TAKAI & ANAYA, 1996; TAKAI *et al.*, 2000). This locality is 26 Ma (KAY *et al.*, 1998), or late Oligocene age (Deseadan South American Land Mammal Age, SALMA). The phylogenetic relations of *Branisella* and *Szalatavus* are still under debate.

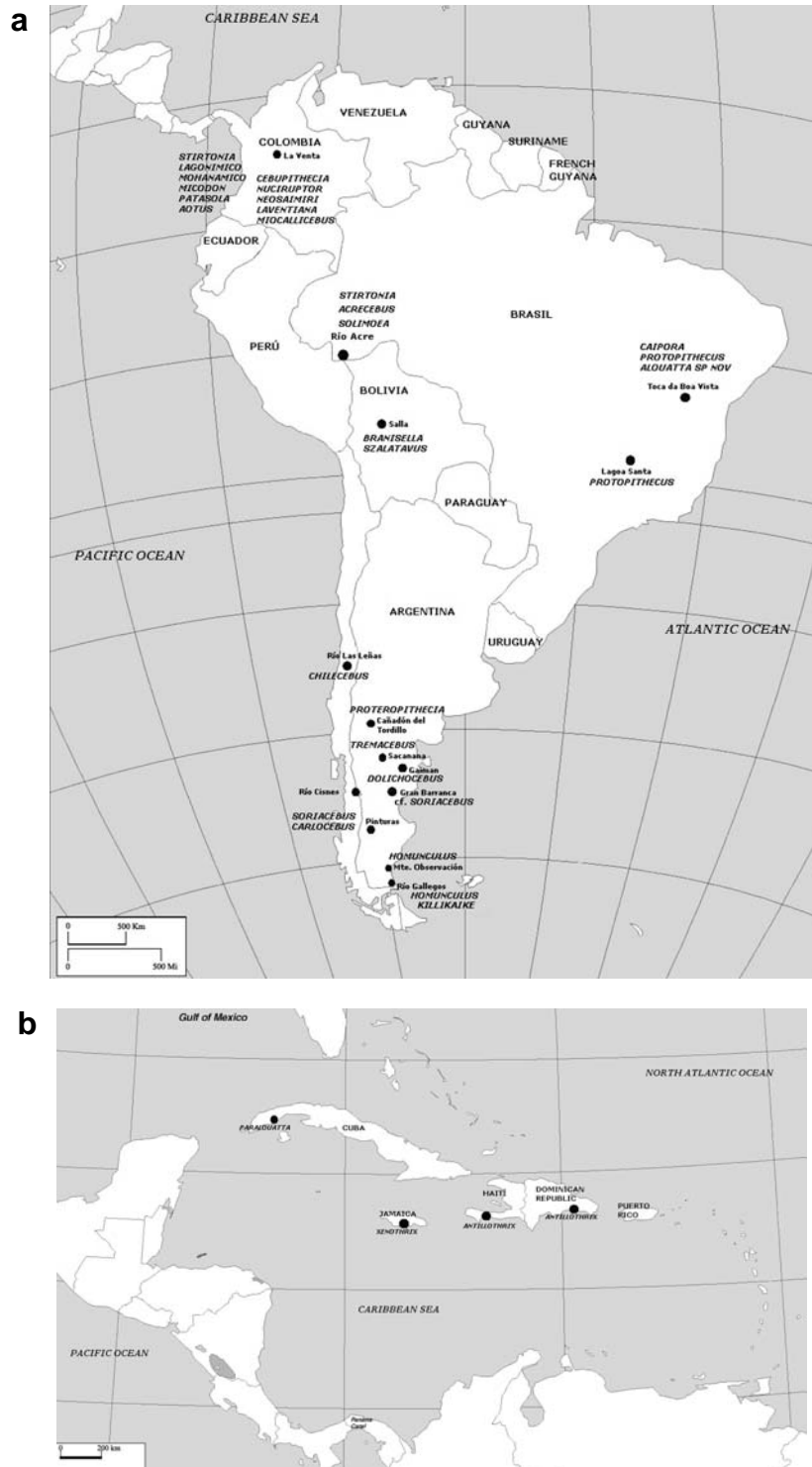


Fig. 1- Geographic distribution of the fossil platyrrhine localities and genera in South America (a) and the Caribbean (b).

TABLE 1. Temporal and geographic distribution of the platyrrhine fossil genera.

AGE (MA)	EPOCH	SALMA	PRIMATE-BEARING SITES	FOSSIL TAXA
	HOLOCENE		Hispaniola	<i>Antillothrix</i>
10,000	PLEISTOCENE	Lujanian	Lagoa Santa-Toca da Boa Vista	<i>Protopithecus-Caipora-Alouatta sp nov</i>
2-5-		Ensenadan	Caribbean localities	<i>Xenothrix</i> <i>Paralouatta</i>
	PLIOCENE	Uquián		
8-11-		Chapadmalalan	Rio Acre	<i>Solimoea-Stirtonia-Acrecebus</i>
14-17-	MIOCENE	Montehermosan	La Venta	<i>Stirtonia-Neosaimiri-Cebupithecia-Aotus-Mohanamico-Micodon-Lagonimico-Patasola-Laventiana-Nuciraptor-Miocallicebus</i>
20-		Huayquerian		Cañadón del Tordillo
		Chasicoan	Santa Cruz Fm	<i>Homunculus-Killikaike</i>
		Mayoan	Pinturas Fm	<i>Soriacebus-Carlocebus</i>
		Laventan		
		Colloncuran		
		Santacruccian		
		Colhuehuapian		
		Deseadan	Sacanana-Gaiman-Gran Barranca	cf. <i>Soriacebus</i>
			Rio Las Leñas	<i>Tremacebus-Dolichocebus</i> <i>Chilecebus</i>
23-26-	OLIGOCENE		Salla	
29-32-				<i>Branisella-Szalatavus</i>
35-				

Some characters relate them more closely to the Callitrichinae, such as triangular shape of the upper premolars and molars (ROSENBERGER *et al.*, 1991a), as well as the shape of p2 (TAKAI & ANAYA, 1996). Based on several new specimens found more recently, some authors (*i.e.*, Takai, Kay) suggested that *Szalatavus* is a synonym of *Branisella*.

CHILE

In the western Andean cordillera, south of the city of Santiago, in Chile, a remarkable primate skull was discovered in the 1990s. The taxon, *Chilecebus carrascoensis*, is 20 Ma old (Colhuehuapian SALMA; early Miocene; FLYNN *et al.* (1995) and is another odd fossil primate with a rare combination of traits. Following FLYNN *et al.*, 1995; see also FLEAGLE & TEJEDOR, 2002), *Chilecebus* may be related more closely to the Cebinae, based on the premolar morphology, which are buccolingually elongated. *Chilecebus* also has a rounded skull, small orbits, and dental arcade diverging posteriorly; the upper molars are quadrate with a well developed

hypocone; M3 is considerably reduced and has no metacone nor a hypocone, which is also characteristic or consistent with cebine morphology. Unusual characters for a cebine are the very small P2 compared with P3-4, and also the small upper canine.

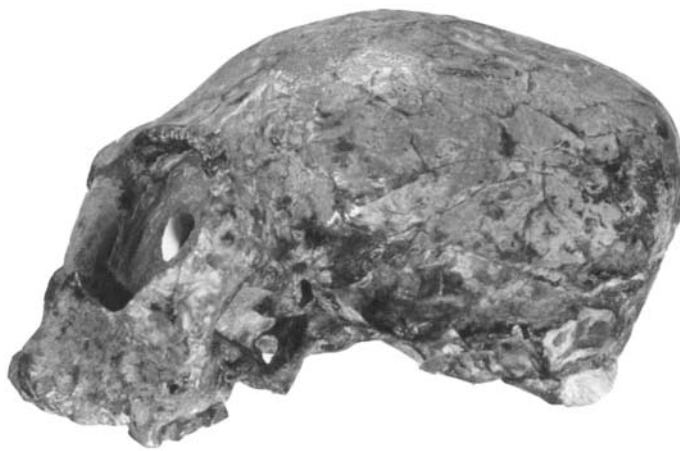
An isolated primate talus from the type locality of the "Friasian" SALMA (Middle Miocene), Alto Río Cisnes, in southern Chile, was described by TEJEDOR (2003). It shares overall similarities and locomotor adaptations with some Pinturas tali reported previously (MELDRUM, 1990).

ARGENTINA

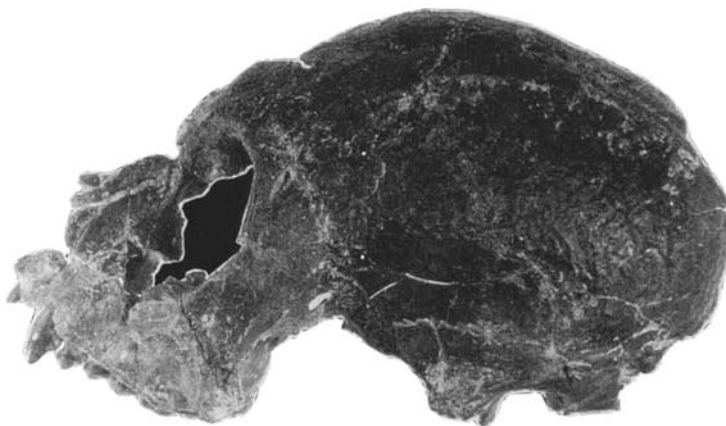
There are somewhat younger records of fossil platyrrhines in the Argentine Patagonia, coming from the provinces of Neuquén, Chubut, and Santa Cruz, with diverse and relatively abundant taxa (TEJEDOR, 2000, and references therein; FLEAGLE & TEJEDOR, 2002). The primates from Chubut Province are all of the Colhuehuapian SALMA, with an age of *ca.* 20 Ma, and come from

three classic localities: Gaiman, Sacanana, and Gran Barranca. From Gaiman, a locality in the lower valley of the Chubut river, the edentulous type skull of *Dolichocebus gaimanensis* is known since 1942, after the original description by BORDAS (1942, see also KRAGLIEVICH, 1951). This taxon is closely related to the living genus *Saimiri* (ROSENBERGER, 1979a; ROSENBERGER & FLEAGLE, 1981). The skull shows small orbits with a narrow interorbital region and long braincase, as in the living *Saimiri*, and an apparently well developed

interorbital fenestra (ROSENBERGER, 1979a; for an alternative view, see HERSHKOVITZ, 1982), also typical of *Saimiri*. Unfortunately, all of the teeth are missing but, judging from the alveolous and broken roots, it is possible to observe buccolingually broad postcanine dentition. Some isolated teeth from Gaiman have been also attributed to *Dolichocebus* (FLEAGLE & BOWN, 1983; FLEAGLE & KAY, 1989), but they are still under study. Their specific attribution to *Dolichocebus* appears difficult.



a



b

Fig.2- Lateral views of the type of *Tremacebus harringtoni* (a; courtesy of Alfred L. Rosenberger) and a partial skull of *Homunculus patagonicus* (b; courtesy of Adán Tauber).

Also from the Colhuehuapian is *Tremacebus harringtoni*, from the locality of Sacanana, in north-central Chubut Province (RUSCONI, 1935; HERSHKOVITZ, 1974). *Tremacebus* is represented by another edentulous skull that shows large orbits and a short face (Fig.2a), certainly synapomorphies shared with the living *Aotus*. The broken upper molars of *Tremacebus* do not provide much information. From the same locality, FLEAGLE & BOWN (1983) described a mandibular fragment preserving a distal p4 and complete m1 that was tentatively allocated to *Tremacebus*; however, FLEAGLE (1990) later suggested that it is most probably related to *Soriacebus ameghinorum* (see below). In a recent paper, TEJEDOR (2005a) has compared several specimens of *Soriacebus* along with the mandible from Sacanana and reached similar conclusion. The molar has a short trigonid and long and wide talonid, but poorly developed cusps and crests.

Also Colhuehuapian, but from the locality of Gran Barranca, is another mandibular fragment with p4 described as *Homunculus* sp. by HERSHKOVITZ (1984). FLEAGLE (1990) also related this mandible to *Soriacebus*, mainly because of the expanded buccal enamel. KAY *et al.* (1999) briefly reported some specimens from Gran Barranca that resemble *Soriacebus*, but they are still undescribed. However, the most significant contribution of that abstract is the age for the Colhuehuapian primates from Argentina, which was placed at around 20 Ma (KAY *et al.*, 1999).

The Pinturas Formation (BOWN & LARRIESTRA, 1990), in the northwest of Santa Cruz Province, has yielded a relatively abundant and moderately diverse collection of early Santacrucian primates. This material has the potential to contribute to the phylogeny of platyrrhine primates in Patagonia because it includes representatives of early stages in the evolution of some clades. Early researchers (AMEGHINO, 1906) as well as more recent ones (DE BARRIO *et al.*, 1984) observed several faunistic differences between the taxa from Pinturas and others from the typical Santa Cruz Formation, which comes from the Atlantic coast of the homonymous province. They concluded that the former was a little more primitive. Actually, FLEAGLE *et al.*, (1995) have determined an age of *ca.* 17 Ma for the Pinturas fauna, thus being early Santacrucian, compared with the younger Santa Cruz Fm, dated in about 16.4 Ma (FLEAGLE *et al.*, 1995; TEJEDOR *et al.*, in press). Four species included in two genera have been described so far for Pinturas. *Soriacebus ameghinorum* and *S. adrianae* (FLEAGLE *et al.*, 1987; FLEAGLE, 1990; FLEAGLE & TEJEDOR, 2002; TEJEDOR, 2005a; 2005b) are early representatives of the tribe Pitheciini, subfamily Pitheciinae (from now on pitheciins and pitheciines, respectively), characterized by having a derived anterior dentition with procumbent and styliform incisors, and big and projecting canines that resemble those of living pitheciins; also, the p2 is huge and projecting. This morphology was probably an adaptation as a hard seed predator, as in living pitheciins (KINZEY, 1992; ROSENBERGER, 1992). However, the posterior dentition has some autapomorphies that has generated controversy (KAY, 1990; ROSENBERGER *et al.*, 1990; TEJEDOR, 2000). Unlike modern pitheciins, *Soriacebus* lower molars are elongated with well developed trigonids, and the upper molars present a relatively small hypocone with a well developed talon. However, the presence of a well developed talon in upper molars and the anterolingual cingulum pattern are clearly pitheciin features (TEJEDOR, 2000). In addition, as in pitheciines, the entire ramus of the mandible of *Soriacebus* deepens posteriorly. The derived condition of the anterior dentition is clearly similar not only to living pitheciines, but also to the slightly younger Pinturas species, *S. adrianae* (Figs.3a, b), and to the even younger *Proteropithecina*, *Cebupithecina* and *Nuciraptor* (see below), all of which show a large suite of derived pitheciin features which reinforce the relationships of *Soriacebus*.

Other Pinturas species are *Carlocebus carmenensis*

(Fig.3d) and *C. intermedius* (FLEAGLE, 1990; FLEAGLE & TEJEDOR, 2002). These are probably more closely related to *Homunculus* or the living *Callicebus*; however, several specimens tentatively attributed to *Carlocebus* are certainly different in morphology (FLEAGLE, 1990), and thus may be allocated to a different species (TEJEDOR, 2000). The dental proportions of *Carlocebus* differ from *Soriacebus* basically in having small anterior dentition and large, quadrate molars with wide basins and more prominent cusps. *Carlocebus* has a large hypocone in the upper molars and strong lingual cingulum, features considered to be primitive for platyrrhines (TEJEDOR, 2000). The p4 of *Carlocebus* is molariform, and P4 surprisingly has a hypocone, whose phyletic significance remains controversial (KAY, 1990; TEJEDOR, 2000). Adding to the dental, maxillary and mandibular material, several postcranial remains are preserved, all suggesting quadrupedal or climbing locomotor adaptations (ANAPOL & FLEAGLE, 1988; MELDRUM, 1990; STEVENS & FLEAGLE, 1998).

Several isolated canines from Pinturas suggest the presence of additional primate taxa (TEJEDOR, 2002), representing at least one small and one large morph, the latter closely similar to the living *Alouatta*. Moreover, a recently discovered mandibular fragment may represent either a different species of *Soriacebus* or a morphological variant within the species *S. ameghinorum* (Fig.3c) (TEJEDOR, 2005b), since the lower molars are not as elongate and the talonid is broader than in described species of the genus. Thus, the diversity of fossil primates in the Pinturas Formation appears the second richest in all of South America, after the La Venta of Colombia (see below).

Also in Santa Cruz Province, the Santa Cruz Formation has produced fossil primates since the time of the Ameghino's brothers. *Homunculus patagonicus* is the oldest fossil primate found in Argentina (AMEGHINO, 1891) and the second discovered in South America, following LUND's (1840) description of *Protopithecus* from a Pleistocene cave in Brazil. All the *Homunculus* specimens were found along the Atlantic coast of southeastern Santa Cruz, south of the town of Piedrabuena through the city of Río Gallegos (AMEGHINO, 1891, 1906; BLUNTSCHLI, 1931; FLEAGLE *et al.*, 1988; TAUBER, 1991; TEJEDOR, 1996, 2000; KAY *et al.*, 2005). *Homunculus* is the best known Argentine fossil primate, and is represented by partial skulls, teeth, mandibles, and postcranial bones.

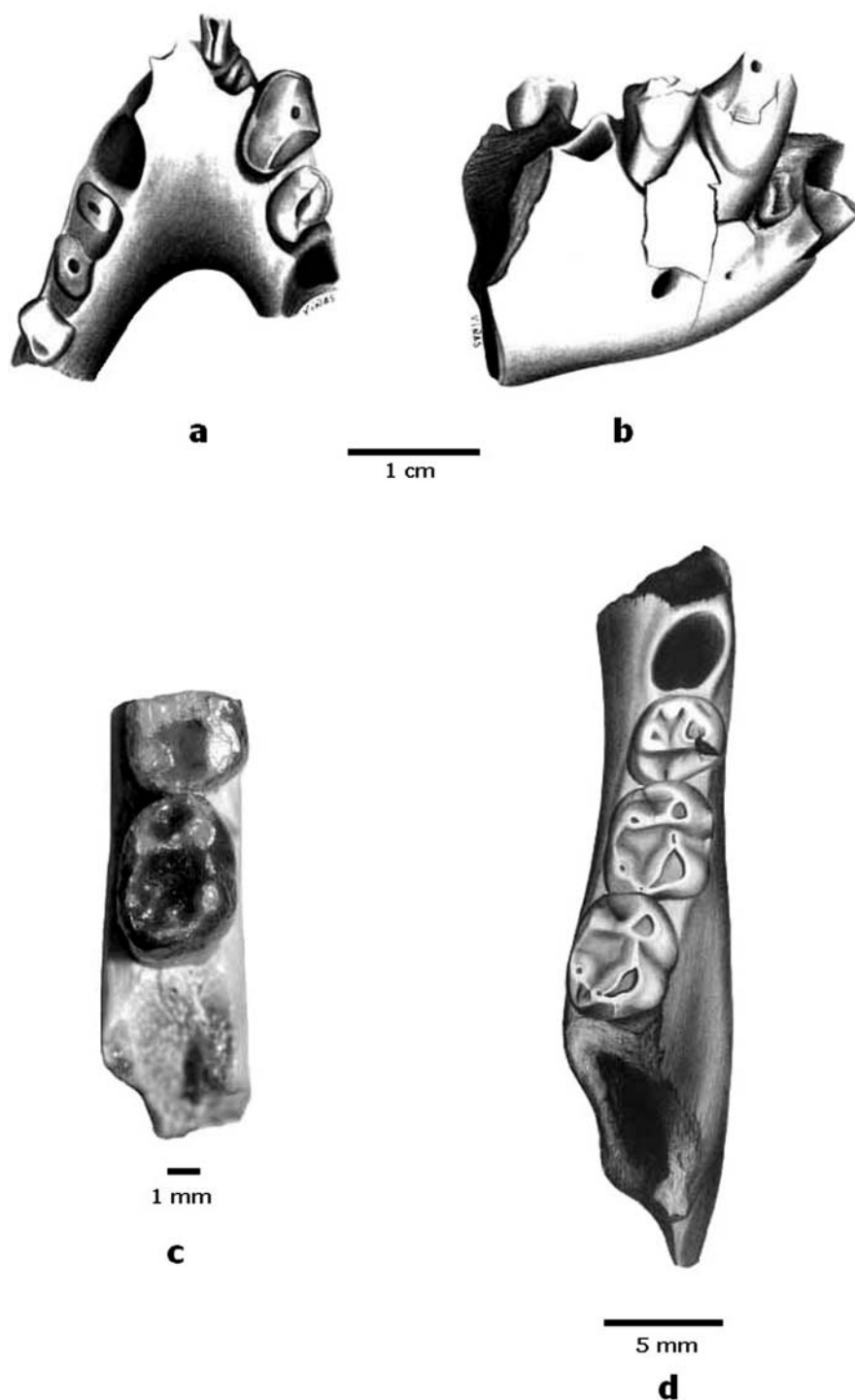


Fig.3- Occlusal (a) and buccal view (b) of *Soriacebus adrianae* (MPM-PV 1605, modified from TEJEDOR, 2005a). Occlusal views of, *Soriacebus cf. ameghinorum*, MPM-PV 36 (c), and MACN-SC 266, holotype of *Carlocebus carmenensis* (d).

The dentition appears also primitive in several characters, such as broad molars with well developed hypocone and lingual cingulum, relatively small anterior teeth, and moderately developed canines. It is similar in general aspects to *Carlocebus*, but the latter has lower and more bunoid cusps, as well as less sharp crests (FLEAGLE, 1990; TEJEDOR, 2000). The skull of *Homunculus* has moderate-sized orbits, a relatively low frontal bone, and a well developed interorbitum. As for *Carlocebus*, the postcranium exhibits adaptations for climbing and quadrupedal habits.

There is a remarkable new partial skull, the new genus and species *Killikaike blakei* (Fig.4), from the coastal Santa Cruz Formation, near Rio Gallegos, that shows strong affinities with cebines and which figures as the southernmost fossil platyrrhine ever described (TEJEDOR *et al.*, 2006). It is the first fossil platyrrhine that preserves the entire face undistorted and an unworn, little damaged dentition that is the best anatomical evidence of the maxillary teeth of any Santacrucian fossil monkey, also providing the first relatively complete and undistorted evidence of the anterior braincase of a fossil platyrrhine. A second maxillary specimen provides additional information on the upper molar morphology. This new taxon lacks diagnostic derived characteristics of the lower face and premolar dentition that are shared by modern



Fig.4- Frontal view of the type of *Killikaike blakei* (MPM-PV 5000).

cebines, but its strongly vaulted frontal bone and capacious anterior cranial fossa indicate the early evolution of an enlarged forebrain.

In the northwest of Patagonia, the Province of Neuquén has yielded a poorly represented fossil pitheciin, *Proteropithecium neuquenensis* (KAY *et al.*, 1998, see also PARDIÑAS, 1991). It is known only by 15 isolated teeth and a talus. However, the interrelationships of this fossil can be firmly established. It has lower incisors that are compressed and procumbent as in pitheciins, and lower molars with low crown relief, shallow basins and crenulated enamel, also as expected for pitheciins. The talus shows overall resemblances to *Callicebus*.

COLOMBIA

An important region where a diverse fauna of middle Miocene primates was found is La Venta, in the valley of the Magdalena River, Colombia. The work at La Venta began in the 1940s, when several primate species were found by Stirton and co-workers (STIRTON, 1951). These first Laventan

primates were *Cebupithecium sarmientoi*, *Neosaimiri fieldsi* and *Stirtonia tatacoensis*, originally described as "*Homunculus*" *tatacoensis*, then properly reassessed as a new genus by HERSHKOVITZ (1970). *Cebupithecium* is one of the most complete fossil platyrrhines ever found (STIRTON, 1951) and is undoubtedly linked with pitheciins. The type is a partial skeleton represented by rather complete hindlimbs and forelimbs, vertebrae, tail and pelvic girdle, and a mandible and maxilla with several teeth. The dentition is clearly synapomorphic with the living pitheciins, displaying procumbent upper incisors, huge and projecting canines that are triangular in cross-section, and quadrate molars with poorly developed cusps and crests.

Neosaimiri fieldsi is an undoubtedly squirrel-monkey fossil relative. It is represented by mandibles and abundant isolated teeth (STIRTON, 1951; TAKAI, 1994) that shows strong affinities with *Saimiri*; some authors have also proposed that it differs from *Saimiri* only at the species level (ROSENBERGER *et al.*, 1991b). However, the upper incisors of *Neosaimiri* are slightly smaller, the upper P4 shows a hypocone and the upper molars are trapezoidal in outline, with a moderate hypocone and well developed crests, and M3 is the smallest molar, a synapomorphy shared with *Saimiri* and *Cebus*. The lower molars develop a buccal cingulum. Postcranial elements of *Neosaimiri* shares similarities with *Saimiri*, *Saguinus* and *Aotus* (MELDRUM *et al.*, 1990, NAKATSUKASA *et al.*, 1997).

Laventiana annectens is a closely related taxon represented by a rather complete mandible and a talus (ROSENBERGER *et al.*, 1991c), very similar to *Saimiri* and *Neosaimiri* in general morphology and size. A buccal cingulid is present in the molars, and also an autapomorphic distinct post-entoconid notch.

Nuciruptor rubricae is another pitheciin primate, represented by a right mandibular corpus with well preserved teeth (MELDRUM & KAY, 1997). The lower incisors clearly show the pitheciin pattern, as in *Cebupithecium*, but the canine and premolars are distinct. The canine is moderately developed by comparison and the premolars do not show a molarized p4; instead, the talonid is short. Although presenting primitive features such as well developed cusps and crests, the molars display distinctive pitheciin morphology.

Mohanamico hershkovitzi (LUCHTERHAND *et al.*, 1986) is represented by a mandible and is most probably related to *Callimico* (ROSENBERGER *et al.*, 1990),

although pitheciin affinities have been also proposed (KAY, 1990). It has relatively high-crowned incisors, a tall canine, large p2, and molars with broad trigonids, moderate talonids and moderate crown relief.

Aotus dindensis is placed among the species of the living genus *Aotus* (SETOGUCHI & ROSENBERGER, 1987) and it is represented by a mandible, a maxillary fragment and an isolated talus. Despite the presence of smaller incisors and less elevated premolar trigonids, the general molar morphology is basically identical to the living species. The talus was referred to *A. dindensis* on the basis of some characters seen in the living *Aotus* and *Callicebus* (GEBO *et al.*, 1990). More recently, TAKAI *et al.* (2001) mentioned a maxillary fragment with P4-M1 of an *Aotus*-like taxon from La Venta, with a general morphology indistinguishable from the living *Aotus*.

Patasola magdalenae is a small callitrichine-like primate known by a right mandible with all molars and the deciduous premolars (KAY & MELDRUM, 1997). Lower molars are narrow but still lack the trigonid enlargement seen in callitrichines. However, it has a third molar, which is slightly smaller than that of *Callimico*.

Another callitrichine from La Venta is *Micodon kyotensis* (SETOGUCHI & ROSENBERGER, 1985), represented by an upper molar tentatively referred to as an M1. There is not much to say about this taxon since it is so poorly represented. The morphology suggests callitrichine affinities especially with reference to its small size, and reduced hypocone and lingual cingulum.

Lagonimico conclucatus is a flattened skull described originally as a giant callitrichine (KAY, 1994) that preserves most of the dentition. *Lagonimico* is larger than any known callitrichine, about the size of *Callicebus*. Among the characters that supposedly link it to marmosets and tamarins are the lack of a hypocone in the upper first and second molars, a very small M3/m3, and wasted upper premolars. However, it has also been suggested that *Lagonimico* is related to pitheciines because of its deep mandible with a flaring gonial region, as in all pitheciines, and also because of the shape of its ascending ramus, which resembles *Callicebus* and *Aotus* (ROSENBERGER, 2002).

Miocallicebus villaviejai is the most recently described primate from La Venta (TAKAI *et al.*, 2001). It has preserved a piece of maxilla with root of M1, damaged M2, and broken M3. Takai suggests it is

closely related to the living *Callicebus*, a homunculin taxon of the Pitheciinae clade. Due to the heavy wear, the crown morphology is not clear but the large hypocone and quadrate molar outline resembles that of *Callicebus*.

Stirtonia tatacoensis and *S. victoriae* (STIRTON, 1951; HERSHKOVITZ, 1970; KAY *et al.*, 1987) are closely comparable in size and dental morphology to the living *Alouatta*. This genus is well known by dental, mandibular and maxillary material, including large molars with tall cusps and sharp crests, prominent buccal cingulum and reduced lingual cingulum in upper molars, a long cristid obliqua, a high and relatively small trigonid in the lower molars, and broad talonids with well developed talonid basin. In general, these characters strongly resemble those of living species of *Alouatta*, thus the generic status of *Stirtonia* - which has already been questioned (DELSON & ROSENBERGER, 1980) - ought to be re-examined.

RÍO ACRE

The Solimões Formation, in the border between Brasil, Perú and Bolivia, has preserved a late Miocene fauna of Huayquerian SALMA (late Miocene, ca. 9-6 Ma), including some isolated primate teeth (KAY & FRAILEY, 1993). The Solimões Fm represents a geologic time with no record of primates in South America, about 12 Ma since the middle Miocene of La Venta through the Pleistocene of Brazil and Caribbean (see below). Two molars were collected at the Bolivian margin of the Acre River. One isolated lower molar has been tentatively assigned to *Stirtonia* sp., for its similarity in crown morphology and size to *Stirtonia tatacoensis*, with the well developed crests that are also seen in the living *Alouatta* species (KAY & FRAILEY, 1993). Another primate from Solimões is an upper molar of a large cebine (KAY & FRAILEY, 1993) that has been named recently as *Acrecebus fraileyi* by KAY & COZZUOL (2006), having inflated cusps, a large hypocone and a metaconule, thus resembling *Cebus* in many aspects. In the same paper, KAY & COZZUOL (2006) described an additional taxon, *Solimoea acensis*, from the Acre river in Brazil, based on an isolated lower molar and a maxillary fragment with P3-4 that they included in their ateline subfamily (Tribe Atelini for the present work), this is the clade formed by *Ateles*, *Lagothrix* and *Brachyteles*, basically because they interpret that the specimens have moderate shearing crests. The authors allocated the two specimens into *Solimoea* based on some dental traits and because they were

found in the same locality. However, the upper premolars are heavily worn and do not allow to predict confidently the morphology, thus leaving some doubts on their generic status.

BRAZIL

Although published later, *Protopithecus brasiliensis* was found by Lund in 1836 inside a Pleistocene cave from the state of Minas Gerais (LUND, 1840). Thus, *Protopithecus* is not only the first fossil primate discovered in South America but also the first in the world. In addition to the partial femur and humerus that Lund discovered in the XIXth century, a skull and mandible along with several postcranial bones were discovered by Cástor Cartelle in the early 1990s in late Pleistocene cave deposits of Toca da Boa Vista, state of Bahia (HARTWIG & CARTELLE, 1996).

Although presenting a mix of traits, *Protopithecus* does display several derived characters shared by all atelines. The skull, which shows some similarities to *Alouatta* (HARTWIG & CARTELLE, 1996), also lacks of the usual specializations for folivory found in the dentition of Howler monkeys. The postcranium is apparently more similar to atelins (*Ateles*, *Lagothrix*, *Brachyteles*), with traits that characterize brachiating locomotor adaptations (HARTWIG & CARTELLE, 1996). However, the postcranium is also much more robust than in other atelines. This is related to the fact that the estimated body weight of *Protopithecus* is about 25kg (HARTWIG, 1995), much larger than the largest living platyrrhines, weighting about 12kg (FLEAGLE, 1999).

Caipora bambuorum is another "giant" primate genus from Toca da Boa Vista, Bahia, represented by a nearly complete skeleton (CARTELLE & HARTWIG, 1996). It is also considerably larger than *Brachyteles*, weighing around 20kg. *Caipora* is more similar to *Ateles* in cranial morphology, with a large, rounded braincase. Its molars are quadrate, bunoid and have low cusp relief. As with *Protopithecus*, the postcranium is generally similar to atelins and exhibits brachiating locomotor adaptations.

Another extinct primate appeared in a Pleistocene cave of Bahia; it is a new species of the living *Alouatta* (TEJEDOR *et al.*, in press) with most major traits undoubtedly demonstrating a relationship to the Howler monkeys.

GREATER ANTILLES

In Cuba, Jamaica, Dominican Republic, and Haiti, several fossil primate remains of controversial

affinities have been found. A remarkable example is *Xenothrix macgregori*, from the late Pleistocene of Jamaica (WILLIAMS & KOOPMAN, 1952; ROSENBERGER, 1977; MACPHEE & FLEAGLE, 1991), a primate that lacks the third molars, among other unusual features. On the basis of several traits of the type mandible, the pitheciine status of *Xenothrix*, as a member of a subclade possibly linked with *Callicebus* and *Aotus*, was proposed years ago by ROSENBERGER (1977). HOROVITZ & MACPHEE (*e.g.*, 1999; MACPHEE & HOROVITZ, 2004) have proposed that *Xenothrix* is part of a unique clade of pitheciines that is more closely related to *Callicebus*. The type mandible has a very deep corpus and preserved m1-2 of bunoid aspect, long and broad with low cusp relief and enamel crenulation. A more recently discovered partial face, with flat P4-M2 on both sides (HOROVITZ & MACPHEE, 1999; MACPHEE & HOROVITZ, 2004), shows pitheciin traits such as expanded trigon/talon basins and poorly developed crown relief. Its morphology suggested to ROSENBERGER (2002) the possibility of closer affinities with genus *Aotus*, a proposal challenged by MACPHEE & HOROVITZ (2004). Another remarkable but non-pitheciin character of *Xenothrix* is the small canine and second premolar in both jaws, evidenced by the small roots. However, moderate canine and p2 characterize the homunculins.

Antillothrix bernensis was originally described as "*Saimiri*" *bernensis* by RÍMOLI (1977), later renamed by MACPHEE *et al.* (1995). The type is a partial maxilla with P4-M2, and other material include a lower m1 in a mandibular fragment, and a distal tibia found in the southeast of Dominican Republic, Hispaniola. The estimated age is 3850 ± 150 rcybrp, thus being late Holocene. Although the affinities with *Saimiri* have been debated, the upper molars resemble at least cebines in its buccolingually broad P4 – a key synapomorphy of cebines – expanded bucal side of M1-2, reduced cingulum and reduced M2 with the hypocone almost absent. To the contrary, based on four unambiguous characters of the skull and canine, MACPHEE *et al.* (1995) and HOROVITZ & MACPHEE (1999) suggested a sister group relationship between *Antillothrix* and *Paralouatta* (see below). As noted above, they hypothesize that *Antillothrix* forms a monophyletic clade along with *Xenothrix*, and that this clade also includes *Callicebus*. However, the dental morphology evidence supports a phylogenetic link with cebines.

Paralouatta varonai was described from a well preserved skull with a damaged dentition and a good part of the face (RIVERO DE LA CALLE & ARREDONDO, 1991). Later, a mandible and isolated teeth were found and

described (HOROVITZ & MACPHEE, 1999). This material came from the Pleistocene (probably early?) of Cuba. The face appears projecting upward, as in *Alouatta*; the braincase is long and low, relatively large with strong temporal and nuchal crests, and large orbits, a set of characters strongly resembling *Alouatta*. But the dentition exhibits several strong differences; the canine is very small, and the cheek teeth are not large and crested like *Alouatta*. While as mentioned above, some associate *Paralouatta* with pitheciines, along with *Xenothrix*, *Antillothrix*, and *Callicebus* (MACPHEE *et al.*, 1995; HOROVITZ, 1999; HOROVITZ & MACPHEE, 1999), several cranial and dental novelties of *Paralouatta* are shared with the howlers, indicating they are cladistically related.

Adding to the above mentioned three taxa of Caribbean platyrrhines, there are other records of importance, such as an astragalus from the early Middle Miocene of Cuba (MACPHEE & ITURRALDE-VINENT, 1995), the oldest platyrrhine recorded until now in the Greater Antilles as well as in the northern Neotropical Region. This talus appears similar to one broken talus assigned to *Paralouatta*, and has been named as the new species *Paralouatta marianae* (MACPHEE *et al.*, 2003). “*Montaneia anthropomorpha*” (AMEGHINO, 1910, later renamed *Ateles anthropomorphus* (ARREDONDO & VARONA, 1983), is an

upper dentition currently thought to pertain to the living species *Ateles fusciceps* (MACPHEE & RIVERO DE LA CALLE, 1996). A tibia from Hispaniola with uncertain taxonomic affinities has been related morphologically to callitrichines, but it approached the size of a *Cebus* (FORD, 1986). Two femora from Jamaica (FORD & MORGAN, 1986; HERSHKOVITZ, 1988) are similar to each other in size and morphology and could be attributable to *Xenothrix* (see MACPHEE & HOROVITZ, 2002), while a third femur is rather unusual (MACPHEE & FLEAGLE, 1991). Finally, several materials from Haitian caves have been mentioned by FORD (1990) but remain undescribed.

DISCUSSION AND CONCLUSION

Before considering particular questions, the systematics of much of the above is summarized here, in the form of a classification. This classification of platyrrhines includes all known living and fossil genera. These taxa are the evidence of a very small part of a history of more than 26 Ma of evolution in South America and the Antilles. An impressive number of genera – twenty four, and twenty eight species, of extinct platyrrhines are described at the present time, as compared with 16 living genera.

Infraorden Platyrrhini E. Geoffroy, 1812

Superfamily Ateloidea Gray, 1825 (Rosenberger, Setoguchi & Shigehara, 1990)

Family Atelidae Gray, 1825

Subfamily Atelinae Gray, 1825 (Pocock, 1925)

Tribe Atelini Gray, 1825 (Szalay & Delson, 1979)

Ateles E. Geoffroy, 1806

Lagothrix E. Geoffroy, 1812

Brachyteles Spix, 1831

†*Protopithecus brasiliensis* Lund, 1838

†*Caipora bambuorum* Cartelle & Hartwig, 1996

Tribe Alouattini Trouessart, 1897 (Szalay & Delson, 1979)

Alouatta Lacépède, 1799

†*Stirtonia* Hershkovitz, 1970

†*Alouatta* sp. nov. (Tejedor, Rosenberger & Cartelle, MS accepted)

Subfamily ?Atelinae

Tribe Aotini Poche, 1908 (Tejedor, 2000)

Aotus Illiger, 1811

†*Tremacebus* Hershkovitz, 1974

†*Aotus dindensis* Setoguchi & Rosenberger, 1987

Subfamily Pitheciinae Gray, 1849 (Mivart, 1865)

Tribe Pitheciini Gray, 1849

Pithecia Desmarest, 1820

Chiropotes Lesson, 1840

Cacajao Lesson, 1840

- † *Cebupithecia* Stirton & Savage, 1951
- † *Soriacebus* Fleagle, Powers, Conroy & Watters, 1987
- † *Nuciraptor* Meldrum & Kay, 1997
- † *Proteropithecia* Kay, Johnson & Meldrum, 1998
- Tribe Homunculini Ameghino, 1894 (Rosenberger, Setoguchi & Shigehara, 1990)
 - Callicebus* Thomas, 1903
 - † *Homunculus* Ameghino, 1891
 - † *Carlocebus* Fleagle, 1990
 - † *Miocallicebus* Takai, Anaya, Suzuki, Shigehara & Setoguchi, 2001
- Tribe indet.
 - † *Xenothrix* Williams & Koopman, 1952
- Subfamily ?Pitheciinae
 - † *Lagonimico* Kay, 1994
- Subfamily *incertae sedis*
 - † *Antillothrix* Rimoli, 1977 (Mac Phee, Horovitz, Arredondo & Jimenez-Vasquez, 1995)
- Family Cebidae Bonaparte, 1831
 - Subfamily Callitrichinae Thomas, 1903 (Cabrera, 1958)
 - Callithrix* Erxleben, 1777
 - Cebuella* Gray, 1886
 - Saguinus* Hoffmannsegg, 1807
 - Leontopithecus* Lesson, 1840
 - Callimico* Thomas, 1913
 - † *Micodon* Setoguchi & Rosenberger, 1985
 - † *Patasola* Kay & Meldrum, 1997
 - † *Mohanamico* Luchterhand, Kay & Madden, 1986
 - Subfamily *incertae sedis*
 - † *Branisella* Hoffstetter, 1969
 - † *Szalatavus* Rosenberger *et al.*, 1991
 - † *Chilecebus* Flynn, Wyss, Charrier & Swisher III, 1995
 - Subfamily Cebinae Bonaparte, 1831 (Mivart, 1865)
 - Cebus* Erxleben, 1777
 - Saimiri* Voigt, 1831
 - † *Dolichocebus* Kraglievich, 1951
 - † *Laventiana* Rosenberger, Setoguchi & Hartwig, 1991
 - † *Neosaimiri* Stirton, 1951
 - † *Killikaike blakei* Tejedor, Tauber, Rosenberger, Swisher & Palacios, 2006

THE OLDEST, THE RAREST

The oldest platyrrhines, *Branisella* and *Szalatavus*, of late Oligocene age, are still controversial. However, their closest affinities appear to be with the cebids, though probably not with either cebines or callitrichine but with another extinct subfamily. A similar case is *Chilecebus*, the younger Colhuehuapian skull from Chile, a taxon especially difficult to understand. *Chilecebus* shows the rare combination of a small but long braincase with large teeth. But the upper premolars are clearly broad, a strong synapomorphy undoubtedly shared with the cebines, as well as a small M3 relative to the other molars. However, unlike cebines,

Chilecebus has large quadrate molars with a prominent hypocone; also, the interorbitum appears wider than in a cebine pattern. The early radiation of cebines appears to have been a complex event, and the scarcity of fossil cebids does not help our understanding of their phylogeny. But it is clear that other clades are involved in their diversification.

AUSTRAL PLATYRRHINES

Patagonia has preserved an important record from the early stages of platyrrhine evolution. The Colhuehuapian primates, *Dolichocebus* and *Tremacebus*, are ancient relatives of *Saimiri* and

Aotus, respectively (ROSENBERGER, 1979b; ROSENBERGER & FLEAGLE, 1981). *Dolichocebus* is the oldest cebine known thus far, and *Tremacebus* is the oldest aotini. If it is confirmed that the Aotini are atelines, as suggested by TEJEDOR (2001), thus the early Miocene *Tremacebus* would be the oldest record of the whole Subfamily Atelinae.

The Santacrucian Pinturas primates display an interesting diversity of ancient models of modern patterns. The most remarkable story is the status of *Soriacebus*, certainly the oldest pitheciin known to date. The anterior dentition and mandibular morphology of *Soriacebus* strongly support this hypothesis, and the more recently described *Protopithecina*, from the younger Colloncuran, reinforces the fact that there was a major pitheciin radiation in Patagonia. *Carlocebus*, as a possible homunculin, is probably related to another Santacrucian monkey, *Homunculus*, coming from a different formation but close in age. Homunculins are generalized, morphologically more primitive representatives of the Pitheciinae, and in this sense they are also the oldest. In addition, as FLEAGLE (1990) pointed out, some material from Pinturas pertain to a bigger monkey, morphologically different from *Carlocebus*, whose affinities are currently under study. And TEJEDOR (2002), on the basis of isolated canines has commented on the possible existence of alouattins in Pinturas, as well as a morph even smaller than *S. adrianae*. Finally, *Killikaike blakei*, the new cebine genus is another example of the diverse and still poorly known radiation in Patagonia (TEJEDOR *et al.*, 2006). In summary, during the early to middle Miocene, Patagonia was the geographic reservoir for pitheciines, pitheciins, aotins, and cebines, four major clades that still survive, as well as possibly alouattins.

LAVENTAN PLATYRRHINES

This middle Miocene rich fossiliferous area is, along with Patagonia, one of the two most important regions for fossil platyrrhines. Two additional pitheciin taxa are present there, *Cebupithecina* and *Nuciruptor*, both with more advanced characters than their Patagonian counterparts, relative to the moderns. *Lagonimico* has been allied either to pitheciines of an indeterminate tribe, basically on the basis of its mandibular morphology (ROSENBERGER, 2002), and to callitrichines, based on the dental morphology (KAY, 1994). Abundant remains of *Saimiri*-like cebines are also present in

La Venta, *Neosaimiri* and *Laurentiana*, both with a general morphology and size very close to living *Saimiri*. The three taxa attributed to callitrichines, *Mohanamico*, *Micodon*, and *Patasola*, none of which are convincing beyond a doubt, have several characters non-typical for that subfamily, but their closest affinities are more likely to be with callitrichines than any other clade. The complex callitrichine radiation in La Venta appeared transitional to more modern lineages (HARTWIG & MELDRUM, 2002).

Among the callitrichine's sister clade, the cebines, *saimiri*ins are quite distinct but there is no trace of the *Cebus* lineage. One may speculate that the more typical callitrichines appeared later in the evolutionary history of cebids, and if all these rare forms (*i.e.*, *Patasola*, *Micodon*, *Mohanamico*) should be considered true callitrichines of cebids indet., or if the lack of typical callitrichines is due to sampling error. Aotins are also present in La Venta, represented by *Aotus dindensis*, which is almost identical to the living species of *Aotus*, thus exemplifying the old branching, conservative morphology, and independent evolution of aotins. Finally, *Stirtonia* is a witness of another old lineage, the howler monkeys. There is no question about the relationships between *Stirtonia* and *Alouatta*, and probably a deeper analysis may demonstrate that they are congeneric.

GIANTS FROM BRAZIL

Protopithecus and *Caipora* are outstanding examples of the complex ateline radiation, and the only two possible atelins (Tribe Atelini) discovered thus far, although the status of *Protopithecus* is still under debate (see also GUEDES & SALLES, 2005). These two giant atelines are filling the latest part of what should have been a long ateline history - virtually unknown - during the Tertiary. As noted by MACPHEE & HOROVITZ (2002), *Protopithecus* and *Caipora* may have been part of the megafauna that became extinct in the late Pleistocene, while other primates associated in the same sites still survive. This means there is probably a large taxonomic gap between the relatively abundant and widespread platyrrhines between the early-middle Miocene and the late Pleistocene that hides much of the information we need to understand the modern radiations. The large-bodied platyrrhines today, subfamily Atelinae, are widely distributed and have a broad adaptive spectrum, but there are no traces of larger ancestors or ancient relatives except for the odd *Caipora* and *Protopithecus*.

FROM THE ISLANDS

If one must choose non-typical platyrrhines, the Antillean genera are outstanding examples. *Paralouatta* resembles *Alouatta* in several aspects, but has very unusual teeth, unusual even compared with all other platyrrhines. *Xenothrix* is very odd, not only because it lacks the third molars, but also for its strange dental morphology, having small p2/P2, a very small canine that may have been functionally incisiform. Apparently, the alveolous for the upper central incisors are enlarged relative to the lateral ones and there is a large intralveolar distance between both I1s, as observed by ROSENBERGER (2002; but see MACPHEE & HOROVITZ, 2004). Also, the orbit appears to be large and preserve the inferior orbital fissure, another argument used by ROSENBERGER (2002) to relate *Xenothrix* with *Aotus*. The P4 and upper molars of *Xenothrix* are certainly related to pitheciins, due to the expanded talon and low occlusal relief with weak crests; P4 has the crest connecting paracone and protocone that divides the tooth in two closely symmetrical parts. This pattern of P4 is not shared by any platyrrhines other than the living pitheciins. The lesson from this rare Antillean primate is that the pitheciins (and the pitheciines as a whole) had a diverse radiation with several "mosaic" patterns. For example, *Xenothrix* differs from pitheciins by having a proportionally smaller anterior dentition, especially a small second premolar and canine, the reverse condition seen in pitheciins.

Antillothrix could be considered as a cebine mainly because of the especially strong synapomorphy of highly transverse P4. The remaining traits (*i.e.*, hypocone reduction and structure, shape of the lingual cingulum, M2 reduction) suggesting cebine affinities may be secondarily important.

And the third case, *Paralouatta varonai*, is the last but best example of oddity among the Caribbean primates. It combines a rather normal, albeit primitive, Howler monkey skull with unusual cheek teeth and very small canines. But, after all, the most readily interpretable traits are in the skull, and they spell Howler.

QUESTIONS TO BE ANSWERED...

As final thoughts based on the descriptions and discussions above, I close with several sets of questions:

a) LESS KNOWN FOSSIL RECORD

- Callitrichinae: origin, radiation, and phylogenetic

status. If the Deseadan primates from Bolivia are callitrichines, then the ancestral morphotype we are searching for probably didn't exhibit the expected pattern. Laventan callitrichines are rather unusual and do not contribute to clarify their phylogenetic relationships at all.

- *Cebus lineage*: lack of fossils, virtually unknown; origin of thick enamel and big brain. There is no fossil record of *Cebus*-like platyrrhines anywhere in the Neotropics. The only related specimen is the upper molar from Río Acre. However, the origin of the extreme bunodonty and thick enamel of the living *Cebus* is unknown, as well as its branching from the sister taxon *Saimiri*.
- *Ateles, Lagothrix, Brachyteles*: oldest radiation?, origin?, significance of the Brazilian giants?: The tribe Atelini has no representatives in the fossil record excepting for *Caipora* and, possibly, *Protopithecus*. Even when all atelines are large-bodied, there are no traces of their ancestral morphotypes. The Tertiary had no relatives of the living *Ateles, Lagothrix, and Brachyteles*.

b) CARIBBEAN RADIATION

- Why is *Xenothrix* so unique? Although its pitheciine affinities are convincing, the origin and adaptive significance of its dental adaptations are confusing.
- Combination of alouattin skull and rare teeth in *Paralouatta*. Following the unusual Caribbean radiation, *Paralouatta* combines rare teeth with an almost typical Howler monkey skull, possibly indicating a long and relatively independent evolution that remains unexplained.
- Examples of island endemisms? This is one of the most probable hypotheses to explain the particular adaptations of all the Caribbean primates, only speculative for now.
- Where do these monkeys come from? The presence of a middle Miocene primate talus in Cuba led us to speculate if the platyrrhines originated first in South America and moved to the Caribbean to undertake such an odd radiation. If so, we should investigate the Caribbean platyrrhines in a different way taking into account a history of an early branching about 17 million years ago.

c) THE MOST CONTROVERSIAL TAXON AMONG PLATYRRHINES, THE *AOTUS* LINEAGE:

- Pitheciine (Rosenberger, 1979b), cebid (Schneider *et al.*, 1996; Horovitz, 1999), ateline (Tejedor, 2000, 2001), something else? Present in the middle Miocene of La Venta, and older relative in the early Miocene of Argentina, *Aotus* is the last

systematic problem among platyrrhines due to its jumping position in the taxonomy. The recent evidences, both morphological and molecular, are far from resolve the controversies.

ACKNOWLEDGEMENTS

For inviting me to participate in the symposium on Gondwanan Mammals as part of the II Congreso Latino-Americano de Paleontología de Vertebrados, I thank Lilian Bergqvist and Marcelo Reguero. Fieldworks in Patagonia from 2000 through 2005 were supported by research grants from the L.S.B. Leakey Foundation to the author.

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