A New Platyrrhine from the Middle Miocene of La Venta, Colombia, and the Phyletic Position of Callicebinae

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Abstract A new platyrrhine, *Miocallicebus villaviejai* gen. et sp. nov., from the middle Miocene of La Venta (Colombia) is described. The specimen consists of a right maxillary fragment preserving a root of M¹, a complete M², and a fragmentary M³. *Miocallicebus* is included in the Callicebinae on the basis of M² structure, but it differs from extant *Callicebus* in its much larger size and the position of the pterygoid process. Morphological analysis of M² structure suggests that the Callicebinae are more closely related to the pitheciinae than to other platyrrhine taxa, supporting the phylogenetic reconstruction proposed by recent molecular biological studies. The *Callicebus*-lineage is likely to have appeared by the middle Miocene age in the La Venta fauna.

Keywords: *Miocallicebus villaviejai*, Callicebinae, Platyrrhini, Colombia, Middle Miocene

Introduction

Since the 1940s many platyrrhine fossils have been recovered from the middle Miocene sediments of La Venta, the Tatacoa desert, *Southern Colombia* (Fig. 1): *Stirtonia tatacoensis* (including “*Kondous*”; Stirton, 1951; HersHKovitz, 1970; Setoguchi et al., 1981) and *S. victoriae* (Kay et al., 1987); *Neosaimiri fieldsi* (including “*Laventiana annectens*”, Stirton, 1951; Rosenberger et al., 1991; Takai, 1994; Nakatsukasa et al., 1997); *Cebupithecia sarmientoi* (Stirton, 1951; Meldrum and Kay, 1997); *Micodon kiotensis* (Setoguchi and Rosenberger, 1985); *Mohanamico hersHKovitz* (Luchterhand et al., 1986); *Aotus dindensis* (Setoguchi and Rosenberger, 1987); *Lagonimico conclutatus* (Kay, 1994), *Patasola magdalenae* (Kay and Meldrum, 1997); and *Nuciruptor rubicae* (Meldrum and Kay, 1997).

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Figure 1. Index map of La Venta, southern Colombia, showing the localities of fossil primates. UC: University of California; KU: Kyoto University; DU: Duke University. The site names, such as Kyoto, Chepe, Masato, Gentil, and Bolivia sites, are of the Kyoto University locality numbers.

Compared with the early/middle Miocene forms of Patagonia, these La Venta platyrrhines are notable in exhibiting very modern aspects, that have remarkable similarities to extant platyrrhine taxa, indicating a phylogenetic relationship with living platyrrhine clades (e.g. Fleagle et al., 1997; Fleagle and Kay, 1997; Fleagle, 1999): *Stirtonia* and *Neosaimiri* are regarded as the ancestral taxa of living howler monkeys (*Alouatta*) and squirrel monkeys (*Saimiri*), respectively (e.g. Stirton, 1951; Hershkovitz, 1970; Rosenberger, 1979); *Cebupithecia* and *Nuciruptor* are thought to be ancestral sakis (pitheciines) (Stirton, 1951; Meldrum and Kay, 1997); *Aotus dindensis* is considered as the middle Miocene species of *Aotus* (and/or *Mohanamico*, see Luchterhand et al., 1986; Setoguchi and Rosenberger, 1987; Kay, 1990; Rosenberger et al., 1990); *Micodon*, *Lagonimico* and *Patasola* are included in the Callitrichinae (Setoguchi and Rosenberger, 1985; Kay, 1990; Kay and Meldrum, 1997).

On the other hand, the phylogenetic relationships of living platyrrhine monkeys have been long discussed by many researchers. At present three main monophyletic groups, callitrichines (including *Callithrix*, *Cebuella*, *Saguinus*, *Leontopithecus*, and

Callimico), pitheciines (including *Pithecia*, *Cacajao*, and *Chiropotes*), and atelines (including *Alouatta*, *Ateles*, *Brachyteles*, and *Lagothrix*) are generally recognized by most researchers. However, the relationships among these three groups and the phyletic positions of other four genera (*Aotus*, *Callicebus*, *Saimiri*, and *Cebus*) have been variously reconstructed by many morphological studies. For instance, Rosenberger (1979, 1981) and Ford (1986) regarded pitheciines and atelines as more closely related to each other than to callitrichines, while Kay (1990) considered atelines and callitrichines as more closely related to each other than to pitheciines.

Among these morphological studies, the arrangements of the remaining four genera are in even more disagreement: Rosenberger (1979, 1981) placed *Cebus* and *Saimiri* most closely to the callitrichines, and *Aotus* and *Callicebus* with the pitheciines; Ford (1986) regarded *Saimiri* as a relative of the *Aotus-Callicebus* clade, and *Cebus* as a stem group of the platyrrhine radiation (or that *Cebus* and *Saimiri* possibly form a clade, see Ford, 1986); Kay (1990) considered *Callicebus* and *Cebus* as two outgroups of the callitrichines, atelines and pitheciines, linking *Saimiri* with callitrichines, and *Aotus* with atelines and callitrichines as a trichotomous clade.

Recently, many molecular biological studies have proposed phylogenetic trees of living platyrrhines (e.g. Schneider et al., 1993; Harada et al., 1995; Porter et al., 1995; Horovitz and Meyer, 1995; Porter et al., 1997a, 1997b; Barroso et al., 1997; Horovitz, 1999). Although all these studies also recognize three main monophyletic groups (the atelines, callitrichines, and pitheciines) in living platyrrhines, it is notable that all these studies propose a *Callicebus*-pitheciines sister relationship, and regard *Saimiri*, *Cebus* and *Aotus* as most closely related to the callitrichines. The fossil record of the *Callicebus* lineage would help to verify these hypothetical phylogenetic trees: that is, the relationship of *Callicebus* to the pitheciines and/or *Aotus*, or other possibilities.

Since 1977, paleontological expeditions by INGEOMINAS (Instituto de Investigaciones en Geociencias, Minería y Química, Colombia) and the Primate Research Institute of Kyoto University (Japan) have recovered many primate fossils from the middle Miocene deposits in La Venta (Fig. 1). During the 1997 field season, a fossil specimen of a new primate was recovered by surface collection. The specimen is a right maxillary fragment preserving a root of M¹, a complete M², and a badly damaged M3. The overall morphology of this specimen suggests that it may be closely related to *Callicebus*, titi monkeys.

Terminology and Abbreviations

In order to avoid confusion in terminology we basically adopt the classification of Primates proposed by Fleagle (1999). Abbreviations used in this paper are as follows: IGM, INGEOMINAS; IGM-KU, INGEOMINAS-Kyoto University; DU, Duke

University; UCMP, University of California Museum of Paleontology; KUPRI, Primate Research Institute, Kyoto University.

Systematic Paleontology

Order Primates Linnaeus, 1758

Infraorder Platyrrhini Geoffroy, 1812

Family Atelidae Gray, 1825

Subfamily Callicebinae

Miocallicebus villaviejai gen. et sp. nov. (Fig. 2)

Type specimen. IGM-KU 97001, a right maxillary fragment preserving the anterior base of the pterygoid process and a partial root of M^1 , complete M^2 , and poorly preserved M^3 .

Age and locality. Middle Miocene (Laventan Land Mammal Age, Madden et al., 1996). Discovered at the “Bolivia Site” ($3^{\circ}16'53''N$; $75^{\circ}11'40''W$) of Los Mesones, on the right side of Quebrada (= small river) Los Hoyos, Tatacoa desert, Huila Department, Colombia (Fig. 1). Just above the “Tatacoa Sandstone Beds” of the La Victoria Formation of Guerrero (1997), from which several radioisotopic dates have been obtained: 13.78 ± 0.08 Ma, 13.34 ± 0.41 Ma, 12.65 ± 0.26 Ma, and 12.49 ± 0.11 Ma (Guerrero, 1997; Fig. 3).

Etymology. “Mio” from the Miocene age, and “callicebus” from *Callicebus*, extant titi monkeys, for the resemblance between them. “Villavieja” is a name of the village where the type specimen was discovered.

Generic diagnosis. Medium size primate with three molars. Upper molars are very low crowned, and M^2 is square in occlusal outline with a distinct hypocone. A paracone and metacone are situated very buccally, and a protocone and metacone are connected by the postprotocrista-metaloph. M^3 is rather obliquely oriented to

Figure 2. *Miocallicebus villaviejai*, IGM-KU 97001, the type specimen (a right maxillary fragment preserving M^2 and fragments of M^1 and M^3 , stereopair). The arrow indicates the base of the pterygoid process. Scale bar = 1 cm.

the tooth row. Upper molars decrease in size from $M^1 > M^2 \gg M^3$. Differs from all extant and extinct callitrichines in the combination of having three molars and a well-developed hypocone on M^2 . Differs from atelines in having a nearly square occlusal M^2 outline, a distinct lingual cingulum on M^2 , and no deep lingual groove on M^2 . Differs from *Saimiri* and *Neosaimiri* in having a square-outlined M^2 with a large hypocone. Differs from *Cebus* in having a nearly continuous lingual cingulum and thin enamel layer on M^2 . Differs from aotines in having a lingual cingulum and in lacking a deep lingual groove on M^2 . Differs from pitheciines in having a distinct crista obliqua, a small but distinct lingual cingulum, no enamel crenula-

tion, and a “not-evenly worn” wear pattern on M^2 . Differs from extant *Callicebus* in its much larger size and in having a pterygoid process more medially situated. Differs from *Branisella* in having a square-outlined M^2 with a well-developed hypocone. Differs from all early-middle Miocene platyrrhines from Patagonia and Chile, such as *Dolichocebus*, *Soriacebus*, *Carlocebus*, in having a more square-outlined M^2 with a buccally situated paracone and metacone. Differs from *Antillothrix* in having a more rectangular occlusal outline and a less developed lingual cingulum on M^2 . Differs from *Paralouatta* in having a protocone more lingually situated and a less developed lingual cingulum on M^2 , and in having a more medially situated pterygoid process.

Specific diagnosis. As for genus.

Description and Comparison with Platyrrhine Monkeys

The M^2 of *Miocallicebus* is much larger than that of extant *Callicebus*, nearly equal to that of extant *Cebus* or slightly smaller than that of *Ateles* (mesiodistal

Figure 4. Bivariate plots of the M^2 of several extant and extinct platyrrhines. Note that the M^2 of *Miocallicebus* is much larger than that of the pitheciines and *Callicebus*. MD, mesiodistal length (mm); BL, buccolingual width (mm). *Cacajao* includes *C. calvus* and *C. melanocephalus*. *Chiropotes* includes *C. albinus* and *C. satanas*. *Pithecia* includes *P. irrorata*, *P. monachus* and *P. pithecia*. *Callicebus* includes *C. brunneus*, *C. caligatus*, *C. cupreus*, *C. hoffmannsi*, *C. moloch*, *C. ornatus*, *C. personatus* and *C. torquatus*.

Figure 5. Scanning electron micrographs (stereopair) of *Miocallicebus villaviejai* (a, IGM-KU 97001), a new specimen of fossil aotine discovered in the La Venta fauna (b, IGM-KU 98003, right M^{2-3}), *Cebupithecia sarmientoi* (c, UCMP 38762, left M^{1-2}), and *Callicebus moloch* (d, KUPRI 700, right M^{1-3}). Scale bars = 1 mm.

length, 4.41 mm and buccolingual width, 5.25 mm; Figs. 4 and 5). The outline of M^2 is nearly square in occlusal view, and slightly smaller than M^1 but much larger than M^3 . Two buccal cusps, the paracone and metacone, are so marginally situated that there is neither a stylar shelf nor a buccal cingulum. The hypocone is situated more lingually than is the protocone. The lingual half of M^2 is very worn exposing a dentine area at the positions of the protocone and hypocone. A small but distinct lingual cingulum runs from the lingual face of the protocone through to the hypocone. The crista obliqua (= the metaloph and postprotocrista) is well developed. The distal fovea, which is formed by the crista obliqua and the distal cingulum, is moderately deep. The M^3 , which is badly damaged by weathering, is likely to be rather oval in occlusal outline and implanted slightly obliquely to the tooth row.

Among living three-molared platyrrhines, *Callimico* and *Saimiri* have a more triangular M^2 with a poorly developed hypocone (Fig. 6d, j). *Alouatta* has highly specialized upper molars with strongly developed shearing crests (Fig. 6c), and other atelines (*Ateles*, *Brachyteles*, *Lagothrix*) have more roundish-outlined upper molars with deep lingual grooves (= lingual cleft, Rosenberger, 1979) (Fig. 6b). In *Cebus* the outline of M^2 is parallelogram-like rather than square, and the upper molars hardly ever show such a sharp wear ridge of the buccal cones as in *Miocallicebus*, probably because of their thick enamel layer (Fig. 6i).

The morphological resemblance in M^2 structure between *Miocallicebus* and extant *Aotus* (rectangular outline, a well developed crista obliqua, the paracone and metacone situated rather buccally, and a poorly developed lingual cingulum, Fig. 6h) suggest a possible close relationship between them. The close relationship between extant *Callicebus* and *Aotus* has previously been proposed by some researchers (Rosenberger, 1979, 1981; Ford, 1986). In the La Venta fauna a fossil owl monkey, *Aotus dindensis*, was discovered in the lowest part of the Villavieja Formation in the 1980s (locality number, 9–86A; see Figs. 1 and 3; Setoguchi and Rosenberger, 1987; Kay, 1990; Rosenberger et al., 1990). The type specimen of this species consists of a left mandibular corpus preserving I^1 – M^3 and a right maxillary fragment preserving a fragment of M^3 , so it is impossible to make a direct comparison between *Miocallicebus* and *A. dindensis*. During the 1998 and '99 field seasons, however, new maxillary and mandibular specimens of an aotine monkey were discovered near the Masato site (Fig. 2; Takai et al., in prep). All these specimens (IGM-KU 98001–008, 99001–003) most probably belong to the same individual, because they were collected from a very small spot and appear almost the same in dental size without overlap of tooth class. The lower dentition of this new material is nearly identical to that of *A. dindensis* except in its larger size, so it could be referred to a new species of fossil *Aotus* (Takai et al., in prep). Compared with M^2 of *Miocallicebus*, the M^2 of this new fossil aotine (IGM-KU 98003, Fig. 5b) is much smaller in size, is buccolingually waisted by deep buccal and lingual grooves, preserves no lingual cingulum, and its

Figure 6. The right M² of *Miocallicebus* (a, the slanting lines indicate an exposure of dentine area) in comparison with schematic drawings of the upper molars of extant platyrrhines (b, *Ateles*; c, *Alouatta*; d, *Callimico*; e, *Saguinus*; f, *Callicebus*; g, *Pithecia*; h, *Aotus*; i, *Cebus*; j, *Saimiri*). Not same scale.

anterior portion is much wider buccolingually than the posterior one. Thus, the middle Miocene species of *Aotus* definitely differs from *Miocallicebus* in M^2 structure.

In extant pitheciines upper molars have minute enamel crenulation and no (or very poorly developed) lingual cingula, and they are usually worn flat, forming a smooth cradle-like wear facet. The M^1 and M^2 are nearly the same size and M^3 is not so small as in *Miocallicebus*. Also in *Cebupithecia*, a fossil pitheciine discovered in the La Venta fauna, the M^2 has a distinct lingual cingulum and none of the buccal and lingual grooves, and the paracone and metacone are situated buccally as in *Miocallicebus* (Fig. 5c). The critical difference in M^2 structure between *Cebupithecia* and *Miocallicebus* is in their wear pattern: as in extant pitheciines, the M^2 of *Cebupithecia* is worn evenly without any distinct dentine exposure, while in *Miocallicebus*, the M^2 is not worn evenly but exposes an island-like dentine area at the protocone-hypocone position (Fig. 5a, c).

Miocallicebus is very similar to extant *Callicebus* in the following features: neither a buccal nor a lingual groove is present on M^2 ; a distinct lingual cingulum is present on M^2 ; the paracone and metacone are rather buccally situated; M^1 is slightly larger than M^2 and M^3 is much smaller than $M^{1,2}$; the outline of M^2 is nearly square (or slightly wider buccolingually); on M^2 the lingual portion (the protocone and hypocone) is worn more rapidly to make a greater dentine exposure than in the buccal portion (Fig. 5a, d). Therefore, considering the M^2 morphology of a contemporary fossil aotine (IGM-KU 98003) and pitheciine (*Cebupithecia*), *Miocallicebus* is likely to be more closely related to the lineage of callicebines than to other platyrrhine lineages, such as aotines, pitheciines, callitrichines and atelines.

There has been very little morphological research on the dentition of *Callicebus* but Kobayashi (1990) studied morphological variation in upper molars in three species of *Callicebus* (*C. torquatus*, *C. moloch*, and *C. personatus*). In his opinion, *C. torquatus* shows the most primitive upper molar morphology of the three species: that is, the development of the buccal cingulum, stylar cusps, paraconule, and prehypocrista are weak; the lingual cingulum does not run around the hypocone distolingually but connects to the hypocone directly; and the metaloph (= crista obliqua) is continuous from the protocone to the metacone. This tentative primitive condition of the *Callicebus*-lineage holds true in *Miocallicebus*, supporting an ancestor-descendant relationship between *Miocallicebus* and extant *Callicebus* and a sister group relationship between the callicebinae and pitheciinae.

MacPhee et al. (1995) discussed the systematic position of *Antillothrix bernensis* (former name is "*Saimiri*" *bernensis*; MacPhee and Wood, 1982; Ford, 1990) and *Paralouatta varonai* (Rivero and Arredondo, 1991), both of which are Pleistocene fossil taxa from the Antillean islands, using parsimony analysis of 32 craniodental characters, and linked them to extant *Callicebus*. However, in the M^2 of *Antillothrix*

the occlusal outline is not rectangular but rather oval; a nearly complete lingual cingulum is strongly developed but the hypocone is absent; and the paracone and metacone are not situated as buccally as in *Miocallicebus*. In *Paralouatta*, on the other hand, although the hypocone is present on the well-developed lingual cingulum, the protocone is situated much more buccally than the hypocone. *Miocallicebus* is likely to be more similar to extant *Callicebus* than to these Caribbean taxa in M² structure.

Position of the Pterygoid Process

In *Miocallicebus* the base of the pterygoid process is situated much more medially than the lingual marginal line of the upper molars, protruding posteriorly from the position distolingual to M³ (Fig. 2). Among extant platyrrhines, although the position of the pterygoid process relative to the upper dentition line shows various patterns (Table 1), in callitrichines, *Saimiri* and *Ateles* the base of the pterygoid process is obviously situated medial to the lingual marginal line of the upper dentition as in *Miocallicebus*. Particularly in *Saimiri* and *Ateles* the base of the pterygoid process is separated from the alveolar process by a deep palatine groove or palatine foramen. In callitrichines, however, the position of the pterygoid process is likely to be influenced by the reduction of the alveolar process and M³, indicating a substantial difference from *Saimiri* and *Ateles* in the pattern of the structure of the pterygoid process.

In other platyrrhines the position of the base of the pterygoid process is slightly medial to the lingual marginal line (*Callicebus*, *Chiropotes*, *Brachyteles* and *Alouatta*) or on the line of the upper molars (*Pithecia*, *Cacajao*, *Lagothrix*, *Cebus*, and *Aotus*). In *Callicebus*, a palatine foramen is located rather anteriorly, medial to M², so the diastema between the pterygoid process and the marginal line of the upper dentition

Table 1. Position of the pterygoid process relative to the marginal line of upper tooth row in *Miocallicebus* and extant platyrrhines

medial	slightly medial	on the line
<i>Cebuella</i>	<i>Chiropotes</i>	<i>Pithecia</i>
<i>Callithrix</i>	<i>Alouatta</i>	<i>Cacajao</i>
<i>Saguinus</i>	<i>Brachyteles</i>	<i>Lagothrix</i>
<i>Leontopithecus</i>	<i>Callicebus</i>	<i>Cebus</i>
<i>Callimico</i>		<i>Aotus</i>
<i>Saimiri</i>		<i>Paralouatta</i>
<i>Ateles</i>		
<i>Miocallicebus</i>		

is very narrow. In *Paralouatta*, which MacPhee et al. (1995) regarded as the sister group of *Callicebus*, the pterygoid process seems to be positioned on the extended line of the lingual margin of the upper molars (Rivero and Arredondo, 1991). In *Cebupithecia* (UCMP 38762) the posterior part of the palatine is also preserved: although in this specimen the base of the pterygoid process is unfortunately broken off, a distinct deep palatine groove is observed at the posterior end of the palatine, suggesting a rather medial position of the pterygoid process.

The position of the pterygoid process of *Miocallicebus* suggests the presence of a relatively deep palatine groove between the alveolar process and the pterygoid process, which is different from the pattern in extant *Callicebus*.

Comparisons with Fossil Platyrrhines from Patagonia and Chile

Several researchers have pointed out the dental resemblance between extant *Callicebus* and *Carlocebus*, an early-middle Miocene form from Patagonia (Fleagle, 1990, 1999; Fleagle et al., 1997; also see Fleagle et al., 1987), suggesting a possible phyletic relationship between them. Indeed, in *Carlocebus* M² has a rectangular outline with a large hypocone on the distinct lingual cingulum as in *Callicebus*. These features are also observed on M² of *Chilecebus*, an early Miocene form from central Chile (Flynn et al., 1995). However, *Carlocebus* and *Chilecebus* differ from *Callicebus* and *Miocallicebus* in that the paracone and metacone are not buccally situated and M² is buccolingually wide rather than it is mesiodistally long. A large cingulum-derived hypocone on M² is observed not only in *Carlocebus*, *Chilecebus* and *Callicebus* but also in other early/middle Miocene southern South American forms, such as *Dolichocebus* and *Soriacebus* (Fleagle, 1990), suggesting that this feature is not a shared derived character of certain taxa but is a primitive state in early platyrrhines. Although some more fossil platyrrhines, such as *Homunculus*, *Tremacebus* and *Proteropithecia*, have been discovered from the early-middle Miocene sediments in Patagonia (Bluntschili, 1931; Hershkovitz, 1970; Tauber, 1991; Fleagle and Bown, 1983; Kay et al., 1998), the upper molars of these genera are preserved so poorly (or unknown) that it is impossible to compare them with *Miocallicebus*.

Phyletic Position of the Callicebines

The phyletic position of *Callicebus* among the extant platyrrhines has been disputed by many researchers (e.g. Rosenberger, 1981; Ford, 1986; Kay, 1990; Schneider et al., 1993; Harada et al., 1995; Porter et al., 1995; Porter et al., 1997a, 1997b; Barroso et al., 1997). Among morphological studies, Rosenberger (1981) proposed the *Aotus-Callicebus* clade, which was considered to be closely related to the pitheciines; Ford (1986) regarded the *Callicebus-Aotus* clade as closely related not to the

pitheciines but probably to *Saimiri*; and Kay (1990) considered that *Callicebus* is the most primitive lineage among the extant platyrrhine clade. Thus, the results of three morphological studies on the phyletic position of *Callicebus* are not consistent with each other. Is *Callicebus* most closely related to *Aotus* or to the pitheciines?

As already discussed above, *Miocallicebus* and *Cebupithecia* are more similar to each other in M^2 structure than to a fossil aotine from the La Venta (IGM-KU 98003): *Miocallicebus* and *Cebupithecia* share a distinct lingual cingulum on M^2 , whereas a fossil aotine obviously lacks the lingual cingulum but retains a rather deep lingual sulcus, showing a strong resemblance to extant *Aotus* (Setoguchi and Rosenberger, 1987). In the La Venta fauna, therefore, the *Aotus* lineage seems to have split off from the *Callicebus* lineage much earlier than when the pitheciine clade diverged from the *Callicebus* lineage.

Recent many molecular biological studies support the *Callicebus*-pitheciine clade, linking *Aotus* not to *Callicebus* but to the *Cebus*-*Saimiri* and/or callitrichine clade. Schneider et al. (1993), Porter et al. (1995), and Porter et al. (1997a, b) proposed the *Callicebus*-pitheciine clade using ϵ -globin gene sequences. Harada et al. (1995) and Barrosa et al. (1997) support the *Callicebus*-pitheciine clade having analyzed the interstitial reinol-binding protein nuclear gene sequences (IRBP). The concurrence of these analyses based on two different gene sequences reinforces the reliability of the *Callicebus*-pitheciine clade.

Further, Horovitz et al. (1998) and Horovitz (1999) proposed phylogenetic trees of extant and extinct platyrrhines by analyzing morphological characters and nuclear (IRBP and ϵ -globin) and mitochondrial (12S and partial 16S) gene sequences. Although in their previous studies using 12S and 16S mitochondrial gene sequences *Callicebus* was not most closely related to the pitheciine clade, the simultaneous analysis of mitochondrial and nuclear genes and morphological characters supported a *Callicebus*-pitheciine clade (Horovitz et al., 1998; Horovitz, 1999).

On the other hand, the M^2 structure of *Antillothrix* and *Paralouatta*, both of which were discovered from the Pleistocene of the Caribbean islands and are considered closely related to the callicebinae, is unlikely to support this hypothesis (MacPhee et al., 1995). Neither of them shows an "intermediate" M^2 morphology between *Miocallicebus* and extant *Callicebus*. In fact, they are less similar to *Callicebus* than is *Miocallicebus*, at least in M^2 structure. In *Antillothrix*, M^2 is much reduced compared to M^1 : the occlusal outline is oval in shape rather than rectangular, and the hypocone is indistinct. In *Paralouatta* the lingual cingulum is so developed that the protocone is situated much more buccally than the hypocone. The M^2 morphology does not support a *Miocallicebus*-*Antillothrix*/*Paralouatta*-*Callicebus* lineage, which is the most simple ancestor-descendant relationship hypothesis.

Divergence Time of Callicebines in Relation to Other Platyrrhine Clades

Recently, several molecular biological studies have estimated the divergence dates among platyrrhine lineages (Table 2, Schneider et al., 1993; Porter et al., 1997a,b; Barroso et al., 1997). In these studies, although the estimated divergence dates of each node differ somewhat, there is no serious inconsistency among them (Table 2). For instance, the divergence time of *Callicebus* and the pitheciines is estimated as 14.5 Ma by using the ϵ -globin gene (Schneider et al., 1993; Porter et al., 1997a), 16.2 Ma by the IRBP gene (Barroso et al., 1997), and 15.2 Ma with the combined data of IRBP and ϵ -globin (Barroso et al., 1997). So, here we adopt the estimation dates (15.2 Ma) by Barroso et al. (1997), which used the combined data of the IRBP and ϵ -globin gene (Fig. 7).

As already mentioned, radioisotopic dates of the La Venta sediments have been reported by some workers. Takemura et al. (1992) reported three fission-track dates (12.6 ± 0.5 , 13.6 ± 0.7 , and 13.6 ± 0.5 Ma) from the upper part of the Tatacoa Red Member of the Villavieja Formation (Fig. 2), and Gurrero (1997) and Flynn et al. (1997) concluded that the age of the sediments of the La Victoria and Villavieja Formations are about 13.5–12.9 Ma and 12.9–11.5 Ma, respectively, based on a combination of paleomagnetic stratigraphy and $^{40}\text{Ar}/^{39}\text{Ar}$ dates. There is no substantial difference between the estimations by these two research groups: that is, the sediments of La Venta badlands producing many platyrrhine fossils were deposited during 13.5–11.5 Ma. Accordingly, the absolute age of the La Venta primates can be estimated as about 13 Ma. The estimated divergence date for *Callicebus*-pitheciines (15.2 Ma) is older than the absolute age for the La Venta sediments (13 Ma), so there is no contradiction between these two estimations (Fig. 7).

Table 2. Estimated divergence time of several platyrrhine clades based on molecular clock calculations. A reference date of 35 Ma for the platyrrhine-catarrhine divergence, which is based on the paleontological studies, was used in these studies. The Cebidae includes *Cebus*, *Saimiri*, *Aotus* and the Callitrichinae. The Atelidae includes the Atelinae, Pitheciinae and *Callicebus*.

Clade	Schneider et al. (1993)	Porter et al. (1997a)	Porter et al. (1997b)	Barroso et al. (1997)
Cebidae-Atelidae	20.1	22.7	21.3	21.3
Atelinae-Pitheciinae	17.0			
<i>Callicebus</i> -Pitheciinae	14.5		14.5	15.2
Atelinae				13.7
<i>Saimiri</i> - <i>Cebus</i> - <i>Aotus</i> -Callitrichinae	17.7			
<i>Saimiri</i> - <i>Cebus</i>		17.0	16.3	16.7
<i>Aotus</i> -Callitrichinae		17.9	16.7	17.5

Figure 7. A hypothetical phylogenetic tree of platyrrhine monkeys mainly based on the molecular analysis by Barroso et al. (1997). Numbers at the main nodes, such as 21.3, are the estimated divergence time between lineages (see Table 2 for more detailed data). Filled circles indicate fossil taxa discovered in the La Venta fauna.

As for estimations on other divergence times, however, there seem to be some problems. Fig. 7 shows a schematic phylogenetic tree of extant platyrrhines reconstructed by these molecular studies, indicating the divergence times of some important nodes proposed by Barroso et al. (1997) and the geological ages of La Venta primates and *Branisella* (filled circles). As mentioned in the introduction, fossil taxa of most extant platyrrhine lineages have been discovered in the La Venta fauna: *Stirtonia* for the *Alouatta* lineage, *Cebupithecia* and *Nuciraptor* for the pitheciines, *Neosaimiri* for *Saimiri*, *Aotus dindensis* (and/or *Mohanamico*?) for extant *Aotus*,

Micodon and *Lagonimico* for the callitrichines. All estimations of the divergence times of these lineages (13.7 Ma for atelines, 15.2 Ma for *Callicebus*-pitheciines, 16.7 Ma for *Cebus-Saimiri*, and 17.5 Ma for *Aotus*-callitrichines) are older than the age of the La Venta primates (13 Ma).

However, the strong dental resemblance, that is a specialization to a folivorous diet, between *Stirtonia* (fossil taxon) and *Alouatta* (extant taxon) suggest that the *Alouatta* lineage might have diverged much earlier than 13.7 Ma. Moreover, if the estimated divergence time for extant platyrrhines is actually 21.3 Ma, *Branisella*, the oldest fossil platyrrhine discovered from the latest Oligocene of Bolivia (about 26–27 Ma, MacFadden et al., 1985; Kay et al., 1998), should be excluded from the extant platyrrhine clade. Although the phyletic position of *Branisella* has not yet been well established, several researchers have pointed out the resemblance between *Branisella* and callitrichine monkeys (Rosenberger et al., 1991; Takai and Anaya, 1996; Takai et al., 2000). The estimated divergence dates for platyrrhine clades seem to be too young for the estimations based on fossil records. More complete fossil materials of *Miocallicebus* would shed more light on the phylogenetic study of platyrrhine monkeys.

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