Primate diversity in the early Miocene Pinturas Formation, southern Patagonia, Argentina

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Abstract: We report ten new dental specimens of primates from the early Miocene Pinturas Formation, Patagonia, Argentina. The new material includes: a left lower canine and a left upper canine whose affinities remain to be determined; a mandibular fragment preserving part of the symphysis; and right p3-4, practically indistinguishable from Soriacebus adrianae; and a lower molar, probably m2, attributable to S. ameghinorum. A lower molar, probably m3, a P4, and an upper molar resemble Carlocebus carmenensis. Three additional specimens, too damaged for an accurate taxonomic assignment, are tentatively assigned to S. ameghinorum. The specimens here described can be assigned to taxa already known from the Pinturas Formation (S. ameghinorum, S. adrianae, and C. carmenensis) and provide new morphological information.

Key words: Platyrhine primates, Soriacebus, Carlocebus, early Miocene, Patagonia.

INTRODUCTION

Fossil platyrrhines have been known since the first half of the XIXth century with the reports by Lund (1840) of the Pleistocene fauna of eastern Brazilian caves. After long intervals when no new fossils were found, a remarkable amount of material has been collected regarding the origin, evolutionary history and paleobiogeography of the group, especially since the 1980s. Although the number of specimens recorded is proportionally small relative to other fossil mammals, platyrrhines had a notable diversity in the past. About 35 extinct platyrrhine genera have been reported from the mid Cenozoic of Central and South America and the Caribbean islands. Most are part of the modern radiation, but the oldest South American primates discovered so far are part of a complex evolutionary scenario, such as the discovery of a possible stem platyrrhine or pre-platyrrhine (Bond et al. 2015), and a parapithecid stem anthropoid (Seiffert et al. 2020), both from the late Paleogene of the Amazon region in Peru; or the controversial the controversial genera from western Bolivia (late Oligocene, Hoffstetter 1969, Rosenberger et al. 1991a, Takai et al. 2000, Kay et al. 2002) and Chile (early Miocene; Flynn et al. 1995). Then, the more modern forms from the Peruvian Amazonia (late Oligocene; Marivaux et al. 2016a, early Miocene; Marivaux et al. 2012, Kay et al. 2019, late Miocene; Marivaux et al. 2016b, 2020), central Colombia (middle Miocene; Stirton 1951, Hershkovitz 1970, Luchterhand et al. 1986, Setoguchi & Rosenberger 1985, Kay et al. 1987, 1997, Rosenberger et al. 1991b, Takai 1994, Takai et al. 2001, 2009), Brazil (late Miocene and Pleistocene; Lund, 1840, Hartwig & Cartelle 1996, Cartelle & Hartwig 1996, Kay & Cozzuol 2006, Tejedor et al. 2008, Rosenberger et al. 2015, Halenar & Rosenberger 2013), Panama (early Miocene; Bloch et al. 2016), and the Greater Antilles (early Miocene and late Cenozoic; Rivero & Arredondo 1991, MacPhee et al. 2003, Williams...
From Argentine Patagonia (early and middle Miocene), eight genera and eleven species of fossil platyrhines have been recorded from different formations. The oldest Patagonian primates were found in early Miocene sediments from four localities of the Sarmiento Formation (Fm.), Chubut Province. Three genera have been recovered: *Tremacebus* from Sacanana (Rusconi 1933, Hershkovitz 1974), *Dolichocebus* from Gaiman (Kraglievich 1951, Kay et al. 2008) and *Mazzonicebus* from the Gran Barranca (Kay 2010) and La Estrella (Novo et al. 2017). The youngest genus, *Proteropithecia*, was found in middle Miocene deposits of the Collón Curá Fm., Neuquén Province (Kay et al. 1998). In addition, primates have been found in the Santa Cruz Fm. (early Miocene), southeastern coastal area of Santa Cruz Province, where the number of existing genera is still controversial. At the moment, *Killikaike* and two species of *Homunculus* have been described (Ameghino 1891, Tejedor et al. 2006, Tejedor & Rosenberger 2008, Perry et al. 2010, 2014, Kay et al. 2012, Novo et al. 2018, Kay & Perry 2019). Finally, the most diverse fossil record of primates comes from the Pinturas Fm. (early Miocene), also in Santa Cruz Province. The Pinturas Fm. contains the second largest collection of fossil platyrhines specimens, after the taxonomically diverse assemblage of La Venta, Colombia (see Tejedor & Novo 2018). To date, at least two genera and four primate species have been recognized in the Pinturas Fm.: *Soriacebus ameghinorum* Fleagle, Powers, Conroy & Watters, 1987, *Soriacebus adrianae* Fleagle 1990, *Carlocebus carmenensis* Fleagle 1990, and *Carlocebus intermedius* Fleagle 1990, with subsequent reports of isolated specimens (Fleagle & Tejedor 2002, Tejedor 2005a, b, Novo & Fleagle 2015), and a third genus remains unpublished (see Tejedor et al. 2012).

It should be noted that the taxonomic assignments at a suprageneric level that we provide below strongly differ from Kay (2015, and references therein), who suggested an alternative hypothesis considering the Patagonian primates as a stem family group, excepting *Proteropithecia* (Pitheciidae).

In this contribution, we report ten new dental specimens of primates from the Pinturas Fm. that provide additional morphological information on several taxa.

**GEOLOGICAL BACKGROUND**

The Pinturas Fm. is a pyroclastic and epilastic succession, around 70–80 m thick, cropping out in the upper valley of the Pinturas river and its tributaries, in the northern Santa Cruz Province, Patagonia, Argentina (Bown & Larriestra 1990). Currently, the Pinturas Fm. is divided into four informal ‘sequences’, separated by unconformities (Krause et al. 2016), a scheme that modifies the former tripartite division scheme of Bown & Larriestra (1990). The 40Ar/39Ar ages of ~17.99 Ma near the base of the Pinturas Fm. at Estancia el Carmen, and ~16.8 Ma of the overlaying Santa Cruz Fm. at Portezuelo Sumich Norte (see Perkins et al. 2012, Fleagle et al. 2012) suggest that the Pinturas Fm. is Burdigalian in age (20.44–15.97 Ma, Cohen et al. 2013). Eight localities of this unit have been described by Bown & Larriestra (1990) as providing confident sedimentary sections and fossil primates: Arroyo Feo (AF), Estancia El Carmen (EEC), Estancia Ana María (EAM) (hereafter ‘Loma de las Ranas (LR)’), Loma de la Lluvia (LL), Cauce Seca (CS), Cerro de los Monos (CM), Portezuelo Sumich Sur (PSS), and Portezuelo Sumich Norte (PSN) (Fig1). The new fossils reported here come from PSN (S 46° 57'
33.09°, W 70° 93 40' 2'"), LR (S 47° 01´ 30,8", W 70° 43´ 50,3"), and PSS (S 46° 94 59' 7.3", W 70° 38' 21.7"). Platyrrhines from PSN and LR derive from the second sequence from the base of the formation. This sequence coincides with the "sandy yellow, green or pink bentonitic mudstone" of Bown & Larriestra (1990), and is composed of fine- to medium-grained sandstone, yellowish grey in color. The lower boundary is represented by an erosional, irregular surface (i.e., unconformity), up to 15 m in relief, which truncates the first sequence, characterized by stacked, pinkish paleosols (‘very mature paleosols’ of Bown and Larriestra 1990). At PSN, this surface is clearly visible and was interpreted as a paleovalley by Bown & Larriestra 1990: fig. 9A). At LR, the base of the section does not crop out. However, observations in surrounding outcrops in the EAM area show the fossiliferous level in a similar stratigraphic position as for PSN; that is, between the very mature paleosols interval (first sequence) and the eolian dunes interval (third sequence, formerly second sequence of Bown & Larriestra 1990). PSS consists of an isolated outcrop distant from other localities, and was not directly correlated to them. Bown and Larriestra (1990: 113), based on the presence of sandy gray volcanic mudrocks in this place, and its strong similarity regarding the interdune beds from the third sequence (former ‘middle sequence’ of Bown and Larriestra 1990), correlated this locality to it, giving a younger relative age for fossils from PSS relative to those from PSN. Our recent observations in the field accord with the higher stratigraphic position of PSS with respect to both PSN and LR. However, we tentative correlate this locality to the lowermost fourth sequence, as the light gray rocks can be followed to the north up to the higher part of the outcrop at PSN.

Figure 1. Map of Patagonia showing the location and detail of the Pinturas River area and the localities mentioned in the text.
MATERIALS AND METHODS

Institutional abbreviations

MACN Pv SC, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; Colección de Paleovertebrados-Santa Cruz; MPM-PV, Museo Regional Provincial Padre Manuel Jesús Molina, Río Gallegos, Argentina.

Anatomical abbreviations

The dentition of the Patagonian fossil primates is discussed using the following abbreviations: M1–3, upper molars; m1–3, lower molars, p/P lower and upper premolars, c/C lower and upper canines, i/I lower and upper incisors. BL: buccolingual; MD: mesiodistal.

Systematic paleontology

Class Mammalia Linnaeus, 1758
Order Primates Linnaeus, 1758
Parvorder Platyrhini Geoffroy Saint-Hilaire, 1812
Family Pitheciidae Gray, 1849 (Mivart, 1865)
Genus Soriacebus Fleagle, Powers, Conroy & Watters, 1987

Type species: Soriacebus ameghinorum Fleagle, Powers, Conroy & Watters, 1987

Soriacebus ameghinorum

Referred material: MPM PV 17413 (Fig. 2e), right lower molar, probably m2.

Figure 2. Occlusal view of new specimens from the Pinturas Formation. a: MPM PV 21646 left P4, b: MPM PV 17417 left M1 or M2, c: MPM PV 17416 left m3, d: MPM PV 17419 symphysis mandibular, e: MPM PV 17413 right m2. Scale bar 1mm.
Geographic and stratigraphic provenance: Portezuelo Sumich Norte, Santa Cruz Province. Second sequence of the Pinturas Fm.

Description: The roots are broken but it possibly had a divided mesial root, and a single, distal one. The trigonid is slightly higher than the talonid, mesially closed, and somewhat expanded mesially beyond the protoconid due to the presence of a straight preprotocristid, not as long as seen in the type of *S. ameghinorum*, giving the latter a more expanded trigonid in proportion to the talonid. The protoconid is moderately developed, connecting to the metaconid obliquely through the lateral protocristid forming the distal wall of the trigonid. The talonid is expanded distally behind the entoconid and hypoconid. The ectoflexid is slightly marked, differing from the type; the cristid obliqua is oriented forward reaching the wall of the trigonid behind the protoconid. There is a small cuspule twinned to the entoconid that may be homologous to the hypoconulid. The general outline of the molar is rounded, unlike the more elongate and quadrangular aspect of the type of *S. ameghinorum*, and more similar to MPM PV 36, described as *Soriacebus cf. ameghinorum* by Tejedor (2005a). However, MPM PV 17413 has an even more rounded aspect, and the lingual side is more inflated than both of the aforementioned specimens. Based on its morphology and size, this m1 could be assigned to *Soriacebus* with certainty, although there are some important morphological differences, as was mentioned for MPM PV 36 (Tejedor 2005a), thus questioning the specific status.

cf. *Soriacebus ameghinorum*

Referred material: MPM PV 17412, left lower molar; MPM PV 17396, talonid of a left lower molar; MPM PV 17415, mandibular fragment with the broken and worn talonid of a lower molar preserving a complete distal root.

Geographic and stratigraphic provenance: The three specimens come from Portezuelo Sumich Norte, Santa Cruz Province. Second sequence of the Pinturas Fm.

Description: MPM PV 17412 is a heavily worn molar with almost no occlusal morphology preserved, except in the talonid basin. The anterior root is complete, but the posterior one is broken, so it is not possible to determine whether it is bifid or not. It is not possible to determine exactly the taxonomic assignment of MPM PV 17415 and MPM PV 17396 due to wear. However, based on the crown outline and size, these three specimens may be comparable to the lower molars of *S. ameghinorum*.

Type species: *Soriacebus adrianae* Fleagle, 1990

*Soriacebus adrianae*

Referred material: MPM PV 17419 (Fig 2d), symphysis with right p3-4 broken and preserving only the base of the cusps, root of right p2, alveolus of the right canine, and partial alveoli of the incisors.

Geographic and stratigraphic provenance: Loma de las Ranas, Santa Cruz Province. Second sequence of Pinturas Fm.

Description: This specimen is indistinguishable from *S. adrianae* especially the holotype, MACN Pv SC59, and the symphysis MPM PV 1605, based on the general size, V-shaped morphology of the dental arcade, procumbent incisors, as indicated by the position of the alveoli, and relatively large alveolous of the canine.

Genus *Carlocebus* Fleagle, 1990

Type species *Carlocebus carmenensis* Fleagle, 1990
**Carlocebus carmenensis**

**Referred material:** MPM PV 21646 (Fig. 2a) left P4; MPM PV 17417 (Fig. 2b) right M1 or M2; MPM PV 17416 (Fig. 2c) left m3.

**Geographic and stratigraphic provenance:** MPM PV 21646 from Portezuelo Sumich Sur, MPM PV 17417 and MPM PV 17416 from Loma de las Ranas, Santa Cruz Province. From the fourth and second sequences, respectively.

**Description:** The MPM PV 21646 P4 has two fused roots, unlike the three roots present in some upper premolars of *S. ameghinorum*. It has a well-developed paracone worn at the tip, and a small protocone separated by a sulcus continuous with a mesial fovea. It shows a moderately developed lingual cingulum bearing a hypocone. There is a short preparacrista and a longer, distally oriented postparacrista delimiting buccally a relatively wide talon basin. In overall morphology, this P4 is almost indistinguishable from the P4 in the maxilla MACN Pv SC400 (from Estancia El Carmen), attributed to *C. carmenensis* (see Fleagle 1990), but differs from the P4 in MACN Pv SC100 (Cerro de los Monos), attributed to an undescribed taxon (Tejedor et al. 2012), which is more elliptical, with more bulbous cusps and the lingual cingulum is expanded distally, thus contrasting with the triangular shape in *C. carmenensis*.

The MPM PV 17417 upper molar has the root area completely broken, as well as the lingual part of the hypocone. The strong lingual cingulum has accessory cuspules and is expanded as a precingulum as in MACN Pv SC317, an M1 assigned to *C. carmenensis*. A very weak labial cingulum is also present. The talon basin is broad, distally expanded. The mesial fovea is present and deeper than in MACN Pv SC90 and MACN Pv SC254, also attributed to *C. carmenensis*, and it is delimited by a developed hypoparacrista descending from the paracone and reaching the prepseudocrista at about the middle and anterior part of the tooth. Paracone and metacone are well developed forming a V-shaped ectoflexid due to the connection of the postparacrista and premetacrista. There is a tiny metaconule at the end of the descending hypometacrista. A quadrangular shape is produced by the well-developed hypocone connected to the labially oriented postprotocrista by a short prehypocrista, unlike some molars assigned to *C. carmenensis*, where the prehypocrista is absent (i.e., MACN Pv SC90 and MACN Pv SC317). Nevertheless, given its similar morphology with previously assigned specimens, such as MACN Pv SC270, MACN Pv SC98, MACN Pv SC230, MPM PV 17403, among others, this new upper molar is assignable to *C. carmenensis*.

The MPM PV 17416 m3 is heavily worn and its mesolingual region is broken. It has two fused roots. The trigonid is shorter and the talonid has a relatively wide basin, although mesiodistally short. The talonid is expanded distally forming a lobe. The hypocone appears broad at the base, larger than the entoconid. There is a small sulcus distal to the entoconid separating a tiny and worn cusp, as well as the distal lobe; this cusp is more evident in MACN Pv SC248, an m3 attributed to *C. carmenensis* (see Fleagle 1990), which this molar resembles in general morphology.

**Genus indeterminate**

**Referred material:** MPM PV 17414 (Fig. 3c, d) left lower canine; MPM PV 17418 (Fig. 3a, b) left upper canine.

**Geographic and stratigraphic provenance:** MPM PV 17414 is from PSN, whereas MPM PV 17418 is from Loma de las Ranas, Santa Cruz province, second sequence of the Pinturas Fm.

**Descriptions:** The MPM PV 17414 lower canine has a well preserved crown, except its...
tip which is worn and somewhat broken. It has moderate distolingual heel and rounded entocristid. It has an elliptical cross-section, but the shaft of the crown between the cingulum and the apex is rather triangular given by the large open lingual surface and the flat distal surface associated with the entocristid. This is a classical lower canine pitheciine morphology in a somewhat more primitive state. This new canine is approximately the same size as MPM PV 17395 and MPM PV 17397, two primate canines indet reported by Novo & Fleagle (2015), although the latter two are more bucolingually compressed with a reduced lingual cingulum. However, MPM PV 17414 resembles the canine in the type of S. ameghinorum in its general outline, well developed lingual cingulum and lingual heel, but differs in its smaller size.

The MPM PV 17418 upper canine has a large and robust crown with a deep mesial groove. It is even larger and more robust compared to the upper canine of S. ameghinorum in the maxilla MACN Pv SC4, especially in buccolingual dimensions. It has moderate talon wear and heavy wear in the lingual region where it occludes with p2. Among all canines reported from the Pinturas Fm., MPM PV 17418 appears more similar to MACN Pv SC328, the largest canine with a distinct morphology which is described by Tejedor (2002).

**DISCUSSION**

The specimens described above have been tentatively assigned to previously known taxa from the Pinturas Fm., including Soriacebus ameghinorum, S. adrianae, and Carlocebus carmenensis, and they provide additional morphological information on the variation of those taxa. Consequently, a thorough revision is needed for the whole primate collection of the Pinturas Fm. in order to better evaluate the taxonomic significance of the morphological variation among them, and to assess the possibility of additional new taxa. (Fleagle 1990, Tejedor 2005a, Tejedor et al. 2012).

The correlations of taxa and sequences at Pinturas are as follows, from the base to the top of the section (Table I): 1) First sequence (Estancia el Carmen), Carlocebus carmenensis; 2) second sequence (Arroyo Feo, Portezuelo Sumich Norte, Loma de las Ranas, Loma de la Lluvia, Cauce Seca), Carlocebus carmenensis, Soriacebus adrianae, Soriacebus ameghinorum, and Carlocebus intermedius; 3) third sequence (Cerro de los Monos), a third genus remains unpublished (see Tejedor et al. 2012). 4) fourth sequence (Portezuelo Sumich Sur), Soriacebus adrianae, Carlocebus carmenensis.
Table I. The Pinturas Formation specimens previously reported and mentioned in the text. Measurements (in mm).

| Collection N° | Species          | Description                        | Location                               | Sequence | BL  | MD  | References     |
|---------------|------------------|------------------------------------|----------------------------------------|----------|-----|-----|----------------|
| MPM-PV 17412  | cf. *S. ameghinorum* | left m1 or 2                       | Portezuelo Sumich Norte Fm. Pinturas Santa Cruz | second   | 3.58| 4.09| new            |
| MPM-PV 17413  | *S. ameghinorum*  | right m, probably m2               | Portezuelo Sumich Norte Fm. Pinturas Santa Cruz | second   | 3.25| 4.07| new            |
| MPM-PV 17414  | indet            | left c                             | Portezuelo Sumich Norte Fm. Pinturas Santa Cruz | second   | 4.45| 3.59| new            |
| MPM PV 17415  | cf. *S. ameghinorum* | mand. frag. with talonid of m1 or 2 | Portezuelo Sumich Norte Fm. Pinturas Santa Cruz | second   |     |     | new            |
| MPM PV 17396  | cf. *S. ameghinorum* | talonid of m1 or 2                 | Portezuelo Sumich Norte Fm. Pinturas Santa Cruz | second   | 3.19|     | new            |
| MPM-PV 17416  | *C. carmenensis* | left m3                            | Loma de las Ranas Fm. Pinturas, Santa Cruz | second   | 4.2 | 5.46| new            |
| MPM-PV 17417  | *C. carmenensis* | right m, probably m2               | Loma de las Ranas Fm. Pinturas, Santa Cruz | second   | 6.85| 4.95| new            |
| MPM-PV 17418  | indet            | left C                             | Loma de las Ranas Fm. Pinturas, Santa Cruz | second   | 3.87| 5.1 | new            |
| MPM-PV 17419  | *S. adrianae*    | symphysis with p3-4                 | Loma de las Ranas Fm. Pinturas, Santa Cruz | second   |     |     | new            |
| MPM-PV-21646  | cf. *C. carmenensis* | left P4                           | Portezuelo Sumich Sur Fm Pinturas, Santa Cruz | fourth   | 5.48| 3.78| new            |
| MACN Pv SC2 (h) | *S. ameghinorum* | mand. frag. with right i1, m3, and left c root | Portezuelo Sumich Norte Fm. Pinturas Santa Cruz | second   |     |     | Fleagle et al. 1987 |
| MACN Pv SC4   | *S. ameghinorum* | max. frag. with left C-M1          | Portezuelo Sumich Norte Fm. Pinturas Santa Cruz | second   |     |     | Fleagle et al. 1987 |
In the succession of the Pinturas primate fauna, the genus *Soriacebus* is represented in successive levels in the section, with *S. ameghinorum*, known from about 25 dental specimens, older and larger than *S. adrianae*, which is known from about 16 dental specimens. The specimen MPM PV10413 reported here is another example of the variation seen among isolated molars of *S. ameghinorum* with respect to the holotype MACN Pv SC2, as the latter is more rectangular and elongate. With the current evidence, we cannot confirm if the differences may be due to an intraspecific variation or a distinct species, as suggested by Tejedor (2005a); however, another non-typical *Soriacebus* specimen such as MPM PV 10413 cautions us about the high morphological diversity in the Pinturas primates that deserves more scrutiny.
The specimen MPM PV 17419 contributes to the knowledge of the poorly known species *S. adrianae*, which is only recorded from localities of the second sequence, such as PSS, LR, and LL. In addition, the lower canine MPM PV 17414 exhibits strong resemblances to the holotype of *S. ameghinorum*, which supports the pitheciine affinities of the latter, whereas the upper canine MPM PV 17718 is more robust than expected for *Soriacebus*, similar to the possible alouattine morph described by Tejedor (2002) with respect to another Pinturas upper canine.

*Carlocebus carmenensis* is widely distributed in the section, with almost 40 specimens reported in all the mentioned localities of the Pinturas Fm., even in Cerro de los Monos. However, several specimens coming only from CM, at the base of the third sequence, are being reallocated to a new genus (see Tejedor et al. 2012; M.F. Tejedor et al., unpublished data); this is the only locality that corresponds to the third sequence, and therefore one of the youngest for primates. Finally, with only two dental specimens, the poorly known *C. intermedius* is only recorded in Portezuelo Sumich Norte.

The fossils comprising the whole “Pinturan fauna” come from the first three sequences, including rodents (Kramarz & Bellosi 2005), native ungulates (Kramarz & Bond 2005), xenarthrans (González et al. 2006, Brandoni et al. 2016, 2019), marsupials (Bown & Fleagle 1993, Goin et al. 2010, Chornogubsky & Kramarz 2012) and a relatively high diversity of primates (Fleagle et al. 1987, Fleagle 1990, Tejedor 2002, 2005a, b, Novo & Fleagle 2015). As mentioned elsewhere (see Brandoni et al. 2016, and literature therein), fossils collected in the fourth sequence correspond to the more typical mammals of the “Santacrucian fauna” from the Santa Cruz Fm., on the Atlantic coast of Santa Cruz Province.

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