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New specimens of *Soriacebus adrianae* Fleagle, 1990, with comments on pitheciin primates from the Miocene of Patagonia

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Introduction

Since the early 1980s, joint paleontological expeditions to the Pinturas Formation (Santacrucian, lateearly Miocene), in northwestern Santa Cruz Province, Argentine Patagonia, by the Museo Argentino de Ciencias Naturales (Buenos Aires) and the State University of New York at Stony Brook, have recovered several new species of platyrrhine primates and other vertebrates. The named primate species are Soriacebus ameghinorum Fleagle et al., 1987, Soriacebus adrianae Fleagle, 1990, Carlocebus carmenensis Fleagle, 1990, and Carlocebus intermedius Fleagle, 1990. The most controversial Pinturas primate has been the genus Soriacebus, represented by several dental and mandibular specimens that provide rather complete information regarding its dentition. There is no consensus about the phylogenetic affinities of Soria*cebus* and different approaches were discussed by some authors after the original description. Fleagle et al. (1987) pointed out that in the anterior dentition and mandibular shape Soriacebus is close to the living pitheciins (Pithecia, Chiropotes, Cacajao), while the lower premolars and molars resemble those of extant callitrichines for their narrowness and morphology of the molar trigonids. However, Fleagle et al. (1987) draw attention to the unique condition of Soriacebus among platyrrhines by having three-rooted upper premolars, although the presence of small hypocones in P⁴ is shared with the living *Callicebus*. Rosenberger et al. (1990) and Tejedor (2000) included Soriacebus in the tribe Pitheciini, together with the living Pithecia, Chiropotes and Cacajao, and the extinct Cebupithecia, from the Laventan of Colombia, for several traits characterizing its dentition and mandible. Proteropithecia is a more recently described pitheciin from Neuquen Province (Kay et al., 1998). Among the

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major shared features are the morphology and size of the lower incisors and the robustness of the projecting canine, followed by a massive and tall P₂. Also, the posterior mandibular depth is a shared similarity with the extant pitheciins and *Callicebus*. Kay (1990) suggested that *Soriacebus* is an early offshoot of platyrrhines, especially because of the cheek teeth which he considers distinct and more primitive than in most living platyrrhines. In several dental characteristics, the author compared *Soriacebus* with *Apidium* and *Aegyptopithecus*, from the Egyptian Oligocene, concluding that *Soriacebus* was a sister taxon of the Platyrrhini.

In March, 2000, two new specimens of Soriacebus adrianae were found in Pinturas at the locality of Portezuelo Sumich Sur (see Bown and Larriestra, 1990), in a joint expedition by members of the State University of New York at Stony Brook, University of Utah, Centro Nacional Patagónico (CENPAT), and Facultad de Ciencias Naturales, Sede Esquel (Universidad Nacional de la Patagonia "San Juan Bosco"). These are important discoveries since S. adrianae is still poorly represented in the record and new information about the anatomy of the species is provided here. One specimen is a fragmentary mandible (figures 1.A-B), including the symphysis, right canine, right P₂, left P₄, roots of right I₁₋₂ and left P₂₋₃, and alveoli of left I₁₋₂, left canine and right P₃. Unfortunately, the teeth are not well preserved but the crown of the right canine, although broken at the apex, shows a clear lingual crest or entocristid running upward from the base of the crown. Having into account the controversies around the phylogenetic position of Soriacebus, this character is of major interest in assessing the affinities of the genus. The other specimen is an isolated right upper canine (figure 1.C).

Results and discussion

The new fragmentary mandible, MPM-PV 1605, is identical and more complete than the type of *Soria*-

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Figure 1. MPM-PV 1605: partial mandible of *Soriacebus adrianae* Fleagle, 1990, in occlusal **(A)**, and buccal view **(B)**. Measurements of the right canine are: MD=2.80 mm; BL=3.82 mm. **(C)** MPM-PV 1606: isolated right upper canine attributed to *Soriacebus adrianae 1 cm./MPM-PV* 1605: *mandibula parcial de* Soriacebus adrianae *Fleagle*, 1990, *en vista oclusal* **(A)** *y bucal* **(B)**. *Medidas del canino derecho:* MD=2.80 mm; BL=3.82 mm. **(C)** MPM-PV 1606: *canino superior derecho aislado atribuido a* Soriacebus adrianae, *en vista* **protocristid**, **in**-P₃ and the trigonid lingually inclined.

cebus adrianae, MACN-SC 59, a right part of a symplysis preserving the canine root and P_{3-4} (see Fleagle, 1990). The canine is high-crowned, projecting well above the occlusal plane and shows a typical pitheciin structure, being buccolingually compressed with an entocristid along the lingual side. The entocristid makes the cross-section of the canine nearly triangular, as shown by more advanced pitheciins and the extremely derived living Pithecia, Chiropotes and Cacajao. This character is universally present in pitheciins. The holotypes of Soriacebus ameghinorum and Soriacebus adrianae (mandibles MACN-SC 2 and MACN-SC 59; see Fleagle et al., 1987; Fleagle, 1990) have the canine crowns broken, but they are large at the base and were certainly high-crowned. There is a smooth root-crown transition characterizing the living pitheciins, so that the crown is not expanded at the base, as is noted in the Soriacebus specimens.

The isolated upper canine, MPM-PV 1606, also demonstrate affinities with pitheciins, having a long and projecting crown, reduced lingual cingulum, no distolingual heel, a relatively deep mesial groove and the base of the crown is not wide relative to the height. This is certainly a pitheciin pattern characterizing Soriacebus (see Tejedor, 2002). Although smaller, the morphology of this upper canine is the same as those attributed to Soriacebus ameghinorum, as discussed elsewhere (Tejedor, 2002). Unquestionably, this upper canine is morphologically indistinguishable from that of the maxillary fragment of Soriacebus ameghinorum, MACN-SC 4 (see Fleagle et al., 1987), excepting for its smaller size that fits well with Soriacebus adrianae. Among the living platyrrhines with projecting canines, upper canines of pitheciins are distinct from Saimiri and Cebus because the latter have a deeper mesial groove and the distolingual side of the canine is thinner, blade-like, in contrast

AMEGHINIANA 42 (1), 2005

with the robustness showed by pitheciins. *Alouatta* also shows a blade-like pattern in upper canines, but even more projecting, with a more robust root.

The above mentioned characters certainly describe a pitheciin primate. However, Soriacebus has an unusual lower premolar and molar morphology. The lower molars are elongate with large trigonids, in contrast to the trend towards reduced trigonids in all other pitheciins. In the type specimen of Soriacebus *ameghinorum*, the talonid is usually narrower than the trigonid, more in M1, but it shows a distal expansion with a small hypoconulid on M₁₋₂. These are the major controversial characters since such morphology is not shared with any other platyrrhine. On the other hand, trigonid and talonid proportions of P₃₋₄ are similar in Cebupithecia and Soriacebus, with a long pre-It is noted that the pitheciin status of Cebupithecia is unquestionable. This similarity is certainly homologous and the premolars of Soriacebus probably evolved their elongate shape secondarily. As mentioned above, Fleagle et al. (1987) compared the lower molar morphology of Soriacebus to callitrichines, where the trigonid is also large in the lower molars. But callitrichines are quite different from Soriacebus by having reduced talonid and talonid cusps. Thus, there is no homologous similarities between callitrichines and Soriacebus, emphasizing the possible autopomorphic condition of the lower molar morphology in the latter. An alternative view suggests an individual variation in the lower molars of the type, based on a new finding of S. ameghinorum (Tejedor, 2003; Tejedor, in prep.). But the major synapomorphies of Soriacebus and pitheciins are the anterior dentition with compressed and procumbent incisors and projecting canines, as well as a strong symphysis and a mandibular corpus that deepens posteriorly, being very deep below the molars.

Other fossil pitheciins were also recovered in Patagonia. Proteropithecia neuquenensis is a poorly represented species from Colloncuran sediments (Middle Miocene) at Cañadón del Tordillo, Neuquén Province (Kay et al., 1998). Soriacebus-like primates were reported from Colhuehuapian deposits in Chubut Province (Kay et al., 1999) but remains undescribed. A left upper canine was recovered at Gran Barranca, in south central Chubut, which shows pitheciin affinities and proportions (Tejedor, 2002) resembling Soriacebus in having a projecting crown with no basal enlargement and a deep mesial groove. Hershkovitz (1981) attributed a mandibular fragment from Gran Barranca with the right P_4 in situ to Homunculus sp, but Fleagle (1990) held the view that it could be allocated to Soriacebus cf. ameghinorum, based especially on the buccal expansion of P₄, long trigonid and reduced occlusal surface. Additionally, this mandible

is deep and thin buccolingually with a robust symphysis, and may have been rather V-shaped.

These additional specimens, along with those collected in the Pinturas Formation, support the view of a broader geographic and temporal radiation of pitheciin primates, having its earliest representatives in Patagonia.

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AMEGHINIANA 42 (1), 2005