NEW PRIMATES FROM THE RÍO SANTA CRUZ AND RÍO BOTE (EARLY–MIDDLE MIOCENE), SANTA CRUZ PROVINCE, ARGENTINA

RICHARD F. KAY¹
JONATHAN M. G. PERRY²

¹Department of Evolutionary Anthropology and Division of Earth and Ocean Sciences, Box 90383, Duke University, Durham, North Carolina, United States of America.
²Department of Functional Anatomy and Evolution, The Johns Hopkins University, Baltimore, Maryland, United States of America.

Recibido: 25 de marzo 2019 - Aceptado: 24 de agosto 2019

Para citar este artículo: Richard F. Kay, and Jonathan M.G. Perry (2019). New primates from the Río Santa Cruz and Río Bote (Early–Middle Miocene), Santa Cruz Province, Argentina. Publicación Electrónica de la Asociación Paleontológica Argentina 19 (2): 230–238.

Link a este artículo: http://dx.doi.org/10.5710/PEAPA.24.08.2019.289
NEW PRIMATES FROM THE RÍO SANTA CRUZ AND RÍO BOTE (EARLY–MIDDLE MIOCENE), SANTA CRUZ PROVINCE, ARGENTINA

RICHARD F. KAY1, AND JONATHAN M.G. PERRY2

1Department of Evolutionary Anthropology and Division of Earth and Ocean Sciences, Box 90383, Duke University, Durham, North Carolina, United States of America. richard.kay@duke.edu
2Department of Functional Anatomy and Evolution, The Johns Hopkins University, Baltimore, Maryland, United States of America. jperry31@jhmi.edu

Abstract. Four specimens of primates were collected from the Santa Cruz Formation (Early–Middle Miocene) during expeditions undertaken by the Museo de la Plata, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, and Duke University in 2013, 2014, and 2017. A new species of Homunculus Ameghino, H. vizcainoi (Platyrrhini, Homunculidae), was identified at Barrancas Blancas, and Segundas Barrancas Blancas localities on the right bank of the Río Santa Cruz (Santa Cruz Province, Argentina). The Barrancas Blancas specimen comes from a tuff dated at 17.04 Ma; those from Segundas Barrancas Blancas are older than a tuff dated at 16.32 Ma and younger than a tuff dated at 17.36 Ma. A Río Bote specimen is confidently identified as Homunculus, but of uncertain species. All these fossil primates are temporally equivalent to those from the coastal Santa Cruz Formation, and younger than those from the Pinturas Formation to the north. By contrast, the lower and middle strata of the Pinturas Formation contain a different but closely related taxon, Carlocebus Fleagle. All known records of Carlocebus from the Pinturas Formation in north central Santa Cruz Province are older than the known occurrences of Homunculus in the Santa Cruz Formation in the Río Santa Cruz valley, Río Bote and elsewhere.

Key words. Homunculus. Carlocebus. Santa Cruz Formation. Pinturas Formation. Platyrrhini. Anthropoidea. Homunculidae.

PRIMATES are rare elements of the Early and Middle Miocene of Argentina and adjacent areas of Chile. The earliest recorded occurrences of the order in Argentina are from the Sarmiento Formation of Chubut Province in the Colhuehuapian South American Land Mammal Age (SALMA) (~21 Ma): Tremacebus harringtoni Rusconi, 1933; Dolichocebus gaimanensis Kraglievich, 1951; and Mazzonicebus almendrae Kay, 2010; an unnamed taxon from the Cerro Bandera Formation, Neuquén Province (Kramarz et al., 2012); and Chilecebus carrascoensis Flynn et al., 1995. Next to occur temporally are specimens from the Pinturas Formation of Santa Cruz Province. These specimens occur in the Pinturan phase of the Santacrucian SALMA (~18–17 Ma; Perkins et al., 2012) and represent two genera: Soriacebus Fleagle et al., 1987, and Carlocebus Fleagle, 1990. Finally, the Santa Cruz Formation (SCF) ranging in age between ~17.8 and 15.6 Ma (Cuitiño et al., 2016; Trayler et al., 2019), has yielded Homunculus Ameghino, 1891a –including the synonymous
Killickaïke Tejedor et al., 2006, according to Perry et al. (2014). Primates last occur in Argentina (before the Recent) in Neuquén Province in the Middle Miocene Collón Curá Formation ~15.9 Ma, as Proteropithecia neuquenensis Kay et al., 1999. The published age of this locality is 15.7 Ma (Kay et al., 1998), but the Fish Canyon sanidine is now accepted to be 28.2 Ma, so all the calculated ages are a bit older, roughly 15.9 Ma for the Pilcaniyeu ignimbrite. Proteropithecia Kay et al., 1999 also occurs in the penecontemporaneous Río Frías Formation in the area of Río Cisnes, Chile (Bostelmann et al., 2012; R. Kay personal observations).

In this communication, we note new records of fossil primates in the SCF from the southern cliffs of the Río Santa Cruz and from the Río Bote locality of western Santa Cruz Province, Argentina. These localities were reported by Fernicola et al. (2014) (see Fernicola et al., 2019). We show how Homunculus and Carlocebus can be distinguished based on the anatomy of the lower molars. The new material, which forms the basis of a new species of Homunculus is slightly younger than Carlocebus.

**MATERIALS AND METHODS**

*Studied specimens.* The described specimens are stored in the permanent collections of Museo Regional Provincial “Padre M. Jesús Molina”, Río Gallegos, Argentina (Tab. 1). Both this publication and the new taxon erected herein are registered in ZooBank and the resulting life science identifiers (LSID) are provided.

**Geological setting.** The specimens discussed come from several localities along the Río Santa Cruz and near Río Bote (Fig. 1). All derive from the Santa Cruz Formation. Details of the geologic setting are provided in Fernicola et al. (2014), Cuitiño et al. (2016, 2019). Specific locality information is summarized in Table 1.

**Institutional abbreviations.** MACN-A, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Colección Nacional Ameghino, Buenos Aires, Argentina; MACN-PvSC, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Colección Santa Cruz, Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MPM-PV, Museo Regional Provincial “Padre M. Jesús Molina”, Río Gallegos, Argentina.

**SYSTEMATIC PALEONTOLOGY**

*Class Mammalia* Linnaeus, 1758  
*Order Primates* Linnaeus, 1758  
*Suborder Anthropoidea* Mivart, 1864  
*Infraorder Platyrrhini* Geoffroy Saint-Hilaire, 1812  
*Family Homunculidae* Ameghino, 1894  

**Genus Homunculus** Ameghino, 1891a

*Type species.* Homunculus patagonicus Ameghino, 1891a. Santa Cruz Formation. Original type (specimen mislaid) from north shore of Río Gallegos, probably Estancia Felton (now Estancia Killik Aike Norte); proposed neotype (MACN-A 5757) from Corriguen Aike (now...
Puesto Estancia La Costa; see Kay et al. (2012) for further details.  
**Revised generic diagnosis.** Homunculidae with marginally positioned molar cusps such that the trigonid and talonid basins are nearly as broad as the entire crowns. By contrast, in the other recognized homunculid, *Carlocebus*, the occlusal surfaces slope more shallowly from the cusp tips (protoconid and metaconid, or hypoconid and entoconid) to the buccal and lingual margins of the crown. Thus, the cusp tips in *Carlocebus* are more internally located on the crown (Fleagle, 1990). Especially on m1, the trigonid basin of *Homunculus* is broader (buccolingual dimension) relative to trigonid breadth, whereas in *Carlocebus* the trigonid is narrower (Feagle, 1990). In the m2 of *Homunculus*, the distolingual basin is very faint or lacking; whereas *Carlocebus* has a well-developed distolingual basin. The distolingual basin is situated distal and buccal to the entoconid; it is the part of the tooth that receives the hypocone (see Fig. 2). In
these two taxa, the size of the basin is a correlative of the size of the hypocone which, in *Carlocebus*, is larger than that of *Homunculus*. On m1, this basin sometimes is less distinct in *Carlocebus*. It is not recorded on the m1 of *Homunculus*. The m3 trigonid breadth of *Homunculus* is 18% to 24% greater than the talonid breadth whereas the trigonid and talonid breadths are more nearly equal in the m3 of *Carlocebus* (range, 5% to 14%) (Figs. 3, 4; Tab. 2). The lower molars of *Homunculus* are higher crowned than those of *Carlocebus* (Fig. 2).

According to Fleagle (1990) *Homunculus* shows a somewhat greater height disparity between the molar trigonids and talonids whereas in *Carlocebus* the trigonids and talonids are more nearly of equal height. However, samples of these taxa collected since 1990 do not confirm this difference.

---

**Figure 3.** Line drawings of occlusal views of m3s of *Homunculus* and *Carlocebus* (drawings not to scale). 1, MACN-Pv SC 306, *Carlocebus*; 2, MACN-Pv SC 314, *Carlocebus*; 3, MPM-PV 3708, *Homunculus patagonicus*; 4, MPM-PV 17452, *Homunculus* sp., m3 from Río Bote.

---

**Figure 4.** Box plot of the distribution of the ratio of m3 trigonid breadth versus m3 talonid breadth for the specimens listed in Table 2, with the addition of a sample of 20 specimens of the extant monkey *Collicebus torquatus* (Hoffmannsegg, 1807). The Río Bote m3 (MPM-PV 17452 *Homunculus* sp.) is indicated by a blue asterisk. Measurements were made with a calibrated reticle through a binocular microscope at 12x magnification.

**Figure 5.** Occlusal views of specimens of *Homunculus vizcainoi* sp. nov. and *Homunculus* sp. from Río Santa Cruz and Río Bote, respectively. 1, MPM-PV 19426 (type of *H. vizcainoi* sp. nov.), left m1, Segundas Barrancas Blancas; 2, MPM-PV 19428 *H. vizcainoi*, left m1-m2, Barrancas Blancas; 3, MPM-PV 17452 *Homunculus* sp., left m3, Río Bote. Scale bar= 5 mm.
**Homunculus vizcainoi** sp. nov.

Figures 5–7

LSID: zoobank.org:pub: 97566577-2B0D-41DE-B2BA-251ADF0A661

**Derivation of name.** In honor of Dr. Sergio F. Vizcaíno for his contributions to the study of the paleobiology of Santacrucian mammals.

**Diagnosis.** Conforms to the m1 of *Homunculus patagonicus*, and differs from *Carlocebus* spp. in having marginally situated molar cusps and in lacking an m1distolingual basin. Distinguished from the m1 of *H. patagonicus* by its smaller size (Fig. 7; Supplementary Online Information Appendix 1) and from *H. patagonicus* and all other Santacrucian primates (*Soriacebus* spp., *Carlocebus* spp.) in having a discrete paraconid situated mesially and slightly buccally from the metaconid and a lingually open trigonid basin. In contrast, *H. patagonicus* and *Carlocebus* spp. have a variably sharp marginal crest bounding the trigonid mesially but lack a discrete swelling that would denote a paraconid. Also, the lingual notch in the trigonid basin is narrower in *H. patagonicus* and *Carlocebus* spp.

**Type material.** MPM–PV 19426, a left m1 in a fragment of a mandible.

**Referred material.** MPM–PV 19427 and MPM–PV 19428.

**Geographic occurrence.** Valley of the Río Santa Cruz, Santa Cruz Province (Fig. 1; Tab. 1).

**Stratigraphic occurrence.** Type specimen from Barrancas Blancas on south side of Río Santa Cruz (Fig. 1) in Estancia Aguada Grande, Santa Cruz Province. Santa Cruz Formation at the level of the RSC–7 tuff dated at 17.04 Ma (Cuitiño et al., 2016). Occurrences of referred material listed in Table 1.

**Description.** Two features of MPM–PV 19426 lead to the conclusion that it is a different species than *Homunculus*

---

**Figure 6.** MPM–PV 19426, left m1, type of *Homunculus vizcainoi* sp. nov., Segundas Barrancas Blancas, Río Santa Cruz. 1, distal view; 2, occlusal view; 3, buccal view. Scale bar= 5 mm.

**Figure 7.** Bivariate plot of the mesiodistal versus buccolingual dimensions of the first lower molars of *Homunculus* species. Also included is a sample of 20 specimens of the extant platyrrhine *Callicebus torquatus* (black dots), which gives a sense of the amount of variation encountered in an extant platyrrhine of similar size. Blue triangles represent *Homunculus patagonicus*. Blue asterisks represent *H. vizcainoi* sp. nov. molars from Río Santa Cruz (MPM–PV 19426, MPM–PV 19428). Outlier blue triangle represents a third, yet unnamed species of *Homunculus* from Puesto Ea. La Costa. Measurements were made with a calibrated reticle through a binocular microscope at 12x. Measurements are given in Supplemental Online Information.
**Table 2 – Lower third molar mesiodistal and buccolingual dimensions of Homunculidae Ameghino, 1894**

| Taxon                              | Catalog number | Formation | Locality¹ | m-d  | trigonid b-l | talonid b-l | trigonid b-l / talonid b-l |
|------------------------------------|----------------|-----------|-----------|------|--------------|-------------|---------------------------|
| *Carlocebus carmenensis*           | MACN-PVSC 306  | Pinturas  | CM        | 5.00 | 4.21         | 3.79        | 1.11                      |
| *Carlocebus carmenensis*           | MACN-PVSC 314  | Pinturas  | LR        | 4.65 | 4.22         | 3.69        | 1.14                      |
| *Carlocebus intermedius*           | MACN-PVSC 248  | Pinturas  | PSS       | 4.86 | 4.19         | 4.00        | 1.05                      |
| *Carlocebus carmenensis*           | MACN-PVSC 68   | Pinturas  | PSN       | 5.14 | 4.11         | 3.59        | 1.14                      |
| *Carlocebus carmenensis*           | MACN-PVSC 76   | Pinturas  | PSN       | 4.65 | 4.15         | 3.97        | 1.05                      |
| *Carlocebus carmenensis*           | MACN-PVSC 378  | Pinturas  | PSN       | 5.33 | 3.98         | 3.83        | 1.04                      |
| *Carlocebus intermedius*           | MACN-PVSC 3103 | Pinturas  | LR        | 5.14 | 3.97         | 3.59        | 1.11                      |
| *Carlocebus intermedius*           | MSCP-NVSC 3100 | Pinturas  | LL        | 5.39 | 3.96         | 3.72        | 1.06                      |
| *Homunculus patagonicus*           | MPM-PV 3504    | Santa Cruz | ELC    | 4.28 | 3.78         | 2.94        | 1.29                      |
| *Homunculus patagonicus*           | MACN-A 5757    | Santa Cruz | PLC    | 4.25 | 3.46         | 2.92        | 1.18                      |
| *Homunculus, sp. nov. not named*   | MPM-PV 3708    | Santa Cruz | PLC    | 4.32 | 3.82         | 3.14        | 1.22                      |
| *Homunculus* sp.                   | MPM-PV 17452   | Santa Cruz | RB     | 4.73 | 3.55         | 2.86        | 1.24                      |

¹Locality abbreviations: CM, Cerro de los Monos; ELC, Estancia La Costa; LL, Loma de la Lluvia; LR, Loma de las Ranas; PLC, Puesto Estancia La Costa; PSN, Portezuelo Sumich Norte; PSS, Portezuelo Sumich Sur; RB, Río Bote.

*patagonicus*. 1) A distinctive feature of this tooth not seen in any *Homunculus patagonicus* specimens (of which we have a sample of 13) is the presence on the mesial trigonid ridge of a discrete paraconid (which is small). 2) MPM-PV 19426 is also very small. Comparing m1 mesiodistal length between a sample of 13 *H. patagonicus* and two *H. vizcainoi* sp. nov., the two sample means are significantly different (t < 0.0007). A Wilcoxon rank sum test yields a probability of 0.0338 that these are drawn from the same sample population. Likewise, comparing m1 areas, the two samples differ at the level of t < 0.0001; the Wilcoxon rank sum test yields a probability of 0.036.

Two referred primate specimens were recovered from the Segundas Barrancas Blancas at Estancia El Tordillo, Santa Cruz Province. The first is MPM-PV 19428, a broken left mandible with m1 and m2 (Fig. 5.2). The second is MPM-PV 19427, a very poorly preserved right mandible with three broken molars. Both come from a weathering clay flat variously recorded as being approximately 90 m above sea level and about 20 m below a rust-red weathering tuff (called CECA-2) dated at 16.32 Ma (Cuitiño *et al.*, 2016).

The mandibular specimen, MPM-PV 19427, is too broken for detailed comparison with other identified primate specimens. Nevertheless, the preserved anatomy suggests it is of similar size and proportions to MPM-PV 19428, and distinct from *H. patagonicus* (see above). Considering the advanced state of wear in MPM-PV 19427, not much can be said about dental morphology other than that the cusps were marginally situated and the m2 lacks a buccolingual basin, both of which are characteristics of *Homunculus*, as distinct from *Carlocebus*. The m1 is too heavily worn and its mesial margin too damaged to determine whether the specimen had an m1 paraconid, which is present in the holotype.

*Homunculus* **spp.**

*Referred material.* MPM-PV 17452, left m3.

*Geographic occurrence.* Río Bote, Santa Cruz Province.

*Stratigraphic occurrence.* Collected from SCF at Río Bote above tuff RSC-27, dated at 17.36 Ma (Cuitiño *et al.*, 2016).

*Description.* MPM-PV 17452 is an m3, as indicated by the
presence of an interproximal wear facet on its mesial face (where it touched m2) and the absence of such a facet on its distal margin. As in Homunculus, but distinct from Carlocebus, the talonid of MPM-PV 17452 is narrower than the trigonid (Tab. 2). Furthermore, the cusps of the trigonid and talonid are marginally situated so that the occlusal surface is quite broad and the sides of the marginal cusps bulge only slightly. Therefore, we conclude that this tooth represents an individual of Homunculus.

The ratio of m3 trigonid breadth to m3 talonid breadth in Carlocebus carmenensis Fleagle, 1990, Carlocebus intermedius Fleagle, 1990, and Homunculus spp. support the allocation of MPM-PV 17452 to Homunculus (see table of lower molar dimensions in the Supplementary Online Information Fig. 4).

Comment. Notohippus toxodontoides Ameghino, 1891b (Family Notohippidae) as well as the astrapotheres Astrapothericulus iheringi (Ameghino, 1899) occur below the tuff RSC-27. This “Notohippus fauna” or “Notohippidense” faunal zone was established as a fossil-based stratigraphic marker by F. Ameghino (1902, 1906) based on the presence of Notohippus (Cassini et al, 2012; Vizcaíno et al, 2012; Fernicola et al, 2019). Thus, MPM-PV 17452 comes from higher in the stratigraphic section than the Notohippus fauna and is younger.

DISCUSSION

The newly recovered Santa Cruz Formation primates described here, falls within the temporal range of Homunculus documented elsewhere and is younger from the homunculid Carlocebus from the Pinturas Formation in north-western Santa Cruz Province. It extends the geographic range of Homunculus north and west from other previously described specimens that are all known from Atlantic coastal Santa Cruz Province and from the estuary of Río Gallegos. These represent a new species, Homunculus vizcainoi, currently known from only the Río Santa Cruz; it is distinctly smaller than H. patagonicus and it can be distinguished from it by the presence of a discrete m1 paraconid.

If there were additional primate material from the Río Santa Cruz, it would be critical to compare the new material from there before describing a new species. The only other fossil primate known to be from the Río Santa Cruz is very dubious and cannot be adequately compared with the new material described here. That material was described by Alcides Mercerat in 1891 as a primate he called Ecphantodon ceboides Mercerat, 1891. Mercerat’s taxon was based on a right mandibular fragment with a damaged m1 from the “Barrancas del Río Santa Cruz” (Mercerat, 1981).

Although Mercerat’s primate was published at a later date than Ameghino’s specimens, and therefore Ecphantodon ceboides is a subjective junior synonym of Homunculus patagonicus Ameghino, 1891, it almost certainly was the first specimen of a Miocene primate discovered in Argentina, although precisely how much earlier it was collected is uncertain.

An additional problem is that Mercerat’s Ecphantodon ceboides can no longer be found. The type specimen was a fragmentary right mandible with a single tooth damaged on its distolingual corner, which Mercerat identified as an m1. One potential candidate was recently considered to be the lost specimen of E. ceboides. This is a right mandibular specimen of a primate in the MLP “old collections” (MLP 66-V-2-2).

MLP 66-V-2-2 consists of a right mandibular fragment with roots for i2, c, single-rooted p2-p3, a broken distal crown of p4, and the mesial (trigonid) portion of the crown of the first molar. Mercerat’s description of the type specimen says there is one tooth, not two broken ones. Possibly Mercerat confused the distal part of p4 and the mesial part of m1 as being two parts of a single tooth. We doubt this to be the case because the mesial tooth part — which would, in fact, be the distal part of the p4 — does not have any indication of the raised mesial margin mentioned in Mercerat’s description. Furthermore, Mercerat reported on the dimensions of the roots of the m1 in his specimen, but there would have been no way to measure the roots of MLP 66-V-2-2 because they are embedded in the mandible and not visible externally. Alternatively, perhaps the distal part of m1 has since been lost. But this seems unlikely because the mandible as a whole is broken off on a plane corresponding to the distal margin of the m1 trigonid, so it is unlikely that the distal part of m1 would have been preserved in the specimen, when collected. A final problem is that MLP 66-V-2-2 is not accompanied by locality information. All we know is that it is from the “old collections”. There is no evidence to suggest that it came from the Río Santa Cruz.

Given the considerable discrepancies between Mercerat’s
description and MLP 66-V–2–2, and in the absence of any contemporaneous locality information, we are disinclined to accept that this specimen is the lost type of *Ecphantodon ceboides*. Therefore, we consider *E. ceboides* to be a *nomen dubium*.

With doubt cast on the status of *Ecphantodon ceboides* due to a lack of definite referable material, this leaves no primate material from the Río Santa Cruz with which to compare the new specimens. Furthermore, we cannot adequately evaluate Ameghino’s claim that Mercerat’s material should be considered *Homunculus patagonicus* because the type and only specimen of *E. ceboides* is lost. The establishment of a new species name for the Río Santa Cruz primate material is warranted on the basis of diagnostic differences between the type and known material of *Homunculus patagonicus* as well as large differences between the type and known material of *Carlocebus*. Currently *Homunculus vizcaínoi* sp. nov. is the only primate definitely known from the Río Santa Cruz. The Río Bote molar certainly belongs with *Homunculus*, not *Carlocebus*, but absence of comparable anatomical parts make allocation to species uncertain.

**ACKNOWLEDGEMENTS**

We thank S.F. Vizcaíno (SFV), and M.S. Bargo (MSB) for the opportunity to collaborate on field expeditions in Río Santa Cruz and for many helpful discussions about the paleobiology of Santa Cruz vertebrates. We thank J. Cuitiño, for help with the geology of the Santa Cruz Formation in the Río Santa Cruz valley. We thank J.C. Fernicola (JCF) for productive discussions about the history of paleontological collecting on the river. G. De lulis provided helpful taxonomic advice. M. Bond, and M. Reguero (MLP) were enormously helpful concerning the history of MLP "old collections" and a search for the lost type of *Ecphantodon*. This research was supported by the following grants: PIP–CONICET 00781 to J.C. Fernicola and SFV, UNLP N867 to SFV and MSB PICT 2013–0389 to SFV PICT 2017–1081 to MSB and NSF BCS 1348259 to R.F. Kay.

**REFERENCES**

Ameghino, F. 1891a. Nuevos restos de mamíferos fósiles descubiertos por C. Ameghino en el Eoceno inferior de la Patagonia austral. Especies nuevas, adiciones y correcciones. *Revista Argentina de Historia Natural* 1: 289–328.

Ameghino, F. 1891b. Caracteres diagnósticos de cincuenta especies nuevas de mamíferos fósiles argentinos. *Revista Argentina de Historia Natural* 1: 129–167.

Ameghino, F. 1894. Enumeración synoptique des espèces de mammières fossiles des formations Eogènes de Patagonie. *Boletín del Academia Nacional de Ciencias Córdoba* 13: 259–451.

Ameghino, F. 1899. Sinopsis geológico-paleontológica. *Suplemento (Adiciones y correcciones)* Imprenta La Libertad La Plata 1–13.

Ameghino, F. 1902. L’age des formations sédimentaires de Patagonia. *Annales de Societé Científica de Argentina* 54: 161–180, 220–240.

Ameghino, F. 1906. Les formations sédimentaires du Crétacé supérieur et du Tertiaire de Patagonie avec un parallèle entre leurs faunes mammalogiques et celles de l’ancien continent. *Anales del Museo Nacional de Buenos Aires, Série* 3: 15–1568.

Bostelmann, E., Bobe, R., Carrasco, G., Alloway, B., Santi-Malnis, P., Mancuso, A., Agüero, B., Alemseged, Z., and Godoy, Y. 2012. The Alto Río Cisnes fossil fauna (Río Frías Formation, early Middle Miocene, Friasian SALMA): a keystone and paradigmatic vertebrate assemblage of the South American fossil record. In: M. Leppe, J.C. Aravena, and R. Villa-Martínez (Eds.), *Abriendo ventas al pasado, 3° Simposio de Paleontología en Chile*. Instituto Antártico Chileno-Centro de Estudios del Cuaternario y Antártica, Punta Arenas, p. 46–49.

Cassini, G.H., Cerdeño, E., Villaña, A.L., and Muñoz, N.A. 2012. Paleobiology of Santacrucian native ungulates (Meridiungulata: Astropotheria, Litopterna and Notoungulata). In: S.F. Vizcaíno, R.F. Kay, and M.S. Bargo (Eds.), *Early Miocene Paleobiology in Patagonia: High–latitude paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, p. 243–286.

Cuitiño, J.I., Fernicola, J.C., Kohn, M., Naipauer, M., Bargo, M.S., Kay, R.F., and Vizcaíno, S.F. 2016. U-Pb geochronology of the Santa Cruz Formation at the Santa Cruz and Bote rivers (southernmost Patagonia, Argentina) and its implications for the fossil vertebrate communities. *Journal of South American Earth Sciences* 70: 198–210.

Cuitiño, J.I., Fernicola, J.C., Raigemborn, M.S., and Krapovickas, V. 2019. Stratigraphy and depositional environments of the Santa Cruz Formation (Early–Middle Miocene) along the Río Santa Cruz, southern Patagonia, Argentina. In: J.C. Fernicola, M.S. Bargo, S.F. Vizcaíno, and R.F. Kay (Eds.), *Early–Middle Miocene Paleontology in the Río Santa Cruz, Southern Patagonia, Argentina. 130 years since Ameghino*, 1887. Publicación Electrónica de la Asociación Paleontológica Argentina 19: 1A–33.

Fernicola, J.C., Cuitiño, J.I., Vizcaíno, S.F., Bargo, M.S., and Kay, R.F. 2014. Fossil localities of the Santa Cruz Formation (Early Miocene, Patagonia, Argentina) prospected by Carlos Ameghino in 1887 revisited and the location of the Notohippidion. *Journal of South American Earth Sciences* 52: 96–107.

Fernicola, J.C., Bargo, M.S., Vizcaíno, S.F., and Kay, R.F. 2019. Historical background for a revision of the paleontology of the Santa Cruz Formation (Early–Middle Miocene) along the Río Santa Cruz, Patagonia, Argentina. In: J.C. Fernicola, M.S. Bargo, S.F. Vizcaíno, and R.F. Kay (Eds.), *Early–Middle Miocene Paleontology in the Río Santa Cruz, Southern Patagonia, Argentina. 130 years since Ameghino*, 1887. Publicación Electrónica de la Asociación Paleontológica Argentina 19: 1–13.

Fleagle, J.G. 1990. New fossil platyrrhines from the Pinturas Formation, southern Argentina. *Journal of Human Evolution* 19: 61–85.

Fleagle, J.G., Powers, D.W., Conroy, G.C., and Watters, J.P. 1987. New fossil platyrrhines from Santa Cruz Province, Argentina. *Folia primatologica* 48: 65–77.

Flynn, J.J., Wyss, A.R., Charrier, R., and Swisher, C.C.I. 1995. An early Miocene anthropoid skull from the Chilean Andes. *Nature* 373: 603–607.

Hoffmannsieg, G. von 1807. Beschreibung vier affenartiger Thiere aus Brasilien. *Magazin Gesellschaft Naturforschungen Freunde, Berlin* 1: 83–104.

Kay, R.F. 2010. A new primate from the Early Miocene of Gran Ba-
rranca, Chubut Province, Argentina: Paleoecological implications. In: R.H. Madden, M.G. Vucetich, A.A. Carlini, and R.F. Kay (Eds.), *The Paleontology of Gran Barranca: Evolution and Environmental Change through the Middle Cenozoic of Patagonia*. Cambridge University Press, Cambridge, p. 220–239.

Kay, R.F., Johnson, D.J., and Meldrum, D.J. 1998. A new pitheciin primate from the middle Miocene of Argentina. *American Journal of Primatology* 45: 317–336.

Kay, R.F., Perry, J.M.G., Malinzak, M.D., Allen, K.L., Kirk, E.C., Plavcan, J.M., and Fleagle, J.G. 2012. The paleobiology of Santacrucian primates. In: S.F. Vizcaíno, R.F. Kay, and M.S. Bargo (Eds.), *Early Miocene Paleobiology in Patagonia: High-latitude paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, p. 306–330.

Kraglievich, J.L. 1951. Contribuciones al conocimiento de los primates fósiles de la Patagonia. I. Diagnosis previa de un nuevo primate fósil del Oligoceno superior (Colheuhuapiano) de Gaiman, Chubut. Comm. *Instituto Nacional Investigaciones Ciencias Naturales, II, Ciencias Zoológicas* 11: 57–82.

Kramarz, A.G., Tejedor, M.F., Forasiepi, A.M., and Garrido, A.C. 2012. New early Miocene primate fossils from northern Patagonia, Argentina. *Journal of Human Evolution* 62: 186–189.

Mercerat, A. 1891. Sobre la presencia de restos de monos en el eoceno de Patagonia. *Revista del Museo de La Plata* 2: 73–74.

Perkins, M.E., Fleagle, J.G., Heizler, M.T., Nash, B., Bown, T.M., Tauber, A.A., and Dozo, M.T. 2012. Tephrochronology of the Miocene Santa Cruz and Pinturas Formations, Argentina. In: S.F. Vizcaíno, R.F. Kay, and M.S. Bargo (Eds.), *Early Miocene Paleobiology in Patagonia: High-Latitude Paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, p. 23–40.

Perry, J.G.M., Kay, R.F., Vizcaíno, S., and Bargo, M. 2014. Oldest known cranium of a juvenile New World monkey (Early Miocene, Patagonia, Argentina): implications for the taxonomy, and the molar eruption pattern of early platyrrhines. *Journal of Human Evolution* 74: 67–81.

Rusconi, C. 1933. Nuevos restos de monos fósiles del Terriario antiguo de la Patagonia. *Anales de la Sociedad Científica Argentina* 116: 286–289.

Tejedor, M.F., Tauber, A.A., Rosenberger, A.L., Swisher III, C.C., and Palacios, M.E. 2006. New primate genus from the Miocene of Argentina. *Proceedings of the National Academy of Sciences* 103: 5437–5441.

Trayler, R.B., Schmitz, M.D., Cuitiño, J.L., Kohn, M.J., Bargo, M.S., Kay, R.F., Stromberg, C.A.E., and Vizcaíno, S.F. 2019. An Improved Approach to Age-Modeling in Deep Time: Implications for the Santa Cruz Formation, Argentina. *Bulletin of the Geological Society of America* doi.org/10.1130/B35203.1

Vizcaíno, S.F., Kay, R.F., and Bargo, M.S. 2012. Background for a paleoecological study of the Santa Cruz Formation (late Early Miocene) on the Atlantic Coast of Patagonia. In: S.F. Vizcaíno, R.F. Kay, and M.S. Bargo (Eds.), *Early Miocene Paleobiology in Patagonia: High-latitude paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, p. 1–22.

---

**Doi:** 10.5710/PEAPA.24.08.2019.289

**Recibido:** 25 de marzo 2019

**Aceptado:** 24 de agosto 2019