

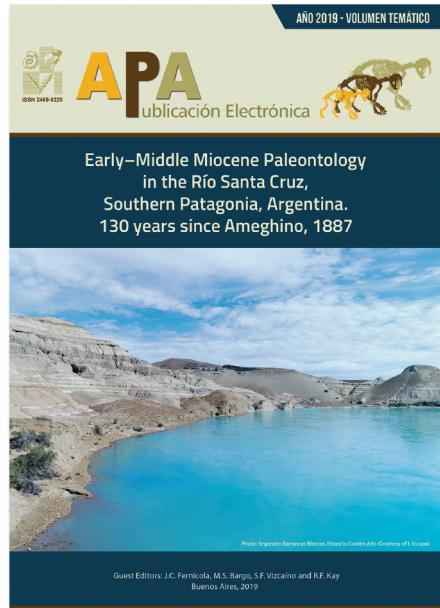
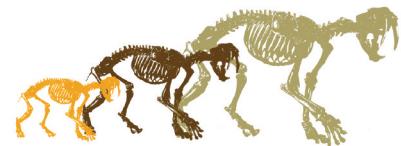


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NEW PRIMATES FROM THE RÍO SANTA CRUZ AND RÍO BOTE (EARLY–MIDDLE MIocene), SANTA CRUZ PROVINCE, ARGENTINA

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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.

Resumen. NUEVOS PRIMATES DEL RÍO SANTA CRUZ Y EL RÍO BOTE (MIOCENO TEMPRANO–MEDIO), PROVINCIA DE SANTA CRUZ, ARGENTINA. Se recuperaron cuatro especímenes de primates de la Formación Santa Cruz (Mioceno Temprano–Medio) durante las expediciones realizadas por el Museo de la Plata, el Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” y la Universidad de Duke en 2013, 2014 y 2017. Una nueva especie de *Homunculus* Ameghino, *H. vizcainoi* (Platyrrhini, Homunculidae), fue identificada en las localidades Barrancas Blancas y Segundas Barrancas Blancas en los afloramientos de la margen derecha del Río Santa Cruz (provincia de Santa Cruz, Argentina). El espécimen de Barrancas Blancas proviene de una toba datada en 17,04 Ma, mientras que aquellos de Segundas Barrancas Blancas son más antiguos que una toba fechada en 16,32 Ma y más jóvenes que una toba fechada en 17,36 Ma. Un espécimen de Río Bote fue identificado sin dudas como *Homunculus*, pero de una especie incierta. Estos primates fósiles son temporalmente equivalentes a los de la Formación Santa Cruz en la costa y más jóvenes que los de la Formación Pinturas al norte. Por el contrario, los estratos inferior y medio de la Formación Pinturas contienen un taxón diferente pero estrechamente vinculado, *Carlocebus* Fleagle. Todos los registros conocidos de *Carlocebus* de la Formación Pinturas en el centro norte de la provincia de Santa Cruz son más antiguos que aquellos conocidos de *Homunculus* en la Formación Santa Cruz en el valle del Río Santa Cruz, Río Bote y en otras localidades.

Palabras clave. *Homunculus*. *Carlocebus*. Formación Santa Cruz. Formación Pinturas. 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 Colhue-huapian 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

Killikaike 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 Cura 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 ANTHROPOOIDEA 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

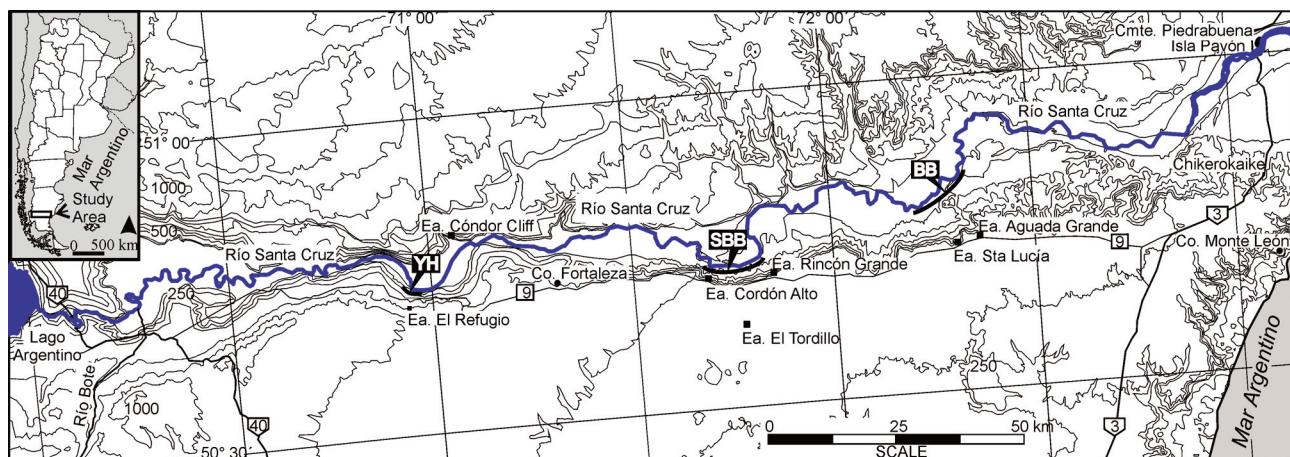


Figure 1. Map of the Río Santa Cruz with the prospected localities and estancias mentioned in the text. BB, Barrancas Blancas; SBB, Segundas Barrancas Blancas; YH, Yaten Huageno; RB, Río Bote; Ea., Estancia. Modified from Fernicola *et al.* (2014).

TABLE 1 – Summary of specimens collected along the Río Santa Cruz and Río Bote

| Year | Collector | Catalog number | Taxon | Material | Locality | Coordinates | Elevation ASL | Stratigraphic position |
|-------------|-------------------------|-------------------------------------|--------------------------------------|---|--------------------------------|------------------------------------|-----------------|--|
| Before 1891 | unknown | No catalog number; specimen missing | <i>Ephantodon ceboides</i> | right mandibular fragment with a damaged m1, per Mercerat, 1891 | "Barrancas del Río Santa Cruz" | — | — | — |
| 2013 | N. Toledo | MPM-PV 19426 (Type) | <i>Homunculus vizcainoi</i> sp. nov. | left m1 in a mandibular fragment | BB (EAG) | — | — | At level of RSC-7 tuff (17.04 Ma) |
| 2014 | J. Spradley | MPM-PV 19427 | <i>Homunculus vizcainoi</i> sp. nov. | very poorly preserved mandible with three molars (broken) | SBB (EET) | 50° 16.689' S 70° 15.282' W | 100.9 m in situ | About 20 m below CECA-2 (16.32 Ma) that weathers rust-red) |
| 2014 | L. Chornogubsky | MPM-PV 19428 | <i>Homunculus vizcainoi</i> sp. nov. | left m1-m2 | SBB (EET) | 50° 16' 41.6" S 70° 15' 16.6" W | 85 m | About 20 m below CECA-2 (16.32 Ma) that weathers rust-red |
| 2017 | S. Bargo S. Vizcaíno | MPM-PV 17452 | <i>Homunculus</i> sp. | left m3 | RB (EME) | | 490 m | Above tuff RSC-27 (17.36 Ma) |

Abbreviations: BB, Barrancas Blancas; SBB, Segundas Barrancas Blancas; RB, Río Bote; EET, Ea. El Tordillo; EAG, Ea. Aguada Grande; EME, Ea. Ma. Elisa.

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 (Feagles, 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

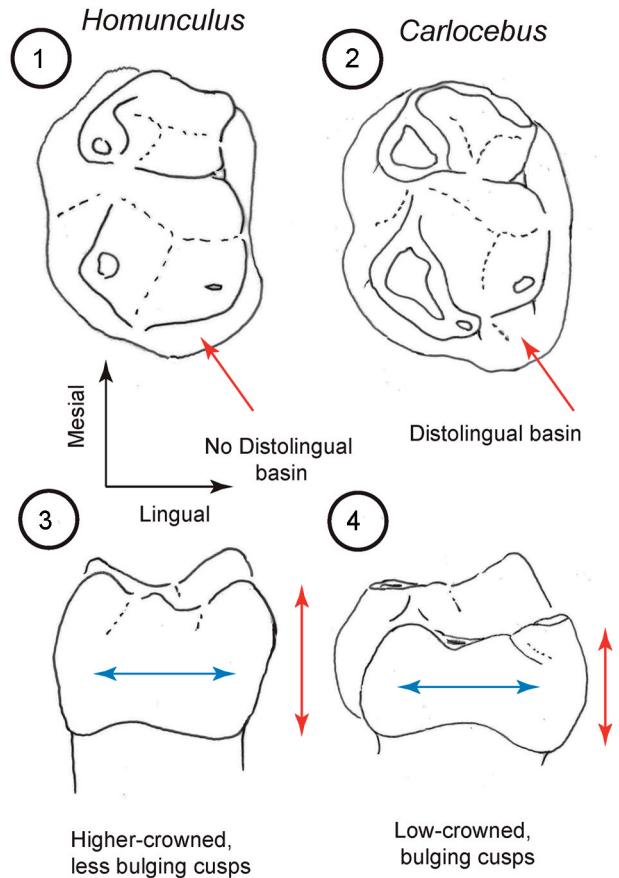


Figure 2. Line drawings illustrating the distinctive features of the lower molars of *Homunculus patagonicus* (MPM-PV 4376; left m2) and *Carlocebus carmenensis* (MACN-PvSC 266, right m2, image reversed). 1–2, Occlusal views of m2; 3–4, distal views of the m2.

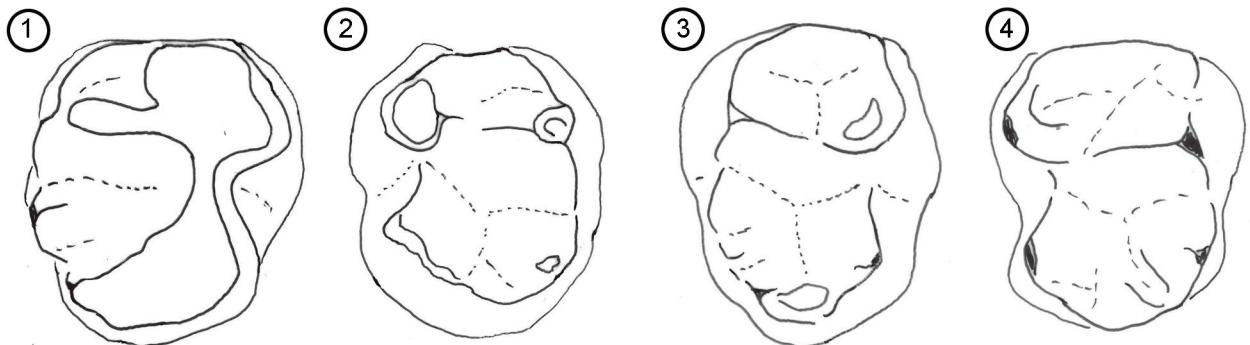


Figure 3. Line drawings of occlusal views of m3s of *Homunculus* and *Carocebus* (drawings not to scale). 1, MACN-Pv SC 306, *Carocebus*; 2, MACN-Pv SC 314, *Carocebus*; 3, MPM-PV 3708, *Homunculus patagonicus*; 4, MPM-PV 17452, *Homunculus* sp., m3 from Río Bote.

these two taxa, the size of the basin is a correlative of the size of the hypocone which, in *Carocebus*, is larger than that of *Homunculus*. On m1, this basin sometimes is less distinct in *Carocebus*. 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 *Carocebus* (range, 5% to 14%) (Figs. 3, 4; Tab. 2). The lower molars of *Homunculus* are higher crowned than those of *Carocebus* (Fig. 2).

According to Fleagle (1990) *Homunculus* shows a somewhat greater height disparity between the molar trigonids and talonids whereas in *Carocebus* the trigonids and talonids are more nearly of equal height. However, samples

of these taxa collected since 1990 do not confirm this difference.

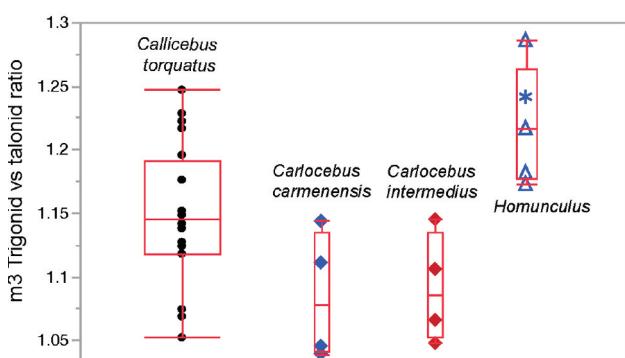


Figure 4. Box plot of the distribution of the ratio of m3 trigonid breadth versus m3 talonid breadth for the specimens listed in Table 2, with the addition of a sample of 20 specimens of the extant monkey *Callicebus torquatus* (Hoffmannsegg, 1807). The Río Bote m3 (MPM-PV 17452 *Homunculus* sp.) is 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.



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.

Homunculus vizcainoi sp. nov.

Figures 5–7

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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 m1 distolingual 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

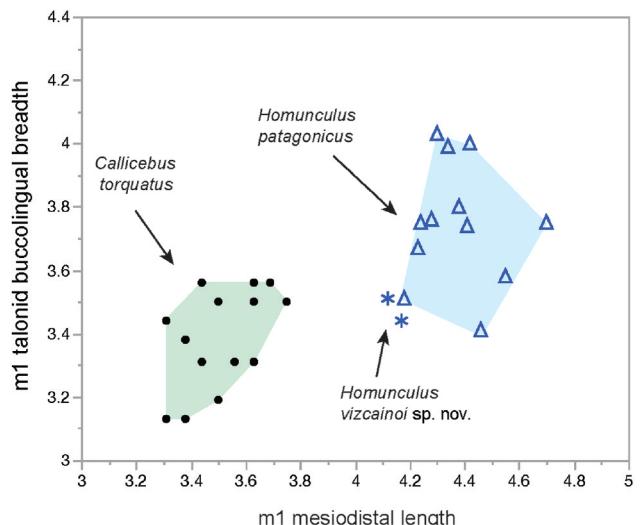


Figure 7. Bivariate plot of the mesiodistal versus buccolingual dimensions of the first lower molars of *Homunculus* species. Also included is a sample of 20 specimens of the extant platyrhine *Callicebus torquatus* (black dots), which gives a sense of the amount of variation encountered in an extant platyrhine 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.

(*Soricebus* 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*

TABLE 2 – Lower third molar mesiodistal and buccolingual dimensions of Homunculidae Ameghino, 1894

| Taxon | Catalog number | Formation | Locality ¹ | <i>m-d</i> | trigonid <i>b-l</i> | talonid <i>b-l</i> | trigonid <i>b-l</i> / talonid <i>b-l</i> |
|--|----------------|------------|-----------------------|------------|---------------------|--------------------|--|
| <i>Carlocebus carmenensis</i> | MACN-PVSC 306 | Pinturas | CM | 5.00 | 4.21 | 3.79 | 1.11 |
| <i>Carlocebus carmenensis</i> | MACN-PVSC 314 | Pinturas | LR | 4.45 | 4.22 | 3.69 | 1.14 |
| <i>Carlocebus intermedius</i> | MACN-PVSC 248 | Pinturas | PSS | 4.86 | 4.19 | 4.00 | 1.05 |
| <i>Carlocebus carmenensis</i> | MACN-PVSC 68 | Pinturas | PSN | 5.14 | 4.11 | 3.59 | 1.14 |
| <i>Carlocebus carmenensis</i> | MACN-PVSC 76 | Pinturas | PSN | 4.65 | 4.15 | 3.97 | 1.05 |
| <i>Carlocebus carmenensis</i> | MACN-PVSC 378 | Pinturas | PSN | 5.33 | 3.98 | 3.83 | 1.04 |
| <i>Carlocebus intermedius</i> | MACN-PVSC 3103 | Pinturas | LR | 5.14 | 3.97 | 3.59 | 1.11 |
| <i>Carlocebus intermedius</i> | MSCN-PVSC 3100 | Pinturas | LL | 5.39 | 3.96 | 3.72 | 1.06 |
| <i>Homunculus patagonicus</i> | MPM-PV 3504 | Santa Cruz | ELC | 4.28 | 3.78 | 2.94 | 1.29 |
| <i>Homunculus patagonicus</i> | MACN-A 5757 | Santa Cruz | PLC | 4.25 | 3.46 | 2.92 | 1.18 |
| <i>Homunculus</i> , sp. nov. not named | MPM-PV 3708 | Santa Cruz | PLC | 4.32 | 3.82 | 3.14 | 1.22 |
| <i>Homunculus</i> 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.

Figure 5.3

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 astrapothere *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 *Ephantodon 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 *Ephantodon ceboides* is a subjective junior synonym of *Homunculus patagonicus* Ameghino, 1891a, 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 *Ephantodon 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 *Ephantodon ceboides*. Therefore, we consider *E. ceboides* to be a *nomen dubium*.

With doubt cast on the status of *Ephantodon 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 vizcainoi* 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.

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