

ANALYSIS OF THE EARLY–MIDDLE MIOCENE MAMMAL ASSOCIATIONS AT THE RÍO SANTA CRUZ (PATAGONIA, ARGENTINA)

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Recibido: 28 de septiembre 2019 - **Aceptado:** 1 de noviembre 2019

Para citar este artículo: Juan C. Fernicola, Sergio F. Vizcaíno, M. Susana Bargo, Richard F. Kay, and José I. Cuitiño (2019). Analysis of the Early–Middle Miocene mammal associations at the Río Santa Cruz (Patagonia, Argentina). *Publicación Electrónica de la Asociación Paleontológica Argentina* 19 (2): 239–259.

Link a este artículo: <http://dx.doi.org/10.5710/PEAPA.01.11.2019.309>

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M.S. Bargo *et al.*

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M. Arnal *et al.*

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Abstract. The Santa Cruz Formation (SCF) records high latitude terrestrial paleoecosystems in the Southern Hemisphere during Burdigalian–early Langhian times (Early–Middle Miocene). Mammalian fossils from Río Santa Cruz (RSC) localities were first collected in the late 19th century, forming the basis for the Santacrucian South American Land Mammal Age. New collections permit an update of the SCF mammalian species along the RSC. The total taxonomic richness is 95 mammalian species. Many species considered by Ameghino as exclusive for the older Notohippidian stage at similar latitude in the west, are not in fact so. The taxonomic richness in three localities along the RSC is substantially different: 47 species from Barrancas Blancas (BB), 60 from Segundas Barrancas Blancas (SBB) and nine from Yaten Huageno. The faunal composition between BB and SBB is also different: they share 31 species, of which six are present only at BB and 20 only at SBB. More than 85 % of all RSC species are also found at Atlantic coastal exposures of the SCF. In spite of BB (~17.04–16.49 Ma) being closer in age to coastal exposures, and SBB fossils (~16.46–15.63 Ma) being younger than the coastal localities (~17.80–16.30 Ma), the greatest similarity is between SBB and the coast. Faunal differences among the localities may be accounted for local variation in climatic and environmental factors. Previously proposed Santacrucian biozones should be set aside. The exposures of the SCF along the RSC should be considered as the type area of this unit and the Santacrucian fauna.

Key words. Santacrucian. Burdigalian. Fossil vertebrates. Taxonomic richness. Biozone.

Resumen. ANÁLISIS DE LAS ASOCIACIONES DE MAMÍFEROS FÓSILES DEL MIOCENO TEMPRANO–MEDIO DEL RÍO SANTA CRUZ (PATAGONIA, ARGENTINA). La Formación Santa Cruz (FSC) registra paleoecosistemas terrestres de alta latitud en el hemisferio sur durante el Burdigaliense–Langhiense temprano (Mioceno Temprano–Medio). Los primeros mamíferos fósiles del Río Santa Cruz (RSC) fueron recolectados a fines del siglo 19 y constituyeron la base de la Edad Mamífero Santacrucense. Nuevas colecciones permitieron actualizar la lista de especies santacrucenses del RSC. La riqueza taxonómica total es de 95 especies. Muchas especies consideradas por Ameghino como exclusivas del más antiguo Piso Notohippidense no lo son en realidad. La riqueza taxonómica en las tres localidades del RSC es sustancialmente diferente: 47 especies en Barrancas Blancas (BB), 60 en Segundas Barrancas Blancas (SBB) y nueve en Yaten Huageno. La composición faunística también es diferente entre BB y SBB; comparten 31 especies, seis presentes solo en BB y 20 solo en SBB. Más del 85 % de las especies de mamíferos RSC también se encuentran en la FSC de la costa atlántica. Aunque BB (~17,04–16,49 Ma) es más próxima cronológicamente a las exposiciones costeras y los fósiles de SBB (~16,46–15,63 Ma) son más jóvenes, se registra mayor similitud entre SBB y la costa (~17,80–16,30 Ma). Las diferencias faunísticas entre las localidades podrían explicarse por la variación local de factores climáticos y ambientales. Las biozonas propuestas previamente deben ser dejadas de lado. Las exposiciones de la FSC a lo largo del RSC deben considerarse como el área tipo de la unidad y la fauna santacrucense.

Palabras clave. Santacrucense. Burdigaliense. Vertebrados fósiles. Riqueza taxonómica. Biozona.

THE SANTA CRUZ Formation (SCF) is an Early–Middle Miocene continental sedimentary succession distributed in a large area of southern Patagonia that contains one of the richest fossil vertebrate assemblages of the Cenozoic of South America and formed the basis of the Santacrucian South American Land Mammal Age (SALMA; Pascual *et al.*, 1965). Its conceptualization as a regional faunal association goes back to the 19th century (Ameghino, 1889).

The first formal geological and paleontological survey of the SCF was carried out on outcrops along the Río Santa Cruz (RSC) in 1887 by Carlos Ameghino, then “Traveling Naturalist” of the Museo de La Plata (Fernicola, 2011a,b; Vizcaíno, 2011; Vizcaíno *et al.*, 2013; Fernicola *et al.*, 2019a). One of Ameghino’s main objectives was to increase the number of fossils that F.P. Moreno (then lifetime Director of the Museo de La Plata since 1884) had collected in that region during an expedition to Southern Patagonia in 1876 and 1877 (Moreno, 1879; Fernicola *et al.*, 2019a). Carlos Ameghino returned to the Museo de La Plata with more than 2000 fossil specimens that were immediately studied by his brother Florentino, who named 110 new species of mammals (Ameghino, 1887a), dramatically increasing the number of Santacrucian taxa from the 12 described earlier (Fernicola *et al.*, 2019a and references therein). When F. Ameghino was relieved of his duties at the Museo de La Plata in 1888, he appropriated a part of the Santacrucian collection made in 1887 (see Fernicola, 2011a,b), among which were a number of type specimens. Carlos Ameghino was expelled from the Museo by Moreno in 1888, but he continued collecting fossils from Patagonia for his brother until 1903 (Vizcaíno *et al.*, 2013). Ameghino (1889) proposed 15 additional species based on specimens from the RSC. Using these collections, he conceptualized a *Fauna Santacrucense* coming from the *Piso Santacrucense*. Between 1888 and 1889, Moreno launched new Museo de La Plata expeditions to collect fossils from the RSC and placed the Swiss geologist Alcides Mercerat in charge of the paleontological collections in the Museo de La Plata. Between 1887 and 1894, approximately 500 added taxa from the SCF were proposed by Ameghino and Mercerat, of which about 120 type specimens came from the RSC (Fernicola *et al.*, 2019a).

Later, Ameghino (1900–02, 1906) subdivided his *Piso Santacrucense* into a supposed older *notohippidéen* and a

younger *santacruzéen* stages. In the process, he transferred to the Notohippidian 15 species originally described for the RSC, thereby obscuring the real distinction between the two stages (Fernicola *et al.*, 2014, 2019a).

Meanwhile, new exposures of the SCF along the Atlantic coast discovered in 1890–91, unlike those of the RSC, produced more complete specimens redirecting the fieldwork and academic study of Santacrucian faunas away from the RSC (Vizcaíno, 2011; Vizcaíno *et al.*, 2012a, 2013; Fernicola *et al.*, 2019a). As a consequence, collecting in the RSC exposures was neglected for more than a century. In fact, it took more than 120 years to reidentify the precise location of the sites prospected by Carlos Ameghino in 1887 (Fernicola *et al.*, 2014). This “coastal” approach has since dominated our thinking about the SCF and its fossils chronologically and geographically. Indeed, Marshall *et al.* (1983, p. 28; 1986, p. 450) considered the formation’s outcrops at the coastal region of Monte León, near the mouth of the RSC, to be the ...“*nominal type locality*”... of the SCF and the Santacrucian SALMA, when in fact it was not (see below).

The embedded inconsistencies in the scientific literature about the distinctness of the Santacrucian and Notohippidian stages, and the incorrect identification of the type region for the Santacrucian fauna as it was originally conceived by Ameghino (1889), added to the effects it has had on comparisons with other Early and Middle Miocene Patagonian faunas, has lead us to reopen the neglected geological and paleontological study of the formation along the river (Fernicola *et al.*, 2019a). The preliminary results of this new study are reported in this volume (Fernicola *et al.*, 2019b).

Our objective in what follows is to compile and analyze an updated mammalian taxonomic list of the SCF at the RSC in order to compare it with earlier studies of the RSC, comparing taxonomic richness of the different localities along the RSC, and assessing the value of the biostratigraphic units (biozones) of the Santacrucian fauna as a whole based upon its type locality.

GEOLOGIC SETTING

The Santa Cruz Formation is situated within the Austral-Magallanes geological basin (Dalziel *et al.*, 1974). This unit corresponds to the younger part of the foreland basin stage and its accumulation is thought to be strongly controlled by

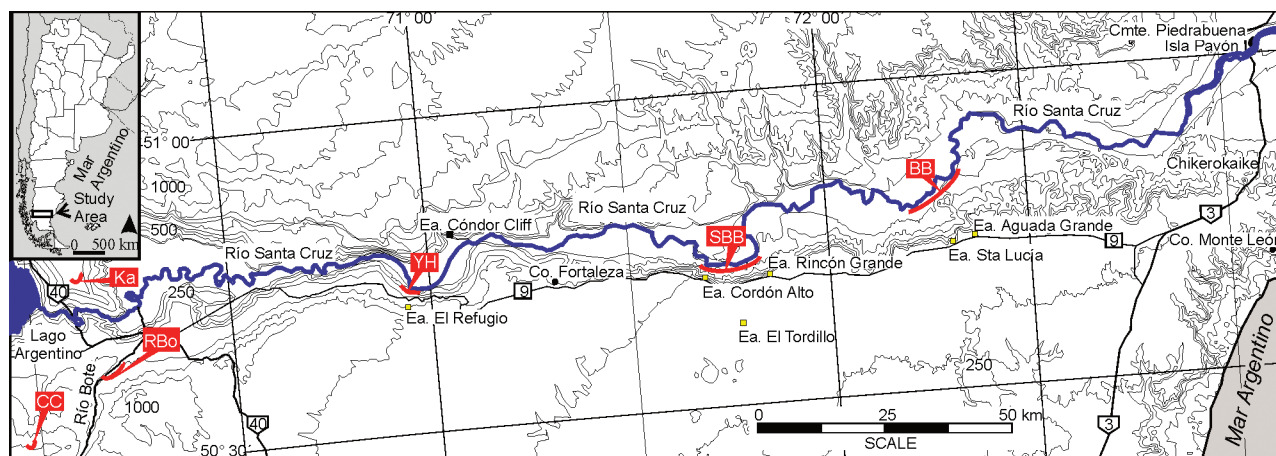


Figure 1. Map of the Río Santa Cruz with the prospected localities and estancias mentioned in the text. BB, Barrancas Blancas; CC, Cerro Centinela; Ea., Estancia; Ka, Karaiken; RBo, Río Bote; SBB, Segundas Barrancas Blancas; YH, Yaten Huageno. Modified from Fernicola *et al.* (2014).

Andean tectonics and arc volcanism (Fosdick *et al.*, 2013; Cuitiño *et al.*, 2016; Ghiglione *et al.*, 2016; Parras and Cuitiño, 2018). Owing to the wide and continuous exposures and the richness of its contained fossils, the SCF represents the most important record of high latitude terrestrial paleoenvironments, paleoclimates, and ecosystems of the Southern Hemisphere during Burdigalian–early Langhian (*e.g.*, Vizcaíno *et al.*, 2012a,b; Raigemborn *et al.*, 2018; Cuitiño *et al.*, 2019a).

The RSC originates in the Lago Argentino and flows through a deeply incised valley stretching 230 km from west to east across the continent. Along the valley's margins, three Miocene sedimentary units can be recognized: (1) the shallow marine Early Miocene Estancia 25 de Mayo Formation (Cuitiño and Scasso, 2010; = the Centinela Formation); (2) the shallow marine to deltaic Monte León Formation (Sacamani and Panza, 2011; Parras and Cuitiño, 2018); and (3) the terrestrial Early–Middle Miocene Santa Cruz Formation (Tauber *et al.*, 2008; Sacamani and Panza, 2011; Cobos *et al.*, 2014; Fernicola *et al.*, 2014; Cuitiño *et al.*, 2016, 2019b). The latter is well exposed in three localities from which we made an extensive fossil collection denominated, from east to west, Barrancas Blancas, Segundas Barrancas Blancas, and Yaten Huageno (Fig. 1). The location, stratigraphy, sedimentology, and geochronology for the SCF in these localities are summarized in Fernicola *et al.* (2014) and Cuitiño *et al.* (2016, 2019b).

The age of the SCF is well constrained radiometrically.

For the coastal zone of southeast of the Province of Santa Cruz the age of the unit is bracketed by means of $\text{Ar}^{39}/\text{Ar}^{40}$, high precision zircon U/Pb, and sedimentation rate estimations between ~ 17.8 and 16.3 Ma (Burdigalian; Tejedor *et al.*, 2006; Perkins *et al.*, 2012; Traylor *et al.*, 2019); in the RSC valley the unit is dated by means of U/Pb on zircons and estimated sedimentation rate between ~ 17.45 and 15.63 Ma (Burdigalian–early Langhian; Cuitiño *et al.*, 2016).

Fernicola *et al.* (2014) and Cuitiño *et al.* (2016; 2019b) reconstructed the fossiliferous locations that Carlos Ameghino studied on the southern margin of the RSC in 1887. These localities, from east to west, are described in what follows.

Barrancas Blancas (BB)

Barrancas Blancas is an outcrop of approximately 6 km in length of horizontal strata from east ($S\ 50^{\circ}\ 09'\ 38.31''$ - $W\ 69^{\circ}\ 40'\ 23.40''$) to west ($S\ 50^{\circ}\ 12'\ 31.70''$ - $W\ 69^{\circ}\ 43'\ 10.66''$). The eastern limit of this exposure is located in Estancia Aguada Grande (EAG) and its western end is found in the Estancia Santa Lucía (ESL). In this region, the fossils were collected from EAG (= EAG2; see Cuitiño *et al.*, 2019b) and ESL (= ESL section; see Cuitiño *et al.*, 2019b). The Monte León Formation crops out at the eastern end of BB and grades transitionally into the SCF, the latter composed of nearly 100 m of well stratified, yellow to greenish siltstone and tabular claystone beds, with evidence of paleosol formation. In this part of SCF, sandstone beds are infrequent

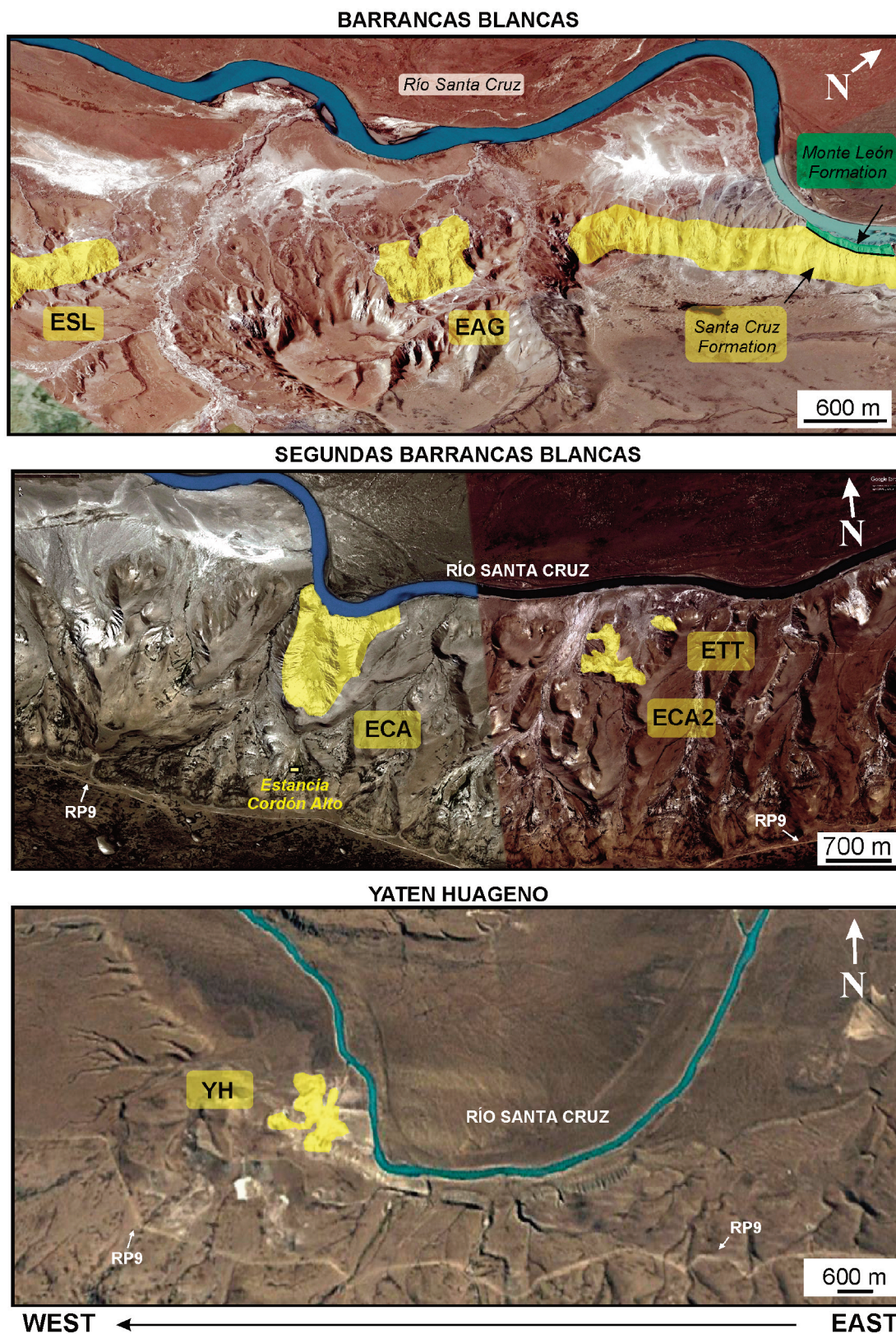


Figure 2. Satellite image (Google Earth TM; 2002) of the Barrancas Blancas, and Segundas Barrancas Blancas (Modified from Cuitiño *et al.*, 2019b); and Yaten Huageno. Section of Monte Observación Member of the Monte León Formation and Santa Cruz Formation are highlighted in green and yellow, respectively. **EAG**, Estancia Aguada Grande Section; **ESL**, Estancia Santa Lucía Section; **ECA**, Estancia Cordón Alto Section; **ECA2**, Estancia Cordón Alto 2 Section; **ETT**, Estancia El Tordillo Section, **YH**, Yaten Huageno.

and abundant pyroclastic material is observed mixed with the epiclastic material, as well as thick tuff beds. In the eastern part of this outcrop a tuff near the base of the SCF was dated at 17.04 ± 0.55 (Cuitiño *et al.*, 2016: fig. 3D); this laterally continuous tuff is used as a marker bed to correlate with Section EAG, where it crops out at the base of the SCF. The ESL Section at BB is a small exposure located 3 km southwest of EAG (Fig. 2; Google Earth images). The correlation of this section with EAG is established from a local tuff layer located 45 m above the 17.04 Ma tuff at (Cuitiño *et al.*, 2019b: fig. 8).

Segundas Barrancas Blancas (SBB)

The SBB locality is a belt of 9 km of exposures in lands of Estancia Cordón Alto (ECA), Estancia El Tordillo (EET), and Estancia Rincón Grande (Fig. 2). Only the SCF crops out at SBB, not the Monte León Formation. Each exposure is identified from east to west as EET (= EET1, see Cuitiño *et al.*, 2019b; S50° 16' 43.00" - W 70° 15' 9.90"), ECA2 (S 50° 16' 55.96" - W 70° 15' 47.33"), and ECA (= ECA 1, Cuitiño *et al.*, 2019b, S 50° 16' 25.56" - W 70° 18' 24.74"). The exposures lie at the bottom of the valley, where the river erodes its southern slope (Fig. 2). Here, SCF is composed of fine-grained sediments deposited in a low-energy fluvial system. The sections are locally correlated using a tuff layer located near the base of the sections (CECA-2 tuff; Cuitiño *et al.*, 2016: fig. 3C) and by distinctive tabular, laterally extensive yellow beds (Cuitiño *et al.*, 2019b). The CECA-2 tuff layer was dated at the EET Section by Cuitiño *et al.* (2016) at 16.32 ± 0.62 Ma.

Yaten Huageno (YH)

Yaten Huageno is an outcrop of about 2 km in length that stretches from East (S 50° 15' 17.48" - W 71° 04' 09.56") to West (S 50° 15' 40.74" - W 71° 03' 48.81") within the Estancia El Refugio (Fig. 2). Only the SCF crops out here, which is composed of 80 m of brown and greenish siltstone, sandstone and tuff beds (Cuitiño *et al.*, 2019b). For this section, a tuff layer located in the middle part of the section has been dated in 16.88 ± 0.65 Ma (Cuitiño *et al.*, 2016: fig. 3B); by sedimentation rate the temporal range of this locality is between ~ 17.22 to ~ 16.67 Ma.

MATERIALS AND METHODS

The specimens were collected by teams of 10–12 people during the Austral summers of 2013 and 2014. On average, they collected fossils during 20 days each season, from the localities BB, SBB, and YH. Almost all identifiable pieces were collected without size or taxonomic bias, and constitute more than 1900 specimens, which are permanently housed at the Museo Regional Provincial "Padre M. Jesús Molina" of Río Gallegos (Province of Santa Cruz, Argentina). The specimens are associated with geographic coordinates, stratigraphic provenance, and/or altitude above sea level.

The taxonomic identifications that form the basis of this paper are taken from the lists provided in this volume: Metatheria (Chornogubsky *et al.*, 2019), Folivora (Bargo *et al.*, 2019), Cingulata (Fernicola and Vizcaíno, 2019), Notoungulata and Astrapotheria (Fernández and Muñoz, 2019), Litopterna (Schmidt *et al.*, 2019), Rodentia (Arnal *et al.*, 2019), and Primates (Kay and Perry, 2019) (Fig 3.1–9).

We performed comparative analyses of mammalian taxonomic richness based on the presence/absence of species. We compared our new collections from the RSC with earlier collections, which we identify as the "old collections" from the RSC (Ameghino, 1885, 1887a; Mercerat, 1891; Cabrera, 1927; Pérez, 2010; Arnal, 2012; Arnal and Vucetich, 2015). We also compared the richness among the three localities BB, SBB, and YH. As earlier publications did not discriminate among the three localities (*e.g.*, Ameghino, 1887a) we considered only information from the new collections. Finally, we compared the taxonomic list of new collections with that of localities along Atlantic Coast (Monte León, Cerro Observatorio, Anfiteatro, Estancia la Costa, Cañadon Silva, Puesto la Costa, Monte Tigre, and Killik Aike Norte; Fernicola *et al.*, 2019a: fig. 1) based on the latest available publications (Tauber, 1996, 1997a; Soria, 2001; Arnal, 2012; Kay *et al.*, 2012; Arnal *et al.*, 2017, 2019; Bargo *et al.*, 2019).

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

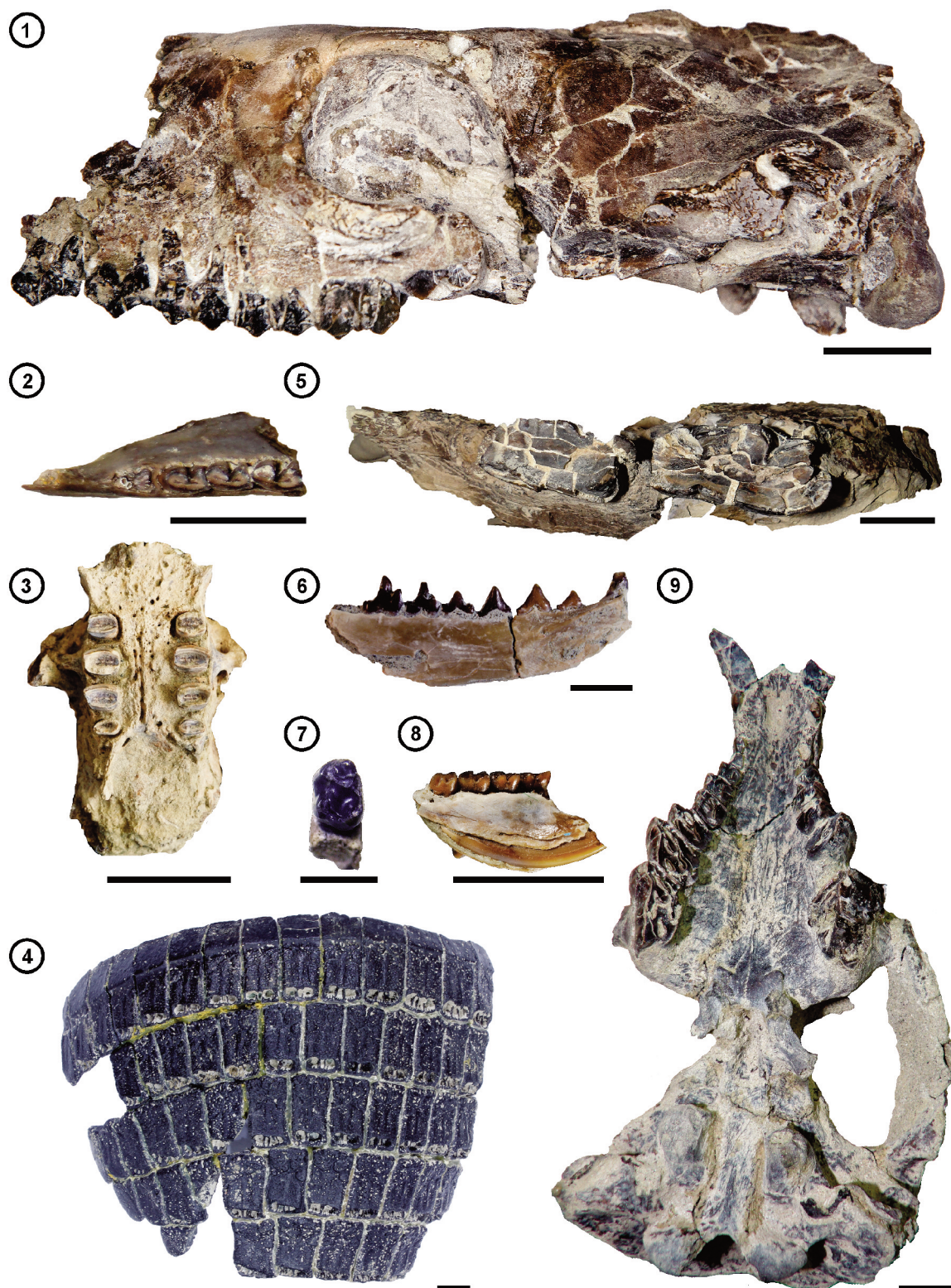


Figure 3. 1, *Tetramerorhinus cingulatus*, MPM-PV 19449, incomplete skull with left and right DP1–DP4 and M1, left lateral view; scale bar= 20 mm; 2, *Pachyrukhos moyani*, MPM-PV 19917, right mandibular fragment with p2–m1, oclusal view; scale bar= 10 mm; 3, *Hapalops* cf. *elongatus*, MPM-PV 19353, anterior portion of skull in palatal view; scale bar= 30 mm; 4, *Proeutatus oenophorus*, MPM-PV 21023, portion of the pelvic shield; scale bar= 10 mm; 5, *Astrapotherium magnum*, MPM-PV 19927, left mandibular fragment with m1–2, in oclusal view; scale bar= 20 mm; 6, *Sipalocyon gracilis*, MPM-PV 19413, lingual view; scale bar= 10 mm; 7, *Homunculus vizcainoi* sp. nov., MPM-PV 19426, left m1, oclusal view; scale bar= 5 mm; 8, *Acarechimys gracilis*, MPM-PV 17430, left mandible with dp4–m3 in lingual view; scale bar= 10 mm; 9, *Adinotherium ovium*, MPM-PV 19717, almost complete skull with associated dentition in palatal view; scale bar= 20 mm.

RESULTS

Appendix 1 presents the taxonomic list of mammals recorded by us in the new RSC collections. Our new collection of fossil mammals consists of 540 specimens collected in BB, 1267 in SBB, and 21 in YH. Species-level identifications were possible for 307 specimens at BB, 647 at SBB, and 11 at YH (Tab. 1). In total, this collection consists of 64 species, adding in six taxa identified at the genus or higher level only when this record implies at least the presence of one species (e.g., *Eucinepeltus* sp., Planopinae indet.). The breakdown is 10 species of metatherians (four Sparassodonta, five Paucituberculata, and one Microbiotheria), 12 species of xenarthrans (five Folivora and seven Cingulata), one astrapotherian species, nine notoungulate species (three Toxodontia and six Typotheria), seven litopterns species (six Proterotheriidae and one Macrauchiidae), 24 rodent species (11 Octodontoidea, two Erethizontoidea, five Caviidae, and six Chinchilloidea), and one primate (Homunculidae).

Appendix 2 is a compilation of mammal species in the new collections of SCF at RSC, as reported in this volume (Fernicola *et al.*, 2019b), compared with those previous reported from RSC. We also list the species present in the three localities at the RSC that are also recorded in outcrops of the SCF from the Atlantic Coast between National Park Monte León and Río Gallegos.

From the old collections as a whole, with the revised taxonomic identifications in this volume there are 79 species: 15 metatherians (six Sparassodonta, seven Paucituberculata, and two Microbiotheria), 16 xenarthrans (nine Folivora and seven Cingulata), two astrapotheres, 16 notoungulates (eight Toxodontia and eight Typotheria), five

litopterns (four Proterotheriidae and one Macrauchiidae), and 25 Rodents (12 Octodontoidea, two Erethizontoidea, five Caviidae, and six Chinchilloidea) (Appendix 2).

Combining the old and new collection lists the taxonomic richness rises to 95 mammalian taxa (Appendix 2). Chornogubsky *et al.* (2019) listed nine of the 15 species of metatherians from the old collections and a new record (*Peratheresutes pungens* Ameghino, 1891), increasing the overall taxonomic richness to 16 species. Bargo *et al.* (2019) and Fernicola and Vizcaíno (2019) identified 12 taxa, of which only six were registered among the 16 species of xenarthrans in the old collections. The xenarthran taxonomic richness rises to 22 species, with new records of three sloths (*Hapalops elongatus* Ameghino, 1891, *Xyophorus atlanticus* Ameghino, 1891, *Nematherium longirostris* Ameghino, 1891, and a species of Planopinae), and two glyptodonts (*Cochlops muricatus* Ameghino, 1889 and *Eucinepeltus* sp. Ameghino 1891). Fernández and Muñoz (2019) identified one of the two previously reported species of *Astrapotherium* Burmeister, 1879 in the new collections, and identify seven of the 16 species of notoungulates in the new collections that also occur in the old collections. Litopterns are represented by seven species, adding two more, *Tetramerorhinus lucarius* Ameghino, 1894 and *T. cingulatum* (Ameghino, 1891), to the five recorded in the old collection list (Schmidt *et al.*, 2019). Arnal *et al.* (2019) recognized 24 species of rodents, one less than in the old collections. But six taxa in our collections (*Perimys incavatus* Ameghino, 1902, "*Eocardia*" *excavata* Ameghino, 1891, *Sciamys latidens* Scott, 1905, *Prospaniomys* sp. nov.?, *Dudumus* sp. nov.?, and *Acarechimys gracilis* Ameghino, 1891) were not found in the old collections, increasing the taxonomic richness to 31 species. A primate identified in the new collections is a new species, *Homunculus vizcainoi* Kay and Perry, 2019, increasing the taxonomic richness to one species. Excluding the first records for the RSC, the total number of species shared between the old and new collections is 44, and the number of unshared species is 35 (Appendix 2).

In the new collections of RSC, SBB has the largest number of taxa (60: 51 species + 8 species assignable to genus but of uncertain species + Planopinae indet.). For BB the numbers are smaller (47: 37 species + 10); at YH we recovered four cingulates, three rodents, one notoungulate,

TABLE 1 – Specimens and species recovered at BB, SBB, and YH

Localities	Total N° of specimens	Specimens identified at specific level	Total N° of species
BB	540	307	37
SBB	1267	647	51
YH	21	11	7
Total	1828	965	–

and *Astrapotherium magnum* Burmeister, 1879. *Astrapotherium magnum* is not certainly present in BB and SBB although several specimens represent an *Astrapotherium* of uncertain species (Fernández and Muñoz, 2019). The specific richness of BB and SBB show differences: of a total of 57 species identified for these localities, they share 31, six are present only at BB (two rodents, one litoptern, one notoungulate, and two cingulates) and 20 only at SBB (10 rodents, two litopterns, two notoungulates, three sloths, and three methaterians).

The great majority of fossil mammal species recorded in the new collections at SCR are also found at Atlantic coastal localities between Monte León and Killik Aike Norte. Of the 37 species identified in BB, 31 are also in the coastal localities (81 %), while of the 51 species identified in SBB, 47 (92 %) are in the coast as well. All seven species recorded in YH are found in coastal localities (Appendix 2).

DISCUSSION

Taxonomic richness: old vs. new collections

Until recently, a major challenge when comparing the taxonomic richness reported for the RSC is a consequence of confusion about the two subdivisions proposed by Ameghino (1900–02, 1906): his *Piso Santacrucense* was divided into a supposedly older *étage notohippidéen* in the West, and a younger *étage santacruzéen* from the RSC and the Atlantic coast. Fifteen of the 54 species said by Ameghino to be exclusively Notohippidian were collected by C. Ameghino in 1887 at the SCF's outcrops at Río Bote, a tributary of the RSC (Fericola *et al.*, 2014). Ameghino (1900–02) claimed that he was able to incorporate into his Notohippidian list, species that were founded more than 10 years earlier because his brother Carlos had provided the precise geographical position of each specimen. However, a review of the data in the Ameghino Catalog (preserved at MACN) does not support, in most cases, the exclusive western origin mentioned by Ameghino (1900–02). For example, the rodent *Neoreomys indivisus* Ameghino, 1887a (= *Neoreomys australis*, Kramarz, 2006) was considered by Ameghino (1900–02) as an exclusively Notohippidian species. However, the taxon was collected by C. Ameghino during his expedition to the *barrancas* of the RSC. Further complicating matters, another specimen of *Neoreomys indivisus* (MACN-A

4329–4337) is recorded in the Ameghino Catalog as being collected by Carlos Ameghino at Cerro Observatorio (= Monte Observación). Other *Neoreomys indivisus* specimens lack geographic information, so it is not possible to establish which could have come from the SCR, if any. A similar situation occurs with the notoungulate *Adinotherium splendidum* Ameghino, 1887a. This species was first collected from the RSC and, according to the Ameghino Catalog, other specimens (MACN-A 5364 and 5365) were collected at the coastal locality Puesto La Costa (= Corriguen Kaik, as recorded in the Ameghino Catalog) and at Cerro Observatorio (MACN-A 5359). Other specimens of *A. splendidum* have no geographic information. These two cases are examples of marked contradictions between the species considered by Ameghino (1900–02, 1906) as exclusive for the Notohippidian, and the geographical distribution of the specimens assigned by him to those species in his catalog. In both cases it is possible that some specimens in the Ameghino Catalog without geographical information could have been collected in the Río Bote or in the Karaiken area, but no information has emerged to indicate that this is the case. What we do know from the Ameghino Catalog is that both species are not exclusive to the Notohippidian stage, because they are reported from areas where Ameghino only recognized a fauna of the Santacrucian stage. An additional but no less important issue is that in 1888 F. Ameghino appropriated from the Museo de La Plata several specimens that had been collected by Carlos in 1887 (Fericola, 2011a,b). The circumstances in which this removal occurred suggest that F. Ameghino did not carry with him any detailed information on the origin of the specimens that remained in the MLP, and we have not found this information in the Ameghino archives in the MACN. Thus, it is not clear how it was possible for Ameghino to assign geographical information to each of the specimens of 1887 still housed in the MLP when he did not have access to them (Fericola, 2011a,b; Fericola *et al.*, 2019a). Finally, the problem of the geographic location of supposed Notohippidian species assemblage is not only with the 1887 collection. For example, *Adinotherium robustum* Ameghino, 1891, collected by Carlos Ameghino after 1887, was considered by Ameghino (1900–02) to be exclusively Notohippidian, but the Ameghino Catalog lists specimens MACN-A 407 and MACN-A 865 as being collected at

Puesto La Costa, indicating that certainly it is not exclusively Notohippidian.

Certainly, the notoungulate *Notohippus toxodontoides* Ameghino, 1891 has so far been recorded only in outcrops of the SCF in the west near Lago Argentino (Ameghino, 1906; Marshall and Pascual, 1977; Fernicola *et al.*, 2014; Cuitiño *et al.*, 2016). Marshall and Pascual (1977) reported a Notohippidian assemblage from lower levels of the SCF at Karaiken, from which they recorded *Notohippus toxodontoides*. Simpson (1940) and Marshall *et al.* (1983) considered this assemblage as an early Santacrucian local fauna. According to Fleagle *et al.* (2012) the lowest levels of the Karaiken deposits correlate with the very lowest levels at Monte León, which would be consistent with primitive nature of the Karaiken fossils relative to those from the coast. Cuitiño *et al.* (2016) place that assemblage slightly younger than ~18.5 Ma, but older than 17.8 Ma. Unlike Ameghino (1906), Marshall and Pascual (1977) report Santacrucian fauna from levels younger than 17.71 Ma (Fleagle *et al.*, 2012; Cuitiño *et al.*, 2016). Marshall and Pascual (1977) claim that Ameghino's specimens of *Notohippus toxodontoides* lack precise stratigraphic provenance and, therefore, cannot be assigned to one of these two faunal levels. They also described a Notohippidian assemblage recovered from the lower SFC levels at Cerro Centinela, 30 km southwest of the Río Bote section (Fig. 1), bracketed between ~18.85 and 18.70 Ma (Cuitiño *et al.*, 2016). Fernicola *et al.* (2014) and Cuitiño *et al.* (2016) recognized the presence of *Notohippus toxodontoides* in the lower levels of the SCF at Río Bote (at ~18.20 to 18.00). Considering *Notohippus toxodontoides* as a reference fossil, the Notohippidian would be older than the Santacrucian, as proposed by Ameghino (1900–02, 1906), which on the Atlantic coast its oldest levels are ~17.80–17.45 Ma (Cuitiño *et al.*, 2016). The part of the section of Karaiken above ~17.71 Ma (Perkins *et al.*, 2012) would be synchronous with the lower levels of the SCF outcropping between Monte Leon and Puesto la Costa (at ~17.80 to 17.50 Ma) (Fig. 4). This scheme must be evaluated with the new taxonomic assignments of the specimens that we have collected in the upper levels of Río Bote and that are currently being studied by us.

The inclusion in the RSC taxonomic list of the taxa of 1887 and 1889 that Ameghino (1900–02, 1906) placed in

the Notohippidian stage, and therefore in the western region of the Province of Santa Cruz, depends ultimately on a comprehensive historical analysis of each of those 15 taxa (Fernicola *et al.*, 2019a). The same consideration applies to the remaining exclusively Notohippidian species identified by Ameghino (1900–02), the remains of which were collected after 1889. For these reasons, the taxonomic lists of Ameghino for the RSC should be taken only as a first approximation of the taxonomic richness in the western region. Clearly, only new faunal lists based on specimens collected in new fieldwork will produce a more accurate understanding of the taxonomic richness of RSC.

After taxonomic revisions, 79 mammalian species were recorded at the old collections of RSC (Appendix 2), not a number exceeding 100 as Ameghino originally supposed. This reduction is due to a great extent to synonymies proposed by several authors (*e.g.*, Scott, 1903; Sinclair, 1909), and despite the establishment of several new RSC taxa (*e.g.*, Cabrera, 1927; Arnal and Vucetich, 2015). At the species-level, the old and new collections share 44 species (Appendix 2). The 35 species not recorded in the new collections, may in part be an artifact because, as several authors conclude, several of the taxonomic groups presented here are taxonomically oversplit and require further revision (*e.g.*, Litopterna, Schmidt *et al.*, 2019; Folivora, Bargo *et al.*, 2019; Notoungulata, Fernández and Muñoz, 2019). The difference may also be overestimated because of the quality of the fossils we recovered. We were able to assign many specimens only to the generic level, not the level of the species due to the absence of the diagnostic parts. For example, we recovered several specimens of *Interatherium*, but none can be assigned with certainty to any of the three species previously reported for the RSC (Fernández and Muñoz, 2019).

Taxonomic richness of the RSC localities

As we mentioned previously, the mammalian associations evaluated in this study correspond to BB, SBB and YH. Unfortunately, at YH (~17.22 –16.67 Ma; Cuitiño *et al.*, 2016) we recovered only 21 specimens among which there are only nine species-level identifications (Appendix 2). The low number of specimens and species in this locality prevents us from considering it in the following discussion. It should be noted that YH is more coarse-grained (higher

energy) and has the lowest areal exposure (0.4 km²) compared with BB (1.35 km²) and SBB (1.5 km²). We suppose that YH is the least fossiliferous locality because our sampling efforts were comparatively similar to that of SSB and BB. Notably, Carlos Ameghino in his fieldbook mentioned that YH was the most fossiliferous of all the localities of the RSC (in Rusconi, 1965). Nevertheless, Clemente Onelli, who visited the RSC, obtained similar result to ours (Brinkman and Vizcaíno, 2014), a fact that allow us to support our perception concerning this site.

With respect to taxonomic richness, SBB has a greater number of species than BB. Excluding the 31 species in common between the two localities, of the 26 remaining species, 20 are unique to SBB and six to BB. This interesting taxonomic difference should be understood within the framework of the temporal ranges of RSC species. According to the dates and sedimentation rates applied to the SBB deposits (Cuitiño *et al.*, 2016) the sedimentary levels in SBB range from ~16.46 to 15.65 Ma, whereas those at BB have a time range between ~17.05 to 16.49 Ma (Cuitiño *et al.*, 2016). Thus, the mammalian associations of both localities are time successive, temporally separate, and non-overlapping.

Comparison with older levels of the SCF

In spite of BB being closer in age to the older Atlantic coastal levels the SCF between Monte León and Río Gallegos, and SBB fossils being younger than the Atlantic coastal levels, the greatest similarity is between SBB and the coast (Appendix 2; Fig. 4). Nineteen of the 20 species present in SBB but absent in BB are present on the Atlantic coast. Twelve species occur at Anfiteatro – Puesto Estancia La Costa (Fericola 2019a: fig. 5), in sedimentary levels older than those of BB (~17.40 to 17.60 Ma; Cuitiño *et al.*, 2016) (Appendix 2): *Microbiotherium tehuelchum* Ameghino, 1887a, *Perathereutes pungens* Ameghino, 1891, and *Cladosictis patagonica* Ameghino, 1887a (Metatheria); *Xyophorus atlanticus* (Pilosa); *Adinotherium ovinum* Owen, 1853 and *Pachyrukhos moyani* Ameghino, 1885 (Notoungulata); *Tetramerorhinus cingulatum* and *Anisolophus floweri* (Ameghino, 1887a) (Litopterna); and *Acarechimys minutus* (Ameghino, 1887a), *Acarechimys constans* (Ameghino, 1887a), *Acaremys murinus* Ameghino, 1887a, and *Stichomys regularis* Ameghino, 1887a

(Rodentia). The rodent *Sciamys latidens*, only known by its holotype, was recorded at SCF from Killik Aike Norte at levels older than BB (~17.00–16.90 Ma; Cuitiño *et al.*, 2016). With respect to the other species, four rodents *Acarechimys gracilis*, *Prolagostomus pusillus* Ameghino, 1887a, *Pliolagostomus notatus* Ameghino, 1887a and *Schistomys erro* Ameghino, 1887a, and the sloth *Nematherium longirostris*, were reported at the SCF from Cerro Observatorio, at sedimentary levels older than or synchronous to those of BB (~17.80–16.30 Ma; Cuitiño *et al.*, 2016). The neotype of the sloth *Schismotherium fractum* Ameghino, 1887a quite possibly was collected in Monte León or Yegua Quemada (Racco *et al.*, 2018) (~17.80–16.20 Ma; Cuitiño *et al.*, 2016) (Fig. 4).

The only SBB taxon not represented on the Atlantic coast corresponds to the rodent *Dudumus* sp. nov.?, which previously was only known from Colhuehuapian sediments (Early Miocene) from Sarmiento Formation, Trelew Member of Chubut Province, Argentina (Arnal *et al.*, 2014).

In summary, 20 mammal species present in the upper levels of RSC (SBB) are absent in BB. Nineteen of this group of 20 distinct SBB species representing in a younger time interval are also found in older Atlantic coastal Santacrucian faunas. In contrast, despite being more similar in age to the Atlantic coastal localities, the fauna of the BB stratigraphic interval is less similar to the Atlantic coastal faunas of similar age. Several obvious possibilities present themselves to explain these differences. First, it could be that the formal difference might be accounted for by sampling error –different amounts of collecting effort between BB and SBB– so that if we more intensely collected at BB we would document the “missing” taxa. This possibility is suggested by the fact that the mammal specimens collected in BB (540) represent 42 % of the specimens recovered in SBB (1267). Despite this difference, the number of specimens from BB identified at specific level (307) represents 47 % of the specimens from SBB identified at the same level. It may be the case that what it is relevant is the difference in relative abundance of specimens rather than the size of the sample. In SBB, three species absent in BB represent 24 % (156) of the specimens collected: *Prolagostomus pusillus* Ameghino, 1887a, *Pliolagostomus notatus* Ameghino, 1887a (Arnal *et al.*, 2019: tab. 2), and *Pachyrukhos moyani* Ameghino, 1885 (Fernández and Muñoz, 2019: appendix 2). A fourth

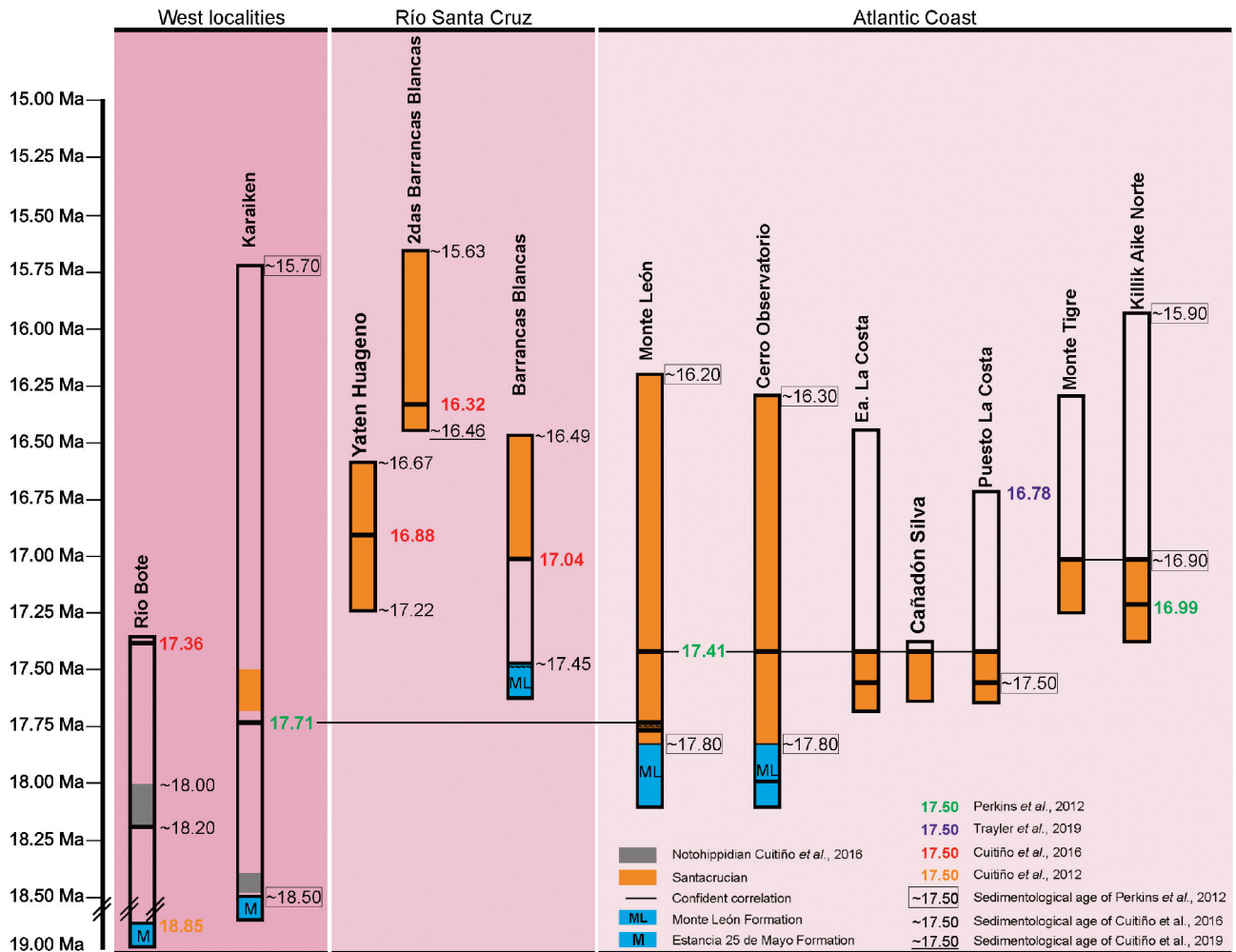


Figure 4. Chronostratigraphic correlation scheme for the Santacrucian sections of the Santa Cruz Formation at the Río Santa Cruz, Río Bote, and Atlantic Coast mentioned in this study. The vertical extension of the columns is calculated assuming an average sedimentation rate of 150 m/Ma (Cuitiño *et al.*, 2016, 2019b), represents time (Ma). Lithostratigraphic units are indicated in capital letters, excepting the Santa Cruz Formation (modified from Cuitiño *et al.*, 2016).

species, *Protypotherium australe* Ameghino, 1887b, is represented in SBB by 60 specimens and by only one specimen in BB (Fernández and Muñoz, 2019: appendix 2). The four species mentioned represent a third (216) of the specimens of SBB. If we exclude from the analysis these four species the number of specimens identified at a specific level in BB (306) would represent 70 % of those of SBB (431). Thus, it is possible that the differences in the number of specimens between both localities are more related to the different abundances of certain species than to a different sampling effort.

Presence or absence of species is not the only phe-

nomenon that supports this view. There also are examples where the local faunas show presence of the same species but extreme variation in its relative abundance (see above). Arnal *et al.* (2019: tab. 2) provide notable examples for this among chinchilloids. For example, *Perimys* is relatively common at BB and SBB, but at SBB the largest species, *Perimys onustus*, is very common (23 specimens) and a smaller species, *P. erutus*, is uncommon (three specimen), whereas at BB, *P. onustus* is represented by only a single specimen, and the smaller species by twelve: *P. erutus* (11 specimens) and *P. incavatus* (one specimen).

Another possibility is that there could be different sedi-

mentological regimes (more coarse or more fine-grained sediment, differential predominance of channels versus overbank deposits, etc.) leading to differential accumulation of the species comprising the vertebrate death assemblages. But the geologic studies of Cuitiño *et al.* (2019b) reveal no obvious sedimentological differences between BB and SBB levels.

Finally, perhaps the variations among the localities are mediated by differences in the environment that could affect local distribution of Santacrucian species. This third option is the one we favor based on the present evidence. To elaborate, we conceive of a relatively stable regional Santacrucian fauna of longstanding inhabiting a mosaic environment with scrublands or grasslands and riverine forests as that proposed by Kay *et al.* (2012) between ~17.5 Ma and ~15.5 Ma. Under this hypothesis, variation in the presence or absence of species within this regional fauna could be accounted for directly by local variation in climatic factors, such as rainfall, temperature, elevation, or distance from a paleo-coastline. Or climatic variations could have indirect effects, casting an influence on overall vegetational composition. In this general scenario of proximate coexistence of different floral communities, relatively minor climatic variations would imply the recession of one plant community and the expansion of the other, each with its accompanying fauna. In this way, a species would be contemporaneously present in a particular part of the landscape but absent in another part, as seems to be the case.

Biozones

Tauber (1997a,b, 1999) identified two sedimentary units in the coastal SCF between the Río Coyle and the Río Gallegos: a lower Estancia La Costa Member and an upper Estancia La Angelina Member. He identified 22 Fossiliferous Levels (FL) in the sequence. Based on his own stratigraphic work, fossil collections and taxonomic identifications, Tauber (1997a) proposed two taxon-range biozones for the Estancia La Costa Member. The lower *Protypotherium attenuatum* biozone comprised of FLs 3 to 7 was based on the exclusive presence of this homonymous typothere. The upper *Protypotherium australe* biozone (FL 8 to 10) was based on the exclusive presence of that taxon in the upper levels. Tauber (1997a, p. 423) noted that in order to formally define

these biozones it would be necessary to confirm its regional applicability with a more complete paleontological record. Later, Krapovickas *et al.* (2008) extended the *P. attenuatum* zone to encompass FL 1 to 7 and the *P. australe* zone from FL 5.3 to 10. They formulated a new biozone restricted to the overlap of the two species (FL 5.3 to 7), which was referred as *P. attenuatum-P. australe* zone. However, Kay *et al.* (2012) recognized the presence of *P. australe* at Estancia La Costa (FL 1 to 4 of Tauber, 1997a). Krapovickas *et al.* (2008, p. 1020) acknowledged that it was necessary to establish the geographic distribution of the *Protypotherium* spp. with more certainty in order to confirm their real value for defining biozones. Tauber *et al.* (2008), in a brief report of the SCF in the RSC, recognized around thirteen genera of fossil mammals collected in Ea. El Refugio, Ea. Cordón Alto, and Ea. Rincón Grande (three of the *estancias* along the RSC mentioned above). Among these taxa, Tauber *et al.* (2008) only provided the geographical position of *Protypotherium attenuatum* (YH) and *Protypotherium australe* (SBB), possibly due to its biostratigraphic importance.

The temporal distribution that we recorded for these species along the RSC makes arguable that these biozones should be set aside. The two *Protypotherium* species overlap extensively, with *P. australe* found at both levels: the BB levels between ~16.80 and 16.57 Ma, and SBB levels between ~16.44 and 16.02 Ma (Fig. 5). Likewise, *P. attenuatum* is recorded in both BB and SBB. The overlapping temporal distribution of *P. australe* and *P. attenuatum* shows that it is not possible to define biozones based exclusively on one of these taxa. Thus, it is clear that the definition of biozones requires a greater knowledge of the spatio-temporal distribution of taxa that could define them.

The type locality for the Santacrucian fauna

As mentioned above, Marshall *et al.* (1983, 1986) proposed that the Monte León local fauna should be designated as the nominal type area of the Santacrucian fauna. Instead, we propose that the exposures along the RSC should be considered as a type area for the Santacrucian. Beyond the complex situation regarding the Ameghino collection and the scant and sometimes ambiguous information associated with its specimens, there is no doubt that the initial concept of this fauna formulated by Ameghino in 1889

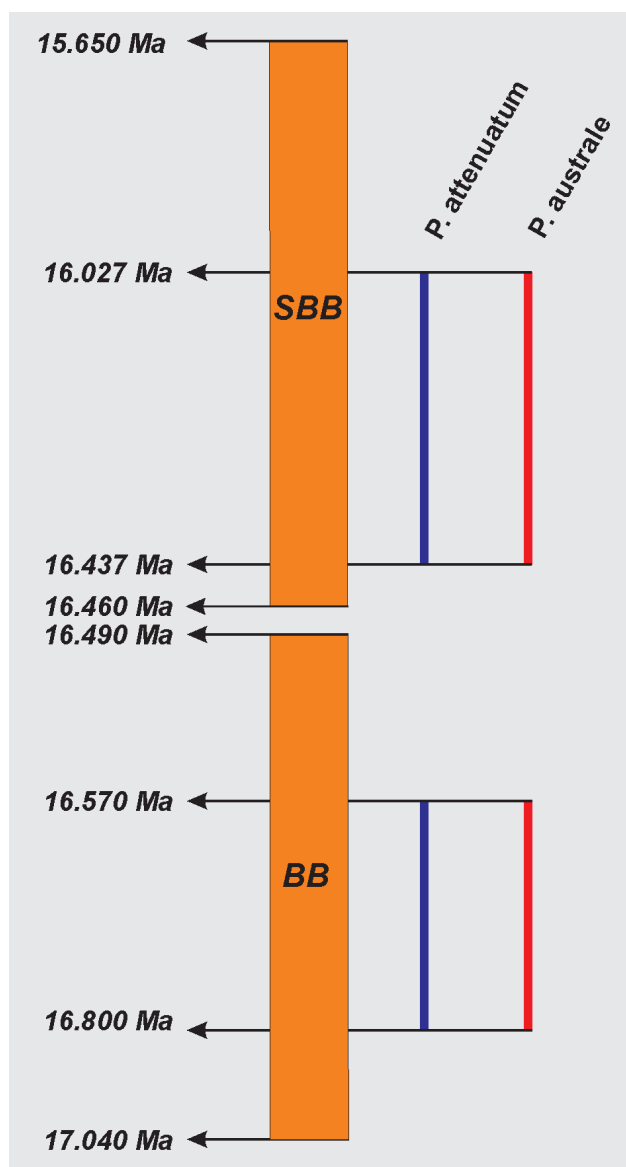


Figure 5. Temporal distribution of *Protypotherium attenuatum* (blue) and *P. australe* (red) at BB and SBB. The specimen of *P. australe* from BB was collected at Estancia Santa Lucía Section which estimated time span between ~16.8 to 16.57 Ma (Cuitiño *et al.*, 2019b).

based on the species collected in the RSC in 1887 and before any substantial collections were made from Monte León or other coastal areas. There are pertinent reasons beyond the purely historical ones. As originally mentioned by Carlos Ameghino (in Rusconi, 1965), BB exposes the transitional contact of the SCF with the underlying marine Monte León Formacion. At SBB, the youngest fossil levels of the entire SCF are in stratigraphic and chronological continuity

with those of BB. Thus, the RSC composite section spans a greater temporal interval than that on the coast. For these reasons, we propose that RSC exposures should be considered as the type locality for the Santacrucian fauna.

CONCLUSIONS

The historical analysis of the 19th century fossil collections from the SCF along the RSC and its tributary Río Bote clarify some of the confusion in the older literature as it relates to the composition of the Santacrucian fauna as distinct from a supposedly older Notohippidian mammalian fauna in the West at Karaiken, and younger Santacrucian from the RSC and the Atlantic coast (Ameghino, 1889). Certainly, several species before considered as exclusive for the Notohippidian have been recorded elsewhere, in levels considered as typically Santacrucian. In this sense, only new faunal lists based on specimens collected in new fieldwork will help to elucidate the real distinction of a Notohippidian fauna and produce an accurate understanding of the taxonomic richness of SCF along the RSC and the West of the Province of Santa Cruz.

The new collection of more than 1900 specimens reported in this volume (Fernicola *et al.*, 2019b) updated the list of SCF mammalian species recorded along the RSC. The new collection rivals the old one in terms of numbers of specimens. Combining the old and new collections lists, including new first reports, the taxonomic richness is of 95 taxa, not the 110 as Ameghino (1887a) originally listed.

The taxonomic richness in the three localities along the RSC is substantially different: 47 species from BB, 60 species from SBB and nine species from YH. The poor sample from YH supports Onelli's *contra* Carlos Ameghino's view about the fossil abundance of the locality and prevented us to analyze it further.

There are also considerable differences in the faunal composition between BB and SBB. The two share 31 species, of which six are present only at BB (two rodents, one litoptern, one notoungulate, and two cingulates) and 20 only at SBB (10 rodents, two litopterns, two notoungulates, three sloths, and three methaterians).

The great majority of fossil mammal species recorded in the new collections at the RSC (more than 85 %) are also found at Atlantic coastal localities. In spite of BB (~17.05 to

~16.49 Ma) being closer in age to the older Atlantic coastal levels the SCF between Monte León and Río Gallegos, and SBB fossils being younger (~16.46 to ~15.65 Ma) than the Atlantic coastal levels, the greatest similarity is between SBB and the coast.

We interpret that faunal differences among the localities largely to result from local variation in climatic factors, such as rainfall, temperature, elevation, or distance from a paleo-coastline. Also, climatic variations could have indirect effects, casting an influence on overall vegetational composition. In this general scenario of proximate coexistence of different floral communities, relatively minor climatic variations would imply the retreat of one plant community and the expansion of another and its accompanying fauna. In this way, certain species would be contemporaneously present in a particular part of the landscape but absent or rare in another part, as seems to be the case.

We have revised and challenged the validity of proposed Santacrucian biostratigraphic units (biozones) based on distributions of the typotheres *Protypotherium australe* and *P. attenuatum* within the Santacrucian fauna as a whole by Tauber (1997a) and Krapovickas *et al.* (2008). After re-evaluation of the stratigraphic distribution of these species, we argue that the Santacrucian is a unified fauna that shows regional and temporal differences that arise from local variation in climatic conditions and propose that these biozones be set aside.

Finally, contrary to Marshall *et al.* (1983, 1986), who considered that the exposures of the SCF at Monte León be designated as the nominal type area of the formation and the Santacrucian fauna, we propose to return to Ameghino's concept that the exposures along the RSC be considered as a type area. This is for two reasons. First, the South side of the RSC was the region that formed the original basis for Ameghino's concept. Second, collectively the richly fossiliferous faunal assemblages at BB and SBB span the whole known temporal range of the Santacrucian fauna: BB exposes the transitional contact of the SCF with the underlying marine Monte León Formation, and the temporally overlapping SBB has the youngest fossil levels of the entire SCF.

130 years after the first paleontological expedition to the RSC, its exposures and fossils remain crucial for under-

standing the successions of mammalian faunas in the Patagonia Cenozoic. They also constitute the most important record of high latitude terrestrial paleoenvironments, paleoclimates, and paleoecosystems in the Southern Hemisphere during Early and Middle Miocene.

ACKNOWLEDGEMENTS

We thank the collection managers of the Vertebrate Paleontology collections at MLP (M. Reguero), and MACN (L. Chornogubsky and M. Ezcurra), and the Dirección de Patrimonio, Secretaría de Cultura de Estado (Province of Santa Cruz), and Museo Regional Provincial P.M.J. Molina. We thank especially L. Acosta, L. Chornogubsky, L. González, V. Krapovickas, S. Hernández del Pino, N.A. Muñoz, A. Racco, and J. Spradley for their collaboration during field work. Also, we acknowledge the work of the two anonymous reviewers and the editor of PE-APA for their comments and corrections. This is a contribution to the projects PIP-CONICET 00781, UNLP 11/N867, PICT 2013-0389 and 2017-1081, National Science Foundation grants 0851272 and 1348259, and National Geographic Society 9167-12.

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- Doi: 10.5710/PEAPA.01.11.2019.309
- Recibido: 28 de septiembre 2019
- Aceptado: 1 de noviembre 2019

Appendix 1. List of the mammalian taxa recorded in the Río Santa Cruz based on the new specimens (MPM-PV) described in the articles of this volume (Fernicola et al., 2019b). It includes 64 species (six at genus of uncertain species and a Planopinae indet.).

METATHERIA

SPARASSODONTA

Hathlyacinidae

- Cladosictis patagonica* Ameghino, 1887a
Sipalocyon gracilis Ameghino, 1887a
Perathereutes pungens Ameghino, 1891

Borhyaenidae

- Borhyaena tuberata* Ameghino, 1887a

PAUCITUBERCULATA

Abderitidae

- Abderites meridionalis* Ameghino, 1887a

Palaeothentidae

- Acdestis oweni* Ameghino, 1887a
Palaeothentes lemoinei Ameghino, 1887a
Palaeothentes intermedius Ameghino, 1887a
Palaeothentes minutus Ameghino, 1887a

MICROBIOTHERIA

Microbiotheriidae

- Microbiotherium tehuelchum* Ameghino, 1887a

XENARTHRA

FOLIVORA

Megatherioidea

- Hapalops* cf. *elongatus* Ameghino, 1891
Schismotherium cf. *fractum* Ameghino, 1887a
Xyophorus atlanticus Ameghino, 1891
Megatheriidae
Planopinae indet.

Myodontoidae

Myodontidae

- Nematherium longirostris* Ameghino, 1891

CINGULATA

Peltephilidae

- Peltephilus pumilus* Ameghino, 1887a

"Dasypodidae"

- Stegotherium tessellatum* Ameghino, 1887a
Prozaedyus proximus (Ameghino, 1887a)
Stenotatus patagonicus (Ameghino, 1887a)
Proeutatus oenophorus (Ameghino, 1887a)

Propalaeohoplophoridae

- Cochlops muricatus* Ameghino, 1889
Eucinepeltus sp.

ASTRAPOTHERIA

Astrapotheriidae

Astrapotherium magnum (Owen, 1853)

NOTOUNGULATA

TOXODONTIA

Homalodotheriidae

Homalodotherium sp.

Toxodontidae

Nesodon imbricatus Owen, 1847

Adinotherium ovinum (Owen, 1853)

TYPOTHERIA

Hegetotheriidae

Hegetotherium mirabile Ameghino, 1887a

Pachyrhoxos moyani Ameghino, 1885

Interatheriidae

Protypotherium australe Ameghino, 1887b

Protypotherium praerutilum Ameghino, 1887a

Protypotherium attenuatum Ameghino, 1887a

Interatherium sp.

LITOPTERNA

Proterotheriidae

Anisolophus australis (Burmeister, 1879)

Anisolophus floweri (Ameghino, 1887a)

Tetramerorhinus lucarius Ameghino, 1894

Tetramerorhinus cingulatum (Ameghino, 1891)

Thoatherium minusculum Ameghino, 1887a

Diadiaphorus majusculus Ameghino, 1887a

Macraucheniiidae

Theosodon sp.

RODENTIA

CAVIOMORPHA

Octodontoidea

Acarechimys minutus (Ameghino, 1887a)

Acarechimys minutissimus (Ameghino, 1887a)

Acarechimys constans (Ameghino, 1887a)

Acarechimys gracilis (Ameghino, 1891)

Dudumus sp. nov.?

Prospaniomys sp. nov.?

Stichomys regularis Ameghino, 1887a

Spaniomys riparius Ameghino, 1887a

Acaremyidae

Acaremys murinus Ameghino, 1887a

Sciamys principalis Ameghino, 1887a

Sciamys latidens Scott, 1905

Erethizontoidea

Erethizontidae

Steiromys detentus Ameghino, 1887a

Steiromys duplicatus Ameghino, 1887a

Cavioidea

Neoreomys australis Ameghino, 1887a

Eocardia montana Ameghino, 1887b

"*Eocardia*" *excavata* Ameghino, 1891

Schistomys erro Ameghino, 1887a

Phanomys mixtus Ameghino, 1887a

Chinchilloidea

Chinchillidae

Prolagostomus pusillus Ameghino, 1887a

Pliolagostomus notatus Ameghino, 1887a

Neopiblemidae

Perimys erutus Ameghino, 1887a

Perimys onustus Ameghino, 1887a

Perimys incavatus Ameghino, 1902

Dinomyidae

Scleromys sp.

PRIMATES

Homunculidae

Homunculus vizcainoi sp.nov. Kay and Perry, 2019

Appendix 2. Comparison of the compiled list of mammal species in the new collections of Santa Cruz Formation at the Río Santa Cruz (RSC) reported in the volume edited by Fernicola *et al.* (2019b), with previous reports from the RSC and the Atlantic Coast. It includes taxa identified at the genus or higher level only when one species of the genus has not been recorded before for the area considered (*i.e.*, the record of the genus implies at least the presence of one species, *e.g.*, *Eucinepeltus* sp.).

Old Collections: list of mammals from old collections of the RSC; **New Collections:** list of mammals from the new collections from the RSC in Fernicola *et al.* (2019b); Barrancas Blancas (**BB**), Segundas Barrancas Blancas (**SBB**), and Yaten Huageno (**YH**). **Atlantic Coast:** list of taxa from the new collections of the RSC also recorded in outcrops of the SCF from the Atlantic Coast between National Park Monte León and Río Gallegos.

	Río Santa Cruz		Río Santa Cruz localities			Atlantic Coast
	Old Collections	New Collections	BB	SBB	YH	
<i>METATHERIA</i>						
<i>SPARASSODONTA</i>						
<i>Cladosictis patagonica</i>	X ¹	X ¹¹	—	X ¹¹	—	X ¹³
<i>Sipalocyon gracilis</i>	X ¹	X ¹¹	X ¹¹	X ¹¹	—	X ¹³
<i>Perathereutes pungens</i>	—	X ¹¹	—	X ¹¹	—	X ¹³
<i>Acrocyon sectorius</i>	X ¹	—	—	—	—	—
<i>Acyon tricuspidatus</i>	X ¹	—	—	—	—	—
<i>Borhyaena tuberculata</i>	X ¹	X ¹¹	X ¹¹	X ¹¹	—	X ¹³
<i>Lycopsis torresi</i>	X ²	—	—	—	—	—
<i>PAUCITUBERCULATA</i>						
<i>Stilotherium dissimile</i>	X ¹	—	—	—	—	—
<i>Abderites meridionalis</i>	X ¹	X ¹¹	X ¹¹	X ¹¹	—	X ¹¹
<i>Acdestis oweni</i>	X ¹	X ¹¹	X ¹¹	X ¹¹	—	X ¹³
<i>Palaeothentes lemoinei</i>	X ¹	X ¹¹	X ¹¹	X ¹¹	—	X ¹³
<i>P. intermedius</i>	X ¹	X ¹¹	X ¹¹	X ¹¹	—	X ¹¹
<i>P. minutus</i>	X ¹	X ¹¹	X ¹¹	X ¹¹	—	X ¹³
<i>P. aratae</i>	X ¹	—	—	—	—	—
<i>MICROBIOTHERIA</i>						
<i>Microbiotherium patagonicum</i>	X ¹	—	—	—	—	—
<i>M. tehuelchum</i>	X ¹	X ¹¹	—	X ¹¹	—	X ¹³
<i>XENARTHRA</i>						
<i>FOLIVORA</i>						
<i>Hapalops elongatus</i>	—	X ²	X ²	X ²	—	X ¹⁴
<i>H. rectangularis</i>	X ¹	—	—	—	—	—
<i>H. indifferens</i>	X ¹	—	—	—	—	—
<i>H. rostratus</i>	X ¹	—	—	—	—	—
<i>H. infernalis</i>	X ¹	—	—	—	—	—
<i>H. adteger</i>	X ¹	—	—	—	—	—
<i>Schismotherium fractum</i>	X ¹	X ²	—	X ²	—	X ¹⁹
<i>Xyophorus atlanticus</i>	—	X ²	—	X ²	—	X ²
<i>Planopinae indet.</i>	—	X ²	—	X ²	—	—
<i>Planops longirostratus</i>	X ¹	—	—	—	—	—
<i>Eucholoeops ingens</i>	X ¹	—	—	—	—	—
<i>Nematherium angulatum</i>	X ¹	—	—	—	—	—
<i>N. longirostris</i>	—	X ²	—	X ²	—	X ²
<i>CINGULATA</i>						
<i>Peltephilus pumilus</i>	X ¹	X ⁴	X ⁴	X ⁴	—	X ¹³
<i>P. strepens</i>	X ¹	—	—	—	—	—
<i>Stegotherium tessellatum</i>	X ¹	X ⁴	X ⁴	—	—	—
<i>Prozaedyus proximus</i>	X ¹	X ⁴	X ⁴	X ⁴	X ⁴	X ¹³
<i>Stenotatus patagonicus</i>	X ¹	X ⁴	X ⁴	X ⁴	X ⁴	X ¹³

Continuated						
	Río Santa Cruz		Río Santa Cruz localities			Atlantic Coast
	Old Collections	New Collections	BB	SBB	YH	
<i>Proeutatus oenophorus</i>	X ¹	X ⁶	X ⁶	X ⁶	X ⁶	X ¹³
<i>Propalaeohoplophorus australis</i>	X ¹	—	—	—	—	—
<i>Cochlops muricatus</i>	—	X ⁶	X ⁶	—	X ⁶	X ¹³
<i>Eucinepeltus sp.</i>	—	X ⁶	X ⁶	X ⁶	—	—
<i>ASTRAPOTHERIA</i>						
<i>Astrapotherium magnum</i>	X ¹	X ⁵	—	—	X ⁵	X ¹³
<i>A. burmeisteri</i>	X ⁶	—	—	—	—	—
<i>Astrapotherium sp.</i>	—	—	X ⁵	X ⁵	—	—
<i>NOTOUNGULATA</i>						
<i>TOXODONTIA</i>						
<i>Homalodotherium cunninghami</i>	X ¹	—	—	—	—	—
<i>Homalodotherium sp.</i>	—	X ⁵	X ⁵	X ⁵	—	—
<i>Nesodon imbricatus</i>	X ¹	X ⁵	X ⁵	—	—	X ¹³
<i>N. conspurcatus</i>	X ¹	—	—	—	—	—
<i>Nesodon sp.</i>	—	—	—	X ⁵	—	—
<i>Adinotherium ovium</i>	X ¹	X ⁵	—	X ⁵	—	X ¹³
<i>A. splendidum</i>	X ¹	—	—	—	—	—
<i>A. nitidum</i>	X ¹	—	—	—	—	—
<i>Adinotherium sp.</i>	—	—	X ⁵	—	X ⁵	—
<i>Phobereotherium silvaticum</i>	X ¹	—	—	—	—	—
<i>Hyperoxotodon speciosus</i>	X ¹	—	—	—	—	—
<i>TYPOTHERIA</i>						
<i>Hegetotherium mirabile</i>	X ¹	X ⁵	X ⁵	X ⁵	—	X ¹³
<i>Pachyrhinos moyani</i>	X ¹	X ⁵	—	X ⁵	—	X ⁵
<i>Protypotherium australe</i>	X ¹	X ⁵	X ⁵	X ⁵	—	X ¹³
<i>P. praerutilum</i>	X ¹	X ⁵	X ⁵	X ⁵	—	X ¹⁴
<i>P. attenuatum</i>	X ¹	X ⁵	X ⁵	X ⁵	—	X ¹⁴
<i>Interatherium rodens</i>	X ¹	—	—	—	—	—
<i>I. excavatum</i>	X ¹	—	—	—	—	—
<i>I. extensum</i>	X ¹	—	—	—	—	—
<i>Interatherium sp.</i>	—	X ⁵	X ⁵	X ⁵	—	—
<i>LITOPTERNA</i>						
<i>Anisolophus australis</i>	X ¹	X ⁸	X ⁸	—	—	X ¹⁶
<i>A. floweri</i>	X ¹	X ⁸	—	X ⁸	—	X ¹⁶
<i>Tetramerorhinus lucarius</i>	—	X ⁸	X ⁸	X ⁸	—	X ¹⁶
<i>T. cingulatum</i>	—	X ⁸	—	X ⁸	—	X ¹⁶
<i>Thoatherium minusculum</i>	X ¹	X ⁸	X ⁸	X ⁸	—	X ¹³
<i>Diadiaphorus majusculus</i>	X ¹	X ⁸	X ⁸	X ⁸	—	X ¹³
<i>Theosodon lydekkeri</i>	X ¹	—	—	—	—	—
<i>Theosodon sp.</i>	—	X ⁸	X ⁸	X ⁸	—	—
<i>RODENTIA</i>						
<i>OCTODONTOIDEA</i>						
<i>Acarechimys minutus</i>	X ¹	X ⁹	—	X ⁹	—	X ¹⁸
<i>Acarechimys minutissimus</i>	X ¹	X ⁹	X ⁹	X ⁹	—	X ¹⁸
<i>Acarechimys constans</i>	X ¹	X ⁹	—	X ⁹	—	X ¹⁸

Continuated						
	Río Santa Cruz		Río Santa Cruz localities			Atlantic Coast
	Old Collections	New Collections	BB	SBB	YH	
<i>Acarechimys gracilis</i>	—	X ⁹	—	X ⁹	—	X ¹⁸
<i>Dudumys sp. nov.?</i>	—	X ⁹	—	X ⁹	—	—
<i>Prospaniomys sp. nov.?</i>	—	X ⁹	X ⁹	X ⁹	—	—
<i>Stichomys regularis</i>	X ¹	X ⁹	—	X ⁹	X ⁹	X ¹⁵
<i>Stichomys sp.</i>	—	—	X ⁹	—	—	—
<i>Spaniomys riparius</i>	X ¹	X ⁹	X ⁹	X ⁹	—	X ¹⁴
<i>Spaniomys sp.</i>	—	—	—	—	X ⁹	—
<i>Spaniomys modestus</i>	X ¹	—	—	—	—	—
<i>Adelphomys candidus</i>	X ¹	—	—	—	—	—
<i>Acaremys murinus</i>	X ¹	X ⁹	—	X ⁹	—	X ¹⁸
<i>Acaremys messor</i>	X ¹	—	—	—	—	—
<i>Acaremys sp.</i>	—	—	X ⁹	—	—	—
<i>Pseudoacaremys kramarzii</i>	X ¹³	—	—	—	—	—
<i>Sciomyes principalis</i>	X ¹	X ⁹	X ⁹	X ⁹	—	X ¹⁷
<i>Sciomyes latidens</i>	—	X ⁹	—	X ⁹	—	X ¹⁸
<i>Sciomyes varians</i>	X ¹	—	—	—	—	—
<i>ERETHIZONTOIDEA</i>						
<i>Steiromys detentus</i>	X ¹	X ⁹	X ⁹	X ⁹	—	X ¹³
<i>Steiromys duplicatus</i>	X ¹	X ⁹	X ⁹	X ⁹	—	X ¹³
<i>CAVIOIDEA</i>						
<i>Neoreomys australis</i>	X ¹	X ⁹	X ⁹	X ⁹	X ⁹	X ¹³
<i>Eocardia montana</i>	X ¹	X ⁹	X ⁹	X ⁹	—	X ¹³
<i>"Eocardia" excavata</i>	—	X ⁹	X ⁹	X ⁹	—	X ¹⁴
<i>"Eocardia" fissa</i>	X ²⁰	—	—	—	—	—
<i>Schistomys erro</i>	X ¹	X ⁹	—	X ⁹	—	X ²⁰
<i>Phanomys mixtus</i>	X ¹	X ⁹	X ⁹	—	—	—
<i>Phanomys sp.</i>	—	—	—	X ⁹	—	—
<i>CHINCHILLOIDEA</i>						
<i>Prolagostomus pusillus</i>	X ¹	X ⁹	—	X ⁹	—	X ²¹
<i>Prolagostomus sp.</i>	—	—	X ⁹	—	—	—
<i>Pliolagostomus notatus</i>	X ¹	X ⁹	—	X ⁹	—	X ²¹
<i>Perimys erutus</i>	X ¹	X ⁹	X ⁹	X ⁹	—	X ¹⁴
<i>Perimys onustus</i>	X ¹	X ⁹	X ⁹	X ⁹	—	—
<i>Perimys incavatus</i>	—	X ⁹	X ⁹	—	—	—
<i>Perimys zonatus</i>	X ¹	—	—	—	—	—
<i>Scleromys angustus</i>	X ¹	—	—	—	—	—
<i>Scleromys sp.</i>	—	X ⁹	X ⁹	X ⁹	—	—
<i>PRIMATES</i>						
<i>Homunculus vizcainoi sp. nov.</i>	—	X ¹⁰	X ¹⁰	X ¹⁰	—	—
TOTAL N° OF SPECIES⁽¹⁾	79	64	47	60	9	—

X¹: Ameghino, 1887a; X²: Cabrera, 1927; X³: Bargo et al., 2019; X⁴: Fernicola and Vizcaíno, 2019; X⁵: Fernández and Muñoz, 2019; X⁶: Mercerat, 1891; X⁷: Ameghino, 1885; X⁸: Schmidt et al., 2019; X⁹: Arnal et al., 2019; X¹⁰: Kay and Perry, 2019; X¹¹: Chornogubsky et al., 2019; X¹²: Arnal and Vucetich, 2015; X¹³: Kay et al., 2012; X¹⁴: Tauber, 1997a; X¹⁵: Tauber, 1996; X¹⁶: Soria, 2001; X¹⁷: Arnal, 2012; X¹⁸: Arnal et al., 2017; X¹⁹: Racco et al., 2018; X²⁰: Pérez, 2010; X²¹: Rasia, 2016.

⁽¹⁾ species + species inferred from specimens identified at generic or suprageneric level