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Early–Middle Miocene Paleontology in the Río Santa Cruz, Southern Patagonia, Argentina. 130 years since Ameghino, 1887

Photo: Segundas Barrancas Blancas, Estancia Cordón Alto (Courtesy of I. Escapa)

Guest Editors: J.C. Fernicola, M.S. Bargo, S.F. Vizcaíno and R.F. Kay
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EARLY–MIDDLE MIOCENE PALEONTOLOGY IN THE RÍO SANTA CRUZ, SOUTHERN PATAGONIA, ARGENTINA. 130 YEARS SINCE AMEGHINO, 1887

J.C. Fernicola, M.S. Bargo, S.F. Vizcaíno, and R.F. Kay
Guest Editors

Buenos Aires
2019

PREFACE

EARLY–MIDDLE MIOCENE PALEONTOLOGY IN THE RÍO SANTA CRUZ, SOUTHERN PATAGONIA, ARGENTINA. 130 YEARS SINCE AMEGHINO, 1887

The fossils of the so-called Santacrucian Mammal Age (Early–Middle Miocene) constitute the most abundant and complete record of a vertebrate fauna in Patagonia during the Middle Miocene Climatic Optimum (MMCO) and prior to the Great American Biotic Interchange (GABI). To explore the effects of MMCO on the Santacrucian fauna, in 2003 we established a paleoecology research program, the first stage of which was reflected in the publication in 2012 of the volume *Early Miocene Paleobiology in Patagonia. High-Latitude Paleocommunities of the Santa Cruz Formation* (S.F. Vizcaíno, R.F. Kay and M.S. Bargo, Eds.; Cambridge University Press). That work focused on the outcrops of the Santa Cruz Formation of the Atlantic coast where the fossils are most abundant and best preserved. We wished then to refine the chronological and faunal correlations of the exposures of this formation in other areas in the Province of Santa Cruz, before extending our paleoecological approach in those outcrops.

Our first step was to recollect localities in the Santa Cruz Formation along the Río Santa Cruz, the first in Patagonia formally explored from a paleontological perspective during the second half of the 19th century. The Río Santa Cruz fossils were seminal for the evolutionary study of the succession of the fossil vertebrate communities of South America during the Miocene in particular, and the Cenozoic in general. The publications of Florentino Ameghino on the Río Santa Cruz fossils, since 1887 and later, strongly marked the focus of vertebrate paleontology in South America. Often without a critical consideration of the context of Ameghino's relationships with other personalities of his time in the field of paleontology and its consequences in the quality of information that remained available for further studies.

Unfortunately, the outcrops of the Río Santa Cruz, distributed discontinuously over approximately 100 km, remained virtually unnoticed since the end of the 19th century. Since then they have been mentioned only as a single locality, in many cases called "Barrancas del Río Santa Cruz". To clarify the status of the various exposures and faunas, in 2009 we began explorations along the river to locate the sites where Carlos Ameghino collected in 1887. With the new work and with careful reading of the contemporaneous notes and letters of Carlos Ameghino we were able to establish the precise locations on the southern margin of the Segundas Barrancas Blancas and Yatén Huageno localities. In 2011 was identified the easternmost locality, Barrancas Blancas, where the contact with the underlying marine Monte León Formation is recorded. In 2012, geological profiles of the three locations were made and rock samples were taken for dating. In 2013–2014 fossil collection fieldwork was carried out that resulted in the recovery of some 1900 specimens for study by various experts of the different groups. Finally, to integrate the new information, we offer this Thematic Volume, *Early–Middle Miocene Paleontology in the Río Santa Cruz, Southern Patagonia, Argentina. 130 years since Ameghino, 1887.*

This synthesis about the Miocene fauna of the Río Santa Cruz includes 13 articles. The first article, by the editors of the volume, summarizes the historical background related to the first explorations of the Río Santa Cruz, the implications of the discoveries and the fate of their fossils. José I. Cuitiño and collaborators describe the geology and sedimentology of the Santa Cruz Formation in the three localities, and provide the timeframe. Leandro M. Pérez and collaborators report the record of freshwater bivalves, Paula Muzzopappa of anurans, and Juan M. Diederle and Jorge I. Noriega of birds. The following seven articles deal with new records of mammals: Laura Chornogubsky and collaborators report the metatheres, M. Susana Bargo and collaborators the sloths, Juan C. Fernicola and Sergio F. Vizcaíno the cingulates, Mercedes Fernández and Nahuel A. Muñoz the astrapotheres and notoungulates, Gabriela I. Schmidt and collaborators the litopterns, Michelle Arnal and collaborators the rodents, and Richard F. Kay and Jonathan M. Perry the primates. They provide descriptions of the new specimens recently recovered, analyze taxonomic aspects referred to the type specimens in the old collections from the Río Santa Cruz, and provide systematic updates. The last article, by Fernicola and collaborators, analyzes the mammal associations recovered from the three localities of the river, based on the information in the previous articles, considering that Barrancas Blancas and Segundas Barrancas Blancas are diachronic. In doing so, they compare the taxonomic richness of these localities with that of the 19th century collections, and those of the outcrops of the Atlantic coast.

We hope to have contributed to improving the understanding of paleontological evidence provided by the outcrops of the Santa Cruz Formation of the Río Santa Cruz, highlighting the need to integrate historical information into geological, geochronological and paleontological analyzes. Our next step will be to extend the focus of this volume to other outcrops of the Santa Cruz Formation to the east and west of the Río Santa Cruz to accomplish more nuanced view of regional and local faunal associations at the end of the MMCO in the Southern Argentine Patagonia.

Our sincere acknowledgement to the 21 authors of the articles, for the excellent willingness and effort to carry out their work in time. Also to the 25 reviewers for their comments and suggestions that substantially improved the manuscripts. Special thanks to the Directors of the PE-APA, Ignacio H. Escapa and Ana P. Carignano, for giving us the opportunity to publish this volume, for their guidance and support during the editorial process. Also to Michelle Arnal of the Editorial Production Team, and the Graphic Editorial Team of PE-APA for their dedication and patience.

We are also grateful to many persons and institutions for making possible the publication of this volume. To the Dirección de Patrimonio Cultural, Secretaría de Estado de Cultura de la Provincia de Santa Cruz for permission to conduct expeditions in the Province of Santa Cruz and for the loan of numerous specimens for study. To the Museo Regional Provincial "Padre Manuel Jesús Molina" of Río Gallegos for administrative and logistic support of different aspects of the work. We thank especially L. Acosta, L. Chornogubsky, J. Cuitiño, L. González, S. Hernández del Pino, V. Krapovickas, N. Muñoz, J. Spradley, N. Toledo, and A. Racco for their collaboration during the field work. To the Museo de La Plata (División Paleontología Vertebrados) and Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" where the collected specimens were prepared. To the people from the estancias along the Río Santa Cruz (Estancias El Vapor, Cordón Alto, Aguada Grande, Santa Lucía) and Río Bote (Estancia María Elisa) who gave us access to the outcrops and provided camp spaces. Financial support for field expeditions and laboratory preparation of fossils PIP-CONICET 00781, UNLP 11/N867, PICT 2013-0389 and 2017-1081, National Science Foundation 0851272 and 1348259, and National Geographic Society 9167-12.

Juan C. Fernicola, M. Susana Bargo,
Sergio F. Vizcaíno and Richard F. Kay
Guest Editors

PALEONTOLOGÍA DEL MIOCENO TEMPRANO–MEDIO EN EL RÍO SANTA CRUZ, PATAGONIA, ARGENTINA. 130 AÑOS DESDE AMEGHINO, 1887

Los fósiles de la llamada Edad Mamífero Santacrucense (Mioceno Temprano–Medio) constituyen el registro más abundante y completo de una fauna de vertebrados de Patagonia durante el Óptimo Climático del Mioceno Medio (OCMM) y anterior al Gran Intercambio Biótico Americano (GIBA). Para explorar los efectos del OCMM en la fauna Santacrucence, en 2003 iniciamos un programa de investigación de paleoecología cuya primera etapa quedó reflejada en la publicación en el año 2012 del volumen *Early Miocene Paleobiology in Patagonia. High-Latitude Paleocommunities of the Santa Cruz Formation* (S.F. Vizcaíno, R.F. Kay, y M.S. Bargo, Eds.; Cambridge University Press). Esa obra se enfocó en los afloramientos de la Formación Santa Cruz de la costa Atlántica, donde los fósiles son abundantes y están muy bien preservados. A partir de los resultados en esa publicación, nos planteamos refinar las correlaciones cronológicas y faunísticas de las exposiciones de la formación en otras áreas de la provincia de Santa Cruz, antes de extender nuestro enfoque paleoecológico a esos afloramientos.

El primer paso fue la revisión de los yacimientos a lo largo del Río Santa Cruz, los primeros de Patagonia explorados formalmente desde una perspectiva paleontológica durante la segunda mitad del siglo XIX. Su contenido fosilífero resultó seminal para el estudio evolutivo de la sucesión de las comunidades de vertebrados fósiles de América del Sur durante el Mioceno en particular y el Cenozoico en general. Las publicaciones de Florentino Ameghino sobre los fósiles del Río Santa Cruz, desde 1887 en adelante, marcaron fuertemente el enfoque de paleontología de vertebrados en América del Sur, muchas veces sin una consideración crítica del contexto de las relaciones de Ameghino con otras personalidades del ámbito paleontológico de su tiempo y sus consecuencias en la calidad de información que quedó disponible para posteriores estudios.

Desafortunadamente los yacimientos del Río Santa Cruz, distribuidos de manera discontinua a lo largo de aproximadamente 100 km, pasaron virtualmente desapercibidos desde fines del siglo XIX. Desde entonces fueron reportados como una única localidad, que en muchos casos se denominó “Barrancas del Río Santa Cruz”. Para esclarecer la situación de las diferentes exposiciones y sus faunas, en 2009 iniciamos las exploraciones a lo largo del Río Santa Cruz para localizar los sitios en los que recolectó Carlos Ameghino en 1887. Con estas exploraciones y la lectura detallada de las notas y cartas de la época de Carlos Ameghino, establecimos la ubicación precisa, sobre la margen sur, de las localidades Segundas Barrancas Blancas y Yatén Huageno. En 2011 identificamos la localidad más oriental, Barrancas Blancas, donde se encuentra el contacto con la infrayacente Formación Monte León, de origen marino. En 2012 se confeccionaron perfiles geológicos de las tres localidades y se tomaron muestras de rocas para dataciones. En 2013–2014 se realizaron las campañas paleontológicas que resultaron en la recolección de unos 1.900 especímenes, para cuyo estudio fueron convocados especialistas en los distintos grupos. Finalmente, para integrar la información generada editamos este Volumen Temático, *Early–Middle Miocene Paleontology in the Río Santa Cruz, Southern Patagonia, Argentina. 130 years since Ameghino, 1887.*

Esta síntesis sobre la fauna del Mioceno en el Río Santa Cruz incluye 13 artículos. El primero, realizado por los editores del volumen, sintetiza los antecedentes históricos vinculados a las primeras exploraciones del Río Santa Cruz, las implicaciones de los hallazgos y el destino de sus fósiles. José I. Cuitiño y colaboradores describen la geología y sedimentología de la Formación Santa Cruz en las tres localidades y brindan el marco cronológico. Leandro M. Pérez y colaboradores reportan el registro de bivalvos de agua dulce, Paula Muzzopappa el de anuros y Juan M. Diederle y Jorge I. Noriega de aves. Los siete artículos siguientes tratan los nuevos registros de mamíferos: Laura Chornogubsky y colaboradores reportan los metaterios, M. Susana Bargo y colaboradores los perezosos, Juan C. Fernicola y Sergio F. Vizcaíno los cingulados, Mercedes Fernández y Nahuel A. Muñoz los astrapoterios y notoungulados, Gabriela I. Schmidt y colaboradores los litopternos, Michelle Arnal y colaboradores los roedores y Richard F. Kay y Jonathan M. Perry los primates. En ellos se brindan descripciones de nuevos especímenes recuperados, se analizan aspectos taxonómicos referidos a los especímenes tipo de las viejas colecciones procedentes del Río Santa Cruz y se efectúan actualizaciones sistemáticas. El último artículo (Fernicola y colaboradores) analiza las asociaciones de mamíferos recuperadas en las tres localidades, sobre la base de la información que surge de los artículos anteriores, considerando la diacronía existente entre Barrancas Blancas y Segundas Barrancas Blancas. Para ello compararon la riqueza taxonómica de estas localidades con la de las colecciones del siglo XIX y la de los afloramientos de la costa Atlántica.

Esperamos haber contribuido a mejorar el entendimiento de la evidencia paleontológica que ofrecen los afloramientos de la Formación Santa Cruz del Río Santa Cruz, resaltando la necesidad de integrar la información histórica a los análisis geológicos, geocronológicos y paleontológicos. Nuestro próximo paso será extender el enfoque de este volumen a otros afloramientos de la Formación Santa Cruz al este y oeste del Río Santa Cruz para concretar una visión mucho más ajustada de las asociaciones faunísticas regionales y locales al final de la OCMM en la Patagonia austral argentina.

Nuestro sincero agradecimiento a los 21 autores de los artículos, por la excelente disposición y esfuerzo para llevar

adelante sus trabajos en tiempo y forma. También a los 25 revisores por sus comentarios y sugerencias que mejoraron sustancialmente los manuscritos. Un agradecimiento muy especial a los Directores de la PE-APA, Ignacio H. Escapa y Ana P. Carignano, por brindarnos la oportunidad de publicar este volumen y por su orientación y apoyo en todo momento y a Michelle Arnal del Equipo Editorial de Producción y al Equipo Editorail de Gráfica de PE-APA por su dedicación y paciencia.

Agradecemos también a muchas personas e instituciones que hicieron posible la publicación de este volumen. A la Dirección de Patrimonio Cultural, Secretaría de Estado de Cultura de la Provincia de Santa Cruz por brindar los permisos para realizar trabajo de campo en la provincia y los préstamos de los numerosos especímenes recolectados para su estudio. Al Museo Regional Provincial "Padre Manuel Jesús Molina" de Río Gallegos por el apoyo logístico y administrativo. Un agradecimiento especial a L. Acosta, L. Chornogubsky. J. Cuitiño, L. González, S. Hernández del Pino, V. Krapovickas, N. Muñoz, J. Spradley, N. Toledo, and A. Racco por su colaboración en los trabajos de campo. Al Museo de La Plata (División Paleontología Vertebrados) y Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" donde se realizó la preparación de los especímenes colectados. A los dueños y/o encargados de las estancias ubicadas a lo largo del Río Santa Cruz (Estancias El Vapor, Cordón Alto, Aguada Grande, Santa Lucía) y del Río Bote (Estancia María Elisa) por brindarnos acceso a las yacimientos y espacios para acampar. Diferentes agencias e instituciones brindaron apoyo económico para realizar los trabajos de campo y preparación de los especímenes: PIP-CONICET 00781, UNLP 11/N867, PICT 2013-0389, and 2017-1081, *National Science Foundation* 0851272 y 1348259 y *National Geographic Society* 9167-12.

Juan C. Fernicola, M. Susana Bargo,
Sergio F. Vizcaíno y Richard F. Kay
Editores Invitados

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EARLY–MIDDLE MIOCENE PALEONTOLOGY IN THE RÍO SANTA CRUZ, SOUTHERN PATAGONIA, ARGENTINA. 130 YEARS SINCE AMEGHINO, 1887

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HISTORICAL BACKGROUND FOR A REVISION OF THE PALEONTOLOGY OF THE SANTA CRUZ FORMATION (EARLY–MIDDLE MIOCENE) ALONG THE RÍO SANTA CRUZ, PATAGONIA, ARGENTINA

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Abstract. In 1887, Carlos Ameghino carried out the first geological and paleontological expedition to the Río Santa Cruz (RSC), Patagonia, Argentina. Between 1887 and 1889, Florentino Ameghino studied the fossils obtained by Carlos, founding more than 120 taxa and establishing his *Formación Santacruceña* and *Piso Santacruceño*. In 1888, F. Ameghino was exonerated from the Museo de La Plata and replaced by Alcides Mercerat in 1889, starting a strong competition for the Santacrucian fossils, which since 1890 were obtained mainly on the Atlantic coast. Until 1894, Ameghino and Mercerat founded more than 500 mammal species, of which 80% correspond to Ameghino who, later, synonymized almost all Mercerat species. At the end of the 19th century, foreign explorers visited Patagonia, but they did not collect in the RSC. So the largest RSC collections were made until 1889. The Santacrucian collections of the 19th century have vague and in some cases contradictory geographical information. This is true for the Santacrucian species reassigned by F. Ameghino to the Notohippidian, an association that he located northwest of the RSC. Recent analyses show that several of these specimens were collected southwest of the RSC. These and other facts demonstrate the inconvenience of using the data from the old collections in biostratigraphic and paleoecological studies without a critical analysis of the history of their provenance. Since 2003, a research program was launched that promoted biostratigraphic and paleoecological studies of the Santa Cruz Formation (SCF). This Thematic Volume compiles contributions on geology, stratigraphy, taxonomy, and mammal association's analyses of the SCF along the RSC.

Key words. Santacrucian. Notohippidian. Fossil mammals. Taxonomy. Ameghino.

Resumen. ANTECEDENTES HISTÓRICOS PARA UNA REVISIÓN DE LA PALEONTOLOGÍA DE LA FORMACIÓN SANTA CRUZ (MIOCENO TEMPRANO–MEDIO) A LO LARGO DEL RÍO SANTA CRUZ, PATAGONIA, ARGENTINA. En 1887, Carlos Ameghino realizó la primera expedición geológica y paleontológica al Río Santa Cruz (RSC), Patagonia, Argentina. Entre 1887 y 1889, Florentino Ameghino estudió los fósiles obtenidos por Carlos, con los que fundó más de 120 taxones y estableció su Formación Santacruceña y Piso Santacruceño. En 1888, F. Ameghino fue exonerado del Museo de La Plata y reemplazado por Alcides Mercerat en 1889, iniciándose una fuerte competencia por los fósiles santacrucenses. A partir de 1890 estos fueron recolectados principalmente en la costa atlántica. Hasta 1894 Ameghino y Mercerat fundaron más de 500 especies de mamíferos, 80% de las cuales le correspondían a Ameghino quien, posteriormente, sinonimizaría casi todas las especies de Mercerat. A fines del siglo XIX exploradores extranjeros recorrieron Patagonia, pero casi no recolectaron en el RSC. Así, las principales colecciones del río se realizaron hasta 1889. Las colecciones santacrucenses del siglo XIX poseen información geográfica vaga y hasta contradictoria. Así sucede con las especies del Santacrucense reasignadas por Ameghino al Notohippidense, asociación por él ubicada al noroeste del RSC. Análisis recientes evidencian que varios de esos ejemplares fueron recolectados al suroeste del RSC. Estas y otras evidencias prueban la inconveniencia de utilizar los datos de las viejas colecciones sin un análisis crítico de la historia de su procedencia. Desde 2003 se inició un programa de investigación que impulsó estudios bioestratigráficos y paleoecológicos en la Formación Santa Cruz (FSC). Este Volumen Temático reúne contribuciones sobre geología, estratigrafía, taxonomía y análisis de asociaciones de mamíferos de la FSC en el RSC.

Palabras clave. Santacrucense. Notohippidense. Mamíferos fósiles. Taxonomía. Ameghino.

The Santa Cruz Formation (SCF) is an Early–Middle Miocene (Burdigalian–early Langhian) continental sedimentary succession within the Austral-Magallanes Basin widely distributed in southern Patagonia (Cuitiño *et al.* 2016, 2019), in the Province of Santa Cruz, Argentina (Fig. 1). It amalgamates historical and scientific values that strongly promoted and influenced the general approach to the study of continental vertebrate paleontology and stratigraphy of the Cenozoic of South America for over a century.

Particularly, the SCF along the Río Santa Cruz (RSC) was the first terrestrial unit of Patagonia formally and exhaustively explored from geologic and paleontological perspectives during the late 19th century, despite Fitzroy and Darwin had walked past them in 1834. New kinds of fossil vertebrates recovered in the first expedition to the RSC by Carlos Ameghino resulted in a massive foundation of names of fossil vertebrates in South America (Ameghino, 1887), albeit weakly described, without illustrations and, in many cases, based on very fragmentary and/or poorly preserved specimens. These and many other taxa described in the following years served Florentino Ameghino as a reference collection for the comparisons with every new Cenozoic fauna of Patagonia recorded in the subsequent two decades (Ameghino, 1906). The SCF constituted Ameghino's *Piso Santacruceño*, and its fauna his *étages notohippidéen* and *santacruzéen*, which provided the basis for the foundation of the Santacrucian South American Land Mammal Age (SALMA; Pascual *et al.*, 1965; Marshall *et al.*, 1983). Ameghino also believed that many of the species he described were more ancient than what we now understand, and that he had documented the ancestors of many mammalian orders in South America, including those of artiodactyls, perissodactyls, and even human beings (Ameghino, 1891a, 1907). These claims prompted researchers from Europe and North America to undertake the study of Santacrucian fossils, either by organizing their own expeditions or getting specimens from Ameghino's collections (Vizcaíno *et al.*, 2012a, 2013).

Simpson (1980) highlighted the importance of the Santacrucian as representative of a phase in South American mammal history in which the communities consisted of a complex mixture of descendants of ancient lineages of the continent (Marsupialia, Xenarthra, Litopterna, Notoungulata, and Astrapotheria) and new forms from other continents (Rodentia and Primates). This and the fact that some localities have provided excellently preserved fossils promoted paleobiological and paleoecological studies of this fauna. Vizcaíno *et al.* (2012b) and Kay *et al.* (2012) reviewed the published paleoecological contributions on the Santacrucian and performed their own studies based on Santacrucian localities from the Atlantic coast. One of their objectives was to provide a model to reconstruct the paleoecology of the SCF, especially the niche structure for a geographicallly and stratigraphically restricted sets of intensely collected localities, by identifying the number of species, and evaluating different biological parameters. Vizcaíno *et al.* (2012b) promoted future studies by which this approach could be applied to a more complete geographic and chronologic range of the SCF, recording different assemblages at different levels and evaluating ecological changes that occurred during the time of deposition of the unit in different areas.

This research program impelled, among other efforts, the initiation of geological and paleontological studies on the mostly forgotten outcrops of the SCF along the RSC, the area from where this unit was originally recognized and the first large fossil collection was first made. The project started with the relocation of the localities prospected in the 19th century by Francisco P. Moreno and Carlos Ameghino (see below), mostly based on a field season in November 2009, reported by Fernicola *et al.* (2014) and dated by Cuitiño *et al.* (2016). Teams of 10–12 people undertook intensive field work during the succeeding Austral summers of 2013 and 2014 (Fig. 2). On average, they collected fossils for 20 days from the localities Barrancas Blancas, Segundas Barrancas Blancas and Yaten Huageno, situated along an approximately 100 km stretch of the RSC. Another factor that catalyzed the project was the imminent construction of dams on the RSC that will affect the accesses and the outcrops themselves, particularly in the localities Yaten Huageno (Condor Cliff dam) and Segundas Barrancas Blancas (La Barrancosa dam; Fig. 3) (*https://www.minem.gob.ar/www/839/25793/represas-aprovechamientos-hidroelectricos-rio-santa-cruz*). The project then became a paleontological rescue. Virtually all identifiable pieces were collected without size or taxonomic bias, constituting more than 1900 specimens that now belong to the Museo Regional Provincial

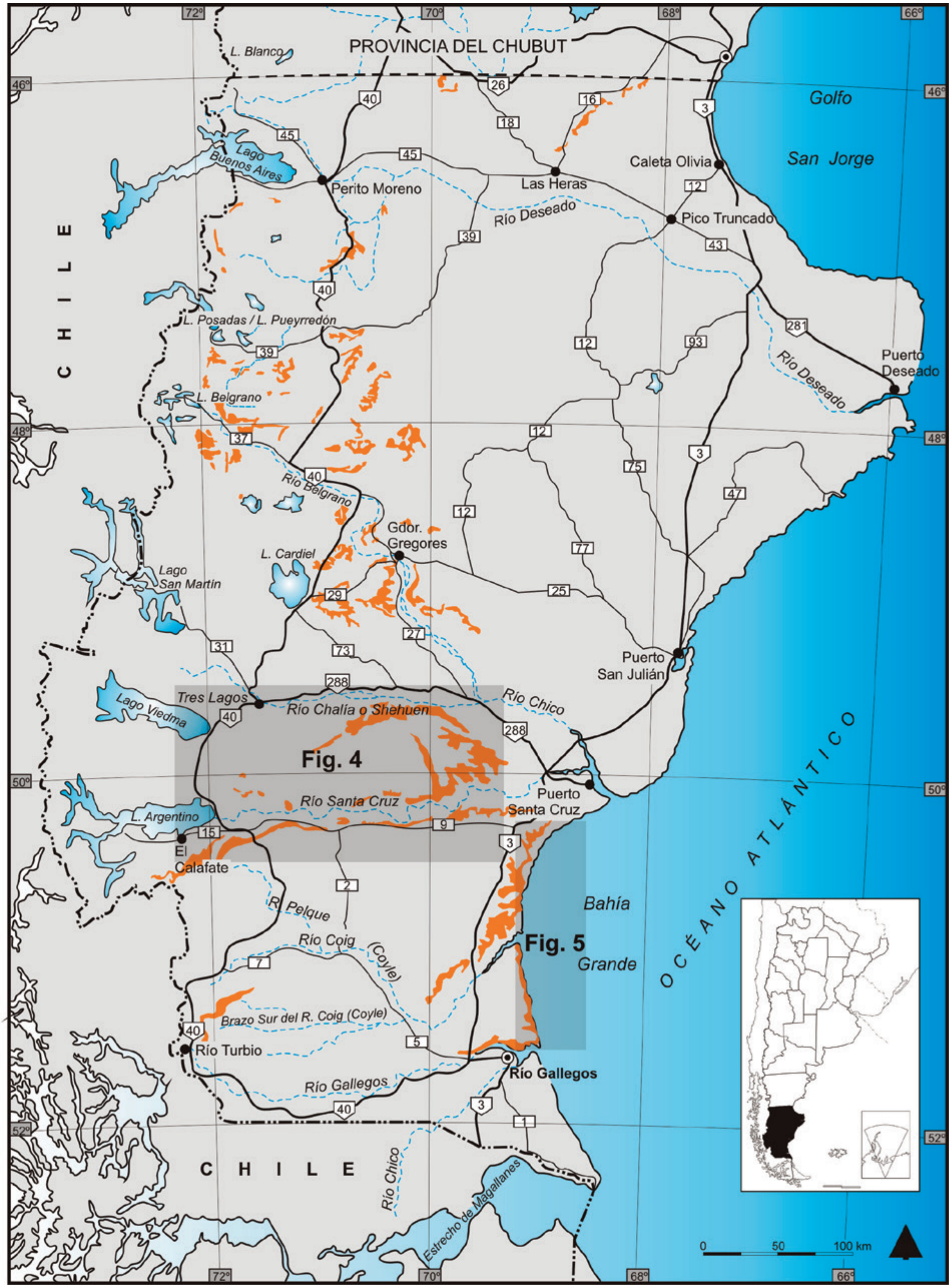

Figure 1. Map of the Province of Santa Cruz showing the distribution of the Santa Cruz Formation (in orange), and the study areas detailed in figures 4 and 5.

Figure 2. Field teams who worked during the summer seasons. **1,** 2013: from left to right, back row R.F. Kay, S. Hernández del Pino, S.F. Vizcaíno, J.C. Fernicola, N. Toledo, and N.A. Muñoz; front row, L. González, V. Krapovickas, L. Chornogubsky, and M.S. Bargo; **2,** 2014: from left to right, back row R.F. Kay, S.F. Vizcaíno, N. Toledo, S. Hernández del Pino, A. Racco, and J. Spradley; middle row, L. Chornogubsky and M.S. Bargo; front row N.A. Muñoz, J.C. Fernicola, J.I. Cuitiño, and L. Acosta.

“Padre M. Jesús Molina” of Río Gallegos (Province of Santa Cruz, Argentina). The specimens were collected recording geographic coordinates, stratigraphic provenance, and/or altitude as precisely as possible.

The project included geologists who recorded stratigraphic profiles and established correlations among the different localities (Cuitiño *et al.*, 2019), and were studied by specialists of the different taxa: invertebrates (Pérez *et al.*, 2019), Anura (Muzzopapa, 2019), Aves (Diederle and Noriega, 2019), Metatheria (Chornogubsky *et al.*, 2019), Rodentia (Arnal *et al.*, 2019), Xenarthra Folivora (Bargo *et al.*, 2019), Xenarthra Cingulata (Fernicola and Vizcaíno, 2019),

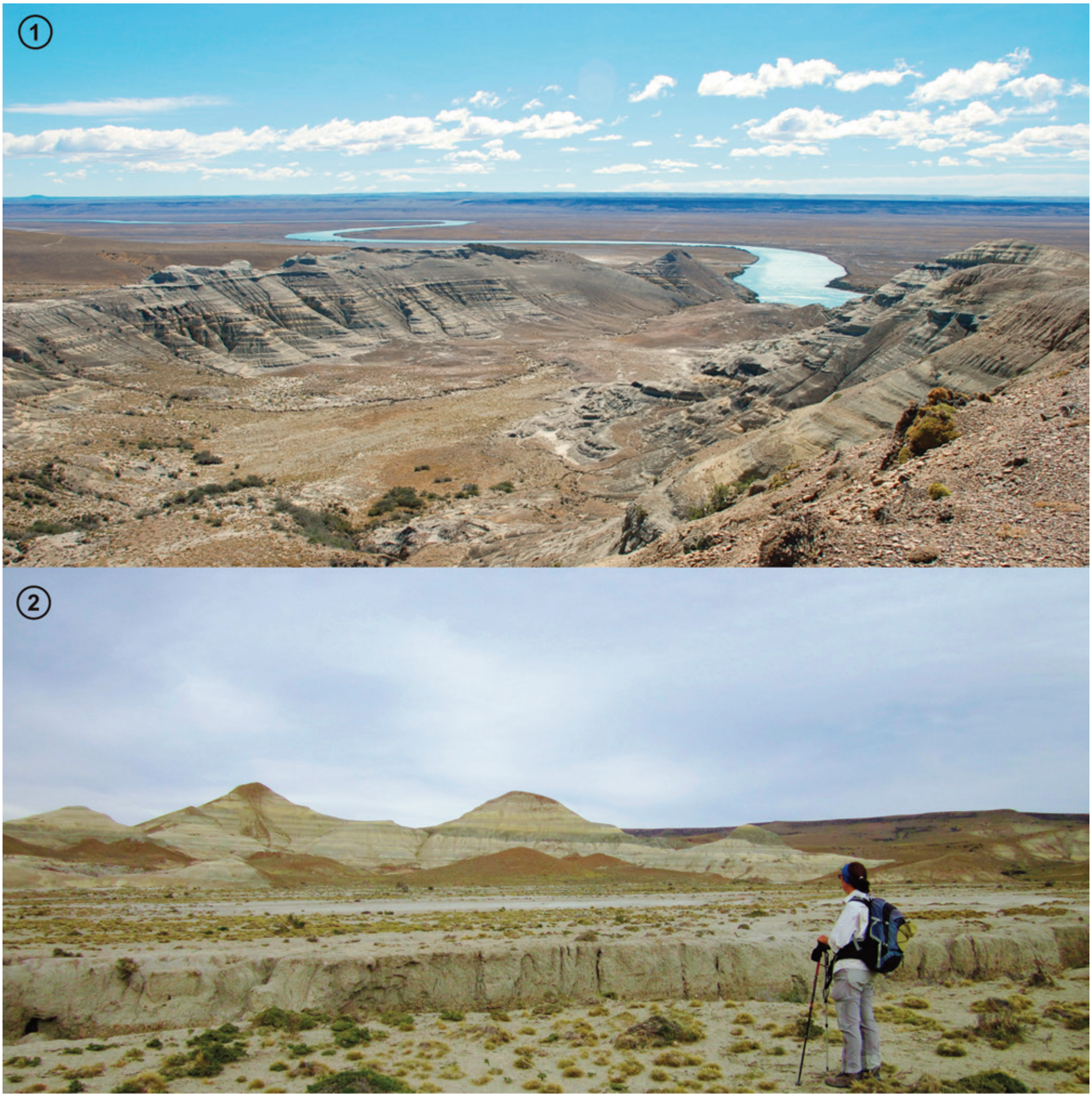

Figure 3. Exposures of the Santa Cruz Formation in the Río Santa Cruz at Segundas Barrancas Blancas locality. La Barrancosa dam will be located in this area. **1,** Ea. Cordón Alto; **2,** Ea. El Tordillo.

Notoungulata and Astrapotheria (Fernández and Muñoz, 2019), Litopterna (Schmidt *et al.*, 2019), and Primates (Kay and Perry, 2019). The results were compiled to undertake an analysis of the mammal associations recorded in the localities along the Río Santa Cruz (Fernicola *et al.*, 2019).

The objective of this contribution is to analyze the historical evidence on how the collections and early publications on the SCF at the Río Santa Cruz, and its fossil vertebrate content, modeled and conditioned the interpretation of its value as temporal or biostratigraphic indicators. In doing so, we expect to provide an accurate, stratigraphically and geographically controlled data upon which to base future bioestratigraphic and paleoecological interpretations generated from the study of new fossil collections from the Río Santa Cruz as they occur.

THE SANTA CRUZ FORMATION IN THE RÍO SANTA CRUZ

Until the first decade of the 20th century, the outcrops of the SCF at the RSC were referred to as discontinuous exposures located in the middle part of the river between Lago Argentino and Puerto Santa Cruz. Thus, Marshall (1976), taking as reference other authors, established that the fossiliferous unit was mainly located from 75 to 125 km east of Lago Argentino. Fernicola *et al.* (2014) were able to establish, from the study of Carlos Ameghino's field book of his 1887 expedition published by Rusconi (1965), the precise collection sites located on the right and left banks of the RSC. They found Carlos Ameghino's localities on the right margin to be, from east to west: Barrancas Blancas (Estancias Santa Lucía and Aguada Grande), Segundas Barrancas Blancas (Estancias Cordón Alto, El Tordillo y Rincón Grande) and Yaten Huageno (Estancia El Refugio). They also located a fourth locality on the Río Bote (Estancia María Elisa), a tributary of the RSC, located southeast of Lago Argentino (Fig. 4) hardly mentioned in Carlos' field notebook (in Rusconi, 1965). According to C. Ameghino (in Rusconi, 1965), on the left margin of the RSC there were three other fossiliferous localities, just in front of those on the right margin. So far, the left bank has not been further prospected.

The fossils from the first paleontological expedition to the Río Santa Cruz

In 1876–77, Francisco P. Moreno collected the first fossils from sediments referred to the SCF up the valley of the RSC during an expedition to Lago Argentino (Moreno, 1879). One of these specimens was published without Moreno's consent as the new species *Astrapotherium patagonicum* Burmeister, 1879 (Fernicola, 2011a,b). Beyond the fact that it unleashed an important conflict among these natu-

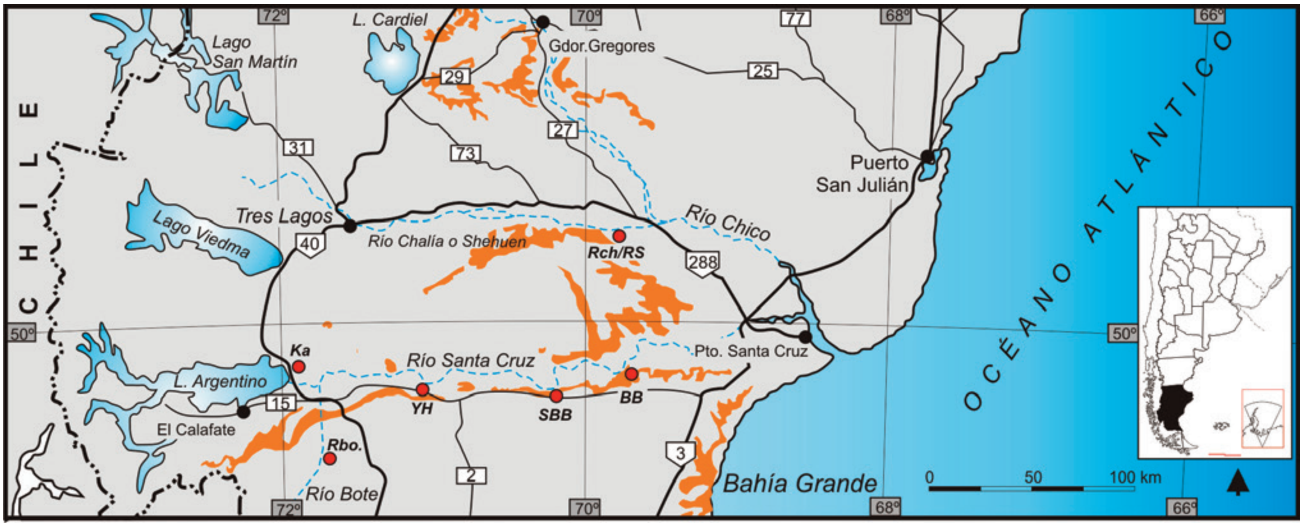

Figure 4. Fossil localities in the Río Santa Cruz, Río Chalía, and the western area in surroundings of Lago Argentino. **BB,** Barrancas Blancas; **SBB,** Segundas Barrancas Blancas, **YH,** Yaten Huageno; **Rch/RS,** Río Chalía (=Río Sehuen); **Ka,** Karaiken; **Rbo,** Río Bote.

ralists, this taxon represents the first formal mention of the deposits of the RSC. Later, in a lecture focused on his Patagonian expedition of 1876–77, Moreno (1882) mentioned the existence of half a dozen new species but never published them formally. In 1885, Florentino Ameghino erected the species *Pachyrukhos moyani* Ameghino, 1885 on the basis of remains collected by Carlos María Moyano about 145 kilometers from the mouth of the RSC.

These circumstances, added to a growing paleontological confrontation (Fernicola, 2011a,b) between Hermann Burmeister, then Director of the Museo Público de Buenos Aires, and F.P. Moreno and F. Ameghino, Director and Vice-Director respectively of the Museo de La Plata. Moreno entrusted C. Ameghino to make a geological and paleontological prospection of the RSC outcrops. Carlos fulfilled the requested work in 1887 (Farro, 2008, 2009; Podgorny, 2009; Fernicola, 2011a,b; Vizcaíno, 2011; Vizcaíno *et al.*, 2012a, 2013).

The expedition was supported by the Museo de La Plata. Carlos had all the field information that Moreno offered him, such as the complete map of the RSC that C.M. Moyano made with great detail during the 1876–77 expedition. The information provided by Moreno and his remarkable performance as a field naturalist allowed Carlos to return to Buenos Aires with more than 2000 fossil vertebrate specimens that were quickly described by his brother Florentino (Ameghino,1887). He recognized 122 taxa, of which 110 were new species, and indicated that more detailed descriptions of these new taxa were going to be published soon. At the beginning of 1888, Florentino was expelled by Moreno from the Museo de La Plata, but this fact did not prevent him from publishing more extensively on the 1887 collections two years later (Ameghino, 1889). This was possible because before leaving the institution he had already finished many of the descriptions, and also because he had retained for himself a considerable portion of the collection made by his brother in 1887 (Fernicola 2011a,b). Fifteen of the 19 new species that Ameghino described in 1889, and whose provenance was recognized by him as the "*Piso santacruceño eoceno inferior*" from the Santa Cruz terrritory, were based on specimens collected in 1887 by Carlos. According to what Florentino asserted (Ameghino 1889, p. 138, 186, 657), the remaining four species corresponded to specimens that Moyano gave him.

Other early collections

Between the years 1888 and 1984, the paleontological collections of the Museo de La Plata increased with new Santacrucian specimens from different localities of the RSC and the Atlantic coast, collected by other explorers of that institution (Vizcaíno *et al.*, 2013; Brinkman and Vizcaíno, 2014). Many of these specimens together with those collected by Carlos in 1887 and housed in the Museo de La Plata were also studied by the Swiss geologist Alcides Mercerat, who superseded F. Ameghino as paleontologist of the Museo de La Plata in 1889. Mercerat (1891a–g) named more than 80 new taxa of vertebrates from Santa Cruz; unfortunately, none of them was figured. In 1892, Mercerat left the Museo de La Plata and abandoned his study of Santacrucian fossils.

When early in 1889 Carlos Ameghino returned from a trip to Chubut commissioned by Moreno, he knew he had been excluded from the Museo de La Plata, completing the definitive rupture between the Ameghino brothers and Moreno after the exoneration of Florentino in 1888 (Fernicola, 2011a,b). Both events affected the study of the SCF. On the one hand, as already mentioned, Florentino retained part of the material of 1887 deposited in the Museo de La Plata. On the other hand, the situation forced Carlos to work in Patagonia without institutional affiliation, but not necessarily without official support (Vizcaíno, 2011; Vizcaíno *et al.*, 2013). Carlos continued doing fieldwork in Patagonia until 1903.

In relation to the outcrops of the *Piso Santacruceño*, in 1889 Carlos crossed the left bank of the RSC reaching the area of Karaiken; in 1890 he stayed in the central area of the Santa Cruz territory, collecting specimens in the Río Chalía (= Sehuen), and from 1890 to 1893 he explored and recovered a large number of specimens along the Atlantic coast between Monte León to Cabo buen Tiempo and along the Río Gallegos (Fig. 5). As soon as the fossils arrived to La Plata from Patagonia, Florentino studied them increasing considerably the species number of fossil vertebrates (Ameghino, 1890, 1891a–c, 1894a).

Between 1890 and 1895, there was a complex dispute concerning the taxonomy of Santacrucian fauna with two taxonomic proposals, the ones by Ameghino and Mercerat, which considerably increased the number of taxa. Ameghino

(1894a) presented his taxonomic synthesis in which he recognized about 300 terrestrial vertebrate Santacrucian taxa in which practically all the taxa founded by Mercerat (1891a–g) were synonymized. This is remarkable because he could not have seen Mercerat's specimens as he was not authorized to visit the collections of the Museo de La Plata (Ameghino, 1889; Fernicola, 2011a).

In the meantime, in 1893, the English paleontologist Richard Lydekker arrived at the Museo de La Plata invited by Moreno (Lydekker, 1894a) to study the paleontological vertebrate collection, including all the museum's Santacrucian specimens. Lydekker spent nearly three months studying the specimens, and published his own taxonomic proposals (Lydekker, 1894a,b). Unlike those previously proposed by Mercerat and Ameghino, he significantly reduced the number of recognized species. As occurred with Mercerat's proposal, Ameghino (1894b, 1895) quickly replied and completely rejected Lydekker's taxonomic arrangement. In this extremely complex context in which none of the naturalists could study the complete collections, the taxonomic proposal that passed to the 20th century was basically that of Ameghino (1894a).

The remarkable interest regarding this fauna promoted several foreign institutions to send expeditions to Patagonia in the succeeding three decades (Vizcaíno *et al.*, 2013, 2016). The most outstanding were conducted between 1886 and 1889 by John B. Hatcher (Princeton University, USA), as part of a research initiative of Professor William B. Scott of Princeton University. Hatcher visited different locations in Santa Cruz Territory, mostly on the Atlantic coast, and spent short time along the RSC (Hatcher, 1903, p. 113). While organizing a series of monographs on the Princeton Expeditions to Patagonia, Scott visited Argentina in 1902 to study and photograph the type materials and Santacrucian specimens in the Museo de La Plata, in the museum in Buenos Aires, and the private collection of Florentino Ameghino. The

Figure 5. Detailed map of the localities in the coastal Santa Cruz Formation, between Monte León and Río Gallegos. These localities have been explored and studied, since 2003 to present, as part of our research program.

album of photographs taken by Scott was rediscovered by Vizcaíno *et al.* (2017). These studies allowed him to carry out an extensive revision of Ameghino's taxonomic arrangement. In a series of lavishly illustrated monographs published between 1903 and 1912 by the Princeton University, every taxonomic group represented in the SCF was reviewed, in general greatly reducing the number of taxa (*e.g.*, Scott, 1903, 1904; Sinclair, 1906, 1909). The new taxonomic proposals such as that of the Xenarthra (Scott, 1903, 1904) were not considered by Ameghino, who continued using his own taxonomic arrangement (Ameghino, 1906) until his death in 1911. In the end, both local and international scientific communities came to adopt, albeit with modifications, the taxonomic proposals published in the Reports of the Princeton University Expeditions to Patagonia between 1901 and 1912.

The Santacrucian/Notohippidian issue

As mentioned above, the great diversity of vertebrates recognized by Ameghino between 1887 and 1889 on specimens recovered from the RSC and other areas (such as Río Chico and Río Gallegos), led Ameghino (1889) to propose a new faunal association that characterized his *Piso Santacruceño*. Almost 90% of the taxa included in this association were founded on specimens from Carlos' 1887 expedition. By 1900, the number of species recognized in the Santacrucian Stage by Ameghino (1894a) was about 400. Unfortunately, the information of the specimens on which the Santacrucian Stage was founded is scarce. Neither the publications of Ameghino nor those of Mercerat, included precise stratigraphic provenance of the specimens; and only in few cases, did they cite a geographic location (see below). In the collection made by C. Ameghino in 1887, he refers only to the Barrancas del Río Santa Cruz (Ameghino, 1889), without indicating a specific locality (*i.e.*, Barrancas Blancas, Segundas Barrancas Blancas or Yaten Huageno) where each specimen came from. This information is neither available in the catalogs of the Museo de La Plata and the Ameghino Collection in the Museo de Buenos Aires.

Ameghino (1900–1902, 1906) subdivided his *Piso Santacruceño* into the older *notohippidéen* and the younger *santacruzéen étages*. In doing so, he listed 72 species for the Notohippidian, 54 of which he considered exclusive of this stage. According to Ameghino (1900–1902, 1906) the specimens on which he based the Notohippidian had been collected by Carlos Ameghino in 1889, from outcrops restricted to a small region in Karaiken, north of the RSC, about 20 km northeast of Lago Argentino (see Ameghino, 1906, fig. 57).

Fernicola *et al.* (2014) provided evidence that some of the specimens included by F. Ameghino in the Notohippidian had been collected by C. Ameghino in 1887, not in 1889. According to these authors, 38 of the supposedly 54 exclusive Notohippidian species listed by Ameghino (1900–1902), were erected by F. Ameghino after 1890, whereas of the remaining 16, 10 were founded by F. Ameghino in 1887 and six in 1889. Furthermore, the specimens of 15 of the 16 species erected before 1889 had been collected by C. Ameghino in 1887.

This implies that the specimens of those 15 species could not have been collected at Karaiken but must come from some locality samples of the 1887 expedition. Fernicola *et al.* (2014) proposed that the specimens of those 15 Notohippidian species were collected by Carlos from rocks cropping out by the Río Bote about 25 km southeast of Lago Argentino. As a consequence, the geographic distribution of the Notohippidian recognized by Ameghino (1900–1902, 1906) would not be restricted to Karaiken locality, but also near Lago Argentino south of the RSC, including Río Bote and probably other outcrops nearby. Furthermore, in the Ameghino's catalog there are specimens collected in different localities along the Atlantic coast, identified as exclusive species of the Notohippidian listed by Ameghino (1900–1902) (Fernicola, pers. obs. 2018). Consequently, it becomes difficult to establish the actual distribution of many species of the RSC involved in Ameghino's distinction between the Santacrucian and Notohippidian stages.

FINAL REMARKS

The complex dispute between paleontologists and institutions occurred during the last 25 years of the 19th century seriously affected the paleontological studies of the SCF during that period. For instance, many of the new species were founded on very fragmentary and/or poorly preserved specimens, poorly described and not figured. Furthermore, most of those specimens do not have original labels indicating their status as types. All these facts implies the need of comprehensive taxonomic revisions of the SCF taxa, carefully reviewing the descriptions by Ameghino (1887, 1889, 1890, 1891a–c, 1894a,b), Mercerat (1891a–g), Lydekker (1894a,b), and Princeton's monographs. But also meticulously searching the location of holotype or syntype specimens and eventually, in the absence of them, the nomination of neotypes. Several Doctoral Dissertations have been conducted in the last decade to solve these problems, such as that on the Cingulata by González Ruiz (2010) and Toxodontia by Hernández del Pino (2017), and others are nearly complete, as is the case of Typotheria and Folivora.

Also, most of the specimens recorded in the historical collections of the museums of La Plata and Buenos Aires lack of precise geographic and stratigraphic information, while those in the Princeton collection (now in Yale Peabody Museum, USA) have the former, but lack the latter. Certainly, biostratigraphic and paleoecological studies require this information, unless it can be established that the levels studied do not differ temporarily from one another.

Recent radiometric dates provide a new chronological scheme for the SCF, including the Atlantic coastal (Fleagle *et al.*, 2012; Perkins *et al.*, 2012; Trayler *et al.*, 2019) and in the RSC (Cuitiño *et al.*, 2016) localities dealt with in this contribution. The latter proposes that the sedimentary sequences in Barrancas Blancas (~17.45 to ~16.49 Ma) and Yaten Huageno (~17.22 to ~16.67 Ma) are older than those at Segundas Barrancas Blancas (~16.32 to ~15.63 Ma). Moreover, the time span of the fossiliferous levels of Barrancas Blancas and Yaten Huageno indicates that the associated faunal assemblage is synchronous with and younger in part than the faunal assemblages of the eastern coastal localities, from Monte León to Killik Aike Norte (~17.85 to ~16.20 Ma). Segundas Barrancas Blancas is partially synchronous and younger than the faunal assemblages from Monte León to Cerro Observatorio (~17.85 to ~16.20 Ma). Interestingly, the higher levels of Segundas Barrancas Blancas overlap chronologically with the Collon Curá Formation from the Province of Río Negro in northern Patagonia, which bears a Colloncuran fauna (Vucetich *et al.*, 1993; González Ruiz *et al.*, 2013).

The absence of precise geographic and stratigraphic information in the old collections, as well as the doubts about the reliability of Ameghino's catalogs regarding the provenance of several Notohippidian species, prevent us from considering Ameghino's references in new biostratigraphic and paleoecological studies of the RSC and reinforced the need to perform our own large-scale field work and collections.

In the following articles of this thematic volume, we compiled a contribution on the stratigraphy of the Santa Cruz Formation on the right banks of the Río Santa Cruz, and an update of the record and systematics of their fossil vertebrates, based on the new collections made during the 2013–2014 fieldworks of our research program. The last article of this volume analyses the associations of mammals of the Santa Cruz Formation along the Río Santa Cruz. This new evidence constitutes the starting point for further comparisons with others Santacrucian exposures in Patagonia.

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REFERENCES

Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de Patagonia Austral y depositados en el Museo de La Plata. *Boletín del Museo de La Plata* 1: 1–26.

Ameghino, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas de la Academia Nacional de Ciencias* 6: 1–1027.

Ameghino, F. 1890. Los Plagiaulacídeos argentinos y sus relaciones zoológicas, geológicas y geográficas. *Boletín del Instituto Geográfico Argentino* 11: 143–201.

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

Ameghino, F. 1891b. Nuevos restos de mamíferos fósiles descubiertos por Carlos Ameghino en el Eoceno inferior de la Patagonia austral. Especies nuevas, adiciones y correcciones. *Revista*

Argentina de Historia Natural 1: 289–328.

Ameghino, F. 1891c. Observaciones críticas sobre los mamíferos eocenos de la Patagonia austral. *Revista Argentina de Historia Natural* 1: 328–382.

Ameghino, F. 1894a. Énumération synoptique des espèces de mammifères fossiles des formations éocènes de Patagonie. *Boletín de la Academia Nacional de Ciencias de Córdoba* 13: 259–455.

Ameghino, F. 1894b. Sur les ongulés fossiles de l'Argentine (Examen critique de l'ouvrage de R. Lydekker: A study on the extinct ungulates of Argentina. *Revista del Jardín Zoológico de Buenos Aires* 2: 193–224; 225–256; 257–288; 289–303.

Ameghino, F. 1895. Sur les édentés fossiles de l'Argentine: Examen critique, revision et correction de l'ouvrage de R. Lydekker: The extinct edentates of Argentina. *Revista del Jardín Zoológico de Buenos Aires* 3: 97–192.

Ameghino, F. 1900–1902. L'âge des formations sédimentaires de Patagonie. *Anales de la Sociedad Científica Argentina* 50: 109–130, 145–165, 209–229; 51: 20–39; 52: 65–91, 189–197, 244–250; 54: 161–180, 220–249, 283–342.

Ameghino, F. 1906. Les formations sédimentaires du Crétacé Superieur et du Tertaire de Patagonie avec un parallele entre leurs faunes mammalogiques et celles de l'ancien continent. *Anales del Museo Nacional de Buenos Aires* 15:1–568.

Ameghino, F. 1907. Notas preliminares sobre el *Tetraprothomo argentinus*: un precursor del hombre del Mioceno superior de Monte Hermoso. *Anales del Museo Nacional de Buenos Aires* 9: 107–242.

Arnal, M., Pérez, M.E., and Deschamps, C.M. 2019. Revision of the Miocene Caviomorph rodents from the Río Santa Cruz (Argentinean Patagonia). 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: 193–229.

Bargo, M.S., De Iuliis R., and Toledo, N. 2019. Early Miocene sloths (Xenarthra, Folivora) from the Río Santa Cruz valley (Southern Patagonia, Argentina). Ameghino, 1887 revisited. 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: 102–137.

Brinkman, P.D., and Vizcaíno, S.F. 2014. Clemente Onelli's sketch map and his first-hand, retrospective account of an early fossil hunting expedition along the Río Santa Cruz, Southern Patagonia, 1888–1889. *Archives of Natural History* 41: 326–337.

Burmeister, G. 1879. *Description physique de la République Argentine. D'après des observations personnelles et étrangères.* Imprenta Paul-Émile Coni, Buenos Aires, 553 p.

Cuitiño, J.I., Fernicola, J.C., Kohn, M., Trayler, R., Naipauer, M., Bargo, M.S., Kay, R.F., and Vizcaíno, S.F. 2016. U-Pb geochronology of the Santa Cruz Formation (early Miocene) at the Río Bote and Río Santa Cruz (southernmost Patagonia, Argentina): implications for the correlation of fossil vertebrate localities*. Journal of South America 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: 14–33.

Chornogubsky, L., Abello, M.A., and Barmak, G. 2019. The Metatheria from the Río Santa Cruz (Santa Cruz Formation, Early–Middle Miocene, Argentina): history and new findings. 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: 62–84.

Diederle, J.M., and Noriega, J.I. 2019. New records of birds from the Santa Cruz Formation (Early–Middle Miocene) at the Río Santa Cruz valley, 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: 55–61.

Farro, M.E. 2008. [*Historia de las colecciones en el Museo de La Plata, 1884–1906: naturalistas viajeros, coleccionistas y comerciantes de objetos de historia natural a fines del Siglo XIX.* PhD Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, 550 p. Unpublished.].

Farro, M.E. 2009. *La formación del Museo de La Plata. Coleccionistas, comerciantes, estudiosos y naturalistas a fines del siglo XIX.* Prohistoria Ediciones, Rosario, 234 p.

Fernández, M., and Muñoz, N.A. 2019. Notoungulata and Astrapotheria (Mammalia, Meridiungulata) of the Santa Cruz Formation (Early–Middle Miocene) along the Río Santa Cruz, Argentine Patagonia. 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: 138–169.

Fernicola, J.C. 2011a. 1886–1888: Ascenso, auge y caída de la sociedad entre Florentino Ameghino y Francisco P. Moreno. *Publicación Especial de la Asociación Paleontológica Argentina* 12: 35–49.

Fernicola, J.C. 2011b. Implicancias del conflicto Ameghino-Moreno sobre la colección de mamíferos fósiles realizada por Carlos Ameghino en su primera exploración al río Santa Cruz, Argentina. *Revista del Museo Argentino de Ciencias Naturales, n.s.* 13: 41–57.

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 Notohippidian. *Journal of South America Earth Sciences* 52: 9–107.

Fernicola, J.C., and Vizcaíno, S.F. 2019. Cingulates (Mammalia, Xenarthra) of the Santa Cruz Formation (Early–Middle Miocene) from the Río Santa Cruz, Argentine Patagonia. 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: 85–101.

Fernicola, J.C., Vizcaíno, S.F., Bargo, M.S., Kay, R.F., and Cuitiño, J.I. 2019. Analysis of the Early–Middle Miocene mammal associations at 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: 239–259.

Fleagle, J.H., Perkins, M.E., Heizler, M.T., Nash, B., Bown, T.M., Tauber, A.A., Dozo, M.T., and Tejedor, M.F. 2012. Absolute and relative ages of fossil localities in the Santa Cruz and Pinturas Formations. 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. 41–58.

González Ruiz, L.R. 2010. [*Los Cingulata (Mammalia, Xenarthra) del Mioceno temprano y medio de Patagonia (edades Santacrucense y "Friasense") revisión sistemática y consideraciones bioestratigráficas*. Phd Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, 471 p. Unpublished.].

González Ruiz, L.R., Góis, F., Ciancio, M.R., and Scillato-Yané, G.J. 2013. Los Peltephilidae (Mammalia, Xenarthra) de la Formación Collón Curá (Colloncurense, Mioceno medio), Argentina. *Revista Brasileira de Paleontologia* 16: 319–330.

Hatcher, J.B. 1903. Narrative of the expedition. In: W.B. Scott (Ed.), *Reports of the Princeton University Expeditions to Patagonia, 1896–1899*. Vol. 1, Princeton University Press, Princeton, p. 1–296.

Hernández Del Pino, S. 2018. [*Anatomía y sistemática de los Toxodontidae (Notoungulata) de la Formación Santa Cruz, Mioceno temprano, Argentina*. PhD Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, 432 p. Unpublished.].

Kay, R.F., Vizcaíno, S.F., and Bargo, M.S. 2012. A review of the paleoenvironment and paleoecology of the Miocene Santa Cruz Formation. 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. 331–365.

Kay, R.F., and Perry, J.M.G. 2019. New primates the Río Santa Cruz and Río Bote (Early–Middle Miocene), Santa Cruz Province, 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: 230–238.

Lydekker, R. 1894a. Contribuciones al conocimiento de los vertebrados fósiles de la Argentina. Part I. *Anales del Museo de La Plata, Paleontología Argentina* 1: 1–83.

Lydekker, R. 1894b. Contribuciones al conocimiento de los vertebrados fósiles de la Argentina. Part II. *Anales del Museo de La Plata, Paleontología Argentina* 2: 1–248.

Marshall, L.G. 1976. Fossil localities for Santacrucian (Early Miocene) mammals, Santa Cruz Province, Southern Patagonia, Argentina. *Journal of Paleontology* 50: 1129–1142.

Marshall, L.G., Hoffstetter, R., and Pascual, R. 1983. Mammals and stratigraphy: Geochronology of the continental mammal-bearing Tertiary of South America. *Paleovertebrata, Mémoire Extraordinaire* 1–93.

Mercerat, A. 1891a. Sinopsis de la familia de los Astrapotheridae (Eoceno de Patagonia). *Revista del Museo de La Plata* 1: 241–255.

Mercerat, A. 1891b. Sinopsis de la familia de los Protoxodontidae conservados en el Museo de La Plata (Eoceno de Patagonia). *Revista del Museo de La Plata* 1: 381–444.

Mercerat, A. 1891c. Sinopsis de la familia Bunodontheridae (Eoceno de Patagonia) conservados en el Museo de La Plata. *Revista del Museo de La Plata* 1: 447–471.

Mercerat, A. 1891d. Datos sobre restos de mamíferos fósiles pertenecientes a los Bruta conservados en el Museo de La Plata y procedentes de los terrenos eocenos de Patagonia. *Revista del Museo de La Plata* 2: 1–46.

Mercerat, A. 1891e. Caracteres diagnósticos de algunas especies del gen. *Theosodon* conservadas en el Museo de La Plata. *Revista del Museo de La Plata* 2: 47–49.

Mercerat, A. 1891f. Caracteres diagnósticos de algunas especies de Creodonta conservadas en el Museo de La Plata. *Revista del Museo de La Plata* 2: 51–56.

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

Moreno, F.P. 1879. *Viaje a la Patagonia Austral, emprendido bajo los auspicios del gobierno nacional, 1876–1877*. Imprenta de La Nación, Buenos Aires, Argentina, 460 p.

Moreno, F.P. 1882. Patagonia, resto de un antiguo continente hoy sumergido. Contribuciones al estudio de las colecciones del Museo Antropológico y Arqueológico de Buenos Aires. *Anales de la Sociedad Científica Argentina* 14: 97–131.

Muzzopapa, P. 2019. *Calyptocephalella* (Anura, Australobatrachia) remains from the Río Santa Cruz (Early–Middle Miocene, Santa Cruz Formation), Santa Cruz Province, 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: 48–54.

Pascual, R., Ortega Hinojosa, E.J., Gondar, D., and Tonni, E.P. 1965. Las edades del Cenozoico mamalífero de la Argentina, con especial atención a aquellas del territorio Bonaerense. *Anales de la Comisión de Investigaciones Científicas* 6: 165–193.

Pérez, L.M., Cuitiño, J.I., Varela, A.N., and Muñoz, N.A. 2019. *Diplodon* cf. *colhuapiensis* (Bivalvia, Hyriidae) in Santa Cruz Formation (Early–Middle Miocene), at the Río Santa Cruz, Patagonia, Argentina. Stratigraphic and paleoenvironmental considerations. 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: 34–47.

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.

Podgorny, I. 2009. *El sendero del tiempo y de las causas accidentales. Los espacios de la prehistoria en la Argentina, 1850–1910*. Prohistoria Ediciones, Rosario, 331 p.

Rusconi, C. 1965. Carlos Ameghino. Rasgos de su vida y obra. *Revista del Museo de Historia Natural de Mendoza* 17: 1–160.

Schmidt, G.I., Hernández del Pino, S., Muñoz, N.A., and Fernández, M. 2019. Litopterna (Mammalia) from the Santa Cruz Formation (Early–Middle Miocene) at Río Santa Cruz, Southern 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: 170–192.

Scott, W.B. 1903. Mammalia of the Santa Cruz beds. Part I. Edentata. In: W.B. Scott (Ed.), *Reports of the Princeton University Expeditions to Patagonia 1896–1899*. Vol. 5, Paleontology 2. Princeton University Press, Princeton, p. 1–226.

Scott, W.B. 1904. Mammalia of the Santa Cruz beds. Part I. Edentata. In: W.B. Scott (Ed.), *Reports of the Princeton University Expeditions to Patagonia 1896–1899*. Vol. 5, Paleontology 2. Princeton University Press, Princeton, p. 227–364.

Simpson, G.G. 1980. *Splendid Isolation: the curious history of South American mammals*. Yale University Press, New Haven, 266 p.

Sinclair, W.J. 1906. Marsupials of the Santa Cruz beds. In: W.B. Scott (Ed.), *Reports of the Princeton University Expeditions to Patagonia, 1896–1899*. Princeton University Press, Princeton, 4: 330–460.

Sinclair, W.J. 1909. Mammalia of the Santa Cruz beds. Part I.

Typotheria. In W.B. Scott (Ed.), *Reports of the Princeton University Expeditions to Patagonia, 1896–1899*, Princeton University Press, Princeton, p. 1–110.

Trayler, R., Schmitz, M., Cuitiño, J.I., Kohn, M., Bargo, M.S., Kay, R.F., Strömberg, C., and Vizcaíno, S.F. 2019. An improved approach to age-modeling in deep time: Implications for the Santa Cruz Formation, Argentina. *GSA Bulletin* doi: 10.1130/B35203.1

Vizcaíno, S.F. 2011. Cartas para Florentino desde la Patagonia. Crónica de la correspondencia édita entre los hermanos Ameghino (1887–1902). In: J.C. Fernicola, A. Prieto, and D. Lazo (Eds.), *Vida y obra de Florentino Ameghino. Publicación Especial de la Asociación Paleontológica Argentina* 12: 51–67.

Vizcaíno, S.F., Bargo, M.S., and Fernicola, J.C. 2013. Expediciones paleontológicas durante los siglos XIX y XX a la Formación Santa Cruz (Mioceno Inferior, Patagonia) y destino de los fósiles. *3º Congreso Argentino de Historia de la Geología* (Salta)*, Actas*: 231–246.

Vizcaíno, S.F., Brinkman, P.D., and Kay, R.F. 2016. On the objectives and results of the Handel T. Martin paleontological expedition (1903–04) to the Santa Cruz Formation in southern Patagonia. *Revista del Museo de La Plata*, *Número Especial* 1: 316–333.

Vizcaíno, S.F., De Iuliis, G., Brinkman, P.D., Kay, R.F., and Brinkman, D.L. 2017. On an album of photographs recording fossils in the "Old collections" of the Museo de la Plata and Ameghino's private collection at the beginning of the 20th century. *Publicación Electrónica de la Asociación Paleontológica Argentina* 17: 14–23.

Vizcaíno, S.F., Kay R.F., and Bargo, M.S. 2012a. 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.

Vizcaíno, S.F., Kay, R.F., and Bargo, M.S. 2012b. *Early Miocene Paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, 370 p.

Vucetich, M.G., Mazzoni, M.M., and Pardiñas, U.F.J. 1993. Los roedores de la Formación Collón Cura (Mioceno Medio), y la Ignimbrita Pilcaniyeu. Cañadón del Tordillo, Neuquén. *Ameghiniana* 30: 361–381.

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ARTÍCULO

STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENTS OF THE SANTA CRUZ FORMATION (EARLY–MIDDLE MIOCENE) ALONG THE RÍO SANTA CRUZ, SOUTHERN PATAGONIA, ARGENTINA

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Abstract. The Santa Cruz Formation is an Early–Middle Miocene terrestrial sedimentary succession widely distributed in southern Patagonia. Particularly, it is exposed along the southern margin of the Río Santa Cruz valley where the sedimentological and stratigraphical features are described for three localities. From east to west these localities are: Barrancas Blancas, Segundas Barrancas Blancas and Yaten Huageno. The facies analysis permits us to identify three associations, representing deposition in 1) low-energy floodplains; 2) crevasse splays and sheet floods; and 3) fluvial channels. The three localities are chronologically equivalent and represent accumulation in an aggradational low-gradient fluvial system that drained towards the east and northeast from the Patagonian Andes to the Atlantic sea. Abundant pedogenic features and some trace fossils are consistent with a temperate subhumid climate and in part, a grassland environment.

Key words. Burdigalian. Sedimentology. Fluvial system. Paleosol. Austral Basin.

Resumen. ESTRATIGRAFÍA Y AMBIENTES DE SEDIMENTACIÓN DE LA FORMACIÓN SANTA CRUZ (MIOCENO TEMPRANO–MEDIO) EN EL RÍO SANTA CRUZ, PATAGONIA AUSTRAL, ARGENTINA. La Formación Santa Cruz consiste en una sucesión de sedimentos continentales del Mioceno Temprano–Medio que se encuentran ampliamente distribuidos en la Patagonia austral. Se describen los atributos sedimentológicos y estratigráficos de tres localidades a lo largo del Río Santa Cruz. De este a oeste estas localidades son: Barrancas Blancas, Segundas Barrancas Blancas y Yaten Huageno. El análisis de facies permitió definir tres Asociaciones que representan acumulación en 1) planicies de inundación; 2) lóbulos de desbordamiento y crecidas en manto; y 3) canales fluviales. Las tres localidades son cronológicamente equivalentes y representan acumulación en un sistema fluvial de bajo gradiente con alta agradación, el cual drenaba hacia el este y noreste desde los Andes Patagónicos hasta la plataforma. Los rasgos de los paleosuelos, más algunas trazas fósiles reconocidas, sugieren un clima templado subhúmedo y en parte, una planicie herbácea.

Palabras clave. Burdigaliense. Sedimentología. Sistema fluvial. Paleosuelo. Cuenca Austral.

The Santa Cruz Formation (SCF) is an Early–Middle Miocene continental sedimentary succession that is distributed in a large area of southern Patagonia within the Austral-Magallanes Basin. This unit represents an important record for Burdigalian–early Langhian high-latitude paleoenvironments, paleoclimates, and terrestrial ecosystems of the Southern Hemisphere (*e.g.*, Vizcaíno *et al.*, 2012; Cuitiño *et al.*, 2019). Early expeditions along the Río Santa Cruz valley summarized by Vizcaíno *et al.* (2013) and Fernicola *et al.* (2019a) noted the abundance and diversity of terrestrial fossil vertebrates from the sedimentary strata of the valley margins; the rich collections formed the basis for the Santacrucian South American Land Mammal Age (SALMA; Pascual *et al.*, 1965; Marshall *et al.*, 1983; Fernicola *et al.*, 2014 and references therein). Currently, the stratigraphy, chronology, sedimentology and paleontology of the SCF is best known for its exposures along the Atlantic coast of southeast of the Province of Santa Cruz (*e.g.*, Tauber, 1999; Vizcaíno *et al.*, 2012; Raigemborn *et al.*, 2018a,b; Zapata, 2018; Trayler *et al.*, 2019). Only recently has interest in the SCF of the Río Santa Cruz area increased, in part prompted by the beginning of a project for the construction of two dams in the Río Santa Cruz valley and the threat of subsequent flooding of fossiliferous outcrops. This resulted in some recent scientific contributions (Fernicola *et al.*, 2014; Cuitiño *et al.*, 2016) as well as the geology, stratigraphy, taxonomy, systematics, biostratigraphy, and paleoecology results presented in this Thematic Volume.

In this contribution we present new sedimentological and stratigraphic data obtained after revisiting some of the best exposures of the SCF along the southern margin of the Río Santa Cruz valley, with two main objectives. First, we aim to reconstruct the general depositional environment for the SCF in the Río Santa Cruz valley, and to compare it to other better known exposures of the unit. Second, we aim to provide a detailed stratigraphic context for the large number of fossils collected in this area.

GEOLOGIC SETTING

The Austral-Magallanes Basin is the southernmost basin of South America (Fig. 1.1) and its sedimentary record starts in the Early Cretaceous. Three main tectonic phases can be recognized for this basin: 1) a synrift phase occurred during the Late Jurassic–Early Cretaceous; 2) a sag phase occurred during the Early Cretaceous; and 3) a retroarc foreland stage occurred during the latest Cretaceous to Cenozoic (*e.g.*, Biddle *et al.*, 1986; Sachse *et al.*, 2016). The sedimentary units outcropping in the Río Santa Cruz valley correspond to the younger part of the foreland stage and are thought to be strongly controlled by the Andean tectonics and arc volcanism (Fosdick *et al.*, 2013; Cuitiño *et al.*, 2016; Ghiglione *et al.*, 2016; Parras and Cuitiño, 2018).

The Río Santa Cruz is one of the largest rivers of Patagonia. It flows through an incised deep and broad valley stretching 230 km from west to east, which was excavated during a relative sea level fall in the Quaternary. The river originates close to the Andean foothills in the eastern margin of Lago Argentino and ends in the Río Santa Cruz estuary that discharges in the Atlantic Ocean (Fig. 1.2–3). Along the valley margins, three Miocene sedimentary units of the Austral Basin can be recognized: (1) the shallow marine Early Miocene Estancia 25 de Mayo –previously named as Centinela Formation; Cuitiño and Scasso (2010)–, (2) the Monte León Formation (Sacomani and Panza, 2011; Parras and Cuitiño, 2018), and (3) the terrestrial Early–Middle Miocene Santa Cruz Formation (Tauber *et al.*, 2008; Sacomani and Panza, 2011; Cobos *et al.*, 2014; Fernicola *et al.*, 2014; Cuitiño *et al.*, 2016). A thin veneer of terrace conglomerates of Late Miocene to Quaternary age covers most of the study area (Sacomani and Panza, 2011; Cobos *et al.*, 2014; Fig. 1).

The age of the SCF is well dated radiometrically. For the coastal zone of southeast of the Province of Santa Cruz the age of the unit is bracketed by means of Ar^{39}/Ar^{40}, high precision zircon U/Pb, and sedimentation rate estimations between ~17.8 and 16 Ma (Burdigalian; Tejedor *et al.*, 2006; Perkins *et al.*, 2012; Trayler *et al.*, 2019), whereas in the Río Santa Cruz valley the unit is dated by means of U/Pb on zircons and sedimentation rate estimations between ~17.45 and 15.6 Ma (Burdigalian–early Langhian; Cuitiño *et al.*, 2016).

Beyond the Río Santa Cruz valley, the SCF and equivalent units are distributed in a wide area within the Austral-Magallanes Basin (Fernicola *et al.*, 2014, fig. 1; Fig. 1.2). It crops out along the foothills of the Andes from the Meseta Cosmelli in Aysén (Chile) (Ugalde *et al.*, 2015; Encinas *et al.*, 2019) and Lago Posadas regions (~400 and ~300 km to the northwest, respectively), where it is time equivalent to the Río Zeballos Group (Cuitiño *et al.*, 2019; Aramendía *et al.*, in press), and south of this area up to the Río Turbio region (~200 km to the southwest; Fig. 1.2). It is also present in the central Santa Cruz Province near Gobernador Gregores and Lago Cardiel (~150 km to the north). Several good exposures occur in the southern of the Province of Santa Cruz (Fig. 1.2), including the Río Chalía (= Sheuhen) (Vizcaíno *et al.*, 2018) and the coastal zone between the Monte León National Park and the Río Gallegos estuary (Bown and Fleagle, 1993; Tauber, 1999; Matheos and Raigemborn, 2012; Raigemborn *et al.*, 2015, 2018a,b; Zapata, 2018). The southernmost counterpart for the SCF is the Cullen Formation, located

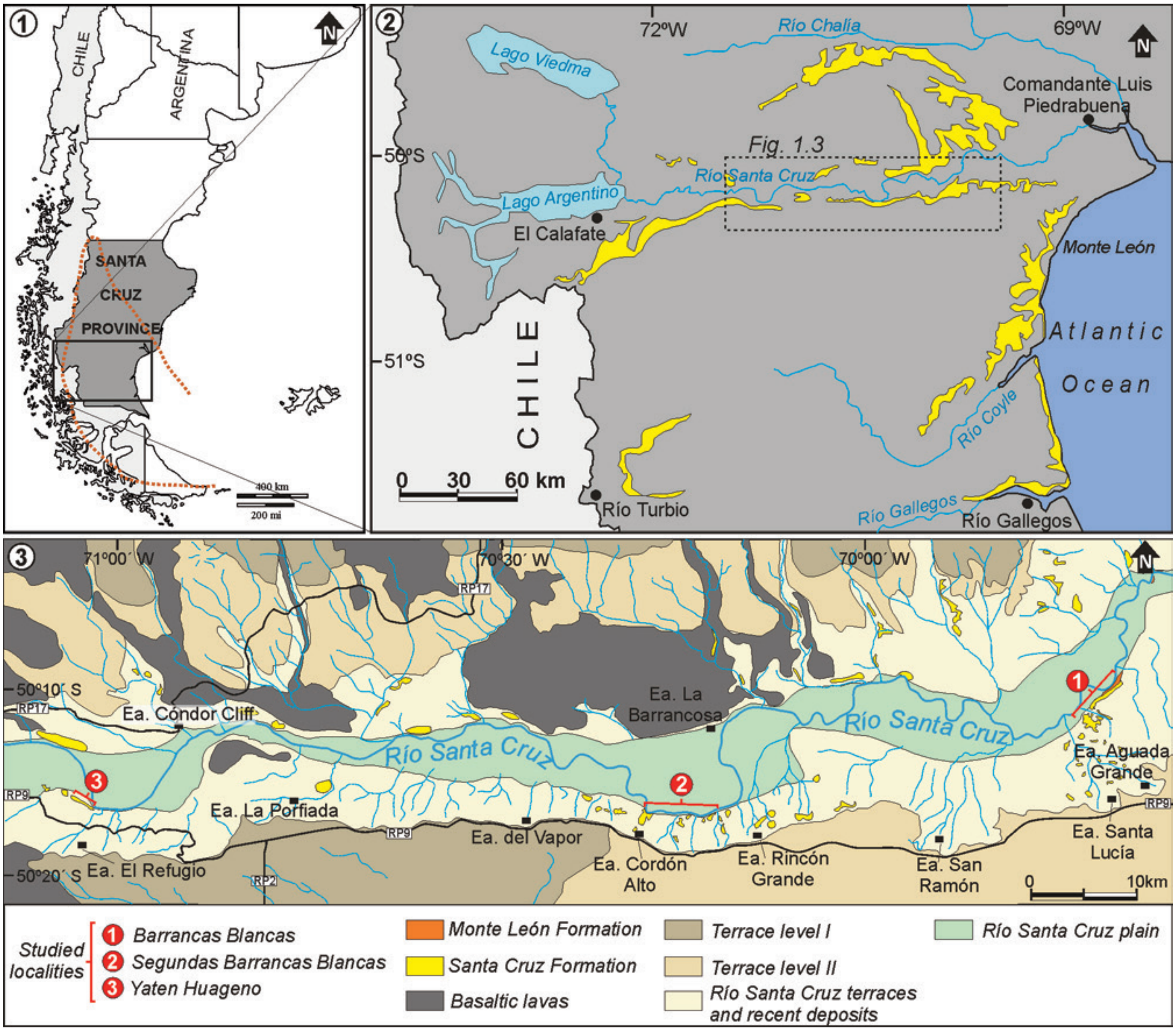

Figure 1. Geographic and geologic context for the studied outcrops. **1,** regional location map showing the position of the study area. The boundary of the Austral-Magallanes Basin is highlighted in dotted red line. **2,** Map of southern Santa Cruz province showing the distribution of the SCF outcrops (in yellow). The dashed-lined box indicates the location of the studied localities. **3,** Detailed geologic map of the Río Santa Cruz valley and the localities studied in this work. Modified after Sacomani and Panza (2011) and Cobos *et al.* (2014).

~300 km to the southeast in the northern part of the Tierra del Fuego Island (Olivero *et al.*, 2015; Bargo *et al.*, 2018).

METHODS

This work is based on data collected in the field, including stratigraphic, sedimentological, macropedological and ichnological observations. The SCF crops out in both the north and south margins of the Río Santa Cruz valley. The three main localities of the southern margin are here described, which correspond to those visited in 1887 by Carlos Ameghino, and recently revisited, as described in Fernicola *et al.* (2014), with new dates presented in Cuitiño *et al.* (2016). From east to west they are (Fig. 1.3): Barrancas Blancas, within the boundaries of the Estancia Aguada Grande (EAG) and Estancia Santa Lucía (ESL); Segundas Barrancas Blancas, in the Estancia Cordón Alto (ECA) and

Estancia El Tordillo (EET); and Yatén Huageno, in the Estancia El Refugio (Fig. 1.3).

The base and top of SCF exposures, as well as guide level elevations, were measured with conventional GPS devices taking care of recording only with the maximum available altitude accuracy. When possible, guide levels such as tuffs or distinctive yellow layers were followed in the field for several kilometers to check their validity as correlation horizons. We logged each outcrop using a Jacob Staff. Sedimentological descriptions include grain-size, primary sedimentary structures, bed thickness and geometry were noted. Paleosol macro pedofeatures noted include structure, mottles, nodules, color, slickensides, root traces, as well as body and other trace fossils (following Retallack, 2001). Colors were described according to the Geological Rock Color Chart (2009). Ages for the base and top of exposures were estimated using the available U/Pb ages and a sedimentation rate of 150 m/Ma estimated by Cuitiño *et al.* (2016), which is roughly coincident with average sedimentation rates of 158 m/Ma obtained by Trayler *et al.* (2019) for the SCF in the coastal zone by means of high precision geochronology. In addition, these values are very close to the sedimentation rate calculated by Sachse *et al.* (2016) for the times of deposition of the SCF in all the Austral Basin (170 m/Ma). Names and numerical ages for formal chronostratigraphic stages are taken from the International Chronostratigraphic Chart 2018/07.

DEPOSITIONAL ENVIRONMENTS

The sedimentological descriptions of the SCF in all the studied sections were the basis for defining a set of facies representing the main depositional processes (Tab. 1). These were grouped in Facies Associations (FAs) representing depositional sub-environments.

TABLE 1 – List of sedimentary facies defined in this work with their distinctive features

Facies Code	*Lithology*	*Physical Sedimentary Structures*	*Other features*	*Depositional process*
Sh	*Fine to medium sandstones, well sorted. Gray to light gray. Intraclasts and pumice common*	*Plane-parallel and low-angle lamination*	-	*Tractive deposits formed through upper flow regime plane bed*
St	*Medium to coarse sandstones*	*Trough cross-bedding. Occasionally with pumice or intraclast particles on the foresets*	*Common reddish to brownish carbonate concretions*	*Migration of 3D subaqueous dunes within fluvial channels*
Sp	*Medium to coarse sandstones*	*Planar cross-bedding.*	-	*Migration of 2D subaqueous dunes*
Sm	*Very fine to medium sandstones. Abundant pyroclastic material*	*Structureless*	*Common root traces. Occasional decapod burrows.*	*Tractive deposits subsequently modified by soil forming processes*
Sr	*Fine sandstones*	*Ripple lamination. Usually observed climbing ripples*	-	*Deposition by tractive currents by current ripple migration*
Fp	*Siltstone and mudstone, with subordinate fine sandstone. Usually greenish or gray*	*Structureless. Remains of plane-parallel or current ripple lamination.*	*Common root traces. Scarce mottles, slickensides, nodules, cutans, peds, rhizoconcretions, organic matter remains. Scarce invertebrate trace fossils and coprolites.*	*Settling from suspension of fine sediments in low energy environments and subsequent modification by soil processes*
Fl	*Silt and clay*	*Plane-parallel lamination*	*Scarce leaf remains.*	*Settling from suspension of fine sediments in low energy environments. Lamination produced by fluctuating energy conditions*
Tm	*Medium to very fine tuffs. White to light yellow or light pink*	*Structureless*	*Abundant in-situ fossil vertebrates. Scarce root traces*	*Ash fallout deposits with subsequent reworking by fluvial and pedogenic processes.*

FA1- Floodplain deposits with paleosols

Description. FA1 is dominant throughout the SCF and is composed of grayish yellow (5Y 8/4), light greenish gray (5GY 8/1) and yellowish gray (5Y 7/2) mudstones, siltstones and light gray very fine to fine sandstones usually lacking any primary sedimentary structure (facies Fp, Sm; Fig. 2.1). A variable degree of intermingled tuffaceous material (facies Tm) like sparse white (N9) to very light gray (N8) thin tuff layers are also observed (Fig. 2.1). Tabular beds of different colorations show large lateral extension, giving the stratified aspect to the unit. Although some layers show delicate parallel laminations (facies Fl; Fig. 2.2), other primary sedimentary structures are hardly observed. In some cases laminated mudstones show poorly preserved oxidized

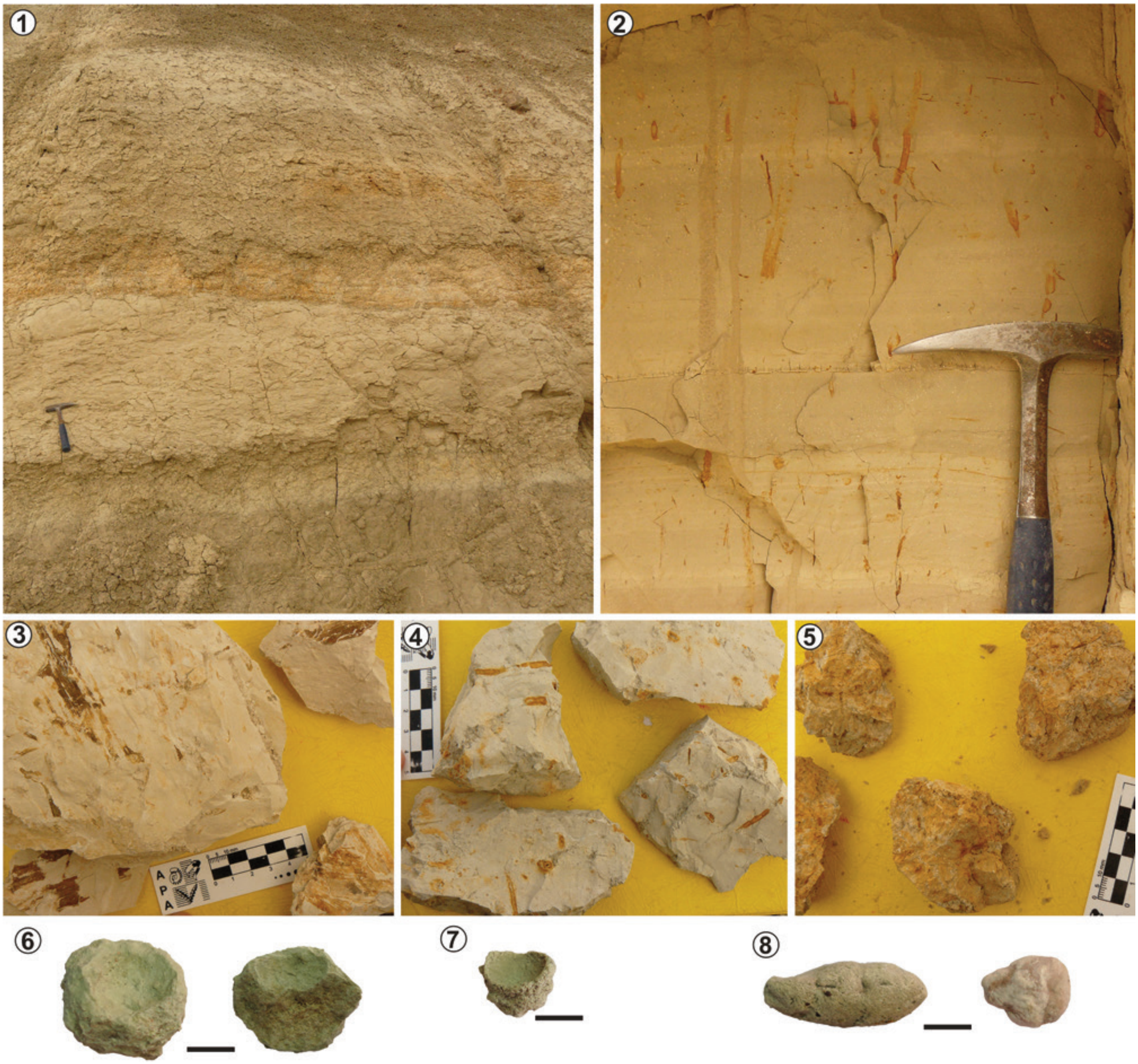

Figure 2. Different features of Facies Association 1 deposits. **1,** succession of structureless strata composed of pedogenically-modified fine tuffaceous sandstones and mudstones. **2,** Detail of laminated siltstones and mudstones with different types of orange-colored root traces. **3,** Plant remains preserved on lamination planes of mudstone. **4,** Detail of angular to subangular blocky peds with ferric delicate and haloed root traces. **5,** Detail of subangular blocky to granular peds with abundant root traces and mottles. **6,** Fragments of ***Coprinisphaera*** isp. **7,** ***Feoichnus challa***. **8,** Coprolites. Scale bars for 6, 7 and 8= 1 cm.

leaf impressions on the lamination planes (Fig. 2.3), some of them tentatively assigned to *Nothofagus* Blume (1851) (Roberto Pujana, personal communication 2018). Pedogenic features are abundant in this FA (Fig. 2.2, 2.4–5), being dominated by very pale brown (10YR 8/2) to moderate yellowish brown (10YR 5/4) ferric and delicate root traces –following the classification of Krapovickas (2012)–. Usually these root traces show dark yellowish orange (10YR 6/6) to light brown (5YR 5/6) haloes –*i.e.*, haloed-root traces *sensu* Krapovickas (2012)– (Fig. 2.4–5). Scarce trace fossils, such as *Feoichnus challa* Krause *et al.*, 2008 (Fig. 2.7) and fragments of *Coprinisphaera* isp. (Fig. 2.6), and scarce coprolites (Fig. 2.8) are recorded. Organic matter, slickensides, ferrous and calcareous nodules, calcareous rhizoconcretions, and mottling are also observed (Fig. 2.5). In general, these pedogenically-modified beds show no evidence of soil horizonation and peds. However, occasionally soil horizons are recognized showing cutans, and a blocky to granular structures (Fig. 2.4–5).

Interpretation. The fine-grained nature of these deposits suggests low-energy environments of deposition. Abundant rhizoliths and other pedogenic features suggest subaerial exposure followed by plant colonization during periods of relative landscape stability that allowed pedogenesis. This is typical of distal fluvial floodplains, which receive sporadic influxes of sediment during flooding episodes with subsequent periods of non-deposition and soil development. Laminated mudstones are interpreted to be deposited in small ponds in the floodplain in which the preservation of leaf impressions took place under acid and oxidizing conditions.

The abundance of small diameter root traces would suggest colonization of the substrate by grasses, herbs, and shrubs (Retallack, 2001; Catena *et al.*, 2016; Raigemborn *et al.*, 2018b). However, we do not rule out the coexistence of this plant community with trees (based on the presence of leaves of *Nothofagus* in this FA) and/or palms indicating mixed environments involving open areas and patches of trees/palms, as has been described in similar paleosols of the SCF southeast of the study area (*e.g.*, Raigemborn *et al.*, 2018a,b). In this context, the record of *Coprinisphaera* and *Feoichnus* are frequently but not exclusively preserved on grassland environments. These features are typical of open vegetated grassland-like soils, which could develop under subhumid to semiarid climates (Retallack, 2001; Catena *et al.*, 2016; Raigemborn *et al.*, 2018b). Particularly, granular structures are typically seen in wooded grassland soils (Retallack, 2001; Stoops *et al.*, 2010). Reduced hues in the matrix paleosols indicate iron-depletion (*e.g.*, Kraus and Hasiotis, 2006). However, the red and brown colors of the ferric root traces result from iron oxides, probably hematite, and represent better-oxidized areas where the Fe was reprecipitated (*e.g.*, Kraus and Hasiotis, 2006). Fe-nodules indicate redox-cycles; haloed root traces, slickensides, mottling and calcareous features suggest well-drained conditions and seasonal rainfall. Remains of organic matter in paleosols could be preserved under wet conditions (Buol *et al.*, 2011), and cutans (*i.e.*, clay-coatings) are signs of improved soil-drainage (Ashley and Driese, 2000). In combination, these features are evidence of fluctuating soil moisture. Paleosols with lack of horizonation and peds, and preservation of relict sedimentary structures as those of the SCF, are considered as very weakly/weakly-developed paleosols, which resemble paleo-Entisols and -Inceptisols present in other sections of the SCF outside the study area (Raigemborn *et al.*, 2018b). However, paleosols with defined horizons, peds, and cutans are compatible with relatively more developed soils (*e.g.*, Retallack, 2001) that probably could be interpreted as Alfisol-like paleosols. The studied paleosol types refer to very short-to-short–moderate pedogenesis, and probably they involved tens, hundreds to more than thousand years of soil formation (*e.g.*, Retallack *et al.*, 2000; Retallack, 2001). Consequently, pauses in sedimentation/erosion or stability of the landscape that allowed pedogenesis in FA1 of the SCF were relatively short (10^1–10^3 yr). The very low/low to moderate degree of paleosol development under the warm-temperate and seasonally humid-to-subhumid environment that prevailed during the Early–Middle Miocene in southern Patagonia (Kay *et al.*, 2012; Raigemborn *et al.*, 2018a,b) is likely the consequence of elevated aggradation rates.

FA2- Sheet flood – crevasse splay deposits

Description. FA2 is composed of centimeter-thick tabular beds of yellowish gray (5Y 8/1) to pale yellowish brown

(10YR 6/2) fine to medium sandstones. Also, up to 1 meter thick, light colored (N9 and N8) tuffaceous horizons show a fining upward trend are present in low proportion (Fig. 3.1). These beds form a distinctive feature of the SCF in the region. They are usually structureless (facies Sm; Tm) although occasionally they show parallel lamination (facies Sh) or ripple lamination (facies Sr), and show sharp bases and gradational tops to fine-grained beds of FA1, producing finning upward successions at the bed-scale. In minor proportion, some small lenticular bodies with planar base and convex tops were observed (Fig. 3.2), showing internal tractive sedimentary structures such as plane-parallel laminations (facies Sh) or small scale cross-bedding (facies St).

At Barrancas Blancas (EAG2), this facies association hosts an extensive burrow system conforming horizontal and vertical networks (Fig. 4.1–3). The individual branches are subcircular in cross section (2–3 cm in diameter) and are passively filled by the overlaying sandstones. The network is composed by burrows of horizontal disposition interconnected to vertical elements. Upward Y-branching and T-branching are commonly recorded (Fig. 4.5). The burrow lining is usually obscured by an external halo conformed by the host rock (Fig. 4.4), even though when visible, are smooth and structureless.

Interpretation. The dominance of relatively thin tabular sandstone deposits suggest accumulation by tractive currents produced by unconfined flows on the floodplain. These flows are interpreted as the result of fluvial flooding episodes when the flow overtopped the channel levees (Burns *et al.*, 2017). In some cases, the repetitive alternation of muddy and sandy tabular layers suggests accumulation confined within levees. Although occasionally observed in our survey, excepting for the Yaten Huageno locality (Fig. 3), lobe-shaped sandy beds are interpreted as crevasse-

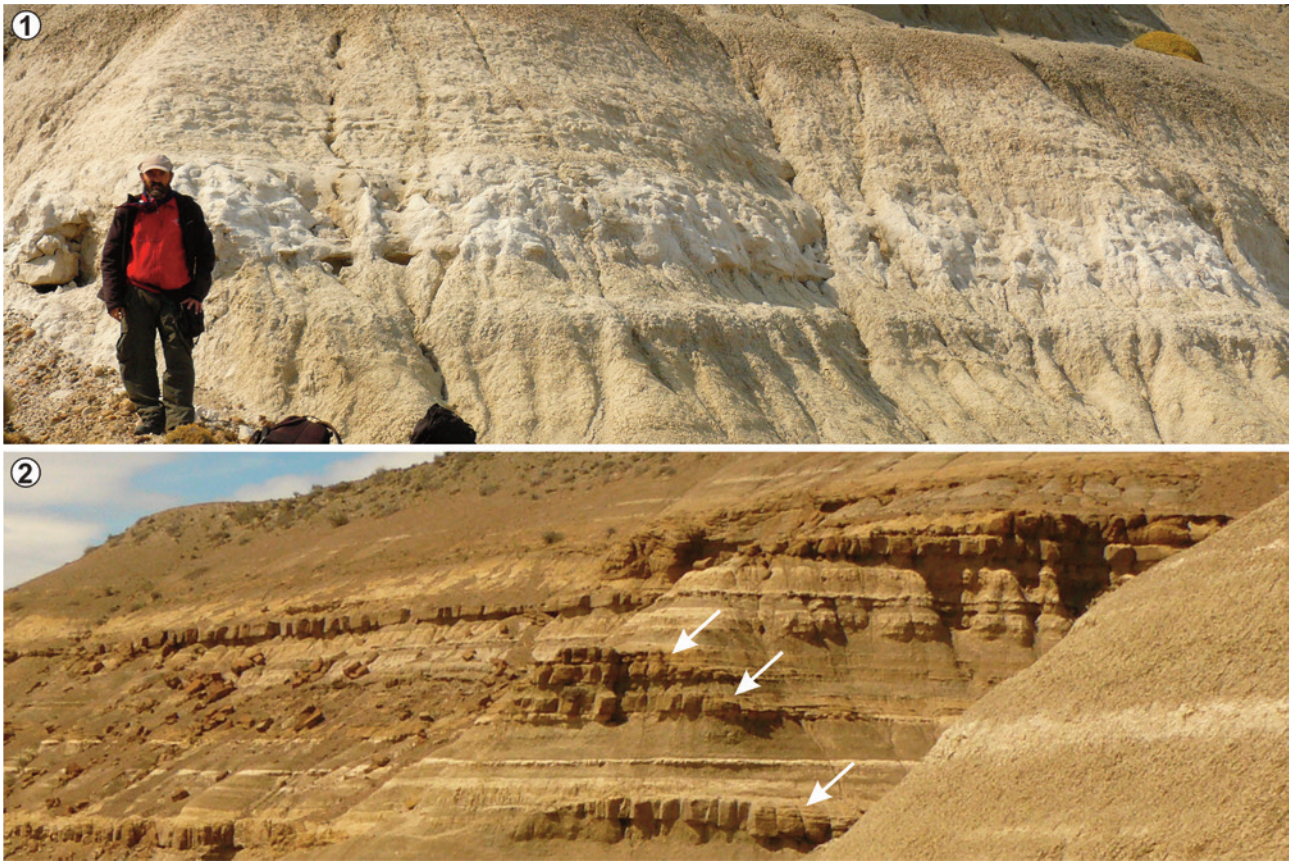

Figure 3. Outcrop views of different features assigned to Facies Association 2. **1,** A ~1 m-thick, tabular whitish tuff horizon showing fining upward trend, interpreted as a sheet flow deposit. **2,** Succession with abundant convex sandstone bodies (arrows), interpreted as lobes formed during crevasse splay events intercalated with floodplain deposits of FA1.

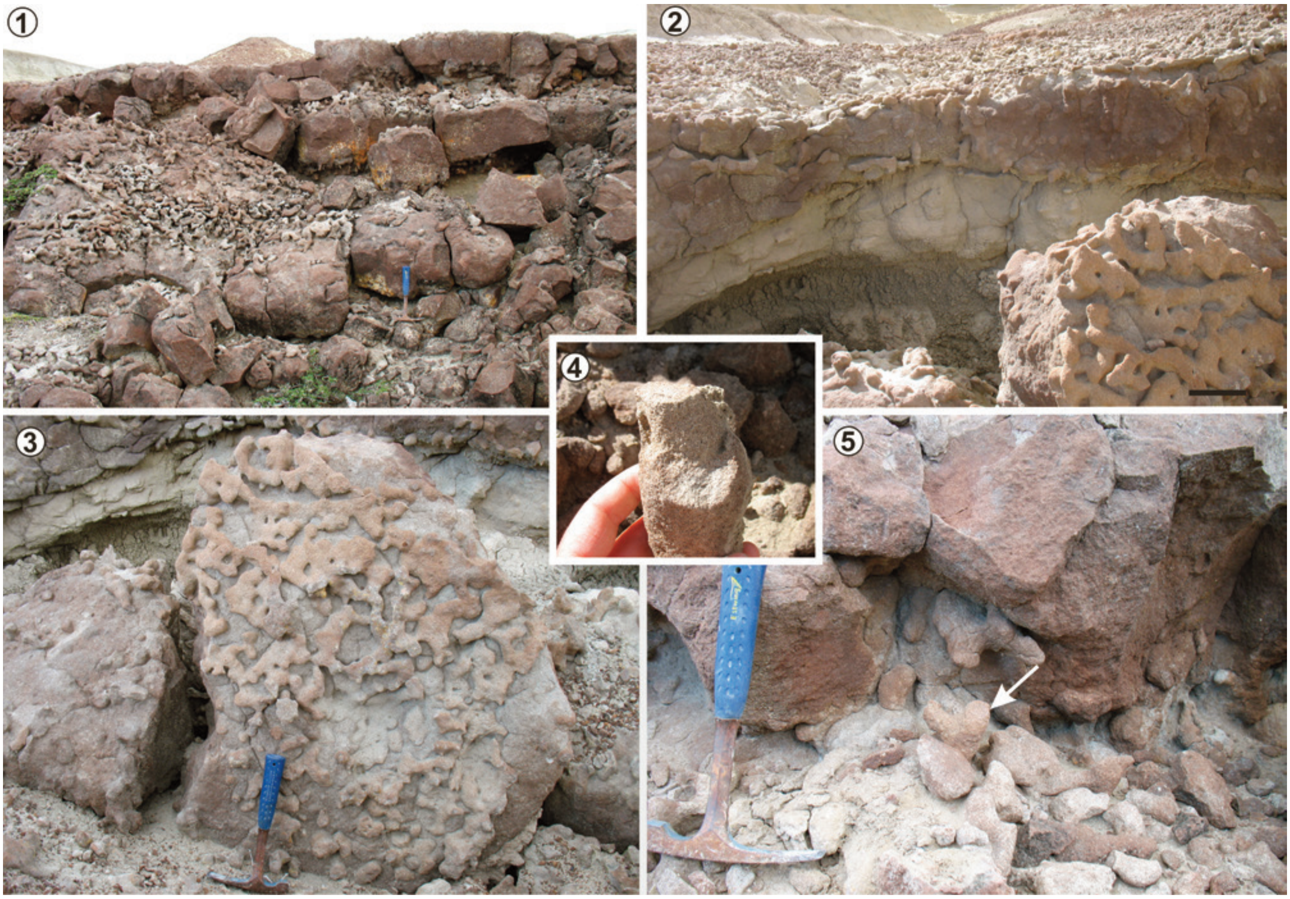

Figure 4. Burrow system described for Facies Association 2. **1–2,** General view of the burrow system and the host medium sandstones. Scale bar in 2= 10 cm. **3,** Detail of the burrows system of horizontal disposition interconnected to vertical elements. **4,** Burrow lining obscured by an external layer. **5,** Detail of an upward Y-branching burrow (indicated by arrow).

splay deposits. These types of sedimentary bodies are a common element in other SCF localities (Zapata, 2018; Cuitiño *et al*., 2019). The lack of primary sedimentary structures in the m-thick, tabular tuff beds makes their interpretation difficult. Some cm-thick tuff layers can be interpreted as primary ash fall deposits. However, considering the distance from the Andes, thin-to-thick tuffs are interpreted as the product of reworking of primary volcanic ash fall deposits either by unconfined flows on the floodplains, aeolian processes, or a combination of both. The occurrence of rhizoliths restricted to the upper part of these tuff beds suggests fast accumulation of the tuffaceous material followed by stable conditions and pedogenic modification.

The architecture of the described burrow systems shows a close morphological resemblance to other burrow systems produced by terrestrial and marginal marine decapod, such as *Camborygma* Hasiotis and Mitchell, 1993, *Lunulichnus* Zonneveld *et al*., 2006, *Loloichnus* Bedatou *et al*., 2008 and *Psilonichnus* Fürsich, 1981*.* They differ from the first three mentioned in this list in lacking vertically dominated structure and differs from *Psilonichnus* by the absence of branches with J and U shape (Fürsich, 1981; Frey *et al*., 1984; Hasiotis and Mitchell, 1993; Zonneveld *et al*., 2006; Bedatou *et al*., 2008). For this reason and until we are able to gather more diagnostic information, we prefer to leave the burrow network without any formal nomenclature.

FA3- Fluvial channel deposits

Description. FA3 is composed essentially by lenticular sandstone deposits with a sharp, concave base and planar top (Fig. 5.1), sometimes grading upwards to fine-grained deposits of FA1 or FA2. Grain sizes vary between fine and coarse sandstone, with subordinate fine gravels. Color ranges from dark gray, grayish yellow (5Y 8/4) to yellowish gray (5Y 7/2). Primary sedimentary structures such as planar and trough cross bedding (facies Sp and St, respectively), as well as plane parallel lamination (facies Sh) are common, forming sets that vary between 0.2 and 1.5 m

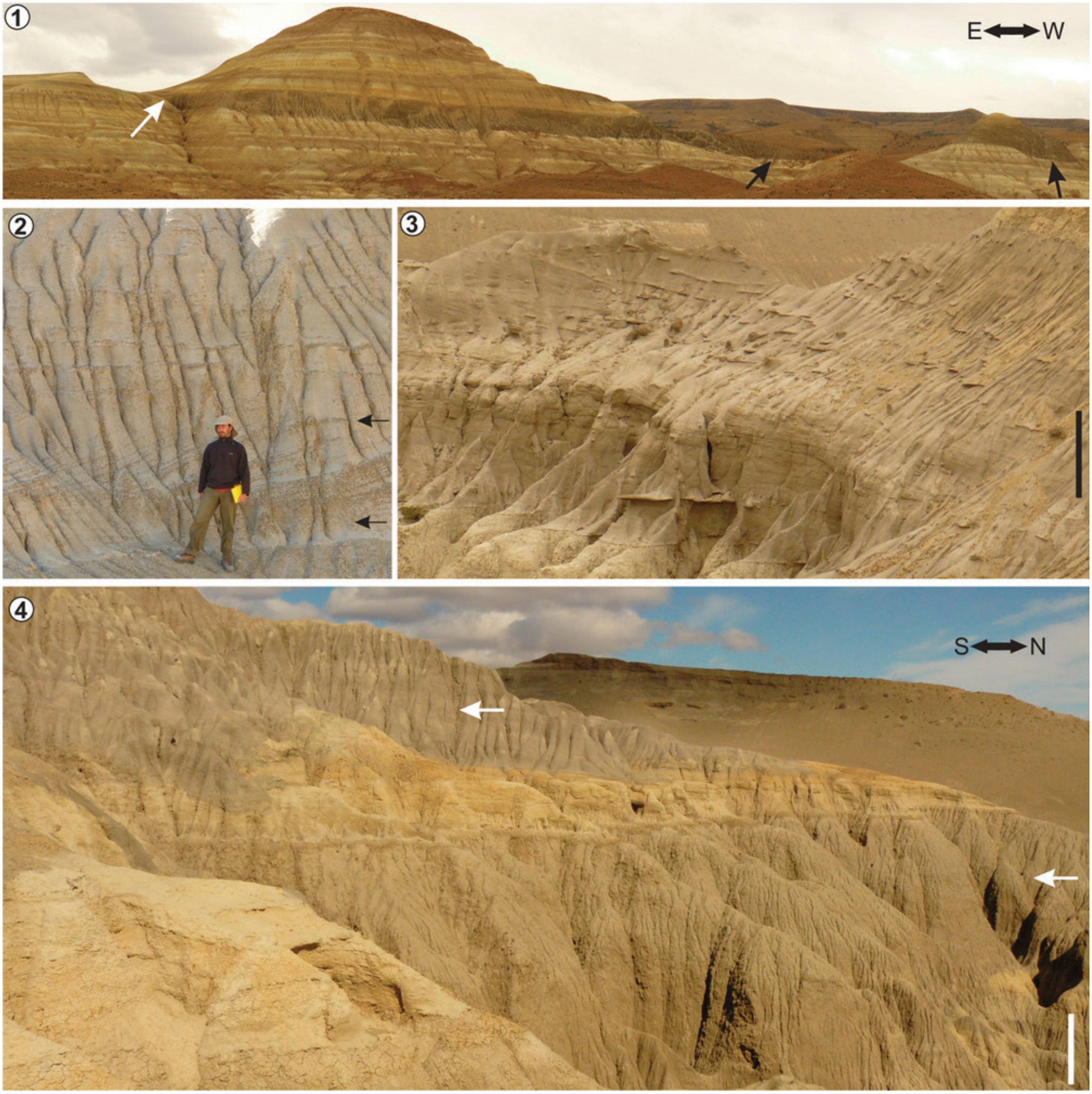

Figure 5. Field photographs of channel deposits of Facies Association 3. **1,** Lenticular dark gray sandstone body with irregular, concave base and planar top. The white arrow points to the lateral pinch-out of the body, whereas the black arrows point to the irregular bottom surface close to the thalweg of the channel. The visible lateral extension of this channel is about 150 m. **2,** Large-scale cross-bedded set (between arrows; 1.1 m) at the base of a thick channel deposit. Upward the sets are no thicker than 0.3 m. **3,** Gray sandstone with trough cross stratification in sets of about 0.5 m thick. Scale bar=1 m. **4,** Two thick channel gray sandstones showing organ pipe weathering (white arrows). Primary sedimentary structures are hardly observed in these bodies, although some relict stratification can be observed for the upper one. Scale bar= 1 m.

thick (Fig. 5.2 and 5.3). The thicker cross-bedded sets are usually observed at the base of these bodies (Fig. 5.2). Due to the poor lithification, many bodies show "organ pipe" weathering patterns without visible structure (Fig. 5.4). Thickness of individual bodies varies between 1 and 7.5 m, whereas apparent width reaches up to 300 m. Some caution on this measurement must be taken because of the limited lateral extension of the exposures and the common lack of paleocurrent indicators useful to locate the cross-current orientation of the bodies. Few paleocurrent measurements from cross bedding show E and NE directions.

Interpretation. Lenticular bodies with erosive bases, infilled with cross bedded sandstones and showing fining upward trends, are interpreted as produced by confined flows typical of fluvial channels (Miall, 2014). They are interbedded within fine-grained deposits of FA1 and FA2. Given the simple infill of the channels and the general reduced thickness of individual bodies, most are interpreted as shallow, single story channels. The lack of evidence for lateral accretion suggests these were fixed channels in a low sinuosity fluvial system (Miall, 2014). In accordance to our interpretation, for the coastal cliff exposures of the SCF, Zapata (2018) also concluded that the most common type of channel for the SCF is the confined, single story channel.

STRATIGRAPHY AND SPATIAL FACIES TRENDS

The SCF along the southern margin of the Río Santa Cruz valley is exposed in a series of isolated small hills and cliffs located near the valley bottom (Fig. 1.2–3). These were exposed by the erosion of ephemeral streams that transect the valley margin or by the cut bank of the Río Santa Cruz. Most of the area is covered by Miocene–Quaternary terrace fluvial conglomerates or recent alluvial deposits (Fig. 1.2–3). For these reasons, plus the large distances between the exposures (tens of kilometers), a field-based physical correlation scheme based on guide levels at the regional scale was not feasible.

The SCF strata are subhorizontal, with local dips no higher than 3° and few normal faults with no more than 10 m of throw. The maximum measured thickness for the SCF in the study area is 167 m corresponding to Segundas Barrancas Blancas; 142 m and 80 m were measured for Barrancas Blancas and Yaten Huageno, respectively.

The base of the SCF, defined as just above the uppermost oyster shell bed recognized in the underlying marine deposits is only visible in Barrancas Blancas, where one can observe the transition with the underlying Monte Observación Member of the Monte León Formation (Parras and Cuitiño, 2018). For the remaining localities, the base of the unit is covered.

Figure 6. Oblique satellite image (Google Earth TM; 2002) of the Barrancas Blancas locality showing the position of the three measured sections just south of the Río Santa Cruz. In the lower part of the EAG1 Section the brownish strata of the Monte Observación Member of the Monte León Formation is highlighted.

Several small outcrops of poor quality record the SCF in higher topographic elevations, up to few meters below the uppermost conglomerate of the Terrace II of Pampa de Monte León (Sacomani and Panza, 2011; Cobos *et al.*, 2014) (*e.g.*, Estancia Santa Lucía, Estancia Rincón Grande; Fig. 1.3), which is estimated to be no more than 10 m thick. Thus, we estimate the thickness of the SCF including covered intervals is about 267 m for Barrancas Blancas, at least 288 m for Segundas Barrancas Blancas and at least 380 m for Yaten Huageno. This westward increase in thickness is consistent with regional trends observed elsewhere for the SCF in southern of the Province of Santa Cruz (Cuitiño *et al.*, 2016).

Considering only the measured thicknesses of the well-exposed stratigraphic intervals studied here, together with the available ages and using a sedimentation rate of 150 m/Ma (Cuitiño *et al.*, 2016), the estimated time span for the SCF in the studied localities is 17.21–16.3 Ma (Burdigalian)

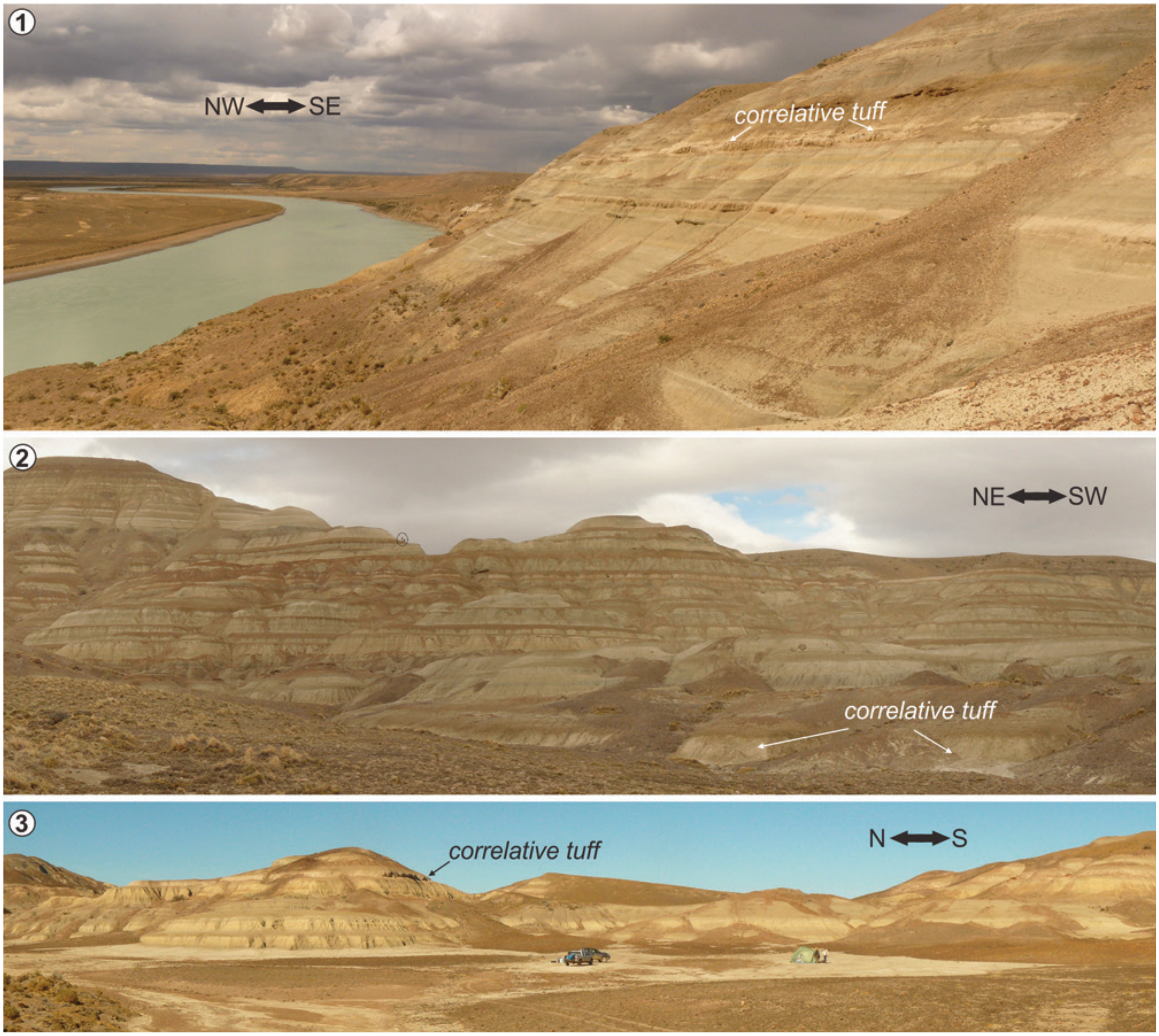

Figure 7. Field panoramic photographs of the three exposures from which sections were measured. **1,** Section EAG1 with the correlative tuff highlighted. **2,** A thick exposure from Section EAG2. The same correlative tuff of Section EAG1 is highlighted. **3,** The small exposure of Section ESL and its correlative tuff. Photographs 1 and 2 taken in December 2012; photograph 3 taken in February 2014.

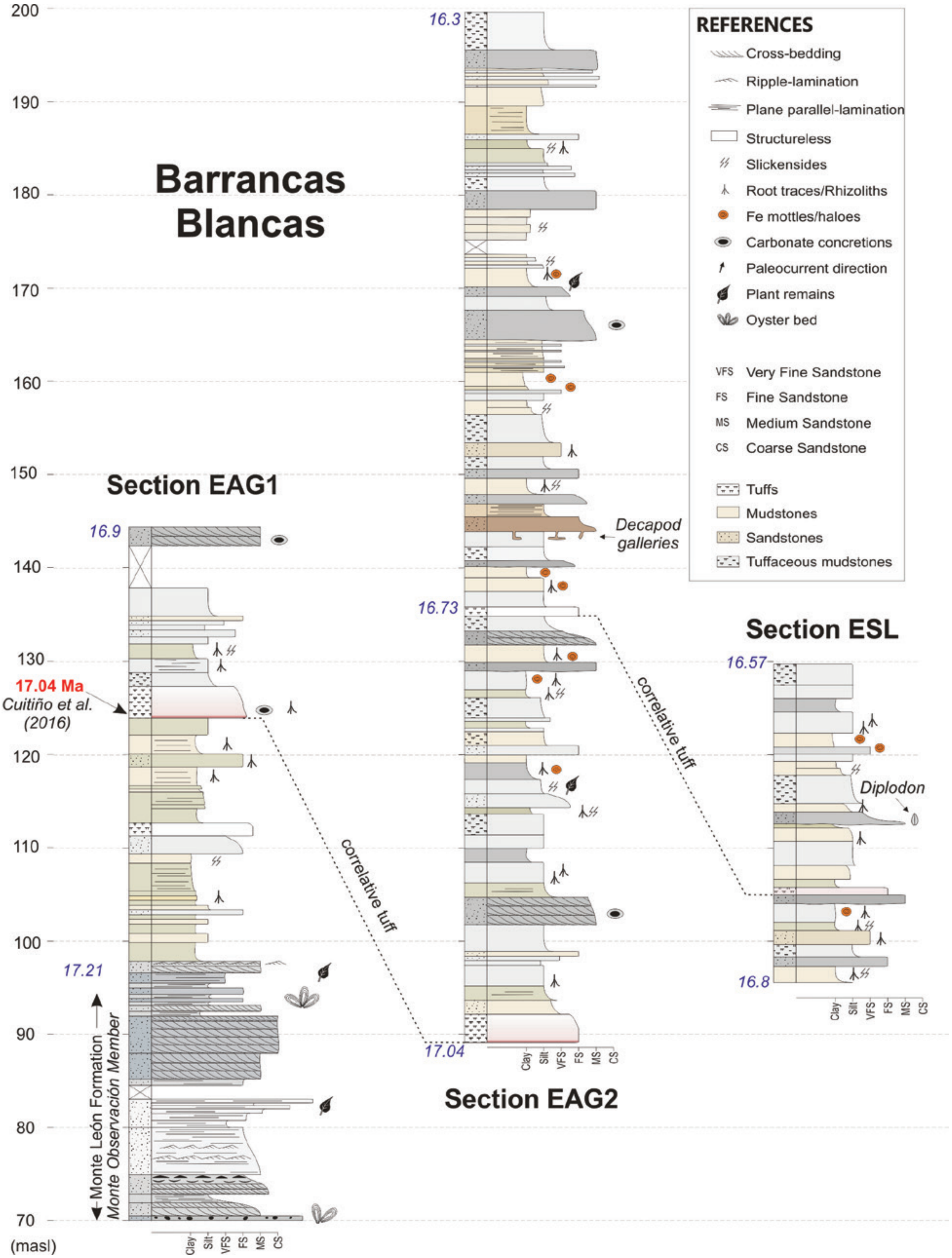

Figure 8. Sedimentary sections measured in Barrancas Blancas locality, showing local correlative horizons. The red number indicates the position of the U-Pb age (Cuitiño *et al.*, 2016) whereas the blue numbers are ages estimated upon sedimentation rates.

for Barrancas Blancas; 16.47–15.3 Ma (Burdigalian–early Langhian) for Segundas Barrancas Blancas; and 17.21–16.68 Ma (Burdigalian) for Yaten Huageno. In addition, it is noted that if the isolated high elevation exposures of the SCF lying just below the Terrace II of Pampa de Monte León conglomerates (see above) are considered in this analysis, the age of the SCF in the Río Santa Cruz should be extended somewhat younger than estimated here and certainly it should comprise part of the Langhian stage.

Barrancas Blancas

This is the easternmost locality of the study area (Fig. 1) and corresponds to a belt of exposures oriented NE-SW in which we measured three sections: Estancia Aguada Grande 1 (EAG1), Estancia Aguada Grande 2 (EAG2) and Estancia Santa Lucía (ESL) (Figs. 6, 7, 8).

Section EAG1 (S 50° 09' 47.6"; W 69° 41' 02.2") begins at the Río Santa Cruz level (Fig. 7.1), and is the only one in the study area where the underlying shallow marine to transitional deposits of the Monte Observación Member of the Monte León Formation can be observed (Figs. 6 and 8). Following the criteria of Parras and Cuitiño (2018) the boundary of this member with the overlying SCF is arbitrarily located in the uppermost *Crassostrea orbignyi* Ihering, 1897 shell bed. Above this contact is a 50 m thick succession of the lower beds of the SCF composed of deposits assigned mostly to FA1 and FA2, with a conspicuous 3 m thick tuff bed located 30 m above the base of the unit (Figs. 7.1 and 8). This tuff was dated in 17.04 ± 0.55 by means of U/Pb on zircons (Cuitiño *et al.*, 2016), and it is used as a marker bed to correlate with Section EAG2 (Fig. 8). In this part of the SCF no terrestrial fossil vertebrates were recovered.

Section EAG2 is 4 km southwest of EAG1 (Fig. 6), it is the thickest and most extensive exposure within Barrancas Blancas (Figs. 7.2 and 8). It is the site of a significant vertebrate fossils collection (Fernicola *et al.*, 2019b) and contains a horizon rich in decapod burrows (Fig. 8). It is mostly composed of floodplain deposits of FAs 1 and 2.

Finally, the ESL Section is a small exposure located 3 km southwest of EAG2 (Figs. 6 and 7.3). The correlation of this section with EAG2 is performed using a local tuff layer (Fig. 8). In this locality, besides the fossil vertebrate collection (Fernicola *et al.*, 2019b), a level bearing the freshwater bivalve *Diplodon* sp. was found (Pérez *et al.*, 2019).

Segundas Barrancas Blancas

This is a belt of 9 km of exposures composed of several isolated outcrops that lie close to the Río Santa Cruz in Es-

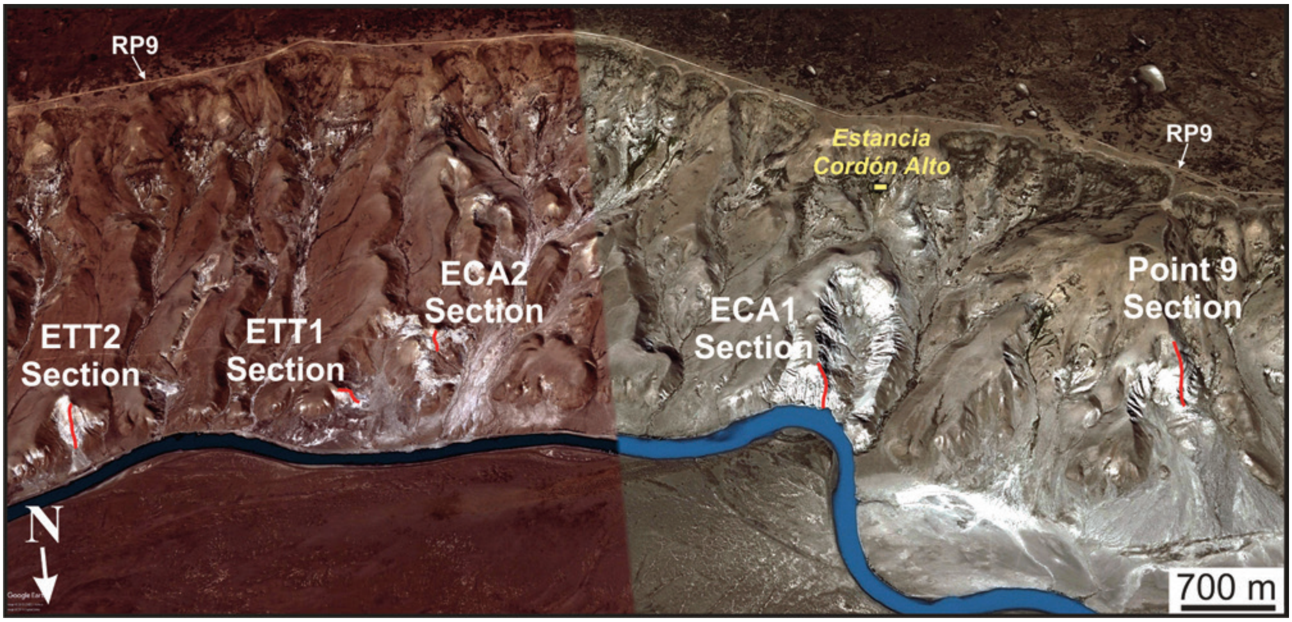

Figure 9. Oblique satellite image of Segundas Barrancas Blancas (from Google Earth TM; 2001), showing the position of the five measured sections.

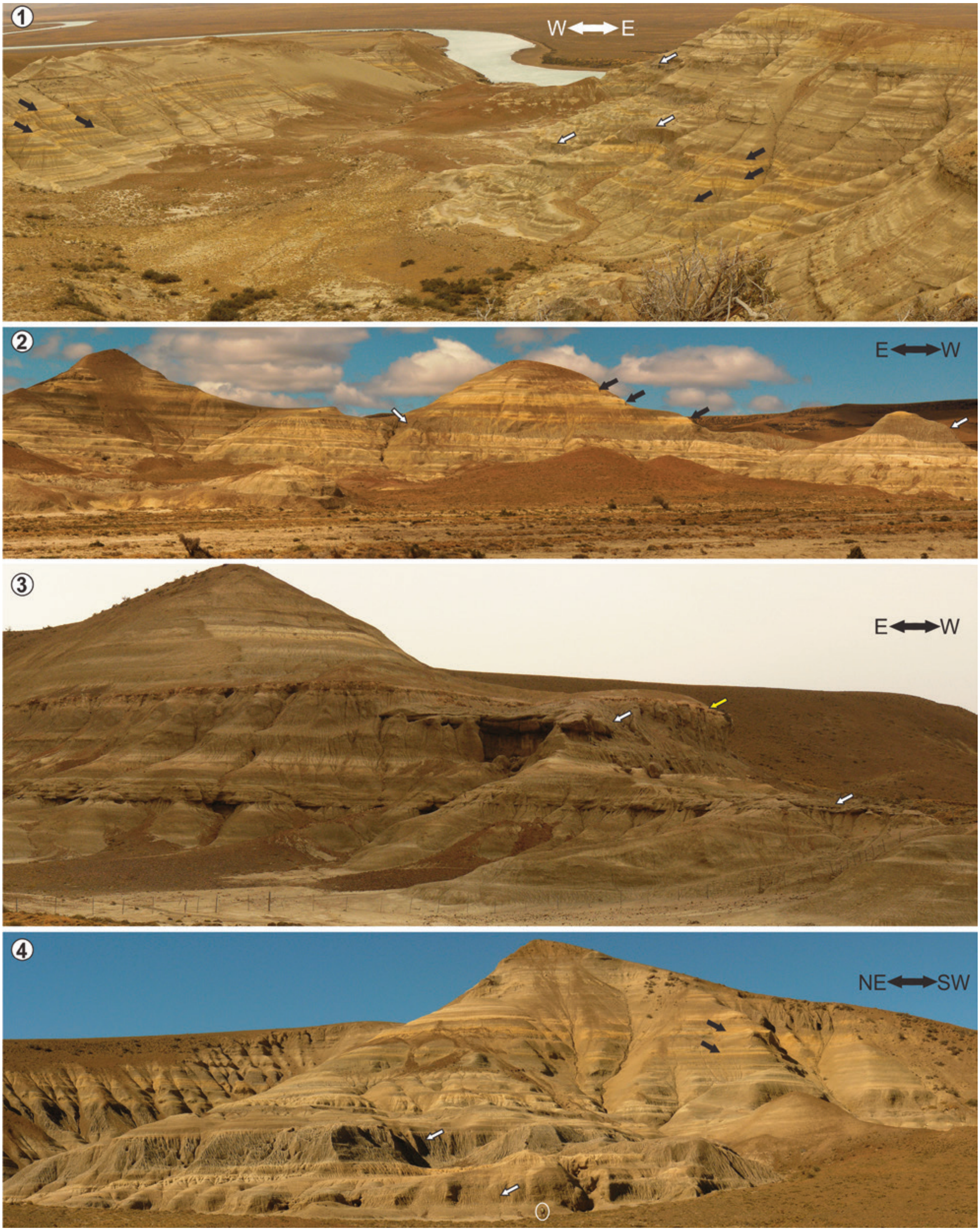

Figure 10. Panoramic photographs of Segundas Barrancas Blancas most representative exposures. In all cases white arrows indicate thick lenticular channel sandstones whereas black arrows point to the yellow beds that were used for correlation. **1,** ECA Section viewed from above. **2,** ECA2 Section. **3**, EET1 Section showing the CECA-2 tuff layer dated by Cuitiño *et al.* (2016) (yellow arrow). **4,** EET2 Section. A person (encircled) as scale. All photographs taken in February 2014.

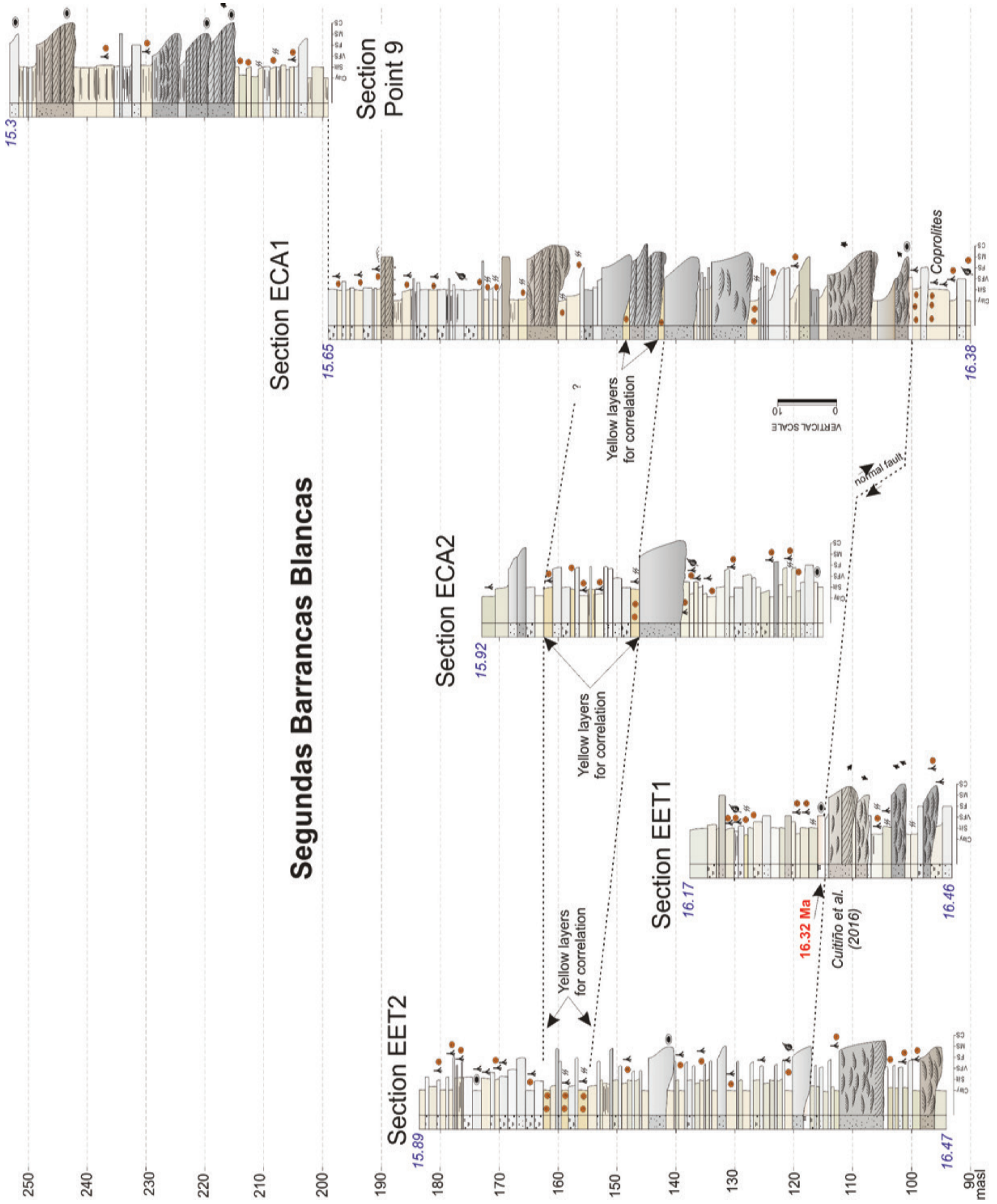

Figure 11. Sections measured for Segundas Barrancas Blancas locality, showing their correlative horizons. All sections are positioned in relation to the altitude above sea-level. The red number indicates the U/Pb age (Cuitiño *et al.*, 2016), whereas the blue numbers are estimated upon sedimentation rates. For references see Figure 8.

tancia Cordón Alto and Estancia El Tordillo (Figs. 1, 9, and 10). Here we measured five sections (Fig. 11), which from east to west are: Estancia El Tordillo 2 (EET2; S 50° 16′ 39.08″; W 70° 13′ 26.18″), Estancia El Tordillo 1 (EET1; S50° 16′ 43.00″; W 70° 15′ 9.90″), Estancia Cordón Alto 2 (ECA2; S 50° 16′ 55.96″; W 70° 15′ 47.33″), Estancia Cordón Alto 1 (ECA1; S 50° 16′ 25.56″; W 70° 18′ 24.74″), and Point 9 (S 50° 16′ 16.30″; W 70° 20′ 48.60″) (Figs. 9 and 11). In each of these sections vertebrate fossils were recovered (Fernicola *et al.*, 2019b).

The SCF here is composed of fine-grained sediments of FAs 1 and 2, although conspicuous lenticular sandstone bodies of FA3 are observed (Fig. 10). The sections are locally correlated using a tuff layer (CECA-2 tuff; Cuitiño *et al.*, 2016) and tabular, laterally extensive and distinctive yellow beds (Figs. 10 and 11). The CECA-2 tuff layer is about 1 m thick (Fig. 10.3) and was dated at the EET1 Section by Cuitiño *et al.* (2016) with an age of 16.32 ± 0.62 Ma. This tuff allows the correlation of Section EET1 with Section ECA1 (Fig. 11) 3.5 km away. Conspicuous yellow beds also used for correlation are a package of about 10 m of fine-grained sediments assigned to FA1 that contains two or three layers that contrast in color with the remaining beds of the SCF (Fig. 10). These beds were used to correlate sections EET2, ECA2 and ECA1 (Fig. 11). Although present in Section ECA, the yellow layers are barely visible due to the presence of thick lenticular sandstone deposits that partly erode them (Figs. 10.1 and 11). Finally, due to the lack of guide levels, Section Point 9 was located in the correlation scheme according to its elevation above sea level (Fig. 11).

Yaten Huageno

This locality has a single section (Fig. 12; S 50° 15′ 40.74; W 71° 3′ 48.81″) in which vertebrate fossils were recovered (Fernicola *et al.*, 2019b). Due to the geographic isolation of this section, physical correlation to other sections is nearly impossible to perform. Here, the SCF is composed of a mixture of fine-grained deposits of FA1 and lenticular to tabular sandy deposits of FA2 and FA3 (Figs. 12 and 13). For this section, a tuff layer has been dated in 16.88 ± 0.65 Ma (Cuitiño *et al.*, 2016).

OVERVIEW AND CONCLUDING REMARKS

Overall, the SCF in the study area is composed of bioturbated and pedogenized poorly consolidated fine-grained sediments with abundant tuffaceous material, mostly represented by floodplain deposits of FA1 and sheet flood to crevasse splay deposits of FA2. Lenticular, cross-bedded sandstone bodies deposited by fluvial channels of FA3 are a minor component of the unit. Conglomerates are only observed as layers of granule to fine-gravel intercalated within sandstone deposits or forming lags at the base of channel sandstone beds. The vertical proportion of the three FAs here defined remains homogeneous for all the studied sections, suggesting an aggradational stacking pattern for the SCF in this region.

The three studied localities of the SCF could not be physically correlated because of the large distances between them and the absence of regional guide levels. However, based on the available U-Pb ages and the estimated sedimentation rates (Cuitiño *et al.*, 2016), they can be

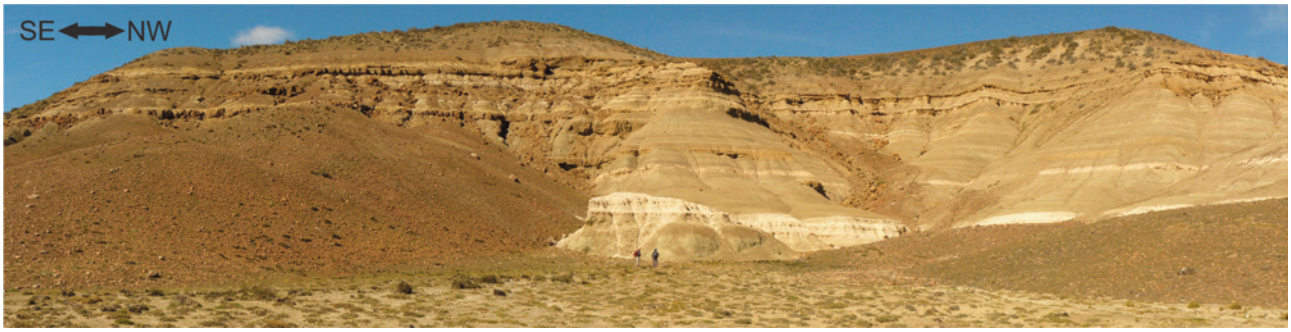

Figure 12. Panoramic photographs of the exposure where the Yaten Huageno section was measured. The whitish strata correspond to tuffs whereas the beds projecting off the exposure are sandstone bodies. Note two persons at the base of the outcrop as scale. Photographs taken in December 2012.

chronologically correlated, being deposited in a time interval between 17.2 and 15.3 Ma (Burdigalian–early Langhian).

Paleocurrent data is scarce because of the poor preservation of primary sedimentary structures. Some isolated measurements point to N, NE and E paleoflows, but this must be taken with caution since the channel sinuosity was not evaluated. The studied exposures of the SCF are arranged in a west to east trend, *i.e.*, approximately parallel to the paleoflow. This is based on the assumption that the Southern Patagonian Andes were a high topographic feature that produced the drainage network to flow eastward, as presently occurs. This is supported by the paleocurrent data and fluvial channel architecture from the coastal localities that show a main paleoflow to the east (Zapata, 2018). This, together with the synchronicity of the SCF among localities of the Río Santa Cruz, implies that Yaten Huageno represents sedimentation roughly 140 km upstream in relation to Barrancas Blancas. In Yaten Huageno several sandstone channels are composed of coarse-sandstones and some reach up to granule-size deposits (Fig. 13), whereas in Barrancas Blancas the sandstone deposits are mostly composed of fine to medium sandstones, with few thin coarse sandstone levels (Fig. 8). This eastward finning grain size trend observed among the channel sandstones in the studied localities supports the idea of a West to East drainage pattern.

The Decapod burrow system recorded at Barrancas Blancas has a strong horizontal component, differing from what has been described until now for crayfish burrows, dominated by vertically components (*e.g.*, Hasiotis and Mitchells, 1993; Bedatou *et al.*, 2008). On the other hand, land crabs as Gecarcinidae and Coenobitidae (Brachyura) typically produce extensive burrow systems along riverbanks, within several kilometers from the sea, where they leave their marine larvae (Maitland and Maitland, 1985; Vannini *et al.*, 2003).The South American freshwater crab Trichodactylidae (Brachyura) excavate along ditches, river banks or wetlands; while the freshwater crayfish Parastacidae excavates burrows not necessary connected to water courses, mostly in soils where they reach the water table (Genise, 2017). Therefore, even though the Barrancas Blancas burrows were found at the easternmost locality, based on the sedimentological evidence for the corresponding terrestrial horizons, the idea of a coastal-influenced paleoenvironment is discounted: freshwater crabs or crayfish could have produced the Barrancas Blancas burrows.

Paleosols developed in the SCF along the Río Santa Cruz valley are abundant although all show an overall very poor/poor to moderate degree of development, which would be assigned to paleo-Entisols, -Inceptisols, and Alfisol-like paleosols. They occur mostly on fine-grained deposits interpreted as distal floodplain deposits (FA1).

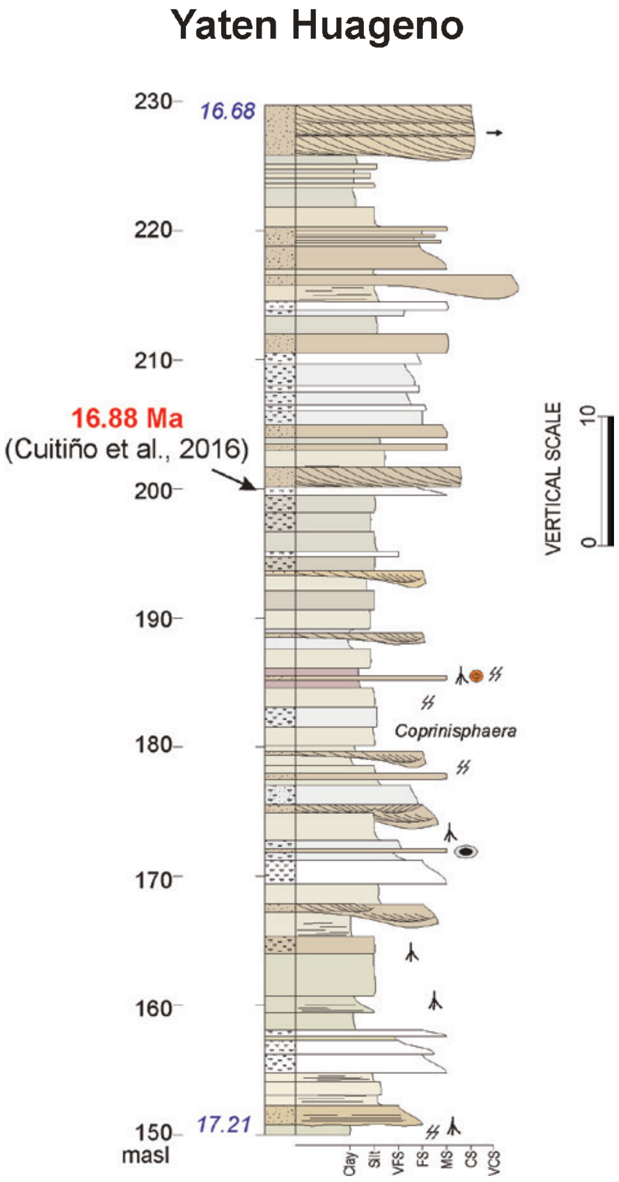

Figure 13. Sedimentary section measured for Yaten Huageno locality showing the dated horizon. The red number indicates the U/Pb age whereas the blue numbers are estimated upon sedimentation rates. For references see Figure 8.

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REFERENCES

Aramendía, I., Cuitiño, J.I., Ghiglione, M.C., and Bouza, P.J. in press. Tectonostratigraphic significance of the Neogene sedimentary record of northwestern Austral-Magallanes Basin, Argentinean Patagonia. *Latin American Journal of Sedimentology and Basin Analysis* 26.

Ashley, G.M., and Driese, S.G. 2000. Paleopedology and paleohydrology of a volcaniclastic paleosol interval: implications for early Pleistocene stratigraphy and paleoclimate record, Olduvai Gorge, Tanzania. *Journal of Sedimentary Research* 70: 1065–1080.

Bargo, M.S., Cerdeño, E., Olivero, E.B., López Cabrera, M.I., Reguero, M.A., and Vizcaíno, S.F. 2018. Primer registro de Astrapotheriidae (Mammalia, Astrapotheria) de la Formación Cullen (Mioceno temprano) de Tierra del Fuego. *Publicación Electrónica de la Asociación Paleontológica Argentina* , Suplemento de resúmenes 19: R35.

Bedatou, E., Melchor, R.N., Bellosi, E., and Genise, J.F. 2008. Crayfish burrows from Late Jurassic–Late Cretaceous continental deposits of Patagonia: Argentina. Their palaeoecological, palaeoclimatic and palaeobiogeographical significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* 257: 169–184.

Biddle, K.T., Uliana, M.A., Mitchum, R.M., Fitzgerald, M.G., and Wright, R.C. 1986. The stratigraphy and structural evolution of the central and eastern Magallanes Basin, southern South America. In: P.A. Allen, and P. Homewood (Eds.), *Foreland Basins*. International Association of Sedimentologists, Special Publication 8: 41–61.

Bown, T.M., and Fleagle, J.G. 1993. Systematics, biostratigraphy, and dental evolution of the Palaeothentidae, later Oligocene to early–middle Miocene (Deseadan–Santacrucian) caenolestoid marsupials of South America. *Journal of Paleontology* 67: 1–76.

Buol, W.S., Southard, R.J., Graham, R.C., and McDanield, P.A. 2011. *Soil Genesis and Classifications*. Sixth edition, Wiley-Blackwell, Oxford, 543 p.

Burns, C.E., Mountney, N.P., Hodgson, D.M., and Colombera, L. 2017. Anatomy and dimensions of fluvial crevasse-splay deposits: Examples from the Cretaceous Castlegate Sandstone and Neslen Formation, Utah, USA. *Sedimentary Geology* 351: 21–35.

Catena, A.M., Hembree, D.I., Saylor, B.Z., Anaya, F., and Croft, D.A. 2016. Paleoenvironmental analysis of the Neotropical fossil mammal site of Cerdas, Bolivia (middle Miocene) based on ichnofossils and paleopedology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 459: 423–439.

Cobos, J.C., Rodríguez, M.F., and Panza, J.L. 2014. Hoja Geológica 5172-II, Paso Río Bote, Provincia de Santa Cruz. *Instituto de Geología y Recursos Minerales, Boletín del Servicio Geológico Minero Argentino* 405: 1–99.

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

Cuitiño, J.I., and Scasso, R.A. 2010. Sedimentología y paleoambientes del Patagoniano y su transición a la Formación Santa Cruz al sur del Lago Argentino, Patagonia Austral. *Revista de la Asociación Geológica Argentina* 66: 406–417.

Cuitiño, J.I., Vizcaíno, S.F., Bargo, M.S., and Aramendía, I. 2019. Sedimentology and fossil vertebrates of the Santa Cruz Formation (early Miocene) in Lago Posadas, southwestern Patagonia, Argentina. *Andean Geology* 46: 383–420.

Encinas, A., Folguera, A., Riffo, R., Molina, P., Paz, L.F., Litvak, V.D., Colwyn, D.A., Valencia, V.A., and Carrasco, M. 2019. Cenozoic basin evolution of the Central Patagonian Andes: Evidence from geochronology, stratigraphy, and geochemistry. *Geoscience Frontiers* 10: 1139–1165.

Fernicola, J.C., Bargo, M.S., Vizcaíno, S.F., and Kay, R.F. 2019a. 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.

Fernicola, J.C. Vizcaíno, S.F., Bargo, M.S., Kay. R.F., and Cuitiño, J.I. 2019b. Analysis of the Early- Middle Miocene mammal associations at the Río Santa Cruz (Patagonia, Argentinba). 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: 239–259.

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 Notohippidian. *Journal of South American Earth Sciences* 52: 94–107.

Fosdick, J.C., Grove, M., Hourigan, J.K., and Calderón, M. 2013. Retroarc deformation and exhumation near the end of the Andes, southern Patagonia. *Earth and Planetary Science Letters* 361: 504–517.

Frey, R.W., Curran, H.A., and Pemberton, S.G. 1984. Tracemaking activities of crabs and their environmental significance: the ichnogenus *Psilonichnus*. *Journal of Paleontology* 58: 333–350.

Fürsich, F.T. 1981. Invertebrate trace fossils from the Upper Jurassic of Portugal. *Comunicações dos Serviços Geológicos de Portugal* 67: 153–168.

Genise, J.F. 2017. *Ichnoentomology: insect traces in soils and paleosols*. Topics in Geobiology 37, Springer International Publishing, Switzerland, 695 p.

Ghiglione, M.C., Ramos, V.A., Cuitiño, J.I., and Varberón, V. 2016. Growth of the Southern Patagonian Andes (46–53°S) and their Relation to Subduction Processes. In: A. Folguera, M. Naipauer, L. Sagripanti, M. Ghiglione, D. Orts, and L. Giambiagi (Eds.), *Growth of the Southern Andes*. Springer Earth System Sciences, Springer International Publishing, Switzerland, p. 201–240. Doi: 10.1007/978-3-319-23060-3

Hasiotis, S.T., and Mitchell, C.E. 1993. A comparison of crayfish burrows morphologies: Triassic and Holocene fossil, paleo- and neoichnological evidence and identification of their burrowing signatures. *Ichnos* 2: 291–314.

Kay, R.F., Vizcaíno, S.F., and Bargo, M.S. 2012. A review of the paleoenvironment and paleoecology of the Miocene Santa Cruz Formation. 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. 331–365.

Krapovickas, V. 2012. Ichnology of distal overbank deposits of the Santa Cruz Formation (late Early Miocene): paleohydrologic and paleodimatic significance. 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. 91–103.

Kraus, M.J., and Hasiotis, S.T. 2006. Significance of different modes of rhizolith preservation to interpreting paleoenvironmental and paleohydrologic settings: examples from Paleogene paleosols, Bighorn Basin, Wyoming, U.S.A. *Journal of Sedimentary Research* 76: 633–646.

Maitland, P., and Maitland, D. 1985. The Australian desert crab. *Australian Natural History* 21: 496–498.

Marshall, L., Hoffstetter, R., and Pascual, R. 1983. Mammals and stratigraphy: geochronology of the continental mammal-bearing Tertiary of South America. *Palaeovertebrata, Mémoire Extraordinaire* 1984: 1–76.

Matheos, S.D., and Raigemborn, M.S. 2012. Sedimentology and paleoenvironment of the Santa Cruz Formation. 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. 59–82.

Miall, A.D. 2014. *Fluvial Depositional Systems*. Springer, Switzerland, 316 p.

Olivero, E., López, C.M.I., and Reguero, M. 2015. Icnología de los depósitos fluviales de la Formación Cullen (Mioceno, Tierra del Fuego) y su relación con la Formación Santa Cruz (Mioceno) de Patagonia. *3º Simposio Latinoamericano de Icnología* (Colonia del Sacramento), p. 60.

Parras, A.M., and Cuitiño, J.I., 2018. The stratigraphic and paleoenvironmental significance of the regressive Monte Observación Member, early Miocene of the Austral Basin, Patagonia. *Latin American Journal of Sedimentology and Basin Analysis* 25: 25–47.

Pascual, R., Ortega Hinojosa, E.J., Gondar, D., and Tonni, E.P. 1965. Las edades del Cenozoico mamalífero de la Argentina, con especial atención a aquéllas del territorio bonaerense. *Anales de la Comisión de Investigaciones Científicas de la Provincia de Buenos Aires* 6: 165–193.

Pérez, L.M., Cuitiño, J.I., Varela, A.N., and Muñoz, N.A. 2019. *Diplodon* cf. *colhuapiensis* (Bivalvia, Hyriidae) in the Santa Cruz Formation (Early–Middle Miocene), at the Río Santa Cruz, Patagonia, Argentina. Stratigraphic and paleoenvironmental considerations. 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: 34–47.

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.

Raigemborn, M.S., Krapovickas, V., Beilinson, E., Peral, L.*e.g.*, Zucol, A.F., Zapata, L., and Sial, A.N. 2018a. Multiproxy studies of Early Miocene pedogeniccalcretes in the Santa Cruz Formation of southern Patagonia, Argentina indicate the existence of a temperate warm vegetation adapted to a fluctuating water table. *Palaeogeography, Palaeoclimatology, Palaeoecology* 500: 1–23.

Raigemborn, M.S., Krapovickas, V., Zucol, A.F., Zapata, L., Beilinson, E., Toledo, N., Perry, J., Lizzoli, S., Martegani, L., Tineo, D., and Passeggi, E. 2018b. Paleosols and related soil-biota of the early Miocene Santa Cruz Formation (Austral-Magallanes Basin, Argentina): a multidisciplinary approach to reconstructing ancient terrestrial landscapes. *Latin American Journal of Sedimentology and Basin Analysis* 25: 117–148.

Raigemborn, M.S., Matheos, S.D., Krapovickas, V., Vizcaíno, S.F., Bargo, M.S., Kay, R.F., Fernicola, J.C., and Zapata, L. 2015. Paleoenvironmental reconstruction of the coastal Monte León and Santa Cruz formations (Early Miocene) at Rincón del Buque, Southern Patagonia: A revisited locality. *Journal of South American Earth Sciences* 60: 31–55.

Retallack, G.J. 2001. *Soils of the Past. An introduction to paleopedology*. 2nd edition, Blackwell Science, Oxford, 404 p.

Retallack, G.J., Bestland, E.A., and Fremd, T. 2000. *Eocene and Oligocene Paleosols in Central Oregon. Geological Society of America, Special Paper*s 344. Boulder, 196 p.

Sachse, F.V., Strozyk, F., Anka, Z., Rodriguez, J.F., and di Primio, R. 2016. The tectono-stratigraphic evolution of the Austral Basin and adjacent areas against the background of Andean tectonics, southern Argentina, South America. *Basin Research* 28: 462–482.

Sacomani, L.E., and Panza, J.L. 2011. Hojas Geológicas 5169-I y 5169-II, Puerto Coig y Puerto Santa Cruz, Provincia de Santa Cruz. *Instituto de Geología y Recursos Minerales, Boletín del Servicio Geológico Minero Argentino* 392: 1–133.

Stoops, G., Marcelino, V., and Mess, F. 2010. *Interpretation of Micromorphological Features of Soils and Regoliths*. Elsevier, Amsterdam, 752 p.

Tauber, A.A. 1999. Los vertebrados de la Formación Santa Cruz (Mioceno inferior-medio) en el extremo sureste de la Patagonia y su significado paleoecológico. *Revista Española de Paleontología* 14: 173–182.

Tauber, A.A., Palacios, M.E., Krapovickas, J., and Rodríguez, P. 2008. La Formación Santa Cruz (Mioceno temprano-medio) en la mitad occidental del Río Santa Cruz, Patagonia, Argentina. *17º Congreso Geológico Argentino* (San Salvador de Jujuy), *Actas*: 1500–1501.

Tejedor, M.F., Tauber, A.A., Rosenberger, A.L., Swisher, 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., Schmitz, M., Cuitiño, J.I., Kohn, M., Bargo, M.S., Kay, R., Strömberg, C., and Vizcaíno, S.F. 2019. An Improved Approach to Age-Modeling in Deep Time: Implications for the Santa Cruz Formation, Argentina. *Geological Society of America Bulletin.* Doi: 10.1130/B35203.1

Ugalde, R., Bostelmann, E., Buldrini, K.E., and Oyarzún, J.L. 2015. Lithofacies, architecture, and depositional environments of the Santa Cruz Formation in Chilean Patagonia. *14º Congreso Geológico Chileno* (La Serena), p. 816–820.

Vannini, M., Cannicci, S., Berti, R., and Innocenti, G. 2003. *Cardisoma carnifex* (Brachyura): where have all the babies gone? *Journal of Crustacean Biology* 23: 55–59.

Vizcaíno, S.F., Bargo, M.S., Cuitiño, J.I., Pérez, M.E., Muñoz, N.A., Aramendía, I., Tomassini, R. L., and Kay, R.F. 2018. The outstanding Río Chalía (=Sehuen) outcrops of the Santa Cruz Formation (early Miocene, Burdigalian) and its fossil vertebrate content. *Publicación Electrónica de la Asociación Paleontológica Argentina,* Suplemento de resúmenes 19: R85.

Vizcaíno, S.F., Bargo, M.S., and Fernicola, J.C. 2013. Expediciones paleontológicas durante los Siglos XIX y XX a la Formación Santa Cruz (Mioceno Inferior, Patagonia) y destino de los fósiles. *3° Congreso Argentino de Historia de la Geología* (Salta), *Actas*: 231–246.

Vizcaíno, S.F., Kay, R.F., and Bargo, M.S. 2012. *Early Miocene Paleobiology in Patagonia: High-latitude Paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, 378 p.

Zapata, L. 2018. [*Estudio paleoambiental de la Formación Santa Cruz (Mioceno inferior-medio) entre los ríos Coyle y Gallegos, Patagonia Austral, Argentina*. Ph.D Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 304 p. Unpublished.].

Zonneveld, J.P., Lavigne, J.M., Bartels, W.S., and Gunnell, G.F. 2006. *Lunulichnus tuberosus* ichnogen. andichno sp. nov. from the Early Eocene Wasatch Formation, Fossil Butte National Monument, Wyoming: an arthropod-constructed trace fossil associated with alluvial firmgrounds. *Ichnos* 13: 87–94.

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DIPLODON CF. *COLHUAPIENSIS* (BIVALVIA, HYRIIDAE) IN THE SANTA CRUZ FORMATION (EARLY–MIDDLE MIOCENE) AT THE RÍO SANTA CRUZ, PATAGONIA, ARGENTINA. STRATIGRAPHIC AND PALEOENVIRONMENTAL CONSIDERATIONS

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Abstract. The Santa Cruz Formation (Early–Middle Miocene) is one of the most widespread sedimentary units of the Argentine Patagonia. This unit contains an abundant and taxonomically diverse fossil vertebrate fauna, especially in mammals. Thus, the paleoecological and paleoenvironmental information derives mainly from the analysis of the vertebrate assemblages, as well as from the ichnological and paleobotanical evidence. The record of freshwater bivalves assigned to the species *Diplodon* cf. *colhuapiensis* Ihering, 1903 from the Santa Cruz Formation, collected in the locality of Barrancas Blancas (Estancia Santa Lucía), at Río Santa Cruz, allows us to infer the particular paleoenvironmental conditions setting during the deposition of the bearing levels. Considering this record, we propose that *Diplodon*, which was originally assigned to the "Sehuenense stage" (piso sehuenense of F. Ameghino), could have come from the Early–Middle Miocene of the Santa Cruz Formation. In this sense, the specimens referred to *Diplodon* cf. *colhuapiensis* suggest the existence of an established community of Hyriidae mollusks at the upper-middle levels of the Santa Cruz Formation. The presence of freshwater bivalves suggests that the depositional environment of this unit included the existence of water courses. The identification of the genus in the Santa Cruz Formation validates its presence in the Early Miocene and extends its southern distribution to the latitude of Río Santa Cruz (~ 50° S).

Key words. *Diplodon*. Hyriidae. Sehuenense stage. Neogene. Santa Cruz Formation. Argentine Patagonia.

Resumen. *DIPLODON* CF. *COLHUAPIENSIS* (BIVALVIA, HYRIIDAE) EN LA FORMACIÓN SANTA CRUZ (MIOCENO TEMPRANO–MEDIO) EN EL RÍO SANTA CRUZ, PATAGONIA, ARGENTINA. CONSIDERACIONES ESTRATIGRÁFICAS Y PALEOAMBIENTALES. La Formación Santa Cruz (Mioceno Temprano–Medio), es una de las unidades sedimentarias más extendidas de la Patagonia argentina. Esta unidad contiene una gran abundancia y diversidad taxonómica de vertebrados fósiles, especialmente de mamíferos. De esta manera, la información paleoecológica y paleoambiental proviene principalmente del análisis de la asociación de vertebrados, como también la evidencia icnológica y paleobotánica. El registro de bivalvos de agua dulce asignados a la especie *Diplodon* cf. *colhuapiensis* Ihering, 1903 de la Formación Santa Cruz, recolectado en la localidad Barrancas Blancas (Estancia Santa Lucía), cerca del Río Santa Cruz, permite inferir las condiciones paleoambientales de la depositación de sedimentos de los niveles portadores de los especímenes. Teniendo en cuenta estos restos, proponemos que el material de *Diplodon* originalmente asignado al "piso Sehuenense" (piso sehuenense de F. Ameghino), podrían provenir del Mioceno Temprano–Medio de la Formación Santa Cruz. En este sentido, el registro de *Diplodon* cf. *colhuapiensis* confirma la existencia de una población establecida de moluscos de la familia Hyriidae en los niveles medio-altos de la Formación Santa Cruz. La presencia de bivalvos de agua dulce, probablemente habitando canales fluviales, sugiere la existencia de cursos de agua bien desarrollados en el ambiente depositacional de la unidad. La identificación del género en la Formación Santa Cruz valida su presencia en el Mioceno Temprano y extiende su distribución sur a la latitud actual del Río Santa Cruz (~ 50° S).

Palabras clave. *Diplodon*. Hyriidae. Piso Sehuenense. Neógeno. Formación Santa Cruz. Patagonia argentina.

The Santa Cruz Formation (SCF), Burdigalian–early Langhian in age, is one of the most widespread sedimentary units in the Argentine Patagonia and, particularly, in the Austral (or Magallanes) Basin, Province of Santa Cruz (Feruglio, 1949; Tauber, 1994; Matheos and Raigemborn, 2012; Perkins *et al.*, 2012; Raigemborn *et al.*, 2015; Cuitiño *et al.*, 2016). This lithostratigraphic unit represents a continental sedimentation lapse associated with the rise of the Southern Patagonian Andes (Ghiglione *et al.*, 2016). Its fossil richness gave it a great geological and paleontological appeal and has spurred the interest of naturalists since the end of the 19th century (*e.g.*, Ameghino, 1893, 1906; Hatcher, 1900; Feruglio, 1949; Vizcaíno *et al.*, 2013). It contains a great abundance and diversity of fossil vertebrate remains, especially mammals (Tauber, 1997; Kay *et al.*, 2012), and most of the paleoecological and paleoenvironmental information of this unit derives from the analysis of the vertebrate fauna (Kay *et al.*, 2012) together with sedimentological and paleopedological analyses of the stratigraphic sequences (Raigemborn *et al.*, 2018; Montalvo *et al.*, 2019). The faunal association, mostly represented by mammalian remains, encouraged the definition of the Santacrucian "mammalian age" of South America (Ameghino, 1906; Pascual *et al.*, 1965; Fernicola *et al.,* 2019). Associated with the vertebrates, the SCF contains other fossil taxa; *i.e.*, plants (Brea *et al.*, 2017), marine mollusks in the lower levels (Griffin and Parras, 2012) and continental pulmonate gastropods (Rodríguez *et al.*, 2012). Likewise, ichnofossils produced by continental invertebrates and mammals have also been described (Krapovickas, 2012; Zapata *et al.*, 2016; Raigemborn *et al.*, 2018, 2019; Cuitiño *et al.*, 2019).

The order Unionida (Bivalvia) is widespread in the Neotropical region, in which it presents the greatest diversity, with 249 species distributed in eight families (Torres *et al.*, 2018). It is found throughout South America, from the Equator to the Patagonian lakes and rivers of Argentina and Chile. The family Hyriidae, in particular, is represented in South America by seven genera (Miyahira *et al.*, 2017). Two of them are present in Argentina: *Diplodon* and *Castalia*, the former with 14 living species and the latter, with only two (Torres *et al.*, 2018). *Diplodon* is well-known in the Argentine Patagonia by several fossil findings reported from different stratigraphic units throughout the Cenozoic. Parras and Griffin (2013) reported *Diplodon bodenbenderi* Doello Jurado, 1927, from locations in northern Neuquén and southern Mendoza, and assigned all of them to the Cretaceous–Paleogene. Ihering (1903, p. 217), reported *Diplodon colhuapiensis* Ihering, 1903, from "Colhuapi" (Province of Chubut), based on findings by Carlos Ameghino, and "Río Sehuen" (Province of Santa Cruz), by Rudolf Hauthal (*sensu* Parodiz, 1969), and referred it to the "Salamanqueano" (Cretaceous) and "Sehuenense" (Upper Cretaceous), respectively (vide infra). Years later, Parodiz (1969) reassigned the same materials to a Paleogene age (Paleocene). Manceñido, and Damborenea (1984) reported three species from locations in central-west Río Negro: *Diplodon* (*Prodiplodon*) *amphitheatri* Manceñido and Damborenea, 1984; *Diplodon* (*Antediplodon*?) *bodenbenderi* Doello Jurado, 1927; and *Diplodon pehuenchensis* Doello Jurado, 1927, while Morton, and Sepúlveda (1988) reported *Diplodon* aff. *colhuapiensis* Ihering, 1903, *Diplodon* aff. *pehuenchensis* Doello Jurado, 1927, and *Diplodon* aff. *oponcitonis* Pilsbry and Olsson, 1935 from the north-west of the Province of Chubut.

The aim of this paper is to report freshwater bivalves assigned to the species *Diplodon* cf. *colhuapiensis* Ihering, 1903 from the SCF, which were collected in Barrancas Blancas (Estancia Santa Lucía) in the Río Santa Cruz area (Fig. 1). From this record, we also infer the paleoenvironmental conditions of the fossil bearing beds, considering both the depositional environment of the sedimentary materials and the ecological requirements of the genus *Diplodon*. The age of the holotype of *D. colhuapiensis* is also discussed.

STUDY AREA AND GEOLOGICAL SETTING

Río Santa Cruz is located in southern Santa Cruz, where the SCF is sporadically exposed (Fig. 1). This unit stretches from the foothills of Cordillera de los Andes (Lago Argentino/Río Turbio region) to the cliffs along the Atlantic coast, especially between Río Gallegos and the Parque Nacional Monte León (Fig. 1). In all the localities in which its base is visible, it is concordantly overlying the marine sediments of the Early Miocene assigned to the Patagonian transgression (Feruglio, 1938; Cuitiño and Scasso, 2010a,b; Cuitiño *et al.*, 2012, 2016; Griffin and Parras, 2012; Raigemborn *et al.*, 2015).

The SCF essentially consists of fine-grained and well-

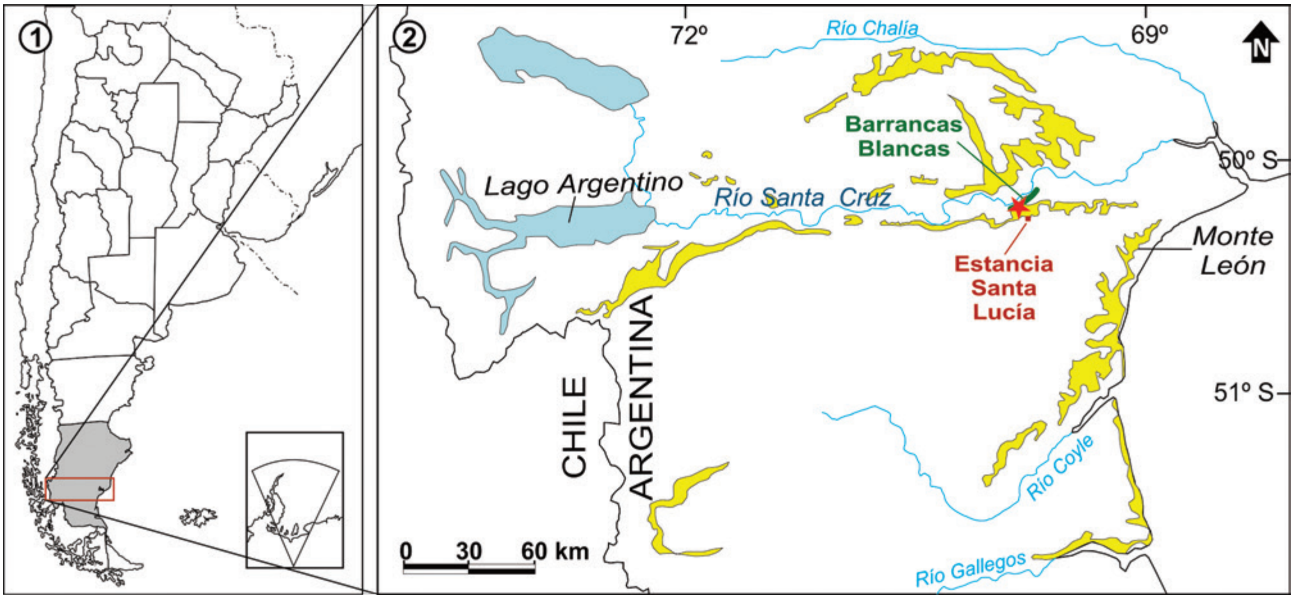

Figure 1.1, Location map of the study area in Argentina. Province of Santa Cruz indicated in gray. **2,** Study area with extension of the outcrops of the Santa Cruz Formation (yellow). The Estancia Santa Lucía site is indicated with a square. The locality Barrancas Blancas is indicated with a green bar. The geographic provenance of the studied material is indicated with a red star.

stratified sediments, mostly silts and fine sandstones, with poorly developed paleosol levels and a high proportion of fine pyroclastic material intercalated in the form of discrete levels of tuffs or mixed with epiclastic sediments. These sediments are interpreted as deposits of a low-gradient fluvial system with extensive floodplains and low sinuosity anastomosed channels (Raigemborn *et al.*, 2015, 2018; Cuitiño *et al.*, 2016, 2019; Zapata, 2018).

The age of the SCF is estimated on the basis of stratigraphic relationships and numerous ^{40}Ar/^{39}Ar and U/Pb radiometric datings, which indicate a Burdigalian–early Langhian age range (17.45–15.3 Ma) for the study area (Perkins *et al.*, 2012; Cuitiño *et al.*, 2016, 2019). Westward, along the foothills of the Southern Patagonian Andes, the sediment depositions of the SCF are also Burdigalian–Langhian, approximately at 19 Ma, and would have continued until approximately 14 Ma (Cuitiño *et al.*, 2012, 2016; Bostelmann *et al.*, 2013).

Between the mountain range to the West and the coast to the East, the SCF crops out in several localities of the valley of Río Santa Cruz, of which some have recently been the object of paleontological (Fernicola *et al.*, 2014, 2019, and other articles in this volume) and geological (Cuitiño *et al.*, 2016, 2019) studies. The remains of *Diplodon* herein described come from Estancia Santa Lucía (50° 12′ 59″ S; 69° 44′ 51″ W). This section (Fig. 2.1) is located at the westernmost area of the locality named Barrancas Blancas by Carlos Ameghino (see Fernicola *et al.* 2014, 2019). In the study area, the SCF is composed of light green and yellowish silts with little development of paleosols, which are intercalated with dark gray to brown, fine- to medium-grained sandstones arranged in lenticular banks (Fernicola *et al.*, 2014; Cuitiño *et al.*, 2016, 2019). The SCF concordantly overlays the Monte León Formation and is ~150 m thick (Fernicola *et al.*, 2014). The top of the unit is truncated by Quaternary terraced conglomerate deposits of Río Santa Cruz. Bivalves were found 3.5 km southwest of the section showed by Fernicola *et al.* (2014).

The Piso Sehuenense of F. Ameghino

Ameghino (1893) described plesiosaur teeth (*Polyptychodon patagonicus*) in what he then called the Santa Cruz Formation. Regarding its stratigraphic and geographic origin, Ameghino (1893, p. 76) indicated that "*La formación que he designado con el nombre de Santacruceña, ocupa la mayor parte de la región de la Patagonia Austral, que cruzan los ríos Santa Cruz,*

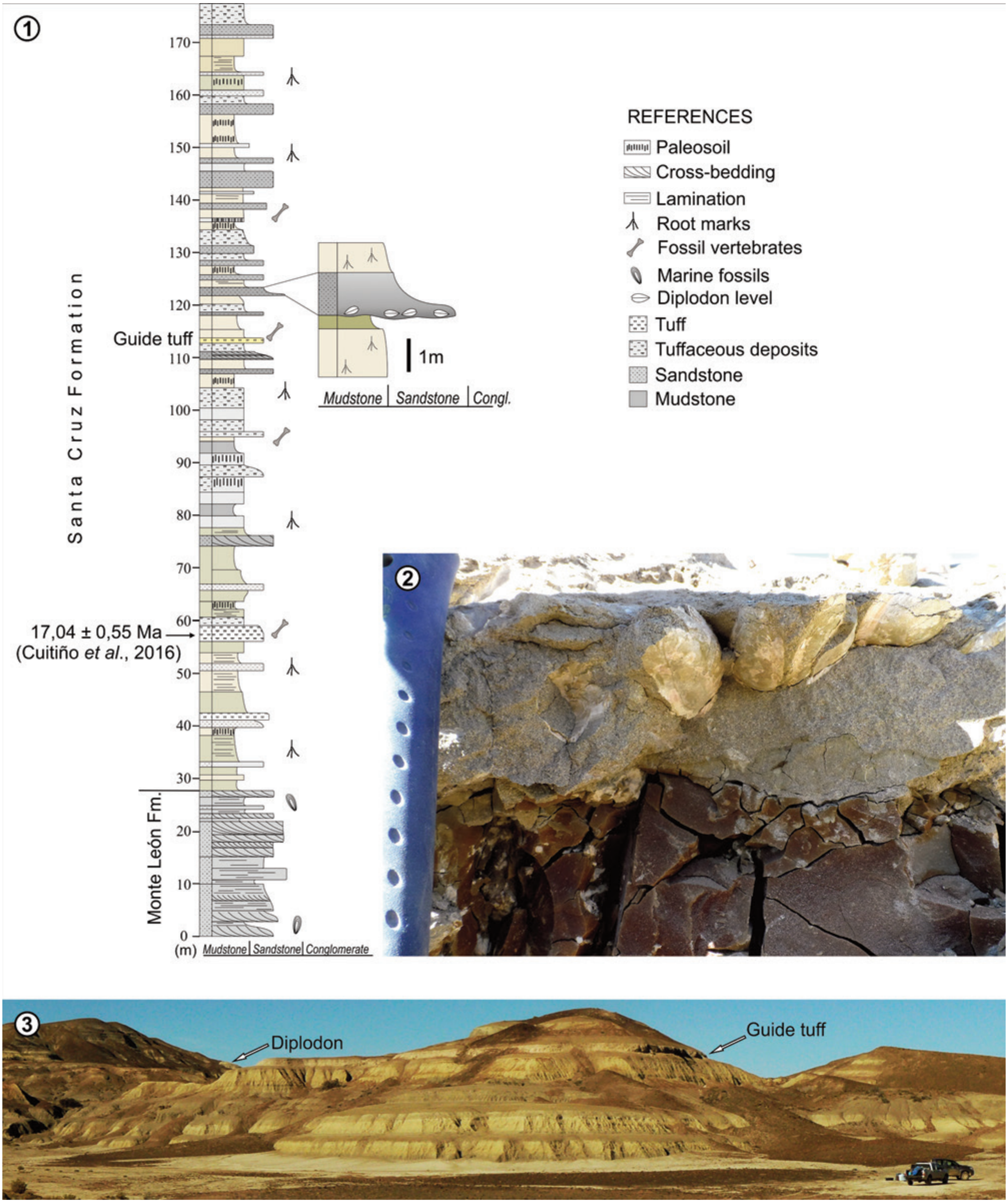

Figure 2. 1–3, The study section of the Santa Cruz Formation in Barrancas Blancas (Early Miocene–Burdigalian). **1,** The section includes ~150 m of silicoclastic rocks, sandy to silty beds with little development of paleosols. **2,** level with the *Diplodon* specimens within the sedimentary matrix. **3,** general view of the outcrops indicating the fossiliferous level and the dated tuff.

Sehuen y Gallegos" (The formation that I have designated with the name of Santacruceña occupies most of the region of Southern Patagonia, crossed by the Santa Cruz, the Sehuen, and the Gallegos rivers). Along Río Sehuen (= Chalía), the Cretaceous Mata Amarilla Formation is exposed (Feruglio in Fossa Mancini *et al.*, 1938; Arbe, 1989, 2002; O'Gorman and Varela, 2010; Varela *et al.*, 2012) associated with the Santa Cruz Formation. This would indicate that the "*Formación Santacruceña*" of Ameghino (1893) is only in part equivalent to what is now known as the Santa Cruz Formation, and that Ameghino also included what is now known as the Mata Amarilla Formation in his "*Formación Santacruceña*" (Ameghino, 1893, p. 76).

Ameghino's interpretation is understandable considering the lithological similarity of both formations. Regarding the age, he referred the "*Formación Santacruceña*" to the "Lower Eocene (Paleocene)" (Ameghino, 1893, p. 76). In the introduction, Ameghino (1893) referred to the problematic association of primates and other clearly Tertiary mammals together with Cretaceous taxa in this formation. Therefore, the association of *Polyptychodon patagonicus* teeth with mammals was based only on a lithostratigraphic similarity.

Ameghino (1906) separated the section of Río Sehuen from his Santa Cruz Formation and named the former the "Sehuenense o *Sehuénéen*" stage. In the same work, he published the map made by his brother, Carlos, and continued to cite the Cretaceous taxa as coming from the "Sehuenense" and not from the Santa Cruz Formation.

MATERIALS AND METHODS

The systematic classification of the living species of Unionida, from Argentina, follows Torres *et al.* (2018).

In order to place the material in a stratigraphic/paleoenvironmental context, a Selley-type sedimentological column was logged, highlighting grain size, sedimentary structures, pedogenetic features, discontinuities and strata shapes, among others. Additionally, we searched for elements that would help to correlate and integrate the stratigraphic information with the Barrancas Blancas section published by Fernicola *et al.* (2014; see also Cuitiño *et al.*, 2019) and dated by Cuitiño *et al.* (2016).

The analysis of the sedimentary matrix bearing the fossils was performed with a Nikon Eclipse E200 binocular petrographic microscope with an associated Leica D camera FC290 HD; the images were taken with and without polarized light. This analysis was carried out at Centro de Investigaciones Geológicas (CIG-CONICET), La Plata. The specimens used for comparison, housed in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" collection, were photographed with a Canon EOS XSi camera. The measurements of the specimens photographed for comparison were taken with the ImageJ 1.50i software (Schneider *et al.*, 2012).

***Institutional abbreviations*.** **CM,** Carnegie Museum of Natural History, Pittsburgh, United States of America; **ICZN,** International Commission on Zoological Nomenclature; **MACN,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad Autónoma de Buenos Aires, Argentina; **MPM,** Museo Regional Provincial "Padre Manuel J. Molina", Río Gallegos, Argentina; **SALMA,** South American Land Mammal Age.

SYSTEMATIC PALEONTOLOGY

Class Bivalvia Linnaeus, 1758
Subclass Palaeoheterodonta Newell, 1965
Order Unionida Gray, 1854
Superfamily Hyrioidea Swainson, 1840
Family Hyriidae Swainson, 1840

Genus ***Diplodon*** Spix in Wagner, 1827

***Type species*.** *Diplodon ellipticus* Spix in Wagner, 1827; OD. Recent, Rio São Francisco, Brazil (see Miyahira *et al.*, 2013).

Diplodon* cf. *colhuapiensis Ihering, 1903
(Fig. 3.1–5)

1903 **Diplodon colhuapiensis** sp. n.; von Ihering, pags. 216–217, fig. 2.
1907 **Diplodon colhuapiensis** Ih.; von Ihering, pag. 466.
1914 **Diplodon colhuapensis** Ih.; von Ihering, pag. 36.
1969 **Diplodon colhuapiensis** Ihering; Parodiz, pags. 53–54, pl. 1, figs. 1–4.

***Type material*.** Following the article 73.1.1 of the ICZN and based on Ihering (1903, p. 217 "*L'exemplaire typique figure a...*"), we believe the holotype (CM 61-137) was deposited by Parodiz in the collection of the Carnegie Museum of

Natural History in May 1961 (Fig. 4.1). The measurements of the holotype are: length of 52 mm, height of 30 mm, width of 19 mm (taken from Ihering, 1903, page 216). Part of the presumed lot of cotypes (sic *cotypo*, in the oldest tag) (Paratypes? MACN-Pi 295) remained in the División de Paleontología de Invertebrados of the MACN (Fig. 4.2–3). This link with the material of the CM is made from one of the labels associated with the material in the MACN, which indicates that the material is "cotype" together with the indication "C. Ameghino 1903". According to this label, it is clear that the specimens come from the "*formaçaõ do Pyrotherium*" (sic in the MACN 295 tag) Salamanquense. In another label, the age assigned to the material appears; *i.e.*, "*Cretácico superior–Salamanquense*", and states that it belongs to the Ihering collection. The specimens that conform the "type material" were collected by C. Ameghino in the locality of Colhue Huapi, Province of Chubut, Argentine Patagonia, and were initially published by Ihering (1903, p. 216), who stated that "*M. C. Ameghino a recueilli plusieurs exemplaires de cette espéce á Colhuapi*" (Mr. C. Ameghino has collected several samples of this species in Colhuapi).

In the same article in which he names *D. colhuapiensis*, Ihering (1903) indicated that "*J'ai reçu des moules, correspondant dans leur forme au* Diplodon colhuapiensis*, de M. le docteur R. Hauthal qui les a trouvés au Río Sehuen, et dont le plus grand exemplaire a une longueur de 58 mm*" (I received molds, corresponding in form to the *Diplodon colhuapiensis*, from Mr. Dr. R. Hauthal, who found them at Río Sehuen, and from which the largest specimen has a length of 58 mm). In a later work (1907, p. 466), Ihering indicated that "*J'en ai reçu aussi quelques moules du Rio Séhuen, recueillis par le Dr. R. Hauthal*" (I also received some molds from Rio Séhuen, collected by Dr. R. Hauthal), suggesting that he had a second collection. This last one probably has the number MACN-Pi 296 and includes four internal molds from Río Sehuen-Patagonia, "Upper Cretaceous" (the file indicates: Roth leg, coll. Ihering). Thus, Ihering (1903) considered that all the aforementioned material belonged to the same species, *D. colhuapiensis*.

As Parodiz (1969, p. 40) said, these "Roth" specimens could have been mixed, meaning that they came from different stratigraphic levels and localities of Southern Patagonia, giving way to the confusion about the stratigraphic ages and units in which this species can be found.

Referred material from "Estancia Santa Lucía". Five incomplete specimens, MPM-Pi 19425 (Fig. 3.1–5), and several additional fragments within the rocky matrix. All specimens were found *in situ* but accumulated in a chaotic manner at the base and encased in a psamo-pelitic matrix, mostly with both valves joined. They were found together with somewhat fragmented shells with diagenetic alteration of the outer surfaces of the valves. As discussed by Miyahira *et al.* (2017), the most important features of the shells are their umbo position, their umbonal sculpture and hinge details. The characters preserved in MPM-Pi 19425 prevent a more precise taxonomic assignment.

Geographic and stratigraphic provenance. Barrancas Blancas (Estancia Santa Lucía), Province of Santa Cruz (Argentina), Santa Cruz Formation (Early Miocene).

Description of MPM-Pi 19425. Sub-elliptical medium sized shell, equivalve, inequilateral, slightly compressed, with the anterior margin rounded and the posterior margin slightly acute. Dorsal edge slightly convex, posterior ventral margin somewhat curved. Slightly pronounced prosogyrous umbo with a small sub-umbonal cavity. Thin shell, smooth outer surface, with tenuous regular commarginal concentric lines. Dorsal posterior carina weakly marked. Impressions of sub-circular isomyarian adductor muscles poorly marked. Poorly differentiated cardinal tooth. The inner surface retains part of the pearly layer. The average dimensions for adult individuals are: length of ~76 mm; height of ~43 mm; width of ~25 mm (measurements taken on 3 specimens).

Comments and comparison. The material shows all the characteristics of the genus *Diplodon* with some features comparable to the holotype of *Diplodon colhuapiensis*. Although the holotype and the rest of the specimens originally referred to the species *D. colhuapiensis* correspond to molds, they have features that are recognizable in the specimens of MPM-Pi 19425. Considering the molds labelled "*Cotypos*" (MACN-Pi 295) as part of the original material of the species nominated by Ihering (1903), as suggested by Parodiz (1969, p. 54), a more complete comparison with the specimens MPM-Pi 19425 is possible. The new specimens are larger than the type material of *D. colhuapiensis* and the lot of “cotypes” (*vide supra*), whose size ranges from 58 to 35 mm in length, 33 to 21 mm in height and 17 to 10 mm in width. The rest of the characters recognized in MPM-Pi 19425 do not present differences with the type material of *D. colhuapiensis* that are significant enough to justify the separation of this sample into a different taxonomic entity. This morphological correspondence could be asserted after establishing comparisons with a greater number of speci-

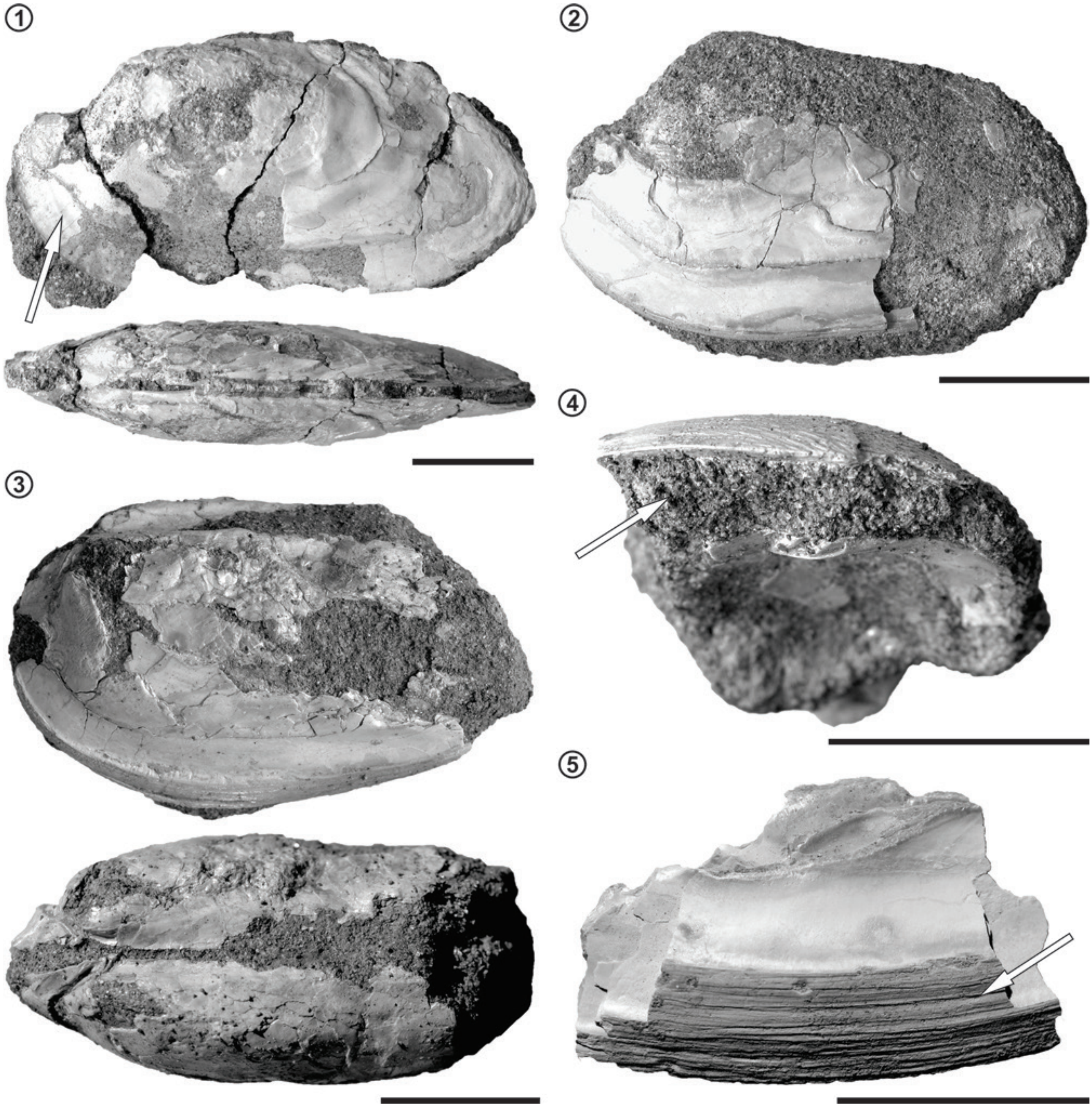

Figure 3. 1–5, ***Diplodon*** **cf.** ***colhuapiensis*** Ihering, **MPM-Pi 19425** (specimens from Estancia Santa Lucía); **1,** lateral (left) and dorsal view (specimen a), the arrow points to the remains of the pearly layer; **2,** lateral (left) view (specimen b); **3,** lateral (left) and dorsal view (specimen c); **4,** umbonal fragment of the left valve (specimen d), arrow points to the expansive sedimentary filling; **5,** lateral external fragment of valve (specimen e), arrow points to the regular commarginal lines in the ventral margin of the shell. Scale bars= 2 cm.

mens. The species remains in open nomenclature until better material becomes available.

Regarding the specimens from Río Sehuen (MACN-Pi 296), they are clearly different from MPM-Pi 19425 in shell size. Although the general morphology is similar, the specimens from Río Sehuen are considerably smaller (length of 51 to 38 mm, height of 28 to 20 mm, width of 18 to 10 mm). These size differences could be considered as within the natural range part of the species given that the three studied samples (MPM-Pi 19425, MACN-Pi 295 and MACN-Pi 296) share the same high/length ratio of ~0.57. There are specimens that are assigned to *D.* aff. *colhuapiensis* from the Ñorquinco Formation, nearby the town of Arroyo Horqueta, Province of Chubut (Morton and Sepúlveda, 1988), based on the form of their valve and, particularly, on the previous depression close to the umbo. These features, together with the image illustrated in Morton and Sepúlveda (1988), do not allow assuring an accurate assignment to the species nominated by Ihering (1903).

Taking into account what occurs in the extant popula-

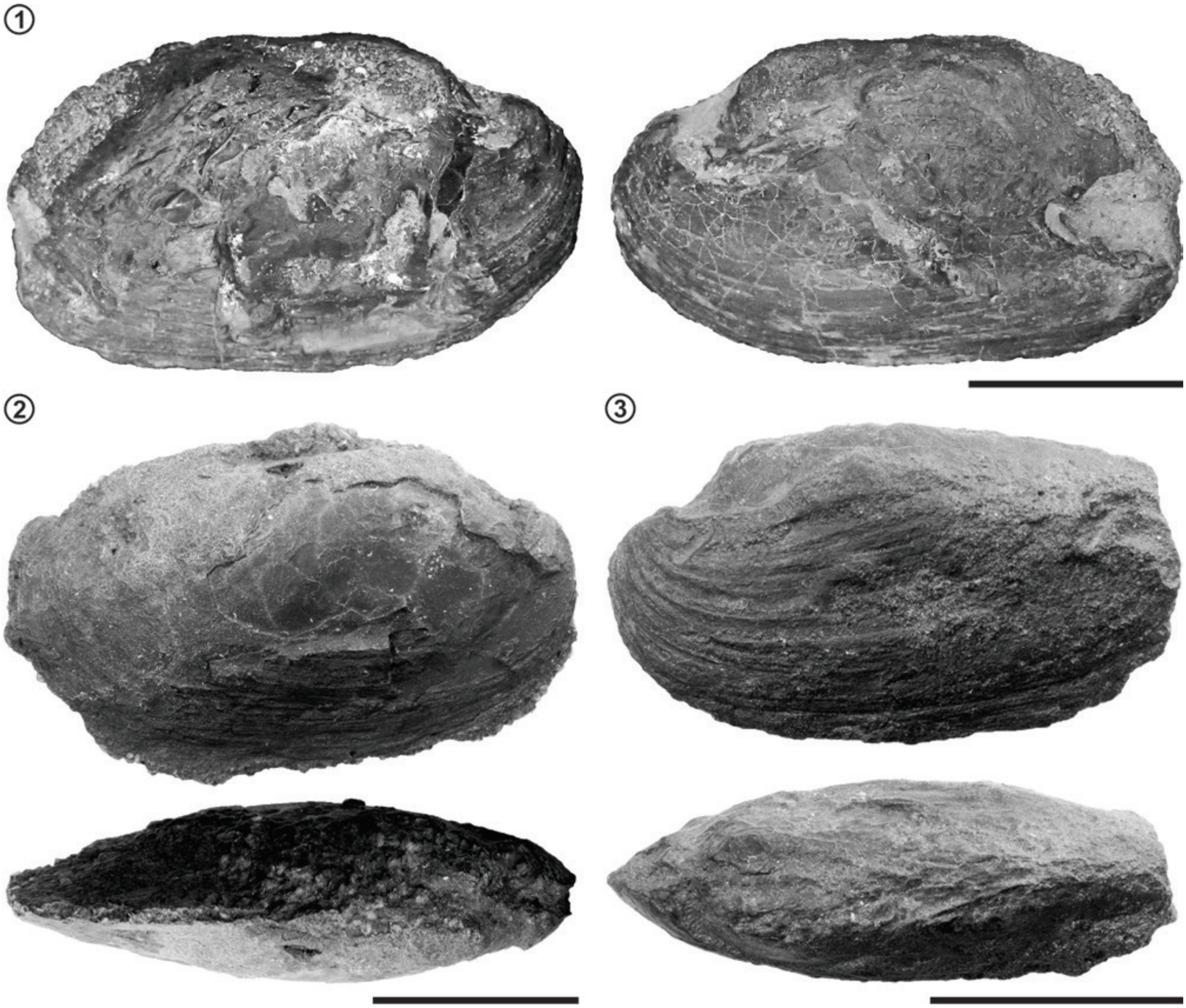

Figure 4. 1–3, ***Diplodon colhuapiensis*** Ihering; **1,** lateral views of specimen **CM 61-137** (Holotype); **2–3**, two specimens, **MACN-Pi 295** (Paratypes?); **2,** lateral (right) and dorsal view of an internal mold and fragments of shell; **3,** lateral (left) and dorsal view of specimen, showing the commarginal lines. Scale bars= 2 cm.

tions of *Diplodon* species, and knowing the existing interpopulation differences within this group of freshwater bivalves, already noticed in the Río Paraná basin (Bonetto and Ezcurra de Drago, 1966), we can expect a variation in size among the individuals of their fossil populations. This would be particularly possible in the case of remains found in different locations and stratigraphic levels in very distant localities, as it happens among the specimens found in northern and southernmost ends of Patagonia.

Sedimentological context. The stratigraphic level of Barrancas Blancas at Estancia Santa Lucía that yielded the specimens of *Diplodon* is approximately 90 m above the contact with the underlying Monte León Formation, and about 60 m above a tuff dated in 17.04 ± 0.55 Ma (Cuitiño *et al.*, 2016) (Fig. 2.1,3). The stratigraphic correlation of this location, using the guide levels in the field, suggests its correspondence with the middle section of Barrancas Blancas, which was measured by Fernicola *et al.* (2014).

The remains of *Diplodon* are concentrated near the base of the section, in a medium grain-size sandstone bed (Fig. 2.2), ~20 cm thick, with irregular erosive surface. The specimens are mostly preserved as articulated valves with their internal space filled with sediments from the surrounding matrix. These shells show no evidence of bioerosion, encrustation and/or fragmentation, although relicts of the internal nacreous layers of the shells are frequent. The shells are articulated, with random orientation, although a few specimens show the commissure plane perpendicular to the stratification with complete and fragmentary remains associated in the same level (Fig. 2.2). Towards the top of the fossil bed, the siltstones display a finning upward trend, with abundant rhizoliths and yellowish ochre coloration. Finally, the base of the fossiliferous bed is irregular and discordant over a brown claystone level, which, in turn, overlays on a bed of yellowish siltstones with abundant ochre rhizoliths.

Under the petrographic microscope, the rock bearing the fossil remains of *Diplodon* is a sandstone dominated by angular clasts of mainly volcanic lithics of andesitic composition with pilotaxitic texture (Fig. 5.1–2) and, to a lesser extent, by sedimentary lithic weathered clasts and acid volcanic lithics with felsitic texture clasts. Among the crystalloclasts of the sedimentary matrix, there are predominantly volcanic type quartz with limpid extinction, feldspars and slightly to moderately weathered plagioclase. The clasts have dense clay coating; a dense filling of compact and laminated clay completely obliterates the pore space (Fig. 5.1–2). This illuvial clay is light brown (with a low luminosity when seen under polarized light) probably due to the mixing between clay and organic matter.

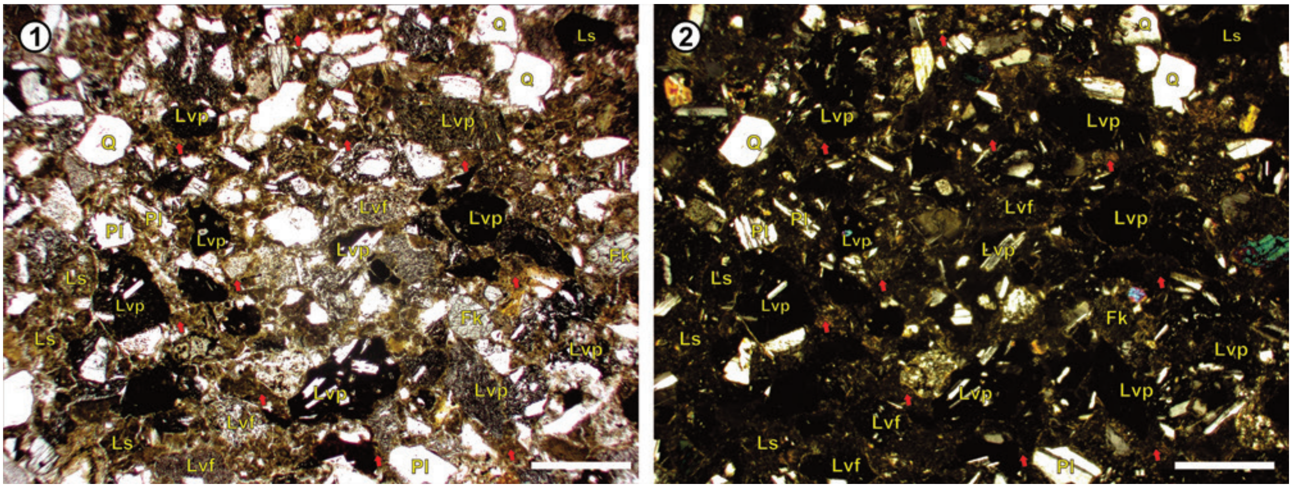

Figure 5. Thin-section photomicrographs of the matrix of *Diplodon* remains. **1,** plane-polarized light. **2,** cross-polarized light; **Fk,** potassium feldspar; **Ls,** sedimentary lithic; **Lvf,** volcanic lithic with felsic texture; **Lvp,** volcanic lithic with pilotaxic texture; **Pl,** plagioclases; **Q,** Clast composition includes quartz. Scale bars= 500 µm.

DISCUSSION

The abundance and taxonomic diversity of the fossil record of vertebrates found in the SCF contributed to characterize the paleocommunities and paleoclimate of southern Patagonia during the Burdigalian (see Kay *et al.*, 2012). By contrast, reports of macroinvertebrates have been scarce and fragmentary. Only a few references dealt with bivalves typical of marine-marginal environments (Griffin and Parras, 2012; Rodríguez *et al.*, 2012). These came from the lower parts of the SCF in the transition with the underlying Monte León Formation, a typically marine lower Miocene unit (Parras *et al.*, 2012). In this sense, the record of *Diplodon* specimens (MPM-Pi 19425), reported from the upper beds of the Estancia Santa Lucia section, contributes with new information to the characterization of the SCF.

The Nayades or "*Almejas Nacaríferas*", as called by Ageitos de Castellanos (1960), are freshwater bivalves that show a wide regional distribution in southern South America (Miyahira *et al.*, 2017). Unionids from the Argentine Patagonia are represented by the Hyriidae, with the genus *Diplodon*, and the Mycetopodidae, with the genus *Anodontites*. Populations of these genera are well-established in northern Patagonia, with species inhabiting cordilleran areas and the extra-Andean sector of Argentina (Parodiz, 1969; Torres *et al.*, 2013). They inhabit clear lentic lakes or lotic water from small streams to large rivers tolerating coarse-grained substrates but preferring fine-grained sediments (usually rich in organic matter). For example, the species *D. chilensis* inhabits lentic and lotic waters of the Manso basin that drain into the Pacific Ocean (Bonetto, 1973). In addition, they are commonly seen in shallow waters, close to 30 cm deep (Miyahira *et al.*, 2017), or in association with roots of aquatic plants (Avelar and Cunha, 2009).

The Family Hyriidae is represented in Argentina by two genera, *Castalia* and *Diplodon*. The latter is marked by a large number of nominal species in the Argentine territory, which inhabit mainly the "*del Plata*" basin (Torres *et al.*, 2013). In this region, the greatest diversity of *Diplodon* is found in the upper basin of Río Paraná, in which the waters are relatively clear, becoming increasingly turbid towards the distal zone where the bottoms are mostly muddy (Bonetto and Ezcurra de Drago, 1966). These conditions are also found in northwestern Patagonia, where the species inhabit similar waters to those of the upper Río Paraná. *Diplodon* (*Diplodon*) *chilensis* (Gray, 1828) is the most widely distributed species, and it is recorded in the provinces of Neuquén, Río Negro, and Chubut as well as in part of the Chilean territory, shared with Argentina, in the Auraucana subregion (Bonetto, 1973). Dense populations of this species inhabit lentic water courses in cordilleran lakes (Bonetto, 1973), such as the forested region of Lago Futalaufquen (~42° 49′ 00″ S; 71° 43′ 00″ O), in which the southermmost records of this taxon can be found (Ageitos de Castellanos, 1959, 1960). The genus *Anodontites* is represented by the species *Anodontites* (*Anodontites*) *patagonicus* (Lamarck, 1819). This species lives in more restricted areas, only present in the Argentine territory, mainly in lotic environments (Bonetto, 1973) such as Río Limay (~38° 59′ 35″ S; 68° 00′ 18″ O), between the provinces of Neuquén and Río Negro (Bonetto, 1973; Torres *et al.,* 2018, see map).

The record of *D.* cf. *colhuapiensis*, in Barrancas Blancas, extends the distribution range of the species several degrees southward, from Lago Colhue Huapi, between 45°–46° S (from where the holotype of the species comes from; Ihering, 1903) to 50° 12′ 58.5″ S. This partially supports the doubtful record mentioned by Parodiz (1969, see map p. 50) for the Oligocene? of Isla Grande of Tierra del Fuego. On the other hand, *D.* cf. *colhuapiensis* of SCF is consistent with the water courses inferred for the upper levels of this unit in previous sedimentological studies (Fernicola *et al.*, 2014), which were confirmed by the presence of dense well-established populations of "*Nayades*" inhabiting the bottoms of these paleoenvironments.

In accordance with the general ecological requirements of this group of freshwater bivalves, the presence of this taxon enables the supposition that in the fluvial watercourses of the SCF, marginal protected areas could probably have been found (backwaters), including the variety of environments in which the extant *Diplodon* (*Diplodon*) *chilensis* currently lives. In these environments, the input of sediments transported by low-energy agents is evidenced in the sedimentary matrix of the bearing deposit of this monospecific population of freshwater bivalves.

Temporal interpretation

The label on the material of *D. colhuapiense*, MACN-Pi 295 (of which the holotype CM 61-137 was most probably part), states that it came from the *Pyrotherium* beds originally regarded as Cretaceous in age. Nevertheless, the *Pyrotherium* beds have been assigned to the Deseadan SALMA (Flynn *et al.*, 2003), for which an Oligocene age of 29.4–24.2 Ma has been estimated (Dunn *et al.*, 2013). Therefore, the age of the specimens MACN-Pi 295 and the holotype CM 61-137 would be Rupelian–Chattian.

MACN-Pi 296, referred in the labels as "Sehuenian (Late Cretaceous)", could either be from the Mata Amarilla Formation (Cretaceous) or from the Santa Cruz Formation (Miocene). However, the Sehuenian of Ameghino (1906) only included marine sediments. This suggests that MACN-Pi 296 should come from the Santa Cruz Formation with continental deposits. In addition, it is similar in morphology to the Santacrucian specimens herein described (although the specimens MACN-Pi 296 are smaller). This would agree with the records of *Diplodon colhuapiensis* being restricted to the Cenozoic, after the reinterpretation of the age of the type material. Then, if our interpretation of the age of MACN-Pi 296 is correct, the fossil record of *Diplodon colhuapiensis* and *D.* cf. *colhuapiensis* (MPM-Pi 19425) would not include the Mesozoic and would be restricted to the Deseadan–Santacrucian SALMA (Oligocene–Miocene).

Interpretation of the sedimentary environment

Due to the abundance of fine-grained deposits with evidence of subaerial exposure (*e.g.*, root traces and sandy paleochannels), the SCF is interpreted as resulting from the accumulation in a low-energy fluvial environment (Fernicola *et al.*, 2014; Cuitiño *et al.*, 2019). In particular, the beds bearing *Diplodon* cf. *colhuapiensis* correspond to a thin sandy level with an erosive base intercalated in mudstone deposits with rhizoliths which suggest it was deposited in fluvial floodplains. This layer shows a lobe-shape geometry and is interpreted as the deposition of overflow channels (*i.e.*, crevasse splay deposits) on the floodplains during episodes of high discharge or river avenues (Mjøs *et al.*, 1993; Bridge, 2003). After their accumulation, these deposits underwent subaerial exposure developing pedogenesis, which is evidenced by illuvial type argillic cement that fills the pore spaces and root traces (Bullock *et al.*, 1985; Retallack, 2001). This supports the interpretation of a proximal floodplain environment. Thick sandstones are scarce in the SCF, in the eastern (middle-distal) basin (Fig. 2.1), and they have been recorded only near the base of some paleochannels. The existence of various specimens of articulated bivalves, chaotically arranged, suggests at least a minimum transport from where they lived (source area). On the other hand, the internal filling of these specimens, which is similar to the surrounding sediment, supports the idea that the individuals were removed from their natural habitat and redeposited in life by means of a high energy current which caused their death during the removal, accumulation and final suffocation processes. This type of flow with erosion capacity is relatively common in anastomosed medium-distal fluvial systems (Miall, 1996; Bridge, 2003) such as those represented in the SCF (Fernicola *et al.*, 2014; Raigemborn *et al.*, 2015; Cuitiño *et al.*, 2016), especially when overflows of the fluvial channels occur and cause overflow or crevasse events on the proximal floodplains. The floodplains recorded in the SCF are composed mainly of yellowish tuffs and siltstones with ochre rhizoliths suggesting a subaerial, well oxygenated environment with vegetation development. As well, a few levels indicate stagnant water accumulation. Because of this, we infer that *Diplodon* cf. *colhuapiensis* would have inhabited marginal protected areas (backwaters) of the fluvial channels in anastomosed rivers and that, due to an overflow process, these were removed and accumulated rapidly in the floodplains.

CONCLUSIONS

This is the first report of freshwater bivalves for the Early–Middle Miocene SCF, in part probably corresponding to the records originally assigned to the "Sehuenense stage" (*piso Sehuenense* of F. Ameghino), represented by specimens referred to *Diplodon* cf. *colhuapiensis* Ihering, 1903. The existence of an established population of mollusks of the Family Hyriidae in the upper-middle beds of the SCF, preserved in fluvial overflow deposits, suggests the existence of well-developed freshwater courses during the deposition of the unit. These deposits are interpreted as fluvial floodplains with evidence of fluvial avenues that excavated the substrate and removed the malacofauna that inhabited the fluvial channels of the SCF. The identification of the genus validates its presence in the lower Miocene and extends its southern distribution to the latitude of Río Santa Cruz (~ 50° S), as already stated by Parodiz (1969). Finally, new specimens of *Diplodon* cf. *colhuapiensis*, from the SCF, showing a better preservation, would enable the establishment of a more precise identification.

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REFERENCES

Ageitos de Castellanos, Z.J. 1959. Algunas consideraciones sobre el género *Diplodon*. *Notas Museo de La Plata (Zoología)* 19: 243–245.

Ageitos de Castellanos, Z.J. 1960. Almejas nacaríferas de la República Argentina. Género *Diplodon* (Moll. Mutélidos). *Secretaría de Estado de Agricultura y Ganadería de la Nación. Dirección general de pesca y conservación de la fauna*. Miscelánea 421: 40 p.

Ameghino, F. 1893. Sobre la presencia de vertebrados de aspecto mesozoico en la formación Santacruceña de la Patagonia austral. *Revista del Jardín Zoológico de Buenos Aires* 1: 76–84.

Ameghino, F. 1906. Les formations sédimentaires du Crétacé Superieur et du Tertiaire de Patagonia. *Anales del Museo Nacional de Buenos Aires (serie 3)* 8: 1–568.

Arbe, H.A. 1989. Estratigrafía, discontinuidades y evolución sedimentaria del Cretácico en la Cuenca Austral, Provincia de Santa Cruz. In: G. Chebli, and L.A. Spalletti (Eds.), *Cuencas Sedimentarias Argentinas*. *Serie de Correlación Geológica* 6, Instituto Superior de Correlación Geológica, Tucumán, p. 419–442.

Arbe, H.A. 2002. Análisis estratigráfico del Cretácico de la Cuenca Austral. In: M.J. Haller (Ed.), *Geología y Recursos Naturales de Santa Cruz. Relatorio 15° Congreso Geológico Argentino.* Asociación Geológica Argentina, Ciudad Autónoma de Buenos Aires, p. 103–128.

Avelar, W.E.P., and Cunha, A.D. 2009. The anatomy and functional morphology of *Diplodon rhombeus fontainianus* (Orbigny, 1835) (Mollusca, Bivalvia, Hyriidae). *Brazilian Journal of Biology* 69: 1153–1163.

Bonetto, A.A. 1973. Nayades de la Patagonia. *Revista de la Asociación de Ciencias Naturales del Litoral* 4: 177–185.

Bonetto, A.A., and Ezcurra de Drago, I. 1966. Notas malacológicas 4. 1) Moluscos paranenses en aguas uruguayas y del sur del Brasil. 2) Notas sobre desoves de algunos gastropodos dulceacuícolas. *Physis* 13: 121–127.

Bostelmann, J.E., Le Roux, J.P., Vásquez, A., Gutiérrez, N.M., Oyarzún, J.L., Carreño, C., Torres, T., Otero, R., Llanos, A., Fanning, C.M., and Hervé, F. 2013. Burdigalian deposits of the Santa Cruz Formation in the Sierra Baguales, Austral (Magallanes) Basin: age, depositional environment and vertebrate fossils. *Andean Geology* 40: 458–489.

Brea, M., Zucol, A.F., Bargo, M.S., and Vizcaíno, S. 2017. First Miocene record of Akaniaceae in Patagonia (Argentina): a fossil wood from the Early Miocene Santa Cruz Formation and its palaeobiogeographical implications. *Botanical Journal of the Linnean Society* 183: 334–347.

Bridge, J.S. 2003. *Rivers and Floodpplains: Forms, Processes, and Sedimentary Record*. Blackwell Science Publishing, Oxford, 491 p.

Bullock, P., Fedoroff, N., Jongerius, A., Stoops, G., and Tursina, T. 1985. *Handbook for Soil Thin Section description*. Waine Research Publication, United Kingdom, 152 p.

Cuitiño, J.I., Fernicola J.C., Kohn, M., Kay, R.F., Trayler, R., Naipauer, M., Bargo, M.S., and Vizcaíno, S.F. 2016. U-Pb geochronology of the Santa Cruz Formation (early Miocene) at the Río Bote and Río Santa Cruz (southernmost Patagonia, Argentina): implications for the correlation of fossil vertebrate localities. *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: 14–33.

Cuitiño, J.I., Pimentel, M.M., Ventura Santos, R., and Scasso, R.A. 2012. High resolution isotopic ages for the "Patagoniense" transgression in southwest Patagonia: stratigraphic implications. *Journal of South American Earth Sciences* 38: 110–122.

Cuitiño, J.I., and Scasso, R.A. 2010a. Sedimentología y paleoambientes del Patagoniano y su transición a la Formación Santa Cruz al sur del Lago Argentino, Patagonia Austral. *Revista de la Asociación Geológica Argentina* 66: 406–417.

Cuitiño, J.I., and Scasso, R.A. 2010b. Large scale, cross-bedded sandstone bodies in a Cenozoic, tide-dominated embayment. *18th International Sedimentological Congress* (Mendoza), *Acta digital*.

Dunn, R.E., Madden, R.H., Kohn, M.J., Schmitz, M.D., Strömberg, C.A., Carlini, A.A., Ré, G.H., and Crowley, J. 2013. A new chronology for middle Eocene–early Miocene South American land mammal ages. *Geological Society of America Bulletin* 125: 539–555.

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) 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.

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 Notohippidian. *Journal of South American Earth Sciences* 52: 94–107.

Feruglio, E. 1938. Relaciones estratigráficas entre el Patagoniano y el Santacruciano en la Patagonia Austral. *Revista del Museo de La Plata (Geología)* 4: 129–159.

Feruglio, E. 1949. *Descripción Geológica de la Patagonia*. Dirección General de Yacimientos Petrolíferos Fiscales, Buenos Aires. Tomos: 1: 1–323; 2: 1–349; 3: 1–331.

Flynn, J.J., Wyss, A.R., Croft, D.A., and Charrier, R. 2003. The Tinguiririca Fauna, Chile: biochronology, paleoecology, biogeography, and a new earliest Oligocene South American Land Mammal "Age". *Palaeogeography, Palaeoclimatology, Palaeoecology* 195: 229–259.

Fossa Mancini, E., Feruglio, E., and Yussen de Campana, J.C. 1938. Una Reunión de geólogos de Y.P.F. y el problema de la Terminología Estratigráfica. *Boletín de Informaciones Petroleras* 171: 31–95.

Ghiglione, M.C., Ramos, V.A., Cuitiño, J., and Varberón, V. 2016. Growth of the Southern Patagonian Andes (46–53°S) and their Relation to Subduction Processes. In: A. Folguera, M. Naipauer, L. Sagripanti, M.C. Ghiglione, D.L. Orts, and L. Giambiagi (Eds.), *Growth of the Southern Andes*. Springer Earth Systems Sciences, Switzerland, p. 201–240.

Griffin, M., and Parras, A. 2012. Oysters from the base of the Santa Cruz Formation (late Early Miocene) 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. 83–90.

Hatcher, J.B. 1900. Sedimentary rocks of southern Patagonia. *American Journal of Science* (1880–1910), Serie 4 9: 85–108.

Ihering von, H. 1903. Les mollusques des terrains crétaciques supérieurs de L´Argentine orientale. *Anales del Museo Nacional de Buenos Aires*, Serie 3 2: 193–228.

Ihering von, H. 1907. Les mollusques fossiles du Tertiaire et du Crétacé supérieur de L´Argentine. *Anales del Museo Nacional de Buenos Aires*, Serie 3 7: 1–608.

Ihering von, H. 1914. Catalogo do Molluscos cretáceos e terciarios da argentina da collecção do autor. *Notas Preliminares*. *Revista do Museu Paulista* 1: 1–113.

Kay, R.F., Vizcaíno, S.F., and Bargo, M.S. 2012. A review of the paleoenvironment and paleoecology of the Miocene Santa Cruz Formation. 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. 331–365.

Krapovickas, V. 2012. Ichnology of distal overbank deposits of the Santa Cruz Formation (late Early Miocene): paleohydrologic and paleoclimatic significance. 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. 91–103.

Manceñido, M.O., and Damborenea, S.E. 1984. Megafauna de invertebrados paleozoicos y mesozoicos. *9° Congreso Geológico Argentino* (San Carlos de Bariloche), *Relatorio* 2–5: 413–465.

Matheos, S.D., and Raigemborn, M.S. 2012. Sedimentology and paleoenvironment of the Santa Cruz Formation. 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. 59–82.

Miall, A.D. 1996. *The geology of fluvial deposits. Sedimentary facies, basin analysis, and petroleum geology*. Springer-Verlag, Berlin, 582 p.

Miyahira, I.C., Barbosa dos Santos, S., and Dreher Mansur, C. 2017. Freshwater mussels from South America: state of the art of Unionida, especially Rhipidodontini. *Biota Neotropica* 17 doi: 10.1590/1676-0611-BN-2017-0341

Miyahira, I.C., Dreher Mansur, M.C., and Barbosa dos Santos, S. 2013. Revision of the type specimens of *Diplodon ellipticus* and *Diplodon expansus* (Bivalvia, Unionoida, Hyriidae). *Spixiana* 36: 173–182.

Mjøs, R., Walderhaug, O., and Prestholm, E. 1993. Crevasse splays sandstone geometries in the Middle Jurassic Ravenscar Group Yorkshire, UK. In: M. Marzo, and C. Puigdefáfregas (Eds.), *Alluvial Sedimentation. International Association of Sedimentologists, Special Publication* 17: 167–184.

Montalvo, C.I., Raigemborn, M.S., Tomassini, R.L., Zapata, L., Bargo M.S., Martínez Uncal, M.C., and Vizcaíno, S.F. 2019. Floodplain taphonomic mode of Early Miocene vertebrates of southern Patagonia, Argentina. *Palaios* 34: 105–120.

Morton, L.S., and Sepúlveda, E.G. 1988. Bivalvos dulceacuícolos de la Formación Ñorquinco (Oligoceno), en la Cuenca del Río Percey, Provincia del Chubut, Argentina. *Ameghiniana* 25: 149–154.

O'Gorman, J.P., and Varela, A.N. 2010. The oldest lower Upper Cretaceous plesiosaurs (Reptilia, Sauropterygia) from the southern Patagonia, Argentina. *Ameghiniana* 47: 447–459.

Parodiz, J.J. 1969. The Tertiary non-marine Mollusca of South America. *Annals of Carnegie Museum* 40: 5–237.

Parras, A., Dix, G., and Griffin, M. 2012. Sr-isotope chronostratigraphy of Paleogene Neogene marine deposits: Austral Basin, southern Patagonia (Argentina*). Journal of South American Earth Sciences* 37: 122–135.

Parras, A., and Griffin, M. 2013. Late Cretaceous (Campanian/Maastrichtian) freshwater to restricted marine mollusc fauna from the Loncoche Formation, Neuquén Basin, west-central Argentina. *Cretaceous Research* 40: 190–206.

Pascual, R., Ortega Hinojosa, E.J., Gondar, D., and Tonni, E.P. 1965. Las Edades del Cenozoico mamalífero de la Argentina, con especial atención a aquellas del territorio bonaerense. *Anales de la Comisión de Investigaciones Científicas de la Provincia de Buenos Aires* 6: 165–193.

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.

Raigemborn, M.S., Krapovickas, V., Beilinson, E., Peral, L.E.G., Zucol, A.F., Zapata, L., and Sial, A.N. 2018. Multiproxy studies of Early Miocene pedogenic calcretes in the Santa Cruz Formation of southern Patagonia, Argentina indicate the existence of a temperate warm vegetation adapted to a fluctuating water table. *Palaeogeography, Palaeoclimatology, Palaeoecology* 500: 1–23.

Raigemborn, M.S., Krapovickas, V., Zucol, A., Zapata, L., Beilinson, E., Toledo, N., Perry, J., Lizzoli, S., Martegani, L., Tineo, D., and Passeggi, E. 2019. Paleosols and related soil-biota of the early Miocene Santa Cruz Formation (Austral-Magallanes basin, Argentina): a multidisciplinary approach to reconstructing ancient terrestrial landscapes. *Latin American Journal of Sedimentology and Basin Analysis* 25: 117–148.

Raigemborn, M.S., Matheos, S.D., Krapovickas, V., Vizcaíno, S.F., Bargo, M.S., Kay, R.F., Fernicola, J.C., and Zapata, L. 2015. Paleoenvironmental reconstruction of the coastal Monte León and Santa Cruz formations (Early Miocene) at Rincón del Buque, Southern Patagonia: A revisited locality. *Journal of South American Earth Sciences* 60: 31–55.

Retallack, G.J. 2001. *Soils of the Past: An introduction to Paleope-*

dology. Blackwell Science Ltd., Oxford, 404 p.

Rodríguez, P.E., Miquel, S.E., Tauber, A.A., and Krapovickas, J.M. 2012. First record of land gastropods of the family Charopidae in the Early to Middle Miocene from Santa Cruz Province, Southern Patagonia, Argentina (Gastropoda Pulmonata, Stylommatophora, Charopidae). *Archiv für Molluskenkunde: International Journal of Malacology* 141: 57–66.

Schneider, C.A., Rasband, W.S., and Eliceiri, K.W. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9: 671–675.

Tauber, A. 1994. [*Estratigrafía y vertebrados fósiles de la Formación Santa Cruz (Mioceno Inferior) en la costa Atlántica de Santa Cruz, República Argentina*. Tesis Doctoral, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Córdoba, 422 p. Inédita.].

Tauber, A.A. 1997. Bioestratigrafía de la Formación Santa Cruz (Mioceno Inferior) en el extremo sudeste de la Patagonia. *Ameghiniana* 34: 413–426.

Torres, S., Cao, L., Gutiérrez Gregoric, D.E., de Lucía, M., Brea, F., and Darrigran, G. 2018. Distribution of the Unionida (Bivalvia, Paleoheterodonta) from Argentina and its conservation in the Southern Neotropical Region. *Plos One* doi: 10.1371/journal.pone.0203616

Torres, S., Darrigran, G., and Damborenea, C. 2013. Distribución del género *Diplodon* (Mollusca, Bivalvia, Hyriidae) en la Cuenca del Plata (Argentina) mediante el uso de Colecciones Biológicas. *AUGM/DOMUS Revista Electrónica del Comité de Medio Ambiente* 5: 90–99.

Varela, A.N., Poiré, D.G., Martin, T., Gerdes, A., Goin, F.J., Gelfo, J.N., and Hoffmann, S. 2012. U-Pb zircon constraints on the age of the Cretaceous Mata Amarilla Formation, Southern Patagonia, Argentina: its relationship with the evolution of the Austral Basin. *Andean Geology* 39: 359–379.

Vizcaíno, S.F., Bargo, M.S., and Fernicola, J.C. 2013. Expediciones paleontológicas durante los siglos 19 y 20 a la Formación Santa Cruz (Mioceno Inferior, Patagonia) y destino de los fósiles. *3º Congreso Argentino de Historia de la Geología* (Salta), *Actas*: 231–246.

Wagner, J.A. 1827. *Testacea fluviatilia quae in itinere per Brasiliam annis 1817-1820 jussu et auspiciis Maximiliani Josephi I. Bavariae Regis augustissimi suscepto, collegit et pingenda curavit Dr. J.B. de Spix, digessit, descripsit et observationibus illustravit Dr. J.A. Wagner*. Monachii. Wolf, p. 1–4, 1–36, Tab. 1–29.

Zapata, L., 2018. [*Estudio paleoambiental de la Formación Santa Cruz (Mioceno inferior–medio) entre los ríos Coyle y Gallegos, Patagonia Austral, Argentina*. Tesis Doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 304 p. Inédita.].

Zapata, L., Krapovicas, V., Raigenborn, M.S., and Matheos, S. 2016. Bee cell trace fossils associations on paleosols from the Santa Cruz Formation: Palaeoenvironmental and palaeobiological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 459: 153–169.

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NOTA BREVE

CALYPTOCEPHALELLA (ANURA, AUSTRALOBATRACHIA) REMAINS FROM RÍO SANTA CRUZ (EARLY–MIDDLE MIOCENE, SANTA CRUZ FORMATION), SANTA CRUZ PROVINCE, ARGENTINA

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Key words. Calyptocephalellidae. *Calyptocephalella canqueli.* Neobatrachia. Neogene. Barrancas Blancas Locality.

Palabras clave. Calyptocephalellidae. *Calyptocephalella canqueli.* Neobatrachia. Neógeno. Localidad Barrancas Blancas.

Recent systematic prospecting in the classic localities of the Santa Cruz Formation (SCF) along Río Santa Cruz have produced a vast collection of vertebrate fossil remains (Fernicola *et al.*, 2014; Cuitiño *et al.*, 2016; Fernicola *et al.*, 2019). The assemblage includes bones of anurans recovered from the two easternmost localities, Barrancas Blancas (Estancia Aguada Grande and Estancia Santa Lucía) and Segundas Barrancas Blancas (Estancia Cordón Alto) (Fig. 1). Outcrops of the SCF have already yielded anuran remains at Estancia La Costa, in the Atlantic coast, which were assigned to *Calyptocephalella* Strand, 1928 by Tauber (1999) and Fernicola and Albino (2012) (see Fernicola *et al.*, 2019: figs. 1 and 4). *Calyptocephalella*, whose record is conspicuous and the most common among extinct anuran genera from Patagonia, has a heavily ossified skull, and inhabited these terrains from the Late Cretaceous (Báez, 1987; Martinelli and Forasiepi, 2004; Agnolín, 2012) to the Miocene (Tauber, 1999; Muzzopappa and Báez, 2009; Fernicola and Albino, 2012; Nicoli *et al.*, 2016). Nowadays, only one representative of this genus, *C. gayi* Duméril and Bibron, 1841, survives along southern central Chile (Cei, 1962), living in ponds, lakes and quiet streams.

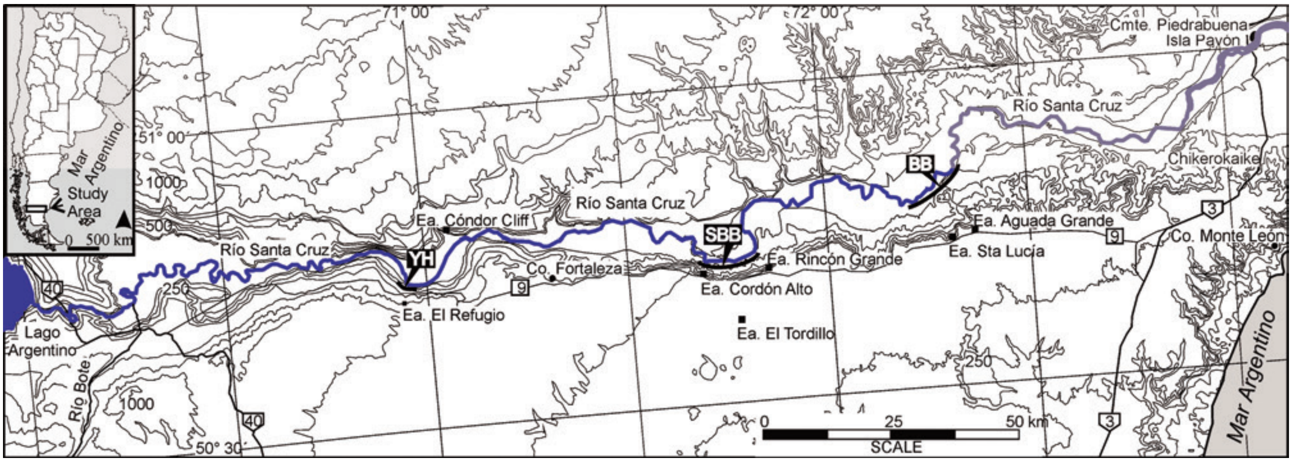

Figure 1. Map of Río Santa Cruz with the prospected localities and estancias mentioned in the text. **BB,** Barrancas Blancas; **SBB,** Segundas Barrancas Blancas; **YH,** Yaten Huageno; **Ea.,** Estancia. Modified from Fernicola *et al.* (2014).

The aim of this contribution is to present the results of investigations on anuran remains from the SCF in Río Santa Cruz. They represent the first anuran record from the original localities of the SCF from which Florentino Ameghino (1889) erected the "Piso Santacruceño" (Fernicola *et al.*, 2014).

The osteological terminology follows that of Trueb (1973), except for the terms fontanella and fenestra, which are used according to Gaupp (1896) as follows: fontanella for openings between dermal bones, and fenestra for openings in the chondrocranium.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; CFA-AN, Colección Fundación Azara, CABA, Argentina; FCEN, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, CABA, Argentina; MACN-HE, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", División Herpetología, CABA, Argentina; MPEF-PV, Museo Paleontológico "Egidio Feruglio", Trelew, Province of Chubut, Argentina; MPM-PV, Museo Regional Provincial "Padre Manuel Jesús Molina", Río Gallegos, Province of Santa Cruz, Argentina.

SYSTEMATIC PALEONTOLOGY

Anura Fischer, 1813
Neobatrachia Reig, 1958
Australobatrachia Frost *et al.*, 2006
Calyptocephalellidae Reig, 1960

Genus ***Calyptocephalella*** Strand, 1928

Type species. *Calyptocephalella gayi* Duméril and Bibron, 1841. Recent, south and central Chile.

Calyptocephalella cf. *canqueli* Schaeffer, 1949
Figure 2.1–3

Holotype. *Calyptocephalella canqueli* Schaeffer, 1949 AMNH FR 3429.

Type locality and age. Rinconada de los López, Scarritt Pocket, Province of Chubut. Late Oligocene (Deseadan).

Referred material. MPM-PV 20025, a left frontoparietal and fragments of both left and right maxillae.

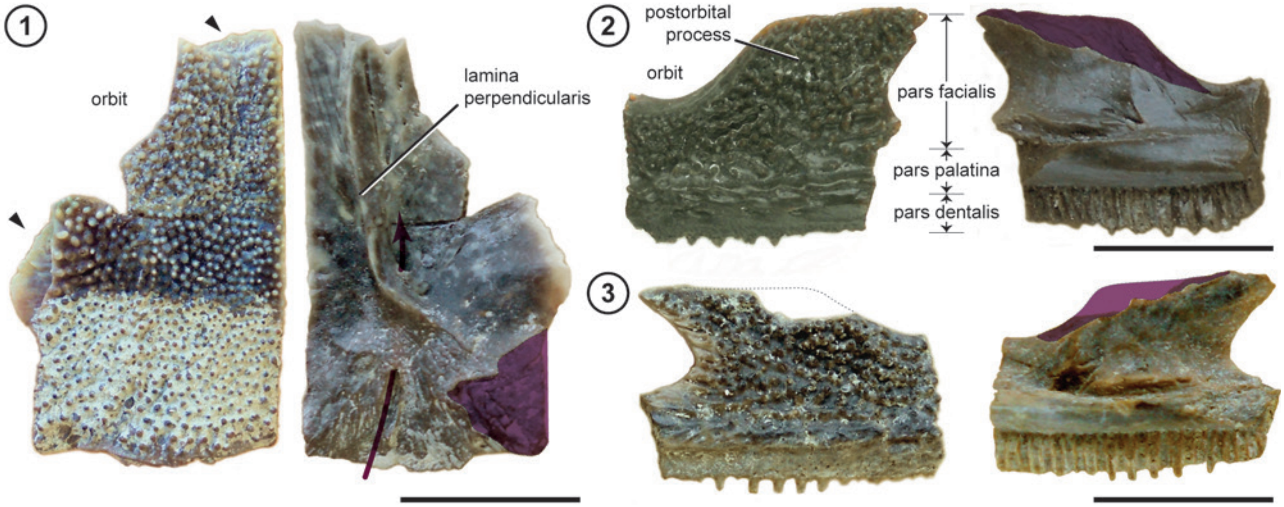

Figure 2. 1–3, ***Calyptocephalella*** **cf.** ***canqueli*****, MPM-PV 20025**; **1,** frontoparietal, dorsal (left) and ventral (right) views; **2–3,** maxillae (fragments), external (left) and internal (right) views. Black arrowheads indicate tongue-like processes; purple surfaces indicate scars left by the squamosal's tongue-like process; the purple arrow indicates the channel for the occipital artery. Scale= 5 mm.

Locality and horizon. Eastern section of Barrancas Blancas (Estancia Aguada Grande), Río Santa Cruz, Province of Santa Cruz, Argentina. Low energy fluvial deposits of Early Miocene (Santacrucian), Santa Cruz Formation (Cuitiño *et al.*, 2016; Cuitiño *et al.*, 2019).

Description. A complete left frontoparietal and fragments of both maxillae constitute, so far, the best preserved remains of anurans recovered from Río Santa Cruz. As they were found close to each other in the field, they are considered to belong to a single individual. Even though these are the only elements that were recovered, several scars imprinted on their surfaces provide significant information regarding the cranial morphology of the specimen. All three elements bear pustular ornamentation on their external surface, the pustules being wide-based, close to one another and not arranged in any particular way. Neither traces of fusions nor coosifications were observed in any of these bones.

The frontoparietal (Fig. 2.1) is a large and conspicuous bone that reached the uttermost posterior border of the neurocranium, extended laterally over the orbit by means of a wide supraorbital flange (whose anterior margin makes the lateral and posterior segments of the orbit), and medially articulated the frontoparietal of the opposite side along its whole length. The supraorbital flange bears two contact facets for articulation with the adjacent squamosal: a triangular scar on the posterolateral portion imprinted by the squamosal, well seen in ventral aspect (purple triangle in Fig. 2.1), and a thin, semicircular tongue-like process (pointed with a black arrowhead in Fig. 2.1), which extends anterior to the aforementioned scar. So, the articulation between the frontoparietal and squamosal is rather complex. Another tongue-like process extends from the anterior end of the frontoparietal, for articulation with the nasal. On the ventral surface of the bone, a conspicuous lamina perpendicularis runs from the anterior border of the frontoparietal up to the level of the otic capsule, where it turns posterolaterally. One can also discern a posterior orifice of the canal through which the occipital artery entered the bone, and another foramen located anteriorly, through which it entered the orbit (purple arrow in Fig. 2.1). It is apparent that the canal for the occipital artery was rather short.

The left and right maxillae (Fig. 2.2–3) are only represented by their orbital and postorbital regions. The external surface bears the same type of ornamentation than that of the frontoparietal, except for the pars dentalis, which is covered by faint ridges parallel to the ventral margin of the bone. On the inner surface, distinct pars facialis, pars palatina and pars dentalis are recognized. The pars facialis is high all along the preserved portion; the anterior section corresponds to the orbital region and its dorsal border constitutes the margin of the orbit, while the posterior section is much higher even and conforms an ample postorbital process (which is not completely preserved on the right side, but complete on the left side). At the level of the orbit, the pars facialis and pars palatina have approximately the same depth, both being higher than the pars dentalis. Noteworthy, there is some intraindividual variation regarding the relative proportions of the pars facialis and the pars palatina when comparing right and left maxillae: the pars facialis is slighly shorter than the pars palatina in the right maxilla, but it is the opposite in the left one. On the inner surface of the postorbital process, a wide and triangular facet can be recognized, in which the tongue-like process projected from the squamosal inserted. Below the orbit, the pars palatina is thicker and more rounded than posteriorly, where —even if it is partially broken— it is evident that it was step-like (*i.e.*, it makes a right angle with both the pars facialis and pars dentalis). Several vertical septa on the inner surface of the pars dentalis indicate the presence of pedicellate teeth along the maxilla. However, neither the total number of tooth position nor the morphology of the teeth can be inferred from these maxillary fragments.

DISCUSSION

The information provided by the specimen MPM-PV 20025 and the scars recognized on it allow the asserting that it belonged to a toothed and casque-headed anuran with frontoparietals completely covering the braincase and meeting in a straight suture along the midline, while leaving no fontanella frontoparietale anteriorly. Also, it is clear that the anterior and lateral tongue-like processes of each frontoparietal were overlapped by the corresponding nasal and squamosal and, moreover, that the squamosal inserted its own tongue-like process below the frontoparietal. These evidences indicate that the frontoparietal had extensive contacts with adjacent elements. Similarly, the squamosal had a steady and straight contact with the maxillary postorbital process by means of a triangular tongue-like process, which took part in the formation of the zygomatic bridge. Despite the scanty record, consisting of three fragmentary bones of the skull roof, MPM-PV 20025 is confidently assigned to the genus *Calyptocephalella*. This assignment is based not only on the overall morphology of each bone and their ornamentation, but also on the presence and position of the tongue-like processes preserved on the frontoparietal, and those inferred for the squamosal. This type of contact between dermatocranial elements by means of tongue-like processes is also observed in extant *C. gayi* (Muzzopappa and Báez, 2009, Muzzopappa, 2013; Fig. 3.1) and in other extinct species of *Calyptocephalella* (*e.g.*, *C. casamayorensis* Schaeffer, 1949 and *C. canqueli*, Schaeffer, 1949; Muzzopappa and Báez, 2009). Such structures, which reinforce contacts between dermal bones, were not found in any other group of frogs (either phylogenetically close or distant) with casqued dermal skull (*e.g.*, *Pelobates* Wagler, 1830, Roček, 1981; Böhme *et al.*, 1982, *Rhinella arenarum* (Hensel), pers. obs. CFA-AN-36, 133, 298), except for some Ceratophryidae (Perí, 1993; pers. obs. FCEN uncatalogued-35) and for some *Latonia* von Meyer, 1843 (Roček, 1994). However, the placement of the tongue-like processes in species of *Ceratophrys* Wied-Neuwied, 1824 is different to that of *Calyptocephalella* (Fig. 3.2–5); for instance, the nasal, instead of the frontoparietal, bears the tongue-like process for the contact of these two dermal bones. Also, in *Ceratophrys*, the maxilla has no orbital margin, as it is excluded from the orbit, and several tongue-like processes are developed for the tripartite articulation between the maxilla, the nasal and the squamosal (Fig. 3.4). In *Latonia*, the frontoparietals are fused along the midline and in broad contact with the nasals, either by interdigitation, as occurs in *L. nigriventer* (Mendelssohn and Steinitz) (Biton *et al.*, 2016), or by the overlap of the tongue-like process ("anterior horns" by Roček, 1994, fig. 7) projected from the anterolateral margin of the frontoparietal, as it happens in *L. seyfriedi* von Meyer, 1843 (Syromyatnikova *et al.*, 2019). Besides, frontoparietals of *Latonia* do not contact the squamosals.

When the frontoparietal MPM-PV 20025 is compared with that of other species of *Calyptocephalella* for which

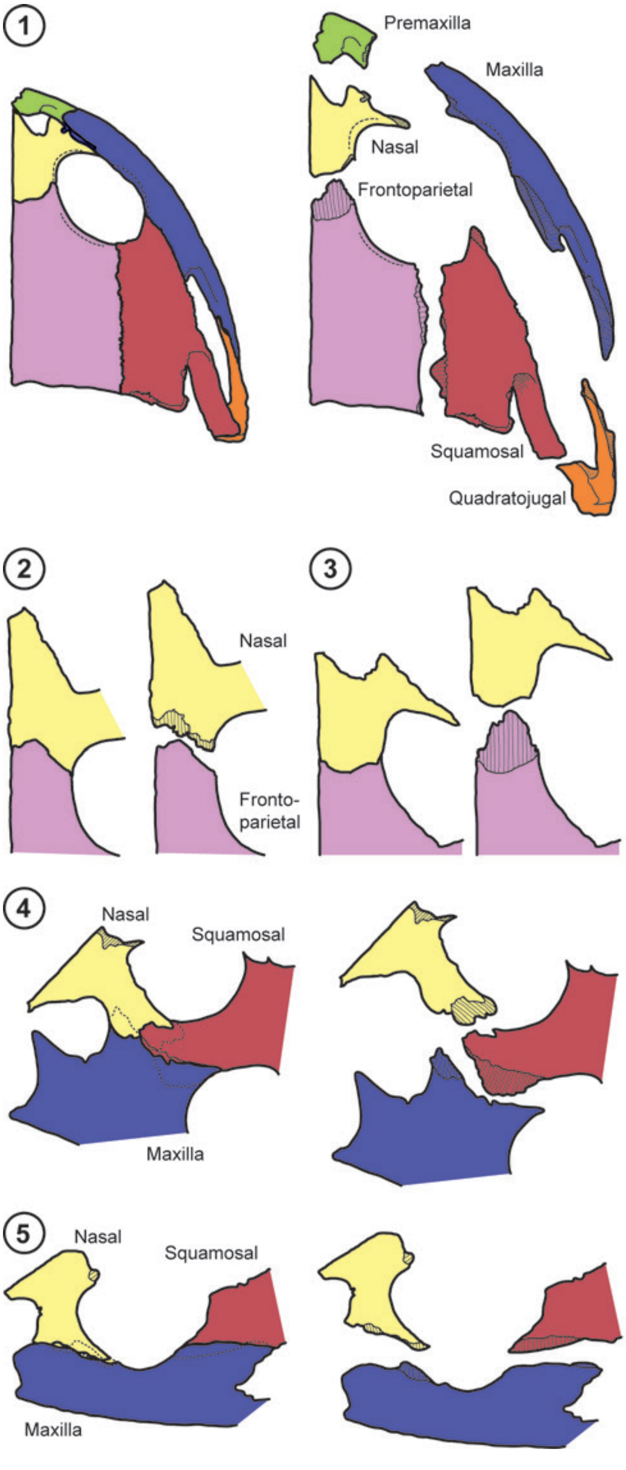

Figure 3. 1, 3, 5, ***Calyptocephalella gayi*****, MACN-HE 45745; 2, 4, 6,** ***Ceratophrys ornata*****, FCEN uncatalogued (35);** schematic comparative drawings of articulated (left) and disarticulated (right) elements of the skull to expose the tongue-like processes; **1,** right half of the skull; **2–3,** nasal and frontoparietal; **4–5,** nasal, maxilla and squamosal. Hatched areas indicate the tongue-like processes.

this element is preserved, its similarity with the frontoparietal of *C. canqueli*, from the Late Oligocene Scarritt Pocket (Schaeffer, 1949: fig. 2, AMNH 3429) and the Late Oligocene–Early Miocene of the Puesto Baibián (Muzzopappa and Báez, 2009: fig. 1, MPEF-PV 1498, 1881, 1886) localities, becomes obvious when regarding the proportions and the pustular ornamentation. As in *C. canqueli*, the frontoparietal of MPM-PV 20025 differs from that of *C. gayi* in having a longer orbital portion and a shorter postorbital portion, which may indicate a more posterior placement of the orbit. The well-preserved tongue-like process projecting from the frontoparietal towards the squamosal differs from that of *C. gayi* in being laterally broader and antero-posteriorly shorter in the fossil specimen (see Fig. 2.1 *versus* Fig. 3.1). The orbit of the Eocene *C. pichileufensis* Gómez, Báez and Muzzopappa, 2011 is antero-posteriorly longer and latero-medially narrower than in *C. canqueli*; furthermore, the frontoparietal in this species does not contact the squamosal, hence there is no postorbital bridge (Gómez *et al.*, 2011). No other species of *Calyptocephalella*, nor *Gigantobatrachus parodii* Casamiquela, 1958 (formerly in synonymy with *Calyptocephalella* but recently recovered as a separate genus, still within Calyptocephalellidae, Agnolín, 2012), preserved frontoparietals to establish comparisons. The comparisons of maxillae MPM-PV 20025 with other species of *Calyptocephalella* and *Gigantobatrachus parodii*, show, aside from variations in the ornamentation patterns, significant differences in the morphology of the pars palatina and the length of the postorbital process, which imply different morphologies of both the zygomatic bridge and the orbit. As was the case with the frontoparietal, the preserved portions of the maxillae are similar to those of *C. canqueli* (Schaeffer, 1949: fig. 2, AMNH 3429; Muzzopappa and Báez, 2009: fig. 1, MPEF-PV 1498, 1885, 1889), the pars facialis, pars palatina and pars dentalis having the same proportions and still the same extension of the postorbital process. In addition, the pars palatina of MPM-PV 20025 is flattened at the level of the orbit, a feature restricted to *C. canqueli* (Muzzopappa and Báez, 2009), within the genus *Calyptocephalella.* When comparing the maxillae of MPM-PV 20025 with *C. casamayorensis* from the Eocene of Chubut (Schaeffer, 1949), similar maxillary proportions and length of the postorbital process are observed. However, there are differences in the pitted ornamentation and in the step-like pars palatina below the orbital portion of *C. casamayorensis*. Differences are more significant with *C. gayi*, regardless of sharing the pustular ornamentation. In *C. gayi*, the postorbital process is longer, the pars palatina is step-like below the orbit, the pars dentalis is deeper, and the pars facialis is shorter. Comparisons with *G. parodii* are more restricted due to the poor preservation of the maxilla: for instance, the postorbital process seems to be incomplete on its dorsal and lateral margins. The pars palatina of *G. parodii*, like in *C. gayi* and *C. casamayorensis*, is step-like below the orbit and the pars dentalis is two to three times deeper than that of MPM-PV 20025. Finally, the ornamentation is of the pitted type instead of pustular.

CONCLUSION

The presence of *Calyptocephalella* is reported for the first time in Río Santa Cruz. Its record in the Santa Cruz Formation, however, has already been described (as *Calyptocephalella* sp.) from the Atlantic coastal locality of Estancia La Costa (Tauber, 1999; Fernicola and Albino, 2012), synchronous according to the dates and analyses of Cuitiño *et al.* (2016). The specimen MPM-PV 20025, even though represented only by three cranial elements, is herein assigned to the species *Calyptocephalella* cf. *canqueli* owing to distinctive features that differentiate it from the remaining species of the genus (Muzzopappa and Báez, 2009): flattened pars palatina at the level of the orbit, dense pustular ornamentation, narrow and posteriorly delimited orbit by the postorbital bridge conformed by frontoparietal and squamosal, a shorter postorbital region and a longer antero-posterior orbital diameter, and significantly deeper pars facialis at the level of the orbit. It differs further from *C. gayi* by its shorter extension of the postorbital process of the maxilla and therefore shorter zygomatic bridge. Several of these features correlate with the shape of the orbit; the narrow and posterior position of the orbit of MPM-PV 20025 is due to the long orbital region of the frontoparietal plus the short zygomatic bridge established by the maxilla and squamosal.

The presence of *Calyptocephalella* cf. *canqueli* in the Santa Cruz Formation substantially enlarges the geographic distribution of this species, thus far recorded in the Province of Chubut (Schaeffer, 1949; Muzzopappa and Báez, 2009;

Muzzopappa and Nicoli, 2010). In agreement with data obtained from findings in Puesto Baibián (Gandolfo *et al.*, 2009) and Scarritt Pocket (Marshall *et al.*, 1986) (Province of Chubut), this form inhabited flooded zones and water bodies during warm temperate periods (Cuitiño *et al.*, 2016 and references therein). The area of the geographic distribution of *C. canqueli* is consistent with that of the extant *C. gayi* in Chile, although in different climatic conditions.

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REFERENCES

Agnolín, F. 2012. A new Calyptocephalellidae (Anura, Neobatrachia) from the upper Cretaceous of Patagonia, Argentina, with comments on its systematic position. *Studia Geologica Salmanticensia* 48: 129–178.

Ameghino, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas de la Academia Nacional de Ciencias de Córdoba* 6: 1–1028.

Báez, A.M. 1987. The Late Cretaceous fauna of Los Alamitos, Patagonia, Argentina. Part III Anurans. *Revista de Museo Argentino de Ciencas Naturales Bernardino Rivadavia—Paleontología* 3: 121–130.

Biton, R., Boistel, R., Rabinovich, R., Gafny, S., Brumfeld, V., and Bailon, S. 2016. Osteological observations on the Alytid anura *Latonia nigriventer* with comments on functional morphology, biogeography, and evolutionary history. *Journal of Morphology* 277: 1131–1145.

Böhme, W., Roček, Z., and Špinar, V. 1982. On *Pelobates decheni* Troschel, 1861, and *Zaphrissa eurypelis* Cope, 1866 (Amphibia, Salientia, Pelobatidae) from the Early Miocene of Rott near Bonn, West Germany. *Journal of Vertebrate Paleontology* 2: 1–7.

Cei, J.M. 1962. *Batracios de Chile*. Ediciones de la Universidad de Chile, Santiago de Chile, 128 p.

Cuitiño, J.I., Fernicola, J.C., Kohn, M.J., Trayler, R., Naipauer, M., Bargo, M.S., Kay, R.F., and Vizcaíno, S.F. 2016. U-Pb geochronology of the Santa Cruz Formation (early Miocene) at the Río Bote and Río Santa Cruz (southernmost Patagonia, Argentina): Implications for the correlation of fossil vertebrate localities. *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) 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: 14–33.

Duméril, A.M., and Bibron, G. 1841. *Erpétologie génerale ou Histoire Naturelle complète des Reptiles*. Librairie encyclopédique de Roret, Paris, 793 p.

Fernicola, J.C., and Albino, A. 2012. Amphibians and squamate reptiles from the Santa Cruz Formation (late Early Miocene), Santa Cruz Province, Argentina: paleoenvironmental and paleobiological considerations. 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, New York, p. 129–137.

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 Notohippidian. *Journal of South American Earth Sciences* 52: 94–107.

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.

Gandolfo, M.A., Zamaloa, M.C., Cúneo, N.R., and Archangelsky, A. 2009. Potamogetonaceae fossil fruits from the Tertiary of Patagonia, Argentina. *International Journal of Plant Sciences* 170: 419–428.

Gaupp, E. 1896. *A. Ecker's und R. Wiedersheim's Anatomie des Frosches. Vol I.* Von Friedrich Vieweg und Sohn, Braunschweig, 227 p.

Gómez, R.O., Báez, A.M., and Muzzopappa, P. 2011. A new helmeted frog (Anura, Calyptocephalellidae) from an Eocene subtropical lake in northwestern Patagonia, Argentina. *Journal of Vertebrate Paleontology* 31: 50–59.

Marshall, L.G., Cifelli, R.L., Drake, R.E., and Curtis, G.H. 1986. Vertebrate paleontology, geology, and geochronology of the Tapera de López and Scarritt Pocket, Chubut Province, Argentina. *Journal of Paleontology* 60: 920–951.

Martinelli, A.G., and Forasiepi, A.M. 2004. Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Río Negro province, Argentina, with the description of a new sauropod dinosaur (Titanosauridae). *Revista del Museo Argentino de Ciencias Naturales, n.s.*, 6: 257–305.

Muzzopappa, P. 2013. [*Anatomía esqueletaria y osteogénesis de* Calyptocephalella gayi *(Anura, Neobatrachia): aporte al conocimiento del registro fósil de un linaje gondwánico relictual.* PhD Thesis, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, 259 p. Unpublished.].

Muzzopappa, P., and Báez, A.M. 2009. Systematic status of the mid–Tertiary neobatrachian frog *Calyptocephalella canqueli* from Patagonia (Argentina), with comments on the evolution of the genus. *Ameghiniana* 46: 113–125.

Muzzopappa, P., and Nicoli, L. 2010. A glimpse at the ontogeny of the fossil neobatrachian frog *Calyptocephalella canqueli* from the Deseadan (Oligocene) of Patagonia, Argentina. *Acta Paleontologica Polonica* 55: 645–654.

Nicoli, L., Muzzopappa, P., and Faivovich, J. 2016. The taxonomic placement of the Miocene Patagonian frog *Wawelia gerholdi* (Amphibia: Anura). *Alcheringa* 40: 153–160.

Perí, S.I. 1993. [*Relaciones evolutivas de las especies de la subfamilia*

Ceratophryinae (Anura, Leptdactylidae). PhD Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Buenos Aires, 223 p., Unpublished.].

Roček, Z. 1981. Cranial anatomy of frogs of the family Pelobatidae Stannius, 1856, with outlines of their phylogeny and systematics. *Acta Universitatis Carolinae. Biologic*a 1980: 1–160.

Roček, Z. 1994. Taxonomy and distribution of the Tertiary Discoglossid (Anura) of the Genus *Latonia* v. Meyer, 1843. *Geobios* 27: 717–751.

Schaeffer, B. 1949. Anurans from the early Tertiary of Patagonia. *Bulletin of the American Museum of Natural History* 93: 41–68.

Strand, E. 1928. Miscellanea nomenclatorica zoologica et palaeontologica I-II. *Archiv für Naturgeschichte* 92: 30–75.

Syromyatnikova, E., Roček, Z., and van de Velde, S. 2019. New discoveries in the frog *Latonia seyfriedi* (Anura, Alytidae) and their impact on taxonomy of the genus *Latonia*. *Paläontologische Zeitschrift*. https://doi.org/10.1007/s12542-019-00477-8

Tauber, A.A. 1999. Los vertebrados de la Formación Santa Cruz (Mioceno inferior–medio) en el extremo sureste de la Patagonia y su significado paleoecológico. *Revista Española de Paleontología* 14: 173–182.

Trueb, L. 1973. Bones, frogs, and evolution. In: J.L. Vial (Ed.), *Evolutionary Biology of the Anurans*. University of Missouri Press, Columbia, p. 65–132.

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NOTA BREVE

NEW RECORDS OF BIRDS FROM THE SANTA CRUZ FORMATION (EARLY–MIDDLE MIOCENE) AT THE RÍO SANTA CRUZ VALLEY, PATAGONIA, ARGENTINA

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Key words. Avifauna. Phorusrhacidae. Tinamidae. Rheidae. Neogene.

Palabras clave. Avifauna. Phorusrhacidae. Tinamidae. Rheidae. Neógeno.

THE SANTA CRUZ FORMATION (SCF) constitutes one of the most representative units of the Early–Middle Miocene (Burdigalian–early Langhian) of South America for its abundant fossil record and the richness of its bird species. This record was collected during paleontological expeditions from the mid-nineteenth century along extensive outcrops exposed throughout a large area of the homonymous province. Seventeen species grouped in 15 genera and at least 10 families (Rheidae, Tinamidae, Phorusrhacidae, Cariamidae, Aramidae, Threskiornithidae, Falconidae, Brontornithidae, Anhimidae?, Anatidae and Anhingidae) constitute the diversity of extinct birds known so far (Degrange *et al.*, 2012).

The SCF crops out in much of the territory of the Province of Santa Cruz (Argentina), in the northwest, in the surroundings of Lago Posadas, the central region along Río Santa Cruz (Fernicola *et al.*, 2014; Cuitiño *et al.*, 2016) and Río Chalía (= Sehuén; Vizcaíno *et al.*, 2018) and, in the southeast, along the Atlantic coast (Vizcaíno *et al.*, 2012). It is a continental unit composed of mudstones, tuffaceous sandstones and tuffs deposited in fluvial environments under the influence of intense explosive pyroclastic input. For extensive geological descriptions, see Cuitiño *et al.* (2016, 2019a). The radiometric ages for the entire SCF span the interval ~18 to 15.60 Ma, being ~18–16 Ma for the Atlantic coastal localities (Fleagle *et al.*, 2012; Perkins *et al.*, 2012); ~18.20–15.60 Ma for the Río Bote and the Río Santa Cruz localities (Cuitiño *et al.*, 2016), and ~18–14 Ma for the Lago Posadas region (Perkins *et al.*, 2012; Cuitiño *et al.*, 2019b).

The SCF along Río Santa Cruz was recently studied and described in three locations by Fernicola *et al.* (2014) and Cuitiño *et al.* (2016, 2019a); that is, from east to west: Barrancas Blancas (BB; Estancias Santa Lucía and Aguada Grande), Segundas Barrancas Blancas (SBB; Estancias Cordón Alto, El Tordillo and Rincón Grande) and Yaten Huageno (YH; Estancia El Refugio) (Fig. 1). In the present contribution, we present and describe the first records of birds from these localities, with accurate geographic and stratigraphic provenances, along Río Santa Cruz.

MATERIAL AND METHODS

Recent fieldwork carried out throughout 2013 and 2014 by joint expeditions of Museo de La Plata (MLP), La Plata, Argentina, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires, Argentina, and Duke University, North Carolina, USA, recovered nine remains of fossil birds. This collection belongs to Museo Regional Provincial "Padre Manuel Jesús Molina" (MPM-PV), Río Gallegos, Argentina. The specimens collected exclusively include postcranial elements (*e.g.*, fragmentary long bones, several pes and manus elements). These were recovered from three fossiliferous localities: Barrancas Blancas (BB; seven specimens), Segundas Barrancas Blancas (SBB; one specimen) and Yaten Huageno (YH; one specimen). The osteological nomenclature follows Howard (1929) and Baumel and Witmer (1993).

SYSTEMATIC PALEONTOLOGY

Order Cariamiformes Verheyen, 1957
Family Phorusrhacidae (Ameghino, 1889)

Genus ***Psilopterus*** Moreno and Mercerat, 1891

Type species. *Psilopterus comunis* Moreno and Mercerat, 1891. Santa Cruz Formation, Province of Santa Cruz, Argentina.

Psilopterus lemoinei (Moreno and Mercerat, 1891)
Figure 2.1–14

Referred material. MPM-PV 18897, associated fragments of a single specimen consisting of right scapula, two proximal ends of humeri (one right and one left), distal end of left radius, left proximal phalanx of *digitus majoris*, synsacrum plus pelvis, two distal ends of femora (one right and one left), distal end of left tibiotarsus, right proximal and right distal ends of tarsometatarsi, and proximal end of an indeterminate phalanx of the foot; MPM-PV 18898, synsacrum plus articulated pelvis and partial vertebral column.

Geographic occurrence. Both specimens come from the BB locality in the Estancia Santa Lucía, Province of Santa Cruz.

Stratigraphic occurrence. Santa Cruz Formation (Early–Middle Miocene).

Description. The specimen MPM-PV 18897 is referred to *Psilopterus lemoinei* based on the following diagnostic characters described by Degrange and Tambussi (2011): humerus with *crista deltopectoralis* weakly developed and lacking pneumatic foramen; femur with *crista lateralis* of *sulcus patellaris* interrupted proximally before the contact with shaft; tibiotarsus with *sulcus extensorius* deep and medially positioned; tarsometatarsus with *hypotarsus* possessing two reduced *cristae hypotarsi* on the plantar surface: *crista medialis hypotarsi* lightly furrowed, with short posterior development, and *crista lateralis hypotarsi* slightly convex; margin of *hypotarsus* not protruded proximally; *foramina vascularia proximalia* visible in plantar view and placed at the same level; ridge of *cotyla medialis* high and oval; *eminentia intercotylaris* well developed.

The synsacrum MPM-PV 18898 is also referred to *Psilopterus* based on the presence of a well-developed process of the ilium, which constitutes a cranially directed spine, caudally located with respect to the *foramen ilioischiadicum* (Degrange *et al.*, 2015b). Additionally, the size of this specimen is similar to that of MPM-PV 18897, precluding its

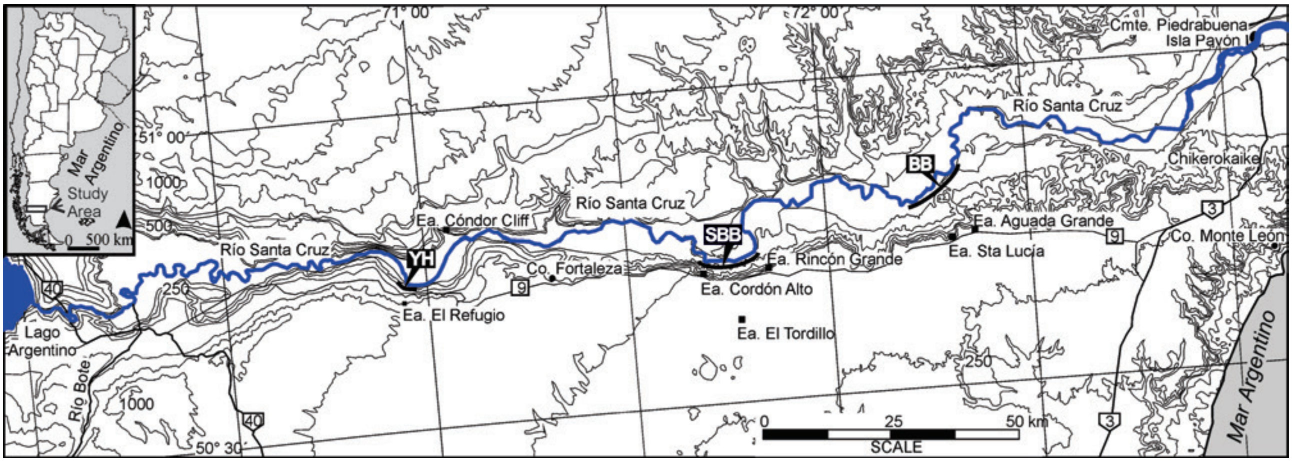

Figure 1. Geographical location of the fossiliferous localities studied at Río Santa Cruz. **SBB,** Segundas Barrancas Blancas; **BB,** Barrancas Blancas; **YH,** Yaten Huageno; **Ea.,** Estancia. Modified from Fernicola *et al.* (2014).

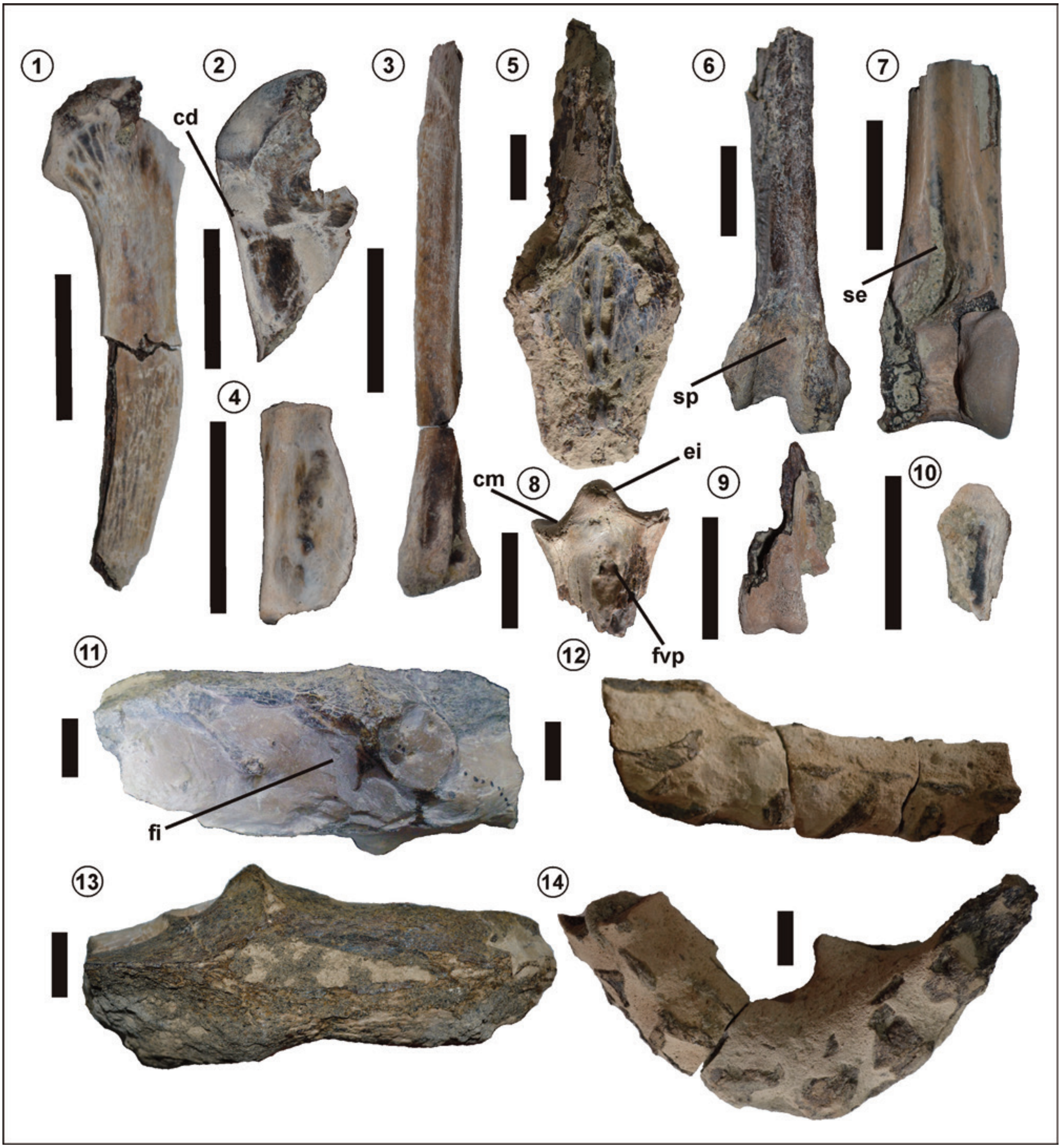

Figure 2. *Psilopterus lemoinei*. **MPM-PV 18897, 1–10; 1**, fragments of right scapula, in dorsal view; **2,** proximal end of right humerus in cranial view; **3,** distal end of left radius in cranial view; **4,** left phalanx proximal *digitus majoris* of the wing in dorsal view; **5,** fragments of synsacrum in dorsal view; **6,** distal end of left femur in cranial view; **7,** distal end of left tibiotarsus, in cranial view; **8,** proximal end of right tarsometatarsus in dorsal view; **9,** distal end of left tarsometatarsus in dorsal view; **10,** proximal end of indeterminate phalanx of the foot, in dorsal view. **MPM-PV 18898, 11–14; 11,** fragments of synsacrum, in lateral view; **12,** fragments of posterior ends of column in lateral view; **13,** fragments of synsacrum in dorsal view; **14,** fragments of anterior ends of column in lateral view. Abbreviations: **cd,** *crista deltopectoralis*; **cm,** *cotyla medialis*; **ei,** *eminentia intercotylaris*; **fi,** *foramen ilioischiadicum*; **fvp,** *foramina vascularia proximale*; **se,** *sulcus extensorius*; **sp,** *sulcus patellaris*. Scale bars= 2 cm.

assignation to *Psilopterus bachmanni* (Moreno and Mercerat, 1891) and *Procariama simplex* Rovereto, 1914 (see Alvarenga and Höfling, 2003, table 8).

Psilopterus sp.

Figure 3.1–2

Referred material. MPM-PV 18901, distal fragment of left tibiotarsus; MPM-PV 18902, distal fragment of left tibiotarsus; MPM-PV 18905, distal end of left tarsometatarsus.
Geographic occurrence. MPM-PV 18901 and MPM-PV 18905 come from BB (Estancia Aguada Grande), while MPM-PV 18902, from SBB (Estancia Cordón Alto), Province of Santa Cruz.
Stratigraphic occurrence. Santa Cruz Formation (Early–Middle Miocene).
Description. The distal end of tarsometatarsus (MPM-PV 18905) resembles that of *Psilopterus lemoinei* because its *trochlea metatarsi* III have flanges more proximally convergent than that of *P. affinis* (Ameghino, 1899) (see Degrange and Tambussi, 2011). The distal fragments of tibiotarsi (MPM-PV 18901, MPM-PV 18902) resemble those of *P. lemoinei* and differ from those *P. bachmanni* by having a wide *pons supratendineus* with a well-developed distal lip and lateral tubercle (Degrange and Tambussi, 2011). In addition, both remains can be distinguished from *P. bachmanni* by their greater size (see Alvarenga and Höfling, 2003, tab. 8). However, both the tibiotarsus and the tarsometatarsus do not present other characters that allow their complete distinction among the species of *Psilopterus* and, hence, their tentative assignment to *Psilopterus* sp.

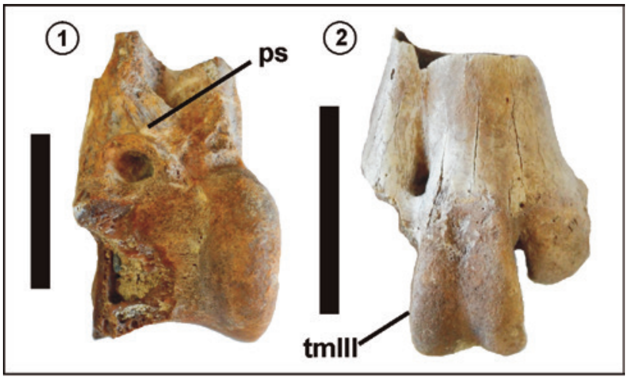

Figure 3. ***Psilopterus*** **sp. 1, MPM-PV 18902**, distal ends of left tibiotarsus in cranial view; **2, MPM-PV 18905,** distal ends of left tarsometatarsus in dorsal view. Abbreviations: **ps**, *pons supratendineus*; **tmIII**, *trochlea metatarsi* III. Scale bars= 2 cm.

Order Rheiformes (Forbes, 1884)

Family Rheidae Bonaparte, 1849

Genus ***Opisthodactylus*** Ameghino, 1891

Type species. *Opisthodactylus patagonicus* Ameghino, 1891. Santa Cruz Formation, Monte Observación, Province of Santa Cruz.

Opisthodactylus patagonicus Ameghino, 1891

Figure 4.1

Referred material. MPM-PV 18903 and MPM-PV 18904, distal ends of left tibiotarsi.
Geographic occurrence. MPM-PV 18903 comes from BB (Estancia Santa Lucía) and MPM-PV 18904, from YH (Estancia El Refugio), Province of Santa Cruz.
Stratigraphic occurrence. Santa Cruz Formation (Early–Middle Miocene).
Description. These specimens are assigned to *Opisthodactylus patagonicus*. They can be distinguished from other extant and extinct Rheidae by the following character combination (Noriega *et al.*, 2017): prominence for attachment of medial ligament continuous with insertion for transverse ligament (not separated by the distal end of the *sulcus extensorius*); *sulcus extensorius* markedly excavated, well delimited and ending proximally; cross-section of distal shaft more markedly compressed anteroposteriorly. Several of the characters observed in both specimens are shared between *O. patagonicus* and *O. kirchneri* Noriega, Jordan, Vezzosi and Areta, 2017 but differ from those of *O. horacioperezi* Agnolín and Chafrat, 2015 (see Noriega *et al.*, 2017): greater size; *trochlea cartilaginis tibialis* larger and more proximodistally developed in anterior view at the point where it joins the medial margin of the *condylus lateralis*; ridge that delimits *trochlea cartilaginis tibialis* proximally higher or more proximally extended; in medial view, medial ligamentary ridge sharper, ending distally in a more robust medial ligamental prominence; in lateral view, *epicondylus medialis* more marked and more proximally placed. The portion of the *sulcus m. fibularis* located medially to the *tuberculum retinaculi m. fibularis* is developed as in *O. patagonicus* but deeper than in *O. kirchneri*.

Order TINAMIFORMES Huxley, 1872
Family TINAMIDAE Gray, 1840

TINAMIDAE gen. et sp. indet.
Figure 4.2

Referred material. MPM-PV 18900, proximal end of left carpometacarpus.

Geographic occurrence. BB (Estancia Santa Lucía), Province of Santa Cruz.

Stratigraphic occurrence. Santa Cruz Formation (Early–Middle Miocene).

Description. A deep pit for an aponeurotic insertion –tentatively identified as the attachment for the *ligamentum ulnocarpometacarpale ventralis* (Bertelli *et al.*, 2014)– located on the ventral surface of the proximal end, caudal to the *processus pisiformis*, which is observed in MPM-PV 18900, is an automorphic character for Tinamidae (Bertelli, 2002). *Nothocercus* Gray, 1867 is the only exception because this pit varies from virtually absent to deep (Bertelli *et al.*, 2014). Additionally, this specimen has the *processus extensorious* well developed, condition shared with all the tinamids and the European *Palaeotis* Lambrecht, 1928 among the palaeognathous genera (Mayr, 2015). Other diagnostic character present in MPM-PV 18900 is the "caudal rim" of the *trochlea carpalis*, which is clearly notched like in some tinamous (*e.g.*, *Nothocercus*, *Tinamus* Hermann, 1783, *Crypturellus* Brabourne and Chubb1914, *Eudromia* Geoffroy Saint-Hilaire, 1832) (Bertelli *et al.*, 2014).

CONCLUDING REMARKS

The state of knowledge of the Santacrucian avian diversity was recently summarized by Degrange *et al.* (2012). The fossil record includes at least 17 formally described species grouped in 15 genera and at least 10 families: rheas (*Opisthodactylus patagonicus*), tinamous (*Crypturellus reai* Chandler, 2012), terror birds (*Phorusrhacos longissimus* Ameghino, 1887; *Patagornis marshi* Moreno and Mercerat, 1891; *Psilopterus bachmanni* (Moreno and Mercerat, 1891), *Psilopterus lemoinei* (Moreno and Mercerat, 1891)), seriemas (*Miocariama patagonica* Noriega and Mayr, 2017), limpkins (*Anisolornis excavatus* (Ameghino, 1891)), spoonbills (*Protibis cnemialis* Ameghino, 1891), falcons (*Badiostes patagoniscus* Ameghino, 1895, *Thegornis musculosus* Ameghino, 1895, *T. debilis* Ameghino, 1895), waterfowls (*Brontornis burmeisteri* Moreno and Mercerat, 1891; *Eoneornis australis* Ameghino, 1895, *Eutelornis patagonicus* Ameghino, 1895, *Ankonetta larriestrai* Cenizo and Agnolín, 2010) and darters (*Anhinga hesterna* (Ameghino, 1895)).

Most of these taxa were originally erected at the end of the 19th century (Ameghino, 1887, 1891, 1895; Moreno and Mercerat, 1891) or restudied at the beginning of the 20th century (Dolgopol de Sáez, 1927; Kraglievich, 1931; Sinclair and Farr, 1932) on the basis of material without precise stratigraphic position or even of dubious geographic provenance.

The most prospected levels of the SCF that have provided the largest amount of avian fossil remains are exposed close to or along the Atlantic Ocean coast (see Fernicola *et al.*, 2019: fig. 5), *e.g.*, Monte León, Monte Observación, La Cueva, Yegua Quemada, Jack Harvey, Puesto Estancia La Costa (Corriguen- Kaik) and Monte Tigre (Ameghino, 1891, 1895; Brodkorb, 1964; Tonni, 1980; Degrange *et al.*, 2012;

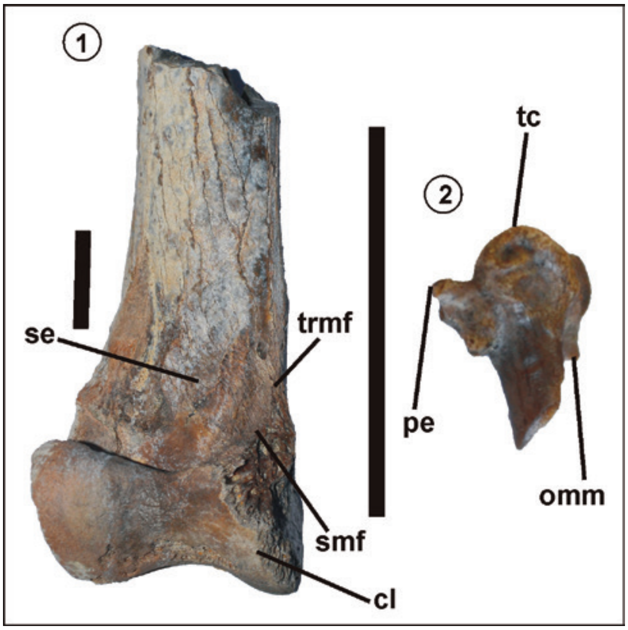

Figure 4. Palaeognathae. 1, ***Opisthodactylus patagonicus*** **MPM-PV 18903**, distal end of left tibiotarsus in cranial view; **2,** Tinamidae indeterminated **MPM-PV 18900**, proximal end of left carpometacarpus in dorsal view. Abbreviations: **cl,** *condylus lateralis*; **omm,** *os metacarpale minus*; **pe,** *processus extensorius*; **se,** *sulcus extensorius*; **smf,** *sulcus m. fibularis*; **tc,** *trochlea carpale*; **trmf,** *tuberculum retinaculi m. fibularis*. Scale bars= 2 cm.

Vizcaíno *et al.*, 2012). Other exposures, such as those in the Río Santa Cruz and Río Chalía (= Sehuén) valleys, have provided limited published information about the fossil record of birds. For example, Carlos Ameghino collected the type specimen of *Phorhusracos longissimus* Ameghino, 1887 from the Río Santa Cruz outcrops but failed to specify a location. Both the distal end of the tarsometatarsus assigned to the purported limpkin *Anisolornis excavatus*, as well as the material referred to *Psilopterus lemoinei* come from Karaiken, north to the rising of Río Santa Cruz, near Lago Argentino; while fragmentary specimens referred to *Opisthodactylus patagonicus* and *Phorhusracos longissimus* are reported from localities in Río Chalía (Brodkorb, 1964; Tonni, 1980). Recently, new remains assigned to *Phorhusracos longissimus* were found near Lago Belgrano (Degrange *et al.*, 2019).

Renewed intensive collecting field trips developed by researchers of MLP, MACN and Duke University, together with paleontological and geologic studies performed since 2003 in the SCF (Vizcaíno *et al.*, 2012; Fernicola *et al.*, 2014), are bringing out the possibility to overcome the historical difficulties concerning the provenances of fossil materials. Thus, the knowledge about some old known Santacrucian bird taxa like the falconid *Thegornis musculosus* (Noriega *et al.*, 2009, 2011; Noriega and Mayr, 2017) or the phorusrhacid *Psilopterus bachmanni* (Degrange *et al.*, 2015a) has been substantially improved with new complete or better-preserved available specimens with accurate provenances.

As a result of the paleontological discoveries within the framework of these projects, we present the first fossil birds collected with precise geological provenance from different localities in the Río Santa Cruz valley. They include fragmentary specimens referred to *Opisthodactylus patagonicus* (Rheidae) and an indeterminate genus and species of tinamous (Tinamidae), as well as other more complete specimens assigned to *Psilopterus lemoinei* (Phorusrhacidae). No new remains of *Phorhusracos longissimus* were recorded.

Santacrucian paleoenvironments were characterized by the presence of alternating areas of herbaceous vegetation with shrubby or wooded areas based on the extrapolation of habitat preferences of living birds for their extinct analogs (Degrange *et al.*, 2012). Habitat preferences of extant rheas, tinamids and seriemas (analog to phorusrhacids) are consistent with open areas because of their cursorial capabilities. Additionally, waterfowls, limpkins, spoonbills and darters would indicate the existence of temporarily flooded savannas or permanent water bodies in forested areas (Degrange *et al.*, 2012).

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REFERENCES

Agnolín, F., and Chafrat, P. 2015. New fossil bird remains from the Chichinales Formation (Early Miocene) of northern Patagonia, Argentina. *Annales de Páleontologie* 101: 87–94.

Alvarenga, H., and Höfling, E. 2003. Systematic revision of the Phorusrhacidae (Aves: Ralliformes). *Papeis Avulsos de Zoologia, Museu de Zoología da Universidade de São Paulo* 43: 55–91.

Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos Eocenos de la Patagonia austral y depositados en el Museo de La Plata. *Boletín del Museo La Plata* 1: 1–26.

Ameghino, F. 1891. Enumeración de las aves fósiles de la República Argentina. *Revista Argentina de Historia Natural* 1: 441–453.

Ameghino, F. 1895. Sur les oiseaux fossiles de Patagonie. *Boletín del Instituto Geográfico Argentino* 15: 501–602.

Ameghino, F. 1899. Sinopsis geológico-paleontológica: adiciones y correcciones. *Segundo Censo de la República Argentina*, p.111–255.

Baumel, J.J., and Witmer, L.M. 1993. Osteologia. In: J.J. Baumel, S.A. King, J.E. Breazile, H.E. Evans, and J.C. Venden Berge (Eds.), *Handbook of Avian Anatomy: Nomina Anatomica Avium, second edition*. Publications of the Nuttall Ornithological Club 23, Cambridge, p. 45–132.

Bertelli, S. 2002. [*Filogenia del orden Tinamiformes (Aves: Palaeognathae)*. Ph.D. thesis, Universidad Nacional de Tucumán, Tucumán, 160 p. Unpublished.].

Bertelli, S., Chiappe, L.M., and Mayr, G. 2014. Phylogenetic interrelationships of living and extinct Tinamidae, flying paleognathous birds from the New World. *Zoological Journal of the Linnean Society* 172: 145–184.

Brabourne W.W.K.-H., and Chubb, C.A. 1914. Key to the species of the genus *Crypturellus*, with descriptions of some new forms. *Annals and Magazine of Natural History* 14: 319–322.

Brodkorb, P. 1964. Catalogue of fossil birds: Part 2 (Anseriformes through Galliformes). *Florida State Museum, Biological Series* 8: 195–335.

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

Cuitiño, J.I., Fernicola, J.C., Raigemborn, M.S., and Krapovickas, V. 2019a. 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: 14–33.

Cuitiño, J.I., Vizcaíno, S.F., Bargo, M.S., and Aramendía, I. 2019b. Sedimentology and fossil vertebrates of the Santa Cruz Formation (early Miocene) in Lago Posadas, a sub-Andean locality of southwestern Patagonia. *Andean Geology* 46: 383–420.

Degrange, F.J., Eddy, D., Puerta, P., and Clarke, J. 2019. New skull remains of *Phorusrhacos longissimus* (Aves, Cariamiformes) from the Miocene of Argentina: implications for the morphology of Phorusrhacidae. *Journal of Paleontology* 93: 1–13.

Degrange, F.J., Noriega, J.I., and Areta, J.I. 2012. Diversity and paleobiology of the santacrucian birds. 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. 138–155.

Degrange, F.J, Noriega, J.I., and Vizcaíno, S.F. 2015a. Morphology of the forelimb of *Psilopterus bachmanni* (Aves, Cariamiformes) (Early Miocene of Patagonia). *Palaöntologische Zeitschrift* 89: 1087–1096.

Degrange, F.J., and Tambussi, C.P. 2011. Re-examination of *Psilopterus lemoinei* (Moreno and Mercerat, 1891), a late early Miocene little terror bird from Patagonia (Argentina). *Journal of Vertebrate Paleontology* 31: 1080–1092.

Degrange, F.J., Tambussi, C.P., Taglioretti, M.L., Dondas, A., and Scaglia, F. 2015b. A new Mesembriornithinae (Aves, Phorusrhacidae) provides new insights into the phylogeny and sensory capabilities of terror birds. *Journal of Vertebrate Paleontology,* 35: 1–18.

Dolgopol de Sáez, M. 1927. *Liornis minor*, una especie nova de ave fósil. *Physis* 8: 584–585.

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.

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 Notohippidian. *Journal of South American Earth Sciences* 52: 94–107.

Fleagle, J.H., Perkins, M.E., Heizler, M.T., Nash, B., Bown, T.M., Tauber, A.A., Dozo, M.T., and Tejedor, M.F. 2012. Absolute and relative ages of fossil localities in the Santa Cruz and Pinturas Formations. 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. 41–58.

Geoffroy Saint-Hilaire, I.S. 1832. *Eudromia*. *Magasin de Zoologie* 47: classe II, pl. 1.

Gray, G.R. 1867. *List of the specimens of birds in the collection of the British Museum. Part V. Gallinae*. The order of the Trustees, London, 97 p.

Hermann, J. 1783. *Tabula Affinitatum Animalium.* Imprensis J.G. Treuttel, Argentorati, Strassburg, 164 p.

Howard, H. 1929. The avifauna of Emerville shellmound. *University of California Publications in Zoology* 32: 301–394.

Kraglievich, L. 1931. Contribución al conocimiento de las aves fósiles de la época araucoentrerriana. *Physis* 10: 304–315.

Lambrecht, K. 1928. *Palaeotis weigelti* n. g. n. sp., eine fossil Trappe aus der mitteleozanen Braunkohle des Geiseltales. *Jahrbuch des Halleschen Verbandes* 7: 1–11.

Mayr, G. 2015. The middle Eocene European “ratite” *Palaeotis* (Aves, Palaeognathae) restudied once more. *Paläontologische Zeitschrift* 89: 503–514.

Moreno, F.P., and Mercerat, A. 1891. Catálogo de los pájaros fósiles de la República Argentina conservados en el Museo de La Plata. *Anales del Museo de La Plata* 1: 7–71.

Noriega, J.I., Areta, J.I., Vizcaíno, S.F., and Bargo, M.S. 2011. Phylogeny and taxonomy of the patagonian Miocene falcon *Thegornis musculosus* Ameghino, 1895 (Aves: Falconidae). *Journal of Paleontology* 85: 1089–1104.

Noriega, J.I., Jordan, E.A., Vezzosi, R.I., and Areta, J.I. 2017. A new species of *Opisthodactylus* Ameghino, 1891 (Aves, Rheidae), from the late Miocene of northwestern Argentina, with implications for the paleobiogeography and phylogeny of rheas. *Journal of Vertebrate Paleontology* 37: e1278005.

Noriega, J.I., and Mayr, G. 2017. The systematic affinities of the putative seriema *Noriegavis santacrucensis* (Noriega *et al.*, 2009) from the Miocene of Argentina. *Contribuciones del Museo Argentino de Ciencias Naturales* 7: 133–139.

Noriega, J.I., Vizcaíno, S.F., and Bargo, M.S. 2009. First record and a new species of seriema (Aves: Ralliformes: Cariamidae) from Santacrucian (early-middle Miocene) beds of Patagonia. *Journal of Vertebrate Paleontology* 29: 620–626.

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.

Rovereto, C. 1914. Los estratos araucanos y sus fósiles. *Anales del Museo Nacional de Historia Natural de Buenos Aires* 25: 1–249.

Sinclair, W., and Farr, M. 1932. Aves of the Santa Cruz beds. In: W. Scott (Ed.), *Reports of the Princeton University expeditions to Patagonia (1896-1899)*. Princeton University Press, New Jersey, p. 157–191.

Tonni, E.P. 1980. The present state of knowledge of the Cenozoic birds of Argentina. *Contributions in Science* 330: 105–114.

Vizcaíno, S.F., Bargo, M.S., Cuitiño, J.I., Pérez, M.E., Muñoz, N.A., Aramendía, I., Tomassini, R.L., and Kay, R.F. 2018. The outstanding Río Chalía (= Sehuén) outcrops of the Santa Cruz Formation (Early Miocene, Burdigalian) and its fossil vertebrate content. *Publicación Electrónica de la Asociación Paleontológica Argentina* 19: 85R.

Vizcaíno, S.F., Kay, R.F., and Bargo, M.S. 2012. *Early Miocene Paleobiology in Patagonia: High-latitude Paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, 370 p.

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THE METATHERIA FROM THE RÍO SANTA CRUZ (SANTA CRUZ FORMATION, EARLY–MIDDLE MIOCENE, ARGENTINA): HISTORY AND NEW RECORDS

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Abstract. Here we summarize the species of Metatheria from the Early–Middle Miocene Santa Cruz Formation at the Río Santa Cruz (RSC; Argentina). We assign newly collected specimens from the RSC localities Barrancas Blancas (BB) and Segundas Barrancas Blancas (SBB) to the known metatherian species. The metatherians from RSC were first described by F. Ameghino in 1887. He did not always establish clearly the type specimens of the species he founded, and often later he chose new type specimens. This led to confusion by future authors when they assumed they were looking at the original types when in fact they were the substitutes. We evaluated the actual and supposed type specimens from the RSC. We have identified the holotype of the Paucituberculata *Palaeothentes aratae* Ameghino and its calcotype. Following the International Code of Zoological Nomenclature (Art. 75), we formally propose neotypes, for the species *Sipalocyon gracilis* Ameghino (Sparassodonta) and for *Microbiotherium patagonicum* Ameghino (Microbiotheria). The species *Perathereutes pungens* Ameghino (Sparassodonta), previously known only from coastal localities, is described for the first time for the RSC. In total, we recognized 16 metatherian species for the RSC: seven Paucituberculata, seven Sparassodonta, and two Microbiotheria. Ten of the 16 species were recorded from recent fieldtrips. All 10 are recorded from SBB, six come from BB, and none from a third RSC locality, Yaten Huageno.

Key words. Marsupial. South America. Early Neogene. Santacrucian.

Resumen. LOS METATHERIA DEL RÍO SANTA CRUZ (FORMACIÓN SANTA CRUZ, MIOCENO TEMPRANO–MEDIO, ARGENTINA): HISTORIA Y NUEVOS REGISTROS. Con el objetivo de enumerar las especies de metaterios presentes en la Formación Santa Cruz (Mioceno Temprano-Medio) en el Río Santa Cruz (RSC; Argentina) y determinar nuevos ejemplares de metaterios del RSC provenientes de las Barrancas Blancas (BB) y Segundas Barrancas Blancas (SBB), se procedió a identificar las especies conocidas para dicha localidad. Los metaterios del RSC fueron descriptos por primera vez por Ameghino en 1887 y, como fue común en sus trabajos, muy pocas veces estableció los ejemplares tipo de las especies por él fundadas o eligió nuevos ejemplares tipo. Esto llevó a que, en algunos casos, los investigadores posteriores tomaran como tipo especímenes que no lo eran. Se procedió al estudio de los tipos de las especies presentes en el RSC y a la determinación de los nuevos ejemplares colectados. El estudio dio como resultado el hallazgo del holotipo y calcotipo de *Palaeothentes aratae* Ameghino (Paucituberculata), la designación formal de dos neotipos siguiendo los requerimientos del Código Internacional de Nomenclatura Zoológica (Art. 75), para las especies *Sipalocyon gracilis* Ameghino (Sparassodonta) y *Microbiotherium patagonicum* Ameghino (Microbiotheria) y se determinó por primera vez para el RSC la especie *Perathereutes pungens* Ameghino (Sparassodonta), previamente conocida para localidades de la Costa Atlántica. Quedan entonces reconocidas un número total de 16 especies para el RSC: siete Paucituberculata, siete Sparassodonta y dos Microbiotheria. Diez de las 16 especies fueron registradas en las campañas recientes. Todas fueron halladas en SBB, mientras que solo seis provienen de BBy ninguna de la tercera localidad del RSC, Yaten Huageno.

Palabras clave. Marsupial. América del Sur. Neógeno temprano. Santacrucense.

THE SANTA CRUZ FORMATION (SCF; Early–Middle Miocene; Burdigalian–early Langhian) forms extensive badlands with mudstones, tuffaceous sandstones, and tuffs cropping out in Southern Argentina, in an extended area of the Province of Santa Cruz. The unit can be studied in the northwest and southeast regions of the province, and in the central area along the Río Santa Cruz and Río Chalía (Vizcaíno *et al.*, 2012; Fernicola *et al.*, 2014; Cuitiño *et al.*, 2016). The Río Santa Cruz (RSC) lies approximately at 50° South in the Province of Santa Cruz and runs from west to east.

Francisco P. Moreno in 1876–1877, following the steps of Fitz Roy (1837), navigated the RSC and explored the outcrops adjacent to its course finding, among other remains, the first marsupial from the SCF (Moreno, 1879, 1882; Fig. 1). In 1886, as director of the Museo de La Plata, Moreno commissioned Carlos Ameghino to carry out a paleontological and geological fieldtrip to the RSC. The trip lasted from January to September 1887 (Ameghino, 1887) and when Carlos returned to La Plata, his brother Florentino quickly studied many of the approximately 2000 fossils, and published an article in which he recognized 122 taxa (Fernicola, 2011), of which 19 are metatherian species (Ameghino, 1887).

The mammalian groups described by Ameghino (1887), currently regarded as metatherians, are Creodonta and Marsupialia. Among the Creodonta (Sparassodonta since Ameghino, 1894) from the RSC, he recognized the following species: *Cladosictis patagonica* Ameghino, 1887, *Hathliacynus lustratus* Ameghino, 1887, *Agustylus cynoides* Ameghino, 1887, *Borhyaena tuberata* Ameghino, 1887, *Anatherium defossus* Ameghino, 1887, *Acrocyon sectorius* Ameghino, 1887, *Acyon tricuspidatus* Ameghino, 1887, and *Sipalocyon gracilis* Ameghino, 1887. Later, Cabrera (1927) described the sparassodont *Lycopsis torresi* also from the RSC. In the recent literature, *Agustylus cynoides*, *Hathliacynus lustratus*, and *Acrocyon sectorius* are regarded as junior synonyms of *Cladosictis patagonica* (Marshall, 1981; Forasiepi, 2009; Prevosti and Forasiepi, 2018).

Ameghino recognized two families of Marsupialia: Plagiaulacidae (regarded later as Paucituberculata) and Microbiotheriidae. The former included *Abderites meridionalis* Ameghino, 1887, *Acdestis oweni* Ameghino, 1887, *Palaeothentes aratae* Ameghino, 1887, *P. lemoinei* Ameghino, 1887, *P. pachygnatus* Ameghino, 1887, *P. intermedius* Ameghino, 1887, *P. pressiforatus* Ameghino, 1887, and *P. minutus* Ameghino, 1887. Almost all these species are still considered valid today, except for *P. pachygnatus* and *P. pressiforatus*, each of which was regarded as a *nomen vanum* by Marshall (1980), because the types are lost and the descriptions are too scant to recognize the diagnostic features of the species. The Microbiotheriidae included *Microbiotherium patagonicum* Ameghino, 1887, *M. tehuelchum* Ameghino, 1887, and *Stilotherium dissimile* Ameghino, 1887. *Stilotherium dissimile* is considered a Paucituberculata Caenolestidae (Trouessart, 1898; Abello, 2013).

Ameghino's (1887) work was seminal for metatherian history in several aspects, since it includes the first description of a fossil fauna from the SCF, and it included the first fossil microbiotherians, paucituberculatans, and sparassodonts ever described (Ameghino, 1887, 1889).

The aim of this work is to reassess the taxonomic history of the metatherians from the RSC fauna identifying the type specimens of taxa named by Ameghino (1887), to study new specimens collected in recent years (Fernicola *et al.*, 2019), and to give an updated list of species for the RSC as are now recognized.

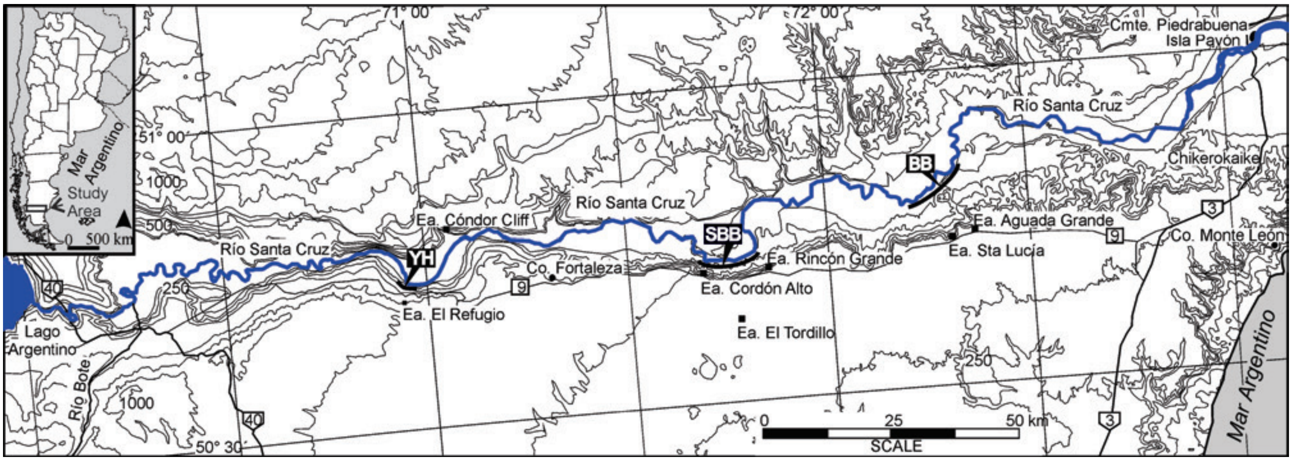

Figure 1. Map of Santa Cruz showing the Río Santa Cruz localities; **BB,** Barrancas Blancas; **SBB,** Segundas Barrancas Blancas; **YH,** Yaten Huageno. Modified from Fernicola *et al.* (2014).

MATERIAL AND METHODS

Institutional abbreviations. **MPM-PV,** Museo Regional Provincial "Padre M. Jesús Molina", Colección de Paleovertebrados; **MLP,** Museo de La Plata; **MACN-A,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Nacional Ameghino; **MACN-Pv,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Nacional de Paleovertebrados; **MACN-Pv SC,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Nacional de Paleovertebrados, Santa Cruz collection.

Anatomical abbreviations. **c,** lower canine; **C,** upper canine; **Ltad,** talonid length; **Ltrgd,** trigonid length; **mx,** lower molar in x position; **Mx,** upper molar in x position; **px,** lower premolar in x position; **Px,** upper premolar in x position; **Wtad,** talonid width; **Wtrgd,** trigonid width.

The new specimens presented in this paper were collected from the southern cliffs of the RSC at the localities Barrancas Blancas (BB, S 50° 9′ 38.31″ - W 69° 40′ 23.40″ to S 50° 12′ 31.70″ - W 69° 43′ 10.66″) and Segundas Barrancas Blancas (SBB, S 50° 16′ 12.48″ - W 70° 22′ 23.21″ to S 50° 16′ 51.90″ - W 70° 17′ 54.76″) (Fernicola *et al.*, 2014, 2019; Cuitiño *et al.*, 2016). A third locality Yaten Huageno (YH) does not contain representatives of Metatheria. Barrancas Blancas crops out in Estancia Aguada Grande (EAG) and Estancia Santa Lucía (ESL). Segundas Barrancas Blancas crops out in Estancia Cordón Alto (ECA) and Estancia El Tordillo (EET) (Fernicola *et al.*, 2014). The localities from the South-East of Province of Santa Cruz follow Vizcaíno *et al.* (2012) and Fernicola *et al.*, (2019: fig. 1).

Ameghino (1887, 1889) considered that the marsupials had four premolars and three molars. However, this view was not shared by subsequent authors (*e.g.*, Mercerat, 1891; Cabrera, 1927; Marshall, 1980, 1981, 1982), since the Metatheria dentary formula include three premolars and four molars. In the following descriptions we will use the present day homologies and we will included Ameghino's hypothesis between brackets [], when necessary.

The systematic arrange for the Sparassodonta, follows Marshall (1978, 1981), Forasiepi *et al.* (2006), Forasiepi (2009), Prevosti *et al.* (2012), and Prevosti and Forasiepi (2018). The Paucituberculata systematics, after Marshall (1980), Abello (2007, 2013), and Abello and Rubilar-Rogers (2012). For the Microbiotheria we follow Marshall (1982).

SYSTEMATIC PALEONTOLOGY

Infraclass METATHERIA Huxley, 1880
Order SPARASSODONTA Ameghino, 1894
Family HATHLIACINIDAE Ameghino, 1894

Genus ***Cladosictis*** Ameghino, 1887

Type species. *Cladosictis patagonica* Ameghino, 1887. Santa Cruz Formation, Barrancas del RSC, Province of Santa Cruz, Argentina.

Cladosictis patagonica Ameghino, 1887
Figure 2.1–7; Table 2

Holotype. MLP 11-103, left maxillary fragment with M3-4.

Stratigraphic and geographic distribution. Río Frías Formation, Aysén (Chile); SCF, Province of Santa Cruz (Argentina) in the following localities: Puesto Estancia la Costa, Río Coyle, Cañadón Silva, Anfiteatro, Campo Barranca, Estancia La Costa, Karaiken, Cerro Observatorio, Río Gallegos, Río Chalía, Corriguen-Kaik, Cañadón Jack, Monte León, 10 miles South of Coy Inlet, Coy Inlet, Lago Pueyrredón, 10 miles North of Coy Inlet, Cañadón de Las Vacas, and RSC.

Referred material. MPM-PV 19416, right dentary fragment with emerging m3; MPM-PV 19417 (Fig. 2.1–7), several dentary fragments pertaining to two mandibles of the same individual; left dentary in two parts, one with m4 and other with m2-3 with broken cusps, right with canine, p1 and roots of p2-3, and several bone fragments; MPM-PV 19419, a lower canine; MPM-PV 19420, a lower canine.

Geographic distribution. SBB, all specimens come from ECA.

Comments on the holotype. In his original description Ameghino (1887) described two teeth, M1-2 [P4-M1]. Both teeth were sectorial, with the posterior tooth smaller and transversely wider. In 1889 Ameghino described these teeth in more detail. From the description, the teeth are probably implanted in a single maxillary fragment. Mercerat (1891) commented on his list of sparassodonts from the MLP collections that the specimen described by Ameghino (1887) corresponds to an M3-4. Later, Cabrera (1927) assigned MLP 11-103 as the type of *C. patagonica* and agreed with Mercerat (1891) on the tooth positions and considered that Ameghino's identification was incorrect. Though incorrect in their position, Ameghino's (1887) description of the mo-

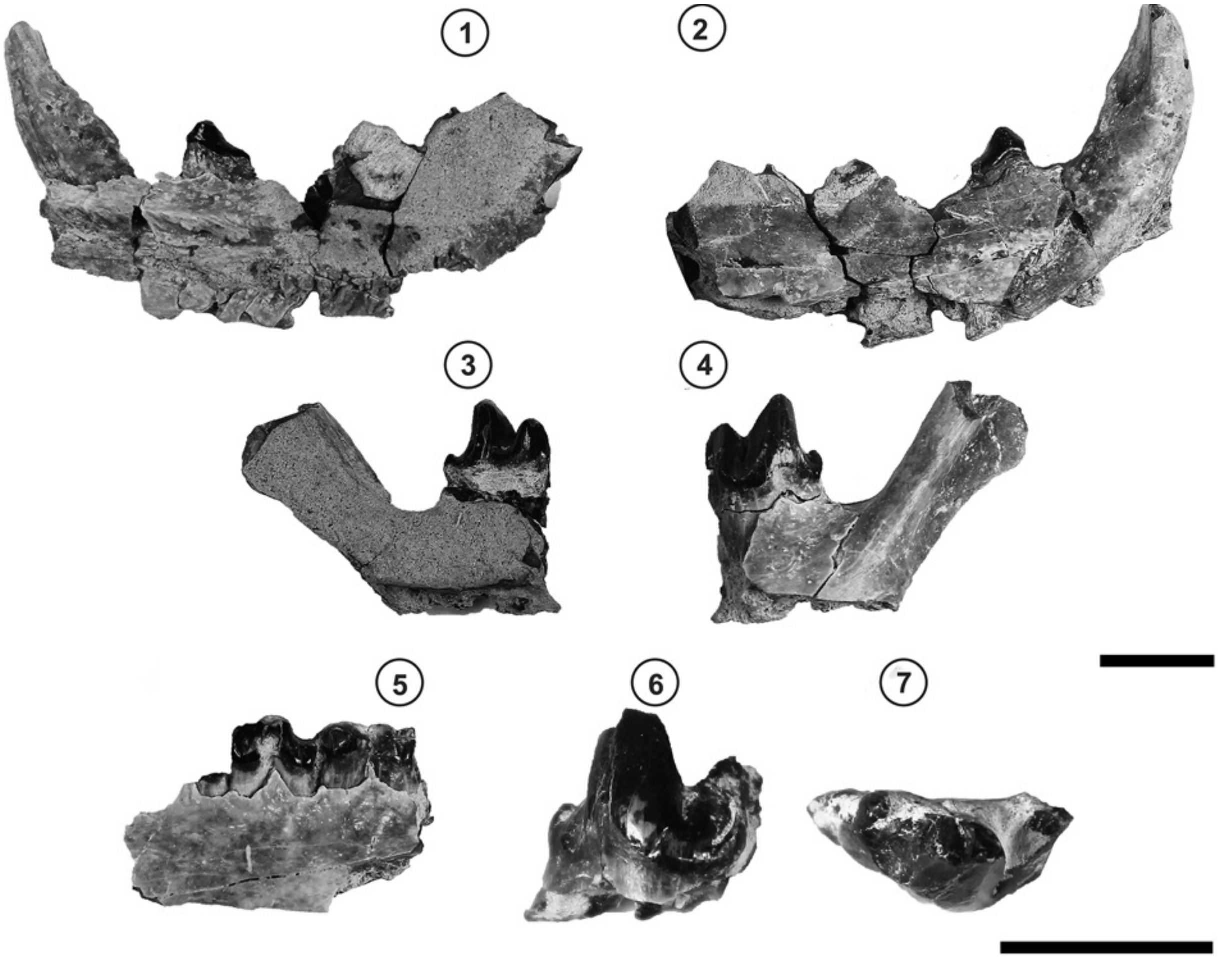

Figure 2. 1–7, ***Cladosictis patagonica*****, MPM-PV 19417**; right dentary fragment with canine, p1 and roots of p2-3 in **1,** lingual view; **2,** labial view; left dentary fragment with m4 in **3,** lingual view; **4,** labial view; left dentary fragment with broken m2-3? in **5,** labial view; isolated right m4 in **6,** labial and **7,** occlusal views. Scale bars= 10 mm.

lars coincides with the MLP 11-103 (indicated as the type in the files from the MLP collections).

Comments on the referred material. The right mandible MPM-PV 19416 corresponds to a juvenile individual with emerging m3, since the talonid is better developed than the one present in the m4 of this species. The specimen MPM-PV 19417 has several fragments and probably was a single individual, since the fragments were found in close proximity and the teeth show similar wear. The size and overall morphology of the molars and premolars are the ones expected for *C. patagonica*, as is the development of the canine, labiolingually broader when compare with other hathliacynids.

The two canines (MPM-VP 19419 and MPM-PV 19420) are here referred to *C. patagonica* by size and similarity to those present in other specimens of the species (*e.g.*, MPM-PV 4333).

Genus ***Acyon*** Ameghino, 1887

Type species. *Acyon tricuspidatus* Ameghino, 1887. Santa Cruz Formation, Barrancas del RSC, Province of Santa Cruz, Argentina.

Acyon tricuspidatus Ameghino, 1887

Figure 3.1–4

Holotype. MLP 11-64, right dentary fragment in two parts, the anterior fragment with roots of c, alveoli for p1 and p2, and a posterior fragment with almost complete p3-m4.

Stratigraphic and geographic distribution. Santa Cruz Formation at the Province of Santa Cruz in the following localities: RSC, Río Chalía, and Cerro Observatorio.

Comments on the holotype. Ameghino (1887) described *A. tricuspidatus* as having eight lower molariforms. Later,

Table 1 – Measurements of the lower molars of new RSC specimens described in this work

	Ltrgd m1	*Wtrgd m1*	*Ltad m1*	*Wtad m1*	*Ltrgd m2*	*Wtrgd m2*	*Ltad m2*	*Wtad m2*	*Ltrgd m3*	*Wtrgd m3*	*Ltad m3*	*Wtad m3*
Abderites meridionalis												
MPM-PV 19374	3.35	1.68	2.27	1.43								
MPM-PV 19375	3.40	2.01	2.14	1.50	1.45	1.66	1.69	1.61	0.82	1.40	1.70	1.11
Acdestis oweni												
MPM-PV 19376	-	-	-	1.84	1.17	1.85	1.14	1.84	0.76	1.36	0.80	1.36
Borhyaena tuberata												
MPM-PV 19321					7.61	4.91	3.05	5.94	8.90	5.46	2.30	6.89
Microbiotherium tehuelchum												
MPM-PV 19372	0.83	0.81	0.61	1.66								
MPM-PV 19373	0.75	0.93	1.11	1.20								
Palaeothentes lemoinei												
MPM-PV 19381	2.47	1.90	1.95	2.36	-	-	-	-				
MPM-PV 19389					1.30	2.04	1.20	1.99	1.18	1.66	0.98	1.56
MPM-PV 19383	1.88	1.57	1.77	1.79	1.21	1.69	1.41	1.68	0.59	1.06	0.65	1.06
MPM-PV 19384	1.68	1.75	1.66	1.61	1.13	1.69	1.12	1.70	0.77	1.34	1.65	1.81
MPM-PV 19385	1.73	1.34	1.65	1.81	1.06	1.98	1.35	1.92				
MPM-PV 19386	1.73	1.41	1.40	1.62	1.01	1.60	1.23	1.59	0.71	1.39	0.70	1.38
MPM-PV 19387					1.40	1.91	1.50	1.90	0.89	1.42	0.88	-
MPM-PV 19388					1.17	1.63	1.16	1.62	-	-	-	-
Palaeothentes minutus												
MPM-PV 19379									0.72	1.54	1.01	1.55
MPM-PV 19391					0.70	1.06	0.72	1.07	0.56	0.74	0.57	0.73
MPM-PV 19392	0.94	0.90	0.95	0.93	0.48	1.15	0.63	1.10	0.40	1.02	0.44	1.04
MPM-PV 19393	0.83	0.82	0.93	0.82	0.63	1.01	0.70	1.02	0.61	0.97	0.63	0.98
MPM-PV 19395					0.62	1.18	0.65	1.18				
MPM-PV 19396					0.61	1.17	0.62	1.17	0.46	0.95	0.50	0.95
MPM-PV 19398	0.81	0.88	0.91	0.92	0.64	1.01	0.75	1.03				
MPM-PV 19399					0.85	1.35	0.92	1.35	0.49	0.94	0.70	0.94
MPM-PV 19401					0.55	1.11	0.57	1.11	0.37	0.90	0.36	0.90
MPM-PV 19402					0.58	0.91	0.59	0.91	0.25	0.82	0.29	0.82
MPM-PV 19403	0.59	0.64	0.76	0.90	0.62	0.78	0.67	0.78				
MPM-PV 19409					0.73	0.96	0.75	0.96	0.42	0.87	0.43	0.87
MPM-PV 19405					0.73	0.90	0.74	0.90				
MPM-PV 19406	0.84	0.80	0.86	0.85	0.53	1.00	0.56	1.01				
Sipalocyon gracilis												
MPM-PV 19413	3.57	1.65	0.97	1.64	3.89	2.57	1.13	2.42	4.78	3.02	1.76	2.49
MPM-PV 19415									5.54	3.98	-	-
Perathereutes pungens												
MPM-PV 19410									3.59	2.66	1.11	1.44

Measurements in mm. – Broken tooth did not allow taking measurement. ***Ltrgd:*** *trigonid length;* ***Wtrgd,*** *trigonid width;* ***Ltad,*** *talonid length;* ***Wtad,*** *talonid width.*

Ameghino (1889) made a more thorough description of the specimen and mentioned that the mandible was in two pieces, the anterior part preserving from the symphyseal region to the second premolar and a posterior fragment with p3-m4 [p4-m4]. According to Mercerat (1891) the anterior fragment corresponds to *Hathliacynus tricuspidatus* and the posterior part to a different genus. Cabrera (1927) described the specimen MLP 11-64 and commented that the material was preserved like when Ameghino described it (Ameghino, 1887, 1889) and argued that the dentary formula included the canine, three premolars and four molars. Since Cabrera's work (Cabrera, 1927: fig. 6) some pieces broke a little more (*e.g.*, the p1 is completely missing) and some were reconstructed (*i.e.*, the p3 has the tip of the main cusp glue together but was not present *in situ* in Cabrera's figure). Cabrera (1927) considered *Acyon* as junior synonym of *Cladosictis*. Later Marshall (1981) considered *A. tricuspidatus* as junior synonym of *Anatherium defossus*. Finally, Forasiepi *et al.* (2006) recognized the genus *Acyon* and the species *A. tricuspidatus* when describing *A. myctoderos*, from the Miocene of Bolivia (see also Engelman *et al.*, 2015).

Genus ***Sipalocyon*** Ameghino, 1887

Type species. *Sipalocyon gracilis* Ameghino, 1887. Santa Cruz Formation, Barrancas del RSC, Province of Santa Cruz, Argentina.

Sipalocyon gracilis Ameghino, 1887

Figure 4.1–5; Tables 1–3

Neotype (designated in this paper). MACN-A 647, right dentary fragment with alveoli of i1-3, root of the canine, alveolus of p1, and a complete p2.

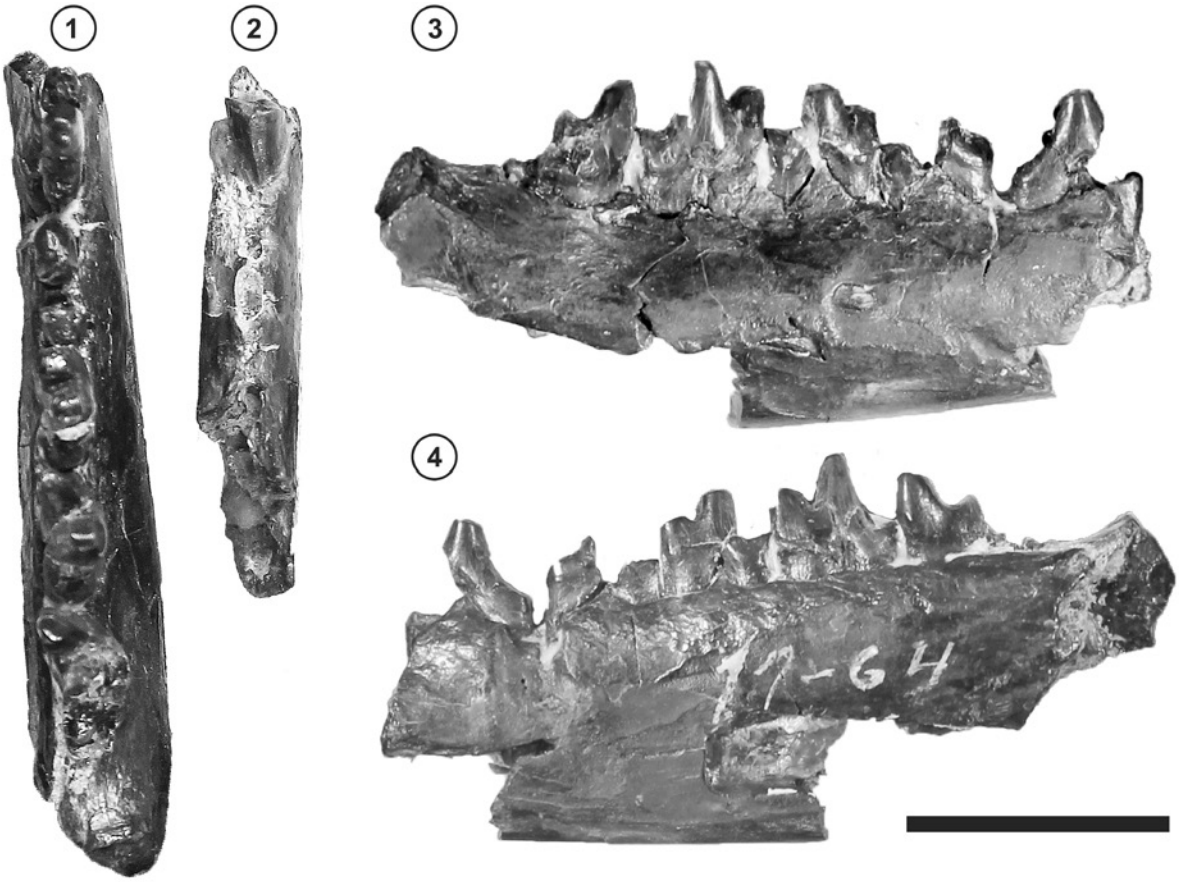

Figure 3. 1–4, ***Acyon tricuspidatus*****, MLP 11-64** (type specimen); **1, 3–4,** right dentary posterior fragment with p3-m4 in **1,** occlusal view; **3,** labial view; **4,** lingual view; **2,** right dentary anterior fragment with roots of c, alveoli for p1 and p2 in occlusal view. Scale bar= 20 mm.

Table 2 – Measurements of the canines and premolars of new RSC specimens described in this work

	W	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*
	C	*p1*	*p1*	*p2*	*p2*	*p3*	*p3*	*P1*	*P1*	*P2*	*P2*	*P3*	*P3*
Acdestis oweni													
MPM-PV 19376						*1.12*	-						
MPM-PV 19478												*2.46*	*1.78*
Microbiotherium tehuelchum													
MPM-PV 19372						*0.92*	*0.63*						
Palaeothentes lemoinei													
MPM-PV 19382										*1.73*	*0.72*	*3.26*	*1.77*
MPM-PV 19390												*2.48*	*1.80*
MPM-PV 19384						*1.70*	*1.15*						
MPM-PV 19385						*1.87*	*1.17*						
MPM-PV 19386						*1.19*	*0.91*						
Palaeothentes minutus													
MPM-PV 19391						*1.15*	*0.65*						
MPM-PV 19393						*0.86*	*0.58*						
MPM-PV 19494						*1.28*	*0.66*						
MPM-PV 19408						*1.01*	*0.55*						
MPM-PV 19398						*0.94*	*0.80*						
Sipalocyon gracilis													
MPM-PV 19413	*3.31*							*3.59*	*1.72*	*4.90*	*1.90*	*5.00*	*2.29*
Perathereutes pungens													
MPM-PV 19410		*3.27*	*1.66*	*4.43*	*1.67*								
Cladosictis patagonica													
MPM-PV 19419	*5.90*	-											
MPM-PV 19420	*6.40*	-											

Measurements in mm. – Broken tooth did not allow to take measurement. ***W:*** *width,* ***L:*** *Length.*

Stratigraphic and Geographic distribution. Río Frías Formation at Aysén (Chile) and in the SCF, Province of Santa Cruz (Argentina) in the following localities: Cerro Observatorio, Monte León, La Cueva, Río Chalía, Yegua Quemada, Killik Aike Norte, Estancia La Costa, Puesto Estancia La Costa (= Corriguen Kaik), Cañadón de las Vacas, 10 miles South from Coy Inlet.

Referred material. MPM-PV 19411, left isolated M4; MPM-PV 19412, skull fragment, right and left isolated M3, and right maxillary fragment with P2-3, probably from the same individual (Fig. 4.1–2); MPM-PV 19413, left dentary fragment with c-m3 (Fig. 4.3–5); MPM-PV 19414, an isolated left M3.

Geographic distribution. BB: MPM-PV 19411 comes from EAG and MPM-PV 19412 comes from ESL. SBB: MPM-PV 19413 was recovered from EET and MPM-PV 19414, from ECA.

Neotype designation. The specimen MACN-A 647 is designated here as the neotype following Art. 75 (75.3.1 to 75.3.7) of the International Code of Zoological Nomenclature, in order to clarify the taxonomic status of the species (Art. 75.3.1). This can be done after establishing that the original type (*e.g.*, holotype, syntypes) is lost (Art. 15.3.4).

When Ameghino (1887) first described this species, he mentioned the measurements of the base of the canine,

Table 3 – Measurements of the upper molars of new RSC specimens described in this work

	W M1	*L M1*	*W M2*	*L M2*	*W M3*	*L M3*	*W M4*	*L M4*
Acdestis oweni								
MPM-PV 19377					*1.64*	*1.30*		
MPM-PV 19378	*3.70*	*2.01*	*2.47*	*1.99*	*1.81*	*1.53*	*1.30*	*1.28*
Borhyaena tuberata								
MPM-PV 19424					*9.66*	*4.86*		
Palaeothentes minutus								
MPM-PV 19397					*1.79*	*1.14*		
MPM-PV 19400			*1.47*	*1.42*				
Sipalocyon gracilis								
MPM-PV 19414					*6.59*	*4.13*		
MPM-PV 19412					*4.71?*	-		
MPM-PV 19418			*4.71*	-				

Measurements in mm. – Broken tooth did not allow to take measurement. ***W:*** *width,* ***L:*** *Length.*

and he described the p1, and his p4-m2 (*i.e.*, m1-3). Later, Ameghino (1889) commented that the monospecific genus *Sipalocyon* was represented by a very incomplete left dentary, but with the base of the canine and almost all its molars severly broken. In Ameghino's unpublished catalogue, the specimen 647 (housed at the MACN-A collection) corresponds to a right dentary fragment with alveoli for i1-3, root of the canine, alveoli of the p1, and complete p2-m2, and it states *tipo*. In 1894 (fig. 55) and in 1898 (fig. 58.e) Ameghino figured this specimen to illustrate *S. gracilis*. MACN-A 647 was then considered as the type by succeeding authors (*e.g.*, Marshall, 1981; Forasiepi, 2009), even though it does not coincide with Ameghino's original description in 1887 or the one from 1889, and was exhumed from SCF levels of Cerro Observatorio (= Monte Observación). When Marshall (1981) study the Hathliacyninae, he assigned several specimens to *S. gracilis*, but only two specimens come from the RSC, MLP 11-7 (type of *Hathliacynus lynchi* Mercerat, 1891) and MLP 11-25. Even though is tempting to consider one of these two specimens as the original type from Ameghino (1887, 1889), there are no correspondence with the preserved loci of these mandibles and the type. After reviewing these specimens and looking for the missing type in both MLP and MACN-A collections, we concluded that it is lost (Art. 75.3.4). We conclude that MACN-A 647 corresponds to the original descriptions of Ameghino (1887, 1889; Art. 75.3.2, 75.3.3, and 75.3.5) and was collected in the same geological unit (SCF; Art. 75.3.6). Moreover, it was considered as the type by the specialists since Ameghino (1894; see also Marshall, 1981; Forasiepi, 2009), thus preserving the name and concept stability.

Comments on the referred material. The specimen MPM-PV 19411 is an isolated M4, with size and transversal development similar to the ones expected for *S. gracilis* (*e.g.*, see MACN-A 691-703). That is why, even though it is an isolated specimen, we assign it to the species.

MPM-PV 19414, an isolated M3, has a broken protocone and the paracone and metacone are shorter than the ones from other specimens assigned to this species, though the stylar shelf and size is similar to the one from it. However, as for the MPM-PV 19411, an assignment to *S. gracilis* is made.

Genus ***Perathereutes*** Ameghino, 1891

Type species. *Perathereutes pungens* Ameghino, 1891. Santa Cruz Formation, Cerro Observatorio, Province of Santa Cruz, Argentina.

Perathereutes pungens Ameghino, 1891
Figure 4.6–14

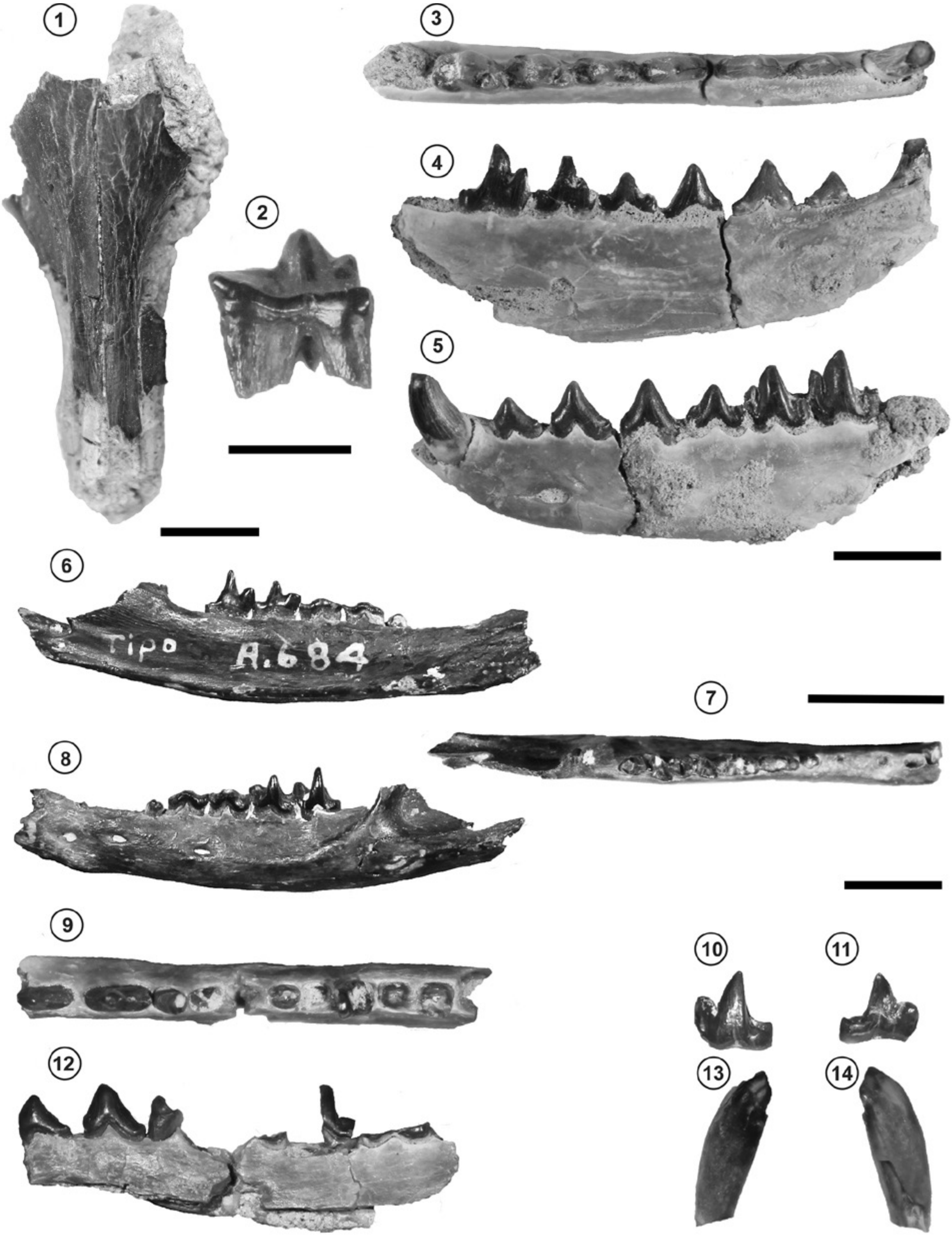

Figure 4. 1–5, ***Sipalocyon gracilis*, MPM-PV 19412**; **1,** cranial fragment in dorsal view; **2,** left isolated M3 in posterolingual view, **MPM-PV 19413**; **3,** occlusal view; **4,** lingual view; **5,** labial view; **6–14,** ***Perathereutes pungens*, MACN-A 684** (type specimen); **6,** lingual view; **7,** occlusal view; **8,** labial view; **MPM-PV 19410**; right mandible with p1-2, and roots of p3-m3 in **9,** occlusal view; **12,** lingual view; m3 in **10,** labial view; **11,** lingual view; and upper canine in **13,** labial view; **14,** lingual view. Scale bars= 10 mm.

Holotype. MACN-A 684, left dentary fragment with alveolus of the canine, roots of p1-3, and complete m1-4 (Fig. 4.6–8).

Stratigraphic and Geographic distribution. Santa Cruz Formation at the Province of Santa Cruz in Cerro Observatorio, La Cueva, and Puesto Estancia la Costa.

Referred material. MPM-PV 19410, left dentary fragment with p1 and p2, anterior root of p3, alveoli for m1, roots of m2, and talonid of m3, and an isolated m3, from the same individual but the contact of the roots is almost lost so it cannot be glue together (Fig. 4.9–14).

Geographic distribution. SBB: MPM-PV 19410 comes from ECA.

Measurements. Tables 1 and 2.

Comments on the referred material. *Perathereutes pungens* has been considered very similar to with *Sipalocyon gracilis* (see Marshall, 1981), but is considered as a valid genus and species (*e.g.*, Prevosti *et al.*, 2012; Ercoli *et al.*, 2014; Prevosti and Forasiepi, 2018). Both species are very similar but they have some distinguishable differences in size, *P. pungens* being smaller than *S. gracilis* and its talonid is less developed than in *S. gracilis* in all lower molars. The specimen MPM-PV 19410 is of smilar size to the holotype. The molar talonids are less developed than the ones from *S. gracilis* (*i.e.*, the hypoconid is less salient). A broken canine is preserved and probably was part of the same individual. This tooth is very gracile.

This is the first time that *Perathereutes pungens* is mentioned for the RSC. This discovery not only improves the knowledge of this species, but also extends its distribution to the West.

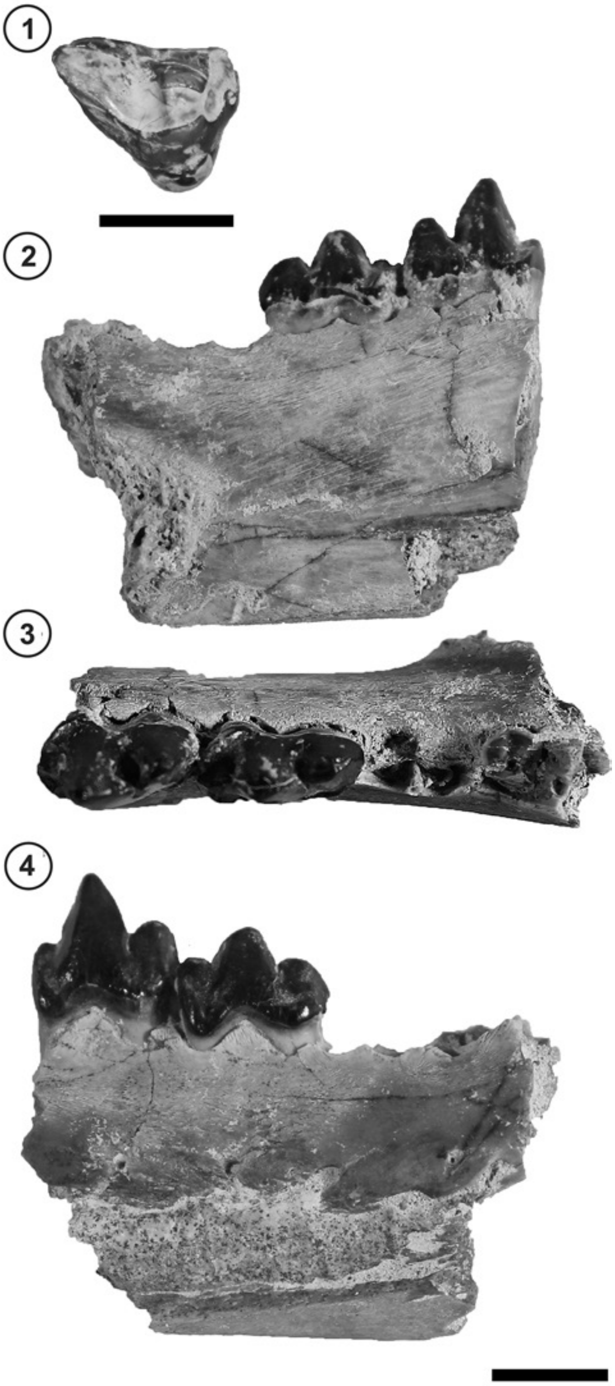

Figure 5. 1–4, ***Borhyaena tuberata*****, MPM-PV 19424; 1,** occlusal view, **MPM-PV 19421; 2,** lingual view; **3,** occlusal view; **4,** labial view. Scale bars= 10 mm.

Superfamily BORHYAENOIDEA Ameghino, 1894
Family BORHYAENIDAE Ameghino, 1894

Genus ***Borhyaena*** Ameghino, 1887

Type species. *Borhyeaena tuberata* Ameghino, 1887. Santa Cruz Formation, Barrancas del RSC, Province of Santa Cruz, Argentina.

Borhyaena tuberata Ameghino, 1887
Figure 5.1–4; Table 1

Holotype. MLP 11-108, an isolated left P3.

Stratigraphic and geographic distribution. Aysén (Río Frías Formation; Chile); In the SCF at the Province of Santa Cruz, the following localities: RSC, Río Coyle, Puesto Estancia La Costa (= Corriguen Aike), Campo Barranca, Anfiteatro, Karaiken, Yegua Quemada, Cerro Observatorio, La Cueva, 6, 10, and 12 miles South of Río Coyle, Estancia Angelina, Monte León.

Referred material. MPM-PV 19421, right dentary fragment with roots of p3-m1 and complete m1-2 (Fig. 5.2–4); MPM-PV 19424, an isolated right M2 (Fig. 5.1).

Geographic distribution. BB: MPM-PV 19421 comes from EAG; SBB: MPM-PV 19424 comes from ECA.

Comments on the referred material. Both specimens have similar size and talonid development as in other specimens of *B. tuberata* (see *e.g.*, MACN-A 6203-6265). MPM-PV 19424, though being an isolated M2, has a vestigial protocone and despite heavy cuspal wear, a paracone is seen to have been large, as occurs on the M2 of *B. tuberata* (MACN-A 9341).

Genus ***Acrocyon*** Ameghino, 1887

Type species. *Acrocyon sectorius* Ameghino, 1887. Santa Cruz Formation, Barrancas del RSC, Province of Santa Cruz, Argentina.

Acrocyon sectorius Ameghino, 1887
Figure 6.1–3

Holotype. MLP 11-70, a right dentary fragment with roots of dp3? and complete m1 (Fig. 6.1–3).

Stratigraphic and geographic distribution. Santa Cruz Formation, Province of Santa Cruz at the following localities: RSC, Río Chalía, and 5 miles south of Coy Inlet.

Comments on the holotype. In his original description Ameghino (1887) described this species as having the last premolars and the first true molars with three cusps on the sectorial line and then provided measurements of the m1 [p4]. Later, Ameghino (1889) commented that the genus *Acrocyon* was erected based on a mandibular fragment with a large complete tooth, probably the m1 [p4] or m2 [m1]. Mercerat (1891) considered that the preserved tooth corresponded to the m2. Cabrera (1927) recognized the type of the species (MLP 11-70) and agreed with Mercerat (1891) concerning the assignment of the single tooth from the mandibular fragment to be the m2. He also described the roots of the anterior, broken tooth. Because of the features of the broken locus, he considered it as the m1, but Marshall (1978) argued that these roots are part, probably, of a deciduous p3.

Figure 6. 1–3, ***Acrocyon sectorius*****, MLP 11-70** (type specimen); **1,** lingual view; **2,** occlusal view; **3,** labial view. Scale bar= 10 mm.

Genus ***Lycopsis*** Cabrera, 1927

Type species. *Lycopsis torresi* Cabrera, 1927. Santa Cruz Formation, RSC, Province of Santa Cruz, Argentina.

Lycopsis torresi Cabrera, 1927
Figure 7.1–4

Holotype. MLP 11-113, two maxillary fragments with M1-4, and a left Px; two mandibles with an incomplete dentition (Fig. 7.1–4).

Stratigraphic and geographic distribution. Santa Cruz Formation, RSC, Estancia la Costa, Province of Santa Cruz, Argentina.

Comments on the holotype. *Lycopsis torresi* was first described by Cabrera (1927) with only the holotype. The specimen comes from the Río Santa Cruz and was recovered by C. Berry in July 1895.

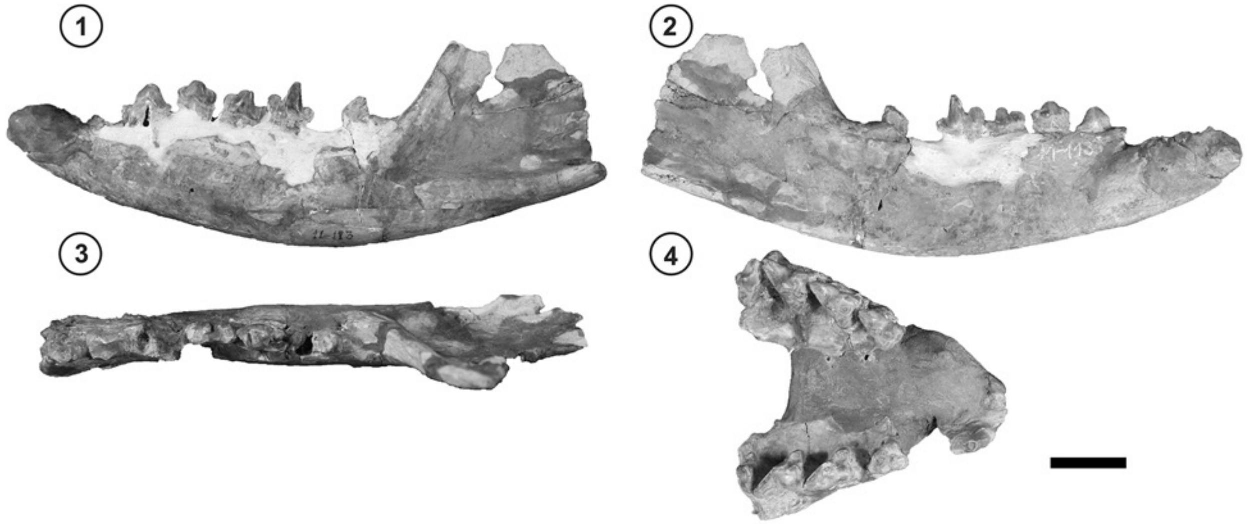

Figure 7. 1–4, ***Lycopsis torresi*****, MLP 11-113** (type specimen); left mandible in **1,** labial view; **2,** lingual view; right mandible in **3,** occlusal view; left and right maxillaries with M1-4 in **4,** occlusal view. Scale bar= 20 mm.

Supercohort Marsupialia Gill, 1872
Orden Paucituberculata Ameghino, 1894
Superfamily Caenolestoidea Trouessart, 1898
Family Caenolestidae Trouessart, 1898

Genus ***Stilotherium*** Ameghino, 1887

Type species. *Stilotherium dissimile* Ameghino, 1887. Santa Cruz Formation, Barrancas del RSC, Province of Santa Cruz, Argentina.

Stilotherium dissimile Ameghino, 1887

Neotype. MACN-A 8464, a right dentary fragment with i2-m4 (Reig, 1955).

Stratigraphic and geographic distribution. Santa Cruz Formation, Province of Santa Cruz in the following localities: RSC, Cerro Observatorio, La Cueva, San Jorge, Río Chalía.

Comments on the holotype. The type of this species is lost, as previously noted by other authors (Reig, 1955; Marshall, 1980). The MACN collection has a specimen labeled as type by Ameghino (MACN-A 5723). However, this specimen does not coincide with Ameghino's (1887) description and was not found during the fieldtrip to the Santa Cruz river by C. Ameghino in 1887 but was collected in the expedition of 1890–1891 at Monte Observación (= Cerro Observatorio). Reig (1955) named the specimen MACN-A 8464 as the neotype because of the completeness of the specimen, even though it does not come from the RSC but from La Cueva. The neotype was accepted by subsequent authors (*e.g.*, Marshall, 1980; Abello, 2007).

We add this taxon to the current study because the original type came from this locality (Ameghino, 1887).

Superfamily Palaeothentoidea Sinclair, 1906
Family Abderitidae (Ameghino, 1889)

Genus ***Abderites*** Ameghino, 1887

Type species. *Abderites meridionalis* Ameghino, 1887. Santa Cruz Formation, Barrancas del RSC, Province of Santa Cruz, Argentina.

Abderites meridionalis Ameghino, 1887
Figure 8.1–5; Table 1

Holotype. MACN-A 12, right mandibular fragment with complete m1-3 (Fig. 8.1–3).

Stratigraphic and Geographic distribution. From Pinturas Formation at Province of Santa Cruz: Cerro de los Monos, Cauce seco, Los Toldos, Estancia El Carmen, Loma de la Lluvia, Loma de las Ranas, Portezuelo Sumich Norte, Portezuelo Sumich Sur, Cañadón del Tordillo; from Province of Chubut, at Gran Barranca. From the SCF, Province of Santa Cruz: RSC, Cerro Observatorio, La Cueva, Río Chalía, Cerro Centinela, and Lago Cardiel.

Referred material. MPM-PV 19374, an isolated m1 (Fig. 8.4–5); MPM-PV 19375, right dentary fragment with m1-3 (Fig. 8.6–7).

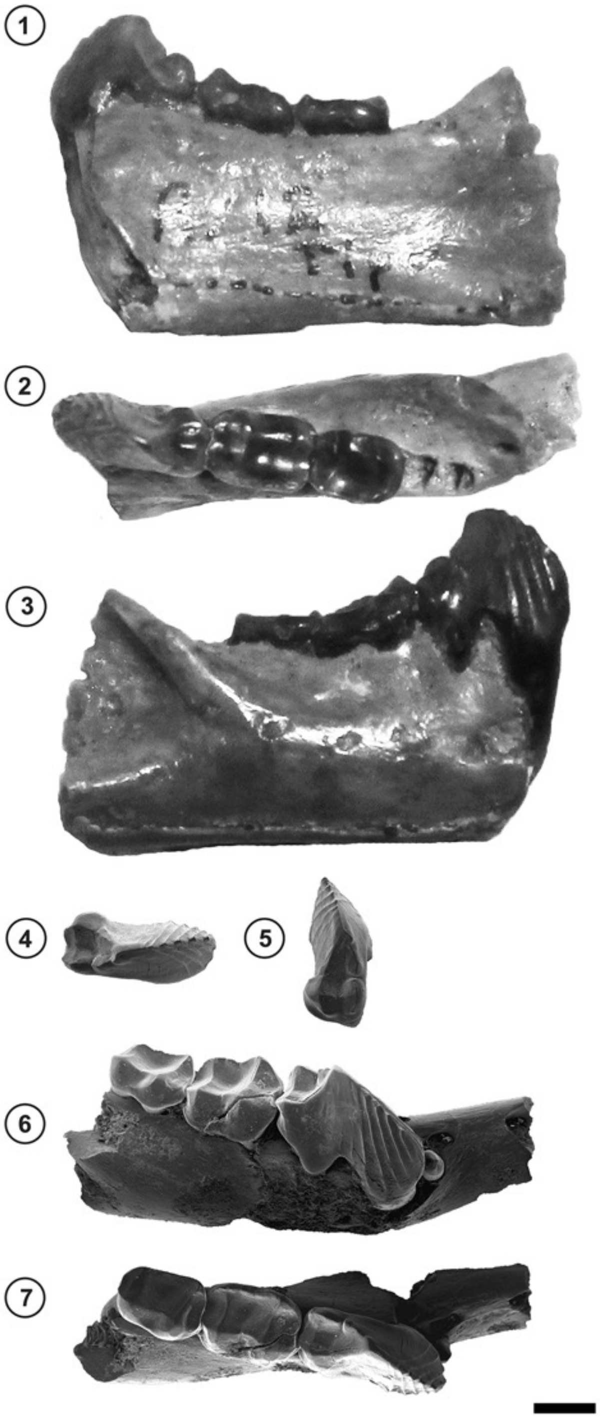

Figure 8. 1–7, ***Abderites meridionalis,*** **MACN-A 12** (type specimen); **1,** lingual view; **2,** occlusal view; **3,** labial views; **MPM-PV 19374**; **4,** occlusal view; **5,** posterior view; **MPM-PV 19375**; **6,** occluso-labial view; **7,** oclusal view. Scale bar= 2 mm.

Geographic distribution. BB: MPM-PV 19374 comes from EAG; SBB**:** MPM-PV 19375 comes from ECA.

Comments on the referred material. The specimens we assign to *A. meridionalis* have the diagnostic features observed for this species (Abello and Rubilar-Rogers, 2012). Moreover, the m1 from MPM-PV 19374 and MPM-PV 19375 have a well developed talonid, with the hypoconid more salient than the expected for other species of the genus, and the dentary MPM-PV 19375 has a diastema mesial to the p3, and the m2 is larger than m1.

Family Palaeothentidae Sinclair, 1906

Subfamily Acdestinae Sinclair, 1906

Genus ***Acdestis*** Ameghino, 1887

Type species. *Acdestis oweni* Ameghino, 1887. Santa Cruz Formation at RSC, Province of Santa Cruz, Argentina.

Acdestis oweni Ameghino, 1887

Figure 9.1–6; Tables 1–3

Holotype. MACN-A 1379, right dentary fragment with broken first incisor, complete p3-m1, and trigonid of m2 (Fig. 9. 1–2).

Stratigraphic and geographic distribution. Collón Cura Formation at Cañadón del Tordillo (Province of Neuquén, Argentina); SCF at the Province of Santa Cruz in the following localities: Monte León, Cerro Observatorio, Lago Cardiel, Gobernador Gregores, Río Chalía, and RSC.

Referred material. MPM-PV 19376, a left dentary fragment with p3-m4 (Fig. 9. 3–4; MPM-PV 19377, an isolated left M3; MPM-PV 19378, a right maxillary fragment with P3-M4 (Fig. 9.5–6).

Geographic distribution. BB: MPM-PV 19376 comes from EAG; SBB: MPM-PV 19377 and MPM-PV 19378 come from ECA.

Comments on the referred material. The specimen MPM-PV 19376 is very worn, but the tooth proportions and size are similar to that expected for *A. oweni*, where the m1 is large when compared to the very reduced m3 and m4.

Likewise, the specimens with upper teeth (MPM-PV 19377 and MPM-PV 19378) agree with other samples of *A. oweni* (*e.g.*, MACN-Pv SC 1461) in terms of size, and cusp and crest arrangement.

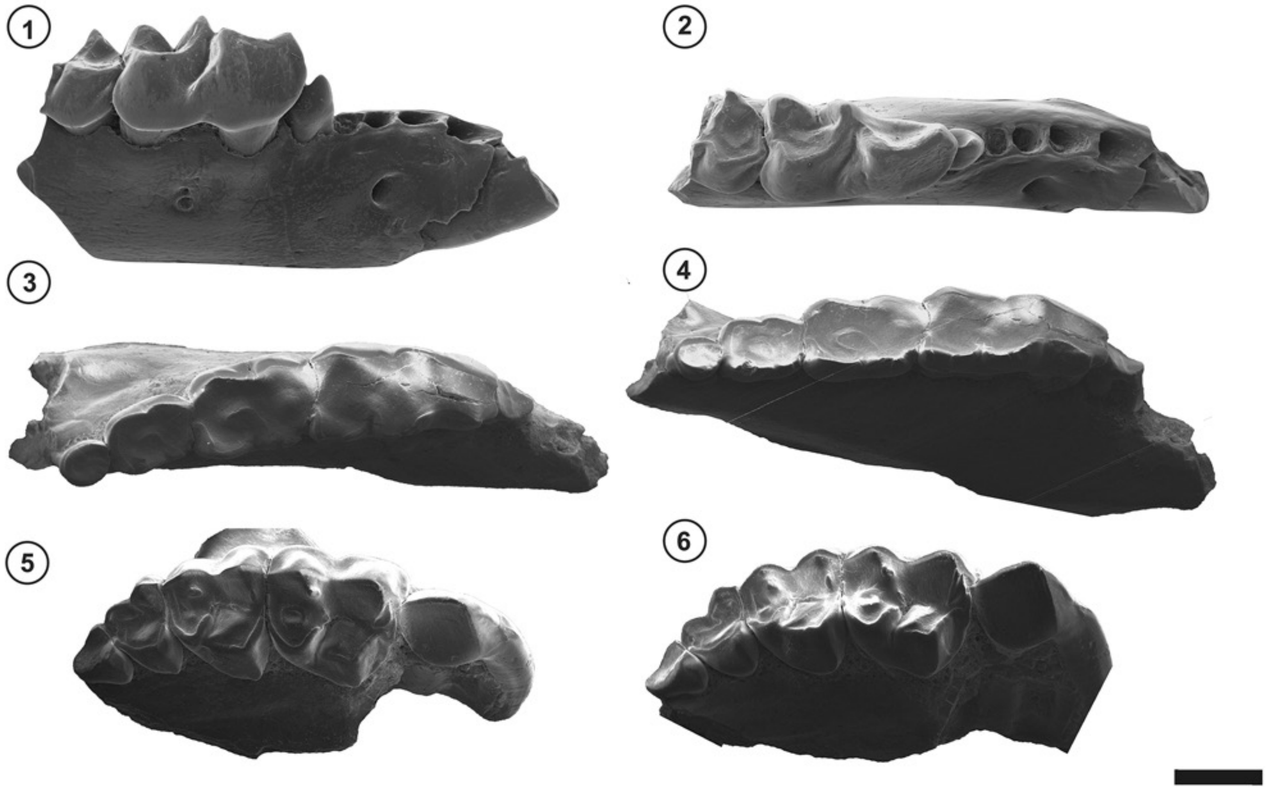

Figure 9. 1–6, ***Acdestis owenii,*** **MACN-A 1379** (type specimen); **1,** labial view; **2,** occlusal view; **MPM-PV 19376**; **3,** occlusal view; **4,** lingual view; **MPM-PV 19378**; **5,** occlusal view; **6,** occluso-lingual view. Scale bar= 2 mm.

Subfamily PALAEOTHENTINAE Sinclair, 1906

Genus ***Palaeothentes*** Ameghino, 1887

Type species. *Palaeothentes aratae* Ameghino, 1887. Santa Cruz Formation, Barrancas del RSC, Province of Santa Cruz, Argentina.

Palaeothentes aratae Ameghino, 1887

Figure 10.1–4

Holotype. MLP 11-93, right dentary fragment with roots of p2, p3, m1, m2, and m4 (Fig. 10.3–4).

Calcotype. MACN-A 1340, right dentary fragment with complete m1, trigonid of m2, roots of p2, p3, and m4 (Fig. 10.1–2).

Stratigraphic and geographic distribution. Santa Cruz Formation at the Province of Santa Cruz in the following localities: RSC, Río Chalía, Cerro Observatorio, Río Gallegos, and Monte León.

Comments on the holotype. Moreno (1882) collected the type specimen from the SCF at the RSC and named it *Palaeothentes aratae*. Later, Ameghino (1887) defined and described the species based on Moreno's findings. The original designation by Moreno is considered as *nomen nudum* (see Marshall, 1980) and Ameghino (1887) is considered as the author of the species by posterior designation (see Abello, 2007). In 1889, Ameghino redescribed the species as *Epanorthus aratae* (Ameghino, 1887) and commented that Moreno (1882) based its species on a single mandibular fragment with a complete m1 and a broken m2 [p4-m1], both very worn. Ameghino (1889) illustrated the specimen collected by Moreno in his Atlas (pl. 1; fig. 11; see also Marshall, 1980). However, on his catalogue, he numbered as type the specimen MACN-A 14, represented by a much more complete mandibular fragment with less worn p3-m4, used as the holotype by subsequent authors (*e.g.*, Sinclair, 1906; Marshall, 1980; Bown and Fleagle, 1993). However, this specimen is not the one collected by Moreno, since it was recovered by C. Ameghino (1890–1891; Marshall, 1980) and does not come from the RSC but from Cerro Observatorio (unpublished catalogue of F. Ameghino).

In Ameghino's collection at MACN there are a few casts representing a single dentary fragment numbered 1340 and named as *Epanorthus aratae*. Different authors considered specimen 1340 as pertaining to *P. aratae* (*e.g.,* Marshall, 1980). This specimen corresponds to the cast of the material figured by Ameghino (1889: pl. 1, fig. 11) and in Ameghino's catalogue figured as collected by Moreno, thus being the original calcotype. Marshall (1980) commented that the original type should have been in the MLP collections but is currently lost. However, in the MLP collection appears the MLP 11-93, considered as *P. aratae* by several authors (*e.g.*, Marshall, 1980; Abello, 2007). It corresponds to a right dentary fragment with broken teeth, and part of the mandible glue together. We suggest that MACN-A 1340 is the cast of MLP 11-93, with the teeth broken off after the original description, thus being the holotype of *P. aratae*.

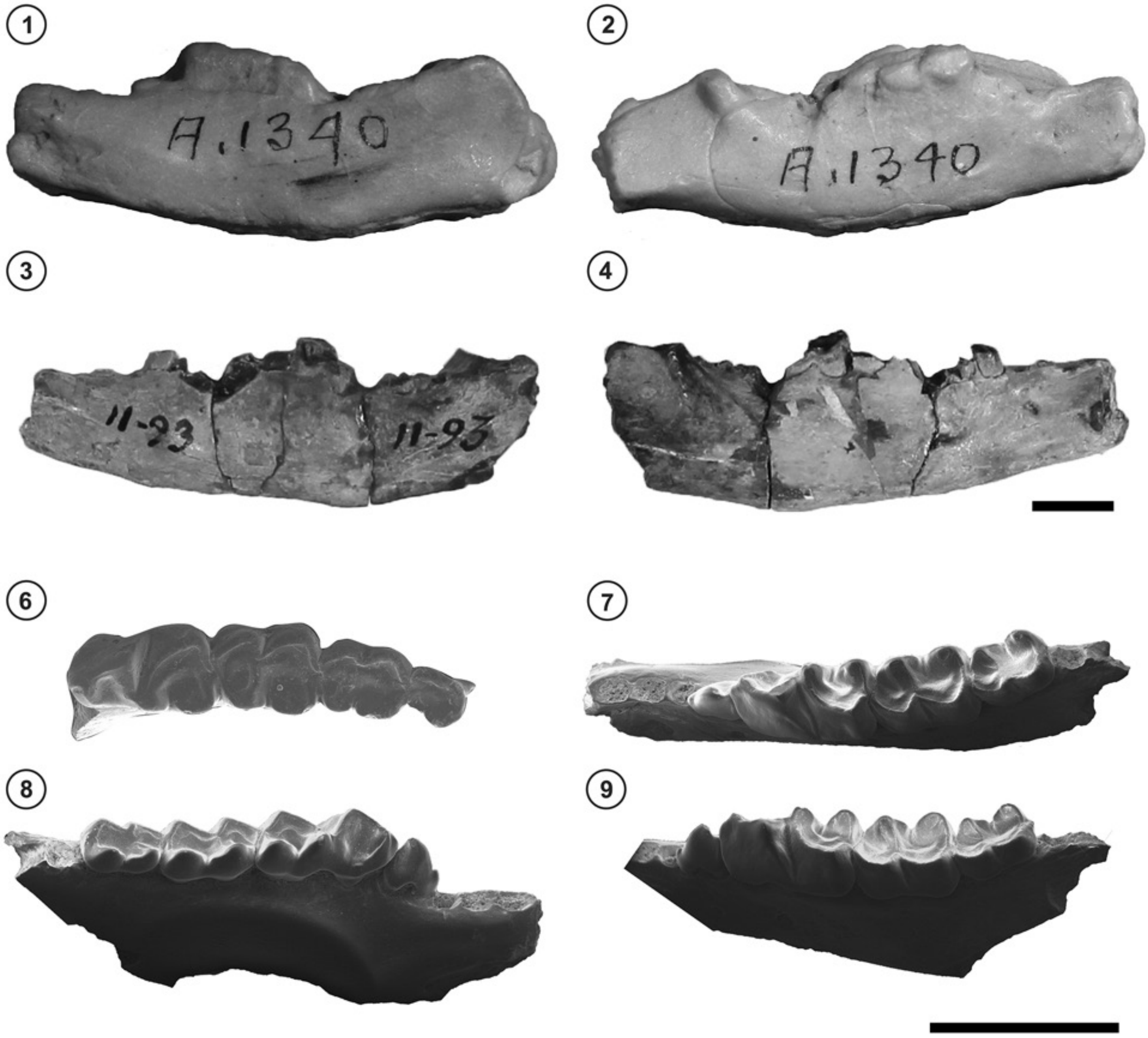

Figure 10. 1–5, ***Palaeothentes aratae***, **MACN-A 1340** (calcotype); **1,** lingual view; **2,** labial view; **MLP 11-93**; **3,** lingual view; **4,** labial view; **6–9,** ***Palaeothentes lemoinei***, **MACN-A 3** (type specimen); **6,** occlusal view; **MPM-PV 19386**; **7,** occlusal view; **8,** labial view; **9,** lingual view. Scale bars= 2 mm.

Palaeothentes lemoinei Ameghino, 1887

Figure 10.6–9; Tables 1, 2

Holotype. MACN-A 3, a right dentary fragment with complete m1-4 (Fig. 10.6).

Stratigraphic and geographic distribution. Santa Cruz Formation, Province of Santa Cruz in the following localities: Cerro Observatorio, Monte León, Puesto Estancia la Costa, La Cueva, Yegua Quemada, Río Chalía, and RSC.

Referred material. MPM-PV 19381, right dentary fragment with m1 and broken m2; MPM-PV 19382, right maxillary fragment with P2-3; MPM-PV 19390, left dentary fragment with p3 and broken m1-2; MPM-PV 19383, right dentary fragment with m1-3; MPM-PV 19384, right dentary fragment with p3-m3; MPM-PV 19385, left dentary fragment with p3-m2; MPM-PV 19386, left dentary fragment with p3-m3 (Fig. 10.7–9); MPM-PV 19387, left dentary fragment with m2-3; MPM-PV 19388, right dentary fragment with m2-3; MPM-PV 19389, right dentary fragment with m2-3.

Geographic distribution. BB: MPM-PV 19381 and MPM-PV 19383 come from ESL, MPM-PV 19389 comes from EAG; SBB: MPM-PV 19382 comes from EET, and MPM-PV 19384, MPM-PV 19385, MPM-PV 19386, MPM-PV 19387, MPM-PV 19388, and MPM-PV 19390 come from ECA.

Comments on the referred material. As seen in Bown and Fleagle (1993) the size and some proportions on the m3 are quite variable in *P. lemoinei*, and all specimens assigned here are encompassed within this variation. In particular, MPM-PV 19383, a dentary fragment with m1-3 has a relatively small m3 when compared to the holotype, but this variant can be observed in other specimens assigned to the species (*e.g.*, MACN-Pv SC 2953 from Río Chalía and MACN-Pv SC 3025, from Cerro Observatorio).

The MPM-PV 19381 and MPM-PV 19390 are very broken and worn, but their overall size and proportions coincides with that of *P. lemoinei*, that is why are here referred to it.

Palaeothentes intermedius Ameghino, 1887

Figure 11.1–2; Table 1

Lectotype. MACN-A 2, right dentary fragment with complete p3-m3 (Marshall, 1980) (Fig. 11.1–2).

Stratigraphic and geographic distribution. All specimens come from the Province of Santa Cruz (Argentina). Pinturas Formation at Río Pinturas: Estancia Los Toldos, Estancia Ana María, Estancia El Carmen, Gobernador Gregores, Cueva de las Manos, and Lago Cardiel. Santa Cruz Formation: Yegua Quemada, Río Chalía, La Cueva, Cerro Observatorio, Monte León, Estancia La Cañada, RSC.

Referred material. MPM-PV 19380, left dentary fragment with m2 and lingually broken m3; MPM-PV 19394, left dentary fragment with p3, and trigonid of m1.

Geographic distribution. BB: MPM-PV 19394 from EAG; SBB: MPM-PV 19380 from ECA.

Comments on the lectotype. Ameghino (1887) described the species on the basis of features of the dentary and lower teeth. Later, Ameghino (1889) commented that the species was based on several specimens and in his unpublished catalogue at MACN collection he considered MACN-A 2 to be the type. MACN-A 2 is figured in Ameghinos's Atlas (pl.1, fig. 15) thus being part of the syntype (from SCF beds in the RSC), even though no data appear in the MACN museum catalog (see Marshall, 1980). In his revision of the Caenolestidae Marshall designated MACN-A 2 as type, even recognizing that other specimens could be part of the syntype. Today, not all of the other specimens constituting the syntype can be located with certainty, but MACN-A 2 has been used by Marshall (1980) and later by other authors (*e.g.*, Marshall, 1980; Bown and Fleagle, 1993; Abello, 2007) as the type of the species.

The ICZN, in its Art. 74.1 states that "*A lectotype may be designated from syntypes to become the unique bearer of the name of a nominal species-group taxon and the standard for its application*". Since it was known to Marshall (1980) that originally the species was defined by a syntype (Ameghino, 1889), it can be assumed that the specimen labelled as type by Marshall (1980) was considered in this sense a lectotype, and applying Art. 74.5 he is considered as the first author of the lectotype.

Comments on the referred material. Specimen MPM-PV 19380 is very worn but it is assigned to *P. intermedius* on behalf of its size and tooth proportions. MPM-PV 19394 preserves only the p3 and the trigonid of the m1. However, we assigned to the species on behalf of its paracristid, almost parallel to the dentary axis, and bifurcates almost at the an-

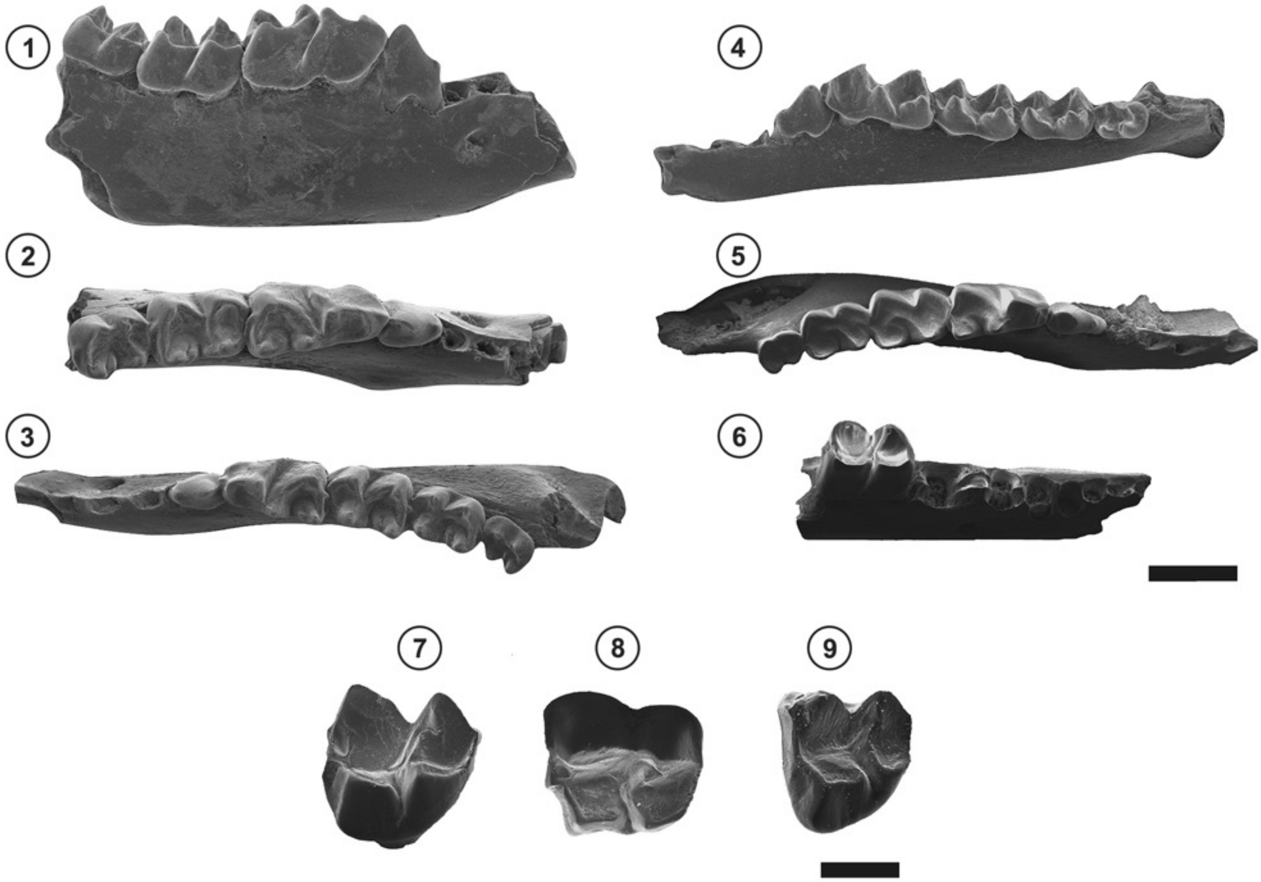

Figure 11. 1–3, ***Palaeothentes intermedius*****, MACN-A 2** (type specimen); **1,** labial view; **2,** occlusal view; **3–9,** ***P. minutus*****, MACN-A 15** (type specimen); **3,** occlusal view; **4,** lingual view; **MPM-PV 19393**; **5,** occlusal view; **MPM-PV 19379**; **6,** occluso-labial view; **MPM-PV 19397**; **7,** lingual view; **8,** occlusal view; **MPM-PV 19400**; **9,** occluso-lingual view. **1–6,** Scale bar 2= mm; **7–9,** Scale bar= 1 mm.

terior margin of the tooth. Finally, its size is intermediate to the smaller *P. minutus* and the larger *P. lemoinei*.

Palaeothentes minutus Ameghino, 1887

Figure 11.3–9; Tables 1–3

Holotype. MACN-A 15, right dentary fragment with p3-m4 (Fig. 11.3–4).

Stratigraphic and Geographic distribution. Province of Santa Cruz (Argentina). Pinturas Formation at Río Pinturas: Estancia Los Toldos, Cerro de los Monos, Estancia Ana María, Loma de la Lluvia, Portezuelo Sumich Sur, Estancia El Carmen, and Río Chalía. Santa Cruz Formation: RSC, Killik-Aike, La Cueva, Río Gallegos, Río Chalía, and Cerro Observatorio.

Referred material. MPM-PV 19379, right dentary fragment with m3 (Fig. 11.6); MPM-PV 19391; left dentary fragment with p3, m2-4; MPM-PV 19392, right dentary fragment with m1-3; MPM-PV 19393, left dentary fragment with p3-m4 (Fig. 11.5); MPM-PV 19395, an isolated right m2; MPM-PV 19396, right dentary fragment with m2-3; MPM-PV 19397, isolated left M2 (Fig. 11.7–8); MPM-PV 19398, right dentary fragment with p3-m2; MPM-PV 19399, left dentary fragment with m2-3; MPM-PV 19400, an isolated left M2 (Fig. 11.9); MPM-PV 19401, left dentary fragment with m2-3; MPM-PV 19402, left dentary fragment with m2-3; MPM-PV 19403, right dentary fragment with m1-2; MPM-PV 19404, right dentary fragment with m1; MPM-PV 19405, right dentary fragment with m2; MPM-PV 19406, left dentary fragment with p3-m2; MPM-PV 19407, right dentary fragment with m2-3; MPM-PV 19408, left dentary fragment with p3, m2-4; MPM-PV 19409, left dentary fragment with m2-3.

Geographic distribution. BB: MPM-PV 19379, MPM-PV 19391, MPM-PV 19392, and MPM-PV 19393 come from EAG, MPM-PV 19395 comes from ESL; SBB: MPM-PV 19396, MPM-PV 19397, and MPM-PV 19408 were exhumed from EET, MPM-PV 19398, MPM-PV 19399, MPM-PV 19400, MPM-PV 19401, MPM-PV 19402, MPM-PV 19403, MPM-PV 19404, MPM-PV 19405, MPM-PV 19406, MPM-PV 19407, and MPM-PV 19409 come from ECA.

Comments on the holotype. Originally, Ameghino (1887) described *Palaeothentes minutus* as the smallest species of the genus and gave measurements of the mandible. He mentioned the p3-m1 [p3-4] and m2-4 [m1-m3]. Ameghino (1889: pl.1, fig. 16) did not give many more details and illustrated a right dentary fragment with m1-3 and the alveoli of the m4. Later, he designated other specimens to the species (*e.g.*, Ameghino, 1894). The specimen MACN-A 15 (labeled as type in Ameghino's catalogue) corresponds to a right dentary fragment. It includes all the dental loci mentioned by Ameghino (1887, 1889), the mental foramen below the m1 [p4], and the measurements are similar to those stated by Ameghino (1887). There is no way of knowing if Ameghino based *P. minutus* in a single specimen or a syntype. We consider, as have other authors (*e.g.*, Marshall, 1980; Abello, 2007), that MACN-A 15 is with almost certainty the type of the species.

Comments on the referred material. *Palaeothentes minutus* is one of the smallest species of the genus, only *P. migueli* and *P. pascuali* are smaller. Among the larger specimens is the holotype, and MPM-PV 19404, MPM-PV 19406, and MPM-PV 19409. The smaller specimens include MPM-PV 19396, MPM-PV 19403, and MPM-PV 19407. The latter specimen is very worn, and the size is almost as small as *P. migueli* and *P. pascuali* but the m1 has a longer and straighter paracristid, while the cristid oblicua is more parallel to the dentary axis, as it occurs in *P. minutus* but not in *P. migueli* and *P. pascuali*.

Order Microbiotheria Ameghino, 1889
Family Microbiotheriidae Ameghino, 1887

Genus ***Microbiotherium*** Ameghino, 1887

Type species. *Microbiotherium patagonicum* Ameghino, 1887. Santa Cruz Formation, Barrancas del RSC, Province of Santa Cruz, Argentina.

Microbiotherium patagonicum Ameghino, 1887

Neotype (designated in this paper). MLP 11-30, right dentary fragment with m1-3 (originally, also m4 was present) and alveoli of p1-3.

Stratigraphic and Geographic distribution. Santa Cruz Formation at Province of Santa Cruz in the following localities: RSC, La Cueva, Río Chalía, Cerro Observatorio.

Neotype designation. Ameghino (1887) made a brief description of a mandible with, at least the m2-3 [m1-2]. Later, Ameghino (1889) commented that the species was based on a left dentary fragment with the three true molars (*i.e.*, today's m2-4) and, anteriorly, only the alveoli of the other loci. Years later, Ringuelet (1953) argued that the right dentary fragment with m1-4 MLP 11-30 was the type specimen of *M. patagonicum* and commented that Ameghino (1889) could made a mistake assigning the type to a left dentary, because he was no longer working in the Museo de La Plata, and he could not see the specimen again (Ringuelet, 1953: pl. 1, fig. 4). Even if that was the case, he omitted to say that the dentary (MLP 11-30) had four complete teeth, not three as he stated. These discrepancies suggest that MLP 11-30 is not the type of the species. The archives from the MLP collection for the specimen MLP 11-30 state that the specimen was collected by C. Ameghino from Santa Cruz, and the label of the specimen also has written that it comes from the "*Bcas. del río Santa Cruz*", but this labels are not the original one and the paper archive has no data but "*Santa Cruz*" and "*Santacrucense*". Since the labels are not the original ones and, by 1887 the term "*Santacrucense*" was not in use, it is possible that the information is inaccurate (see Fernicola, 2011).

Given the information stated above, and trying to clarify the taxonomic status of the species and understanding that the type is lost, we designate MLP 11-30 as the neotype of *Microbiotherium patagonicum,* following Art. 75 (75, 1 to 75.7) of the International Code of Zoological Nomenclature. The neotype comes from the same unit as the type, and has been considered the type by several authors since Riguelet (1953) because the features of the dentary match with those stated in the original description (Ameghino, 1887).

Microbiotherium tehuelchum Ameghino, 1887
Figure 12.1–6; Tables 1, 2

Neotype. MLP 11-36, right dentary fragment with p1-m4 (Marshall, 1982).

Stratigraphic and geographic distribution. In Chile, Río Frías Formation (Aysén). In the Province of Santa Cruz (Argentina) from Pinturas Formation (Río Pinturas): Cerro de Los Monos, and Portezuelo Sumich Sur, and SCF: RSC, Corriguen-Kaik, La Cueva, Yegua quemada, Cerro Observatorio, and Killik Aike Norte.

Referred material. MPM-PV 19372, right dentary fragment with broken p3 and complete m1 (Fig. 12.1, 4–5); MPM-PV 19373, left dentary fragment with m1 (Fig. 12.2–3, 6).

Geographic distribution. SBB: Both specimens come from ECA.

Comments on the holotype. When Ameghino (1887) recognized the species *Microbiotherium tehuelchum*, he described some premolar and molar loci (p3-m4). Ameghino (1889) commented that, even though he based the species on several mandibular fragments, the most complete of them corresponds to a left mandibular ramus with the p3-m4. However, he figured a dentary fragment with two molars (Ameghino, 1889: pl. 1, fig. 17). According to Marshall (1982) this fragment was "*an unidentified member of the caenolestid subfamily Palaeothentinae*". Nevertheless, the resemblance with the caenolestids could be an artifact induced by the extreme wear of the molars, thus giving the appearance of a bilobate occlusal surface (as occurs with MACN-A 2026, dentary fragment with two molars and the trigonid of a third). The interpretation of the figure in Ameghino's Atlas is difficult because of the style of the drawing, and no specimen totally coincides with it.

Ringuelet (1953) described *M. tehuelchum*, and considered the specimen MLP 11-36 as a possible cotype of the species, being similar and with the same measurements than the ones presented by Ameghino (1887, 1889). Pascual and Herrera (1975) considered it the type, and finally Marshall (1982) designated it as the Neotype, based on having a general description coincident with original from Ameghino (1887) and being located in the MLP collection, as was the original sintype, even though he considered it as having no locality data. The problem with this assignation, as recognized by Marshall (1982), is that MLP 11-36 has more preserved premolars than the best specimen described by Ameghino (1887, 1889), thus probably not being part of the original sintype.

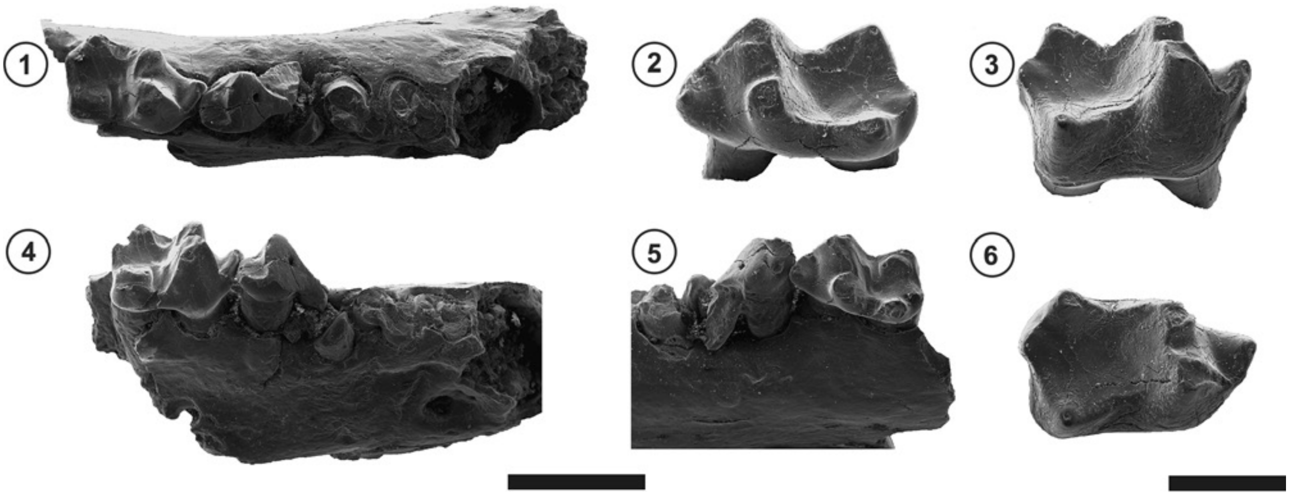

Figure 12. 1–6, ***Microbiotherium tehuelchum*****, MPM-PV 19372**; **1,** occlusal view; **4,** occluso-labial view; **5,** lingual view; **MPM-PV 19373**; **2,** lingual view; **3,** labial view; **6,** occlusal views; **1, 4–5,** scale bar= 2 mm; **2–3, 6,** scale bar= 1 mm.

The record of the catalog of MLP 11-36 indicates "*Barrancas del Río Santa Cruz*", but this could have been written after later interpretations because Marshall (1982) commented that the MLP 11-36 was "*without locality data*".

Finally, there is a specimen, MACN-A 1, labeled as type in Ameghino's catalogue, corresponding to a right dentary fragment with p1-m1. This specimen was considered as part of *Microbiotherium patagonicum* by Marshall (1982), even accepting that could be part of the original sintype of *M. tehuelchum*. This specimen is not the most complete mandible mentioned by Ameghino (1889) and has not the same proportions and we accept Marshall's assignment to *M. patagonicum*.

In this state of knowledge it can be argued that *M. tehuelchum*, following Marshall's neotype that this is the first record of *M. tehuelchum* in the RSC.

Comments on the referred material. The specimen MPM-PV 19372 is similar to *M. tehuelchum* in size and on its molar general features: para- and metaconid are set close together, and the talonid and trigonid are similar in width (contrary to a narrower trigonid in *Oligobiotherium* Ameghino, 1902) but not so much as in *M. patagonicum*.

Specimen MPM-PV 19373 is almost identical to the neotype, only has a slightly more mesially projected paraconid.

DISCUSSION

Ameghino's metatherian types from the RSC

When Ameghino (1887) first described the mammalian fauna from the RSC he based the metatherian species either on a single or several specimens. When he left the Museo de La Plata in 1888 he left some specimens there, but took several others from the RSC with him that were subsequently deposited in the Museo Nacional de Historia Natural, now MACN-A (Marshall, 1980; Fernicola, 2011).

Of the RSC species described by Ameghino (1887, 1889) still considered to be valid there are eleven identifiable type specimens still known. Some of them are in the MLP collections: MLP 11-103 (holotype of *Cladosictis patagonica*), MLP 11-64 (holotype of *Acyon ticuspidatus*), MLP 11-108 (holotype of *Borhyaena tuberata*), MLP 11-70 (holotype of *Acrocyon sectorius*), and MLP 11-93 (holotype of *Palaeothentes aratae*). Other type specimens are retained in the MACN-A collections: MACN-A 684 (holotype of *Perathereutes pungens*), MACN-A 12 (holotype of *Abderites meridionalis*), MACN-A 1379 (holotype of *Acdestis oweni*), MACN-A 3 (holotype of *Palaeothentes lemoinei*), MACN-A 2 (lectotype of *Palaeothentes intermedius*), and MACN-A 15 (holotype of *Palaeothentes minutus*). Since the MACN-A specimens correspond to original type of the species from the RSC, it appears that at least these six type specimens were appropriated by Ameghino from the MLP collection.

From his position in the Museo Nacional de Historia Natural (now MACN), Ameghino started his catalogue and numbered the specimens from his personal collection and, in some cases, designated new types. Moreover, in later papers he figured or described sometimes the species based on other specimens. Because of this, some authors confused such specimens as types (such is the case with *Sipalocyon gracilis*, figured in Ameghino, 1894, and marked as type in his catalogue). In other cases, some reviewers wrongly interpreted which specimen was the original type, as with *Microbiotherium patagonicum* mentioned by Ringuelet (1953). Finally, because several types are not to be found in either the MLP or in MACN collections, a few specimens were selected as neotypes (such as in *Stilotherium dissimile* Reig, 1955). All this changes, confusions, and considerations highlight the need for caution when citing a list of metatherians from the RSC in a biogeographical or a biostratigraphical context; sometimes, even though the species was originally described from RSC, a neotype was erected from another locality or without specific locality data.

The metatherian record from the RSC

In today's view and taking into account the valid species, the taxonomic list of the Metatheria from the RSC is the following (Cabrera, 1927; Marshall, 1978, 1980, 1982; Abello, 2007; Abello *et al.*, 2012; Prevosti *et al.*, 2012; Prevosti and Forasiepi, 2018):

Sparassodonta: *Borhyaena tuberata*, *Acrocyon sectorius*, *Lycopsis torresi*, *Cladosictis patagonica*, *Acyon tricuspidatus, Sipalocyon gracilis, and Perathereutes pungens.*

Paucituberculata: *Palaeothentes aratae*, *P. lemoinei*, *P. intermedius*, *P. minutus*, *Acdestis oweni*, *Abderites meridionalis*, *and Stilotherium dissimile.*

Microbiotheria: *Microbiotherium patagonicum*, *and M. tehuelchum.*

Three localities are recognized for the RSC outcrops of the SCF (Fernicola *et al.*, 2014). From east to west, BB, SBB, and YH. In this study, we recognized 10 species of metatherians from BB and SBB. Nine of them were already described by Ameghino (1887) and one species (*Perathereutes pungens*) was previously known only from Cerro Observatorio, La Cueva and Puesto Estancia la Costa (Prevosti *et al.*, 2012).

No Metatheria is here reported from YH. From BB come the following species: *Borhyaena tuberata*, *Sipalocyon gracilis*, *Acdestis oweni*, *Palaeothentes minutus*, *P. lemoinei*, and *Abderites meridionalis.* From SBB: *B. tuberata*, *S. gracilis*, *P. pungens*, *C. patagonica, A. oweni*, *P. minutus*, *P. lemoinei*, *P. intermedius*, *A. meridionalis*, and *M. tehuelchum.* As can be observed, the species richness varies among the localities, since ten species have been found in SBB, but only six come from BB.

Following Cuitiño *et al.* (2016), SBB have the youngest vertebrate fossil levels from the RSC, but nevertheless, SBB and BB are younger than several localities from the Atlantic coast (*i.e.*, Estancia La Costa, Cañadón Silva, Puesto Estancia La Costa, Monte Tigre, Cabo Buen Tiempo, and Killik Aike Norte).

It is not known whether the RSC species described by Ameghino (1887) come from BB, SBB, or even YH, and whether the species from Cerro Observatorio and Monte León were recorded from the upper or lower parts of those localities. However, the coastal localities mentioned above could better represent a similar time of deposition, older than the ones from SBB and BB (see Cuitiño *et al.*, 2016). Taking into account the species that are restricted in age from the Atlantic coast, and the RSC (BB + SBB), the following are shared: *Borhyaena tuberata*, *Cladosictis patagonica*, *Sipalocyon gracilis*, *Perathereutes pungens*, *Palaeothentes lemoinei*, *P. minutus*, and *Microbiotherium tehuelchum*. *Lycopsis torresi* and *Palaeothentes aratae* are found in both regions, but it is unknown the specific RSC localities from which they were exhumed. Finally, six species with no exact locality are found in the RSC but not in the coastal localities mentioned above (*Acyon tricuspidatus, Palaeothentes intermedius, Acdestis oweni,* and *Microbiotherium patagonicum*), while four species of the coastal older localities are not found in the RSC (*Arctodictis munizi*, *Phonocdromus gracilis*, *Microbiotherium gallegosense*, and *Microbiotherium acicula*). These differences could argue in favor of some differences caused by age or area bias. However, since numerous species recovered from some sites have no stratigraphic data (*e.g.*, old RSC collections, Cerro Observatorio, Monte León; Cuitiño *et al.*, 2016), we lack enough evidence to arrive to a solid conclusion.

CONCLUSIONS

The study of the new records of metatherians from the RSC at BB and SBB led to a thorough searching of Ameghino's (1887) original types and descriptions made by him. We have now identified the lost type of *Paleothentes aratae* (MACN-A 1340), and we designate two neotypes, the MACN-A 647 for *Sipalocyon gracilis* and the MACN-A 11-30 for *Microbiotherium tehuelchum*. The three specimens were erroneously considered as the original types by several authors (*e.g.*, Ringuelet, 1953; Marshall, 1980, 1981, 1982; Abello, 2007; Forasiepi, 2009), the specimen MACN-A 2 is recognized here as the lectotype of *Palaeothentes intermedius* (assigning its implicit recognition to Marshall, 1980).

The study of the new specimens collected in BB and SBB, plus the original ones recognized by Ameghino (1887) give a total of 16 metatherian species from the SCF levels of the RSC: seven Sparassodonta, seven Paucituberculata, and two Microbiotheria. Ten species from the new collections were recognized. Only one species (*Perathereutes pungens*) was not previously recorded in the RSC. In SBB all ten species were recognized, four more than in BB. Several species from the RSC are found also in coastal older localities. However, since much information is lacking on the exact place in the geological section for where the metatherian species occur at several SCF localities (*e.g.*, specimens from RSC and Cerro Observatorio), no precise conclusions can be made as to the age/distribution of the types.

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REFERENCES

Abello, M.A. 2007. [*Sistemática y bioestratigrafía de los Paucituberculata (Mammalia, Marsupialia) del Cenozoico de América del Sur*. Ph.D. Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 456 p. Unpublished.].

Abello, M.A. 2013. Analysis of dental homologies and phylogeny of Paucituberculata (Mammalia: Marsupialia). *Biological Journal of the Linnean Society* 109: 441–465.

Abello, M.A., Ortiz-Jaureguizar, E., and Candela, A.M. 2012. Paleoecology of the Paucituberculata and Microbiotheria (Mammalia, Marsupialia) from the late early Miocene of Patagonia. In: S.F. Vizcaíno, R.F. Kay, and M.S. Bargo (Eds.), *Paleobiology in Patagonia. Reconstructing a high-latitude paleocommunity in the early miocene climatic optimum*. Cambridge University Press, Cambridge, p. 156–172.

Abello, M.A., and Rubilar-Rogers, D. 2012. Revisión del género *Abderites* Ameghino, 1887 (Marsupialia, Paucituberculata). *Ameghiniana* 49: 164–184.

Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de la Patagonia y depositados en el Museo de La Plata. *Boletín del Museo de La Plata* 1: 1–26.

Ameghino, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas de la Academia Nacional de Ciencias de Córdoba* 6: 33–1027.

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

Ameghino, F. 1894. Enumération synoptique des espéces de mamifères fossiles des formations éocènes de Patagonie. *Boletín de la Academia Nacional de Ciencias de Córdoba* 13: 259–452.

Ameghino, F. 1902. Première contribution à la connaissance de la faune mammalogique des couches à *Colpodon*. *Boletín de la Academia Nacional de Ciencias de Córdoba* 17: 71–138.

Bown, T.M., and Fleagle, J.G. 1993. Systematics, biostratigraphy and dental evolution of the Palaeothentidae, Late Oligocene to Early–Middle Miocene (Deseadan–Santacrucian) Caenolestoid marsupials of South America. *Paleontological Society, Memoir* 29: 1–76.

Cabrera, A. 1927. Datos para el conocimiento de los Dasiuroideos fósiles argentinos. *Revista del Museo La Plata* 30: 271–315.

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

Engelman, R.K., Anaya, F., and Croft, D.A. 2015. New specimens of *Acyon myctoderos* (Metatheria, Sparassodonta) from Quebrada Honda, Bolivia. *Ameghiniana* 52: 204–225.

Ercoli, M.D., Prevosti, F.J., and Forasiepi, A.M. 2014. The structure of the mammalian predator guild in the Santa Cruz Formation (late early Miocene). *Journal of Mammalian Evolution* 21: 369–381.

Fernicola, J.C. 2011. Implicancias del conflicto Ameghino-Moreno sobre la colección de mamíferos fósiles realizada por Carlos Ameghino en su primera exploración al río Santa Cruz, Argentina. *Revista del Museo Argentino de Ciencias Naturales, Nueva Serie* 13: 41–57.

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.

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 Notohippidian. *Journal of South American Earth Science* 52: 94–107.

Fitz Roy, R. 1837. Extracts from the diary of an attempt to ascend the River Santa Cruz, in Patagonia, with the boats of H.M.S. Beagle. *Journal of the Royal Geographical Society of London* 7: 1–126.

Forasiepi, A.M. 2009. Osteology of *Arctodictis sinclairi* (Mammalia, Metatheria, Sparassodonta) and phylogeny of Cenozoic metatherian carnivores from South America. *Monografía del Museo Argentino de Ciencias Naturales* 6: 1–174.

Forasiepi, A.M., Sánchez-Villagra, M.R., Goin, F.J., Takai, M., Kay, R.F., and Shigehara, N. 2006. A new Hathliacynidae (Metatheria, Sparassodonta) from the middle Miocene of Quebrada Honda, Bolivia. *Journal of Vertebrate Paleontology* 26: 670–684.

Marshall, L.G. 1978. Evolution of the Borhyaenidae, extinct South American predaceous marsupials. *University of California Publications in Geological Sciences* 117: 1–89.

Marshall, L.G. 1980. Systematics of the South American marsupial family Caenolestidae. *Fieldiana: Geology, New Series* 5: 1–145.

Marshall, L.G. 1981. Review of the Hathlyacyninae, an extinct subfamily of South American "dog-like" marsupials. *Fieldiana: Geology, New Series* 7: 1–120.

Marshall, L.G. 1982. Systematics of the South American marsupial family Microbiotheriidae. *Fieldiana: Geology, New Series* 10: 1–75.

Mercerat, A. 1891. Caracteres diagnósticos de algunas especies de Creodonta conservadas en el Museo de La Plata. *Revista del Museo de La Plata* 2: 51–56.

Moreno, F.P. 1879. *Viaje a la Patagonia Austral, emprendido bajo los auspicios del Gobierno Nacional, 1876–1877*. La Nación Press, Buenos Aires, 246 p.

Moreno, F.P. 1882. Patagonia. Resto de un antiguo continente sumergido. *Anales de la Sociedad Científica Argentina* 14: 97–131.

Pascual, R., and Herrera, H.E. 1975. *Stilotherium* Ameghino, 1887, el más primitivo Caenolestidae conocido. Consideraciones sobre la transicion Didelphidae-Caenolestidae (Marsupialia). *1° Congreso Argentino de Paleontología y Bioestratigrafía* (Tucumán), *Actas* 2: 417–430.

Prevosti, F.J., and Forasiepi, A.M. 2018. *Evolution of South American mammalian predators during the Cenozoic: Paleobiogeographic and Paleoenvironmental Contingencies*. Springer Geology, Springer International Publishing, 196 p.

Prevosti, F.J., Forasiepi, A.M., Ercoli, M.D., and Turazzini, G.F. 2012. Paleoecology of the mammalian carnivores (Metatheria, Sparassodonta) of the Santa Cruz Formation (late early Miocene). 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. 173–193.

Reig, O.A. 1955. Un nuevo género y especie de cenolestinos del Plioceno de la Provincia de Buenos Aires. *Revista de la Asociación Geológica Argentina* 10: 60–71.

Ringuelet, A.B. 1953. Revisión de los Didélfidos fósiles argentinos. *Revista del Museo de La Plata, Nueva Serie* 2: 265–308.

Sinclair, W.J. 1906. Marsupials of the Santa Cruz beds. *Princeton University Expeditions to Patagonia* 4: 330–460.

Trouessart, E.L. 1898. Catalogus mammalium tam viventium quam fossilium. *Nova editio R. Friedländer & Sohn, Berlin* 2: 665–1264.

Vizcaíno, S.F., Kay, R.F., and Bargo, M.S. 2012. *Early Miocene Paleobiology in Patagonia: High-latitude Paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, 378 p.

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CINGULATES (MAMMALIA, XENARTHRA) OF THE SANTA CRUZ FORMATION (EARLY–MIDDLE MIOCENE) FROM THE RÍO SANTA CRUZ, ARGENTINE PATAGONIA

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Abstract. In 1887 Carlos Ameghino carried out the earliest extensive exploration of the fossiliferous localities along the Río Santa Cruz (Patagonia). His brother Florentino erected more than 100 vertebrate species based on the remains that Carlos recovered. The faunal assemblage eventually came to be recognized as the Santacrucian South American Land Mammal Age (Early–Middle Miocene). Over the past several years, an interdisciplinary group from the Museo de La Plata, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Argentina), and Duke University (USA) revisited the Río Santa Cruz localities, including Barrancas Blancas, Segundas Barrancas Blancas, and Yaten Huageno. This contribution presents a taxonomic list of cingulates based on the abundant material recovered during these expeditions. In Barrancas Blancas, we recorded the armadillos *Peltephilus pumilus* Ameghino, *Stenotatus patagonicus* Ameghino, *Proeutatus oenophorus* Ameghino, *Prozaedyus proximus* Ameghino, and *Stegotherium tessellatum* Ameghino, and the glyptodonts *Cochlops muricatus* Ameghino and *Eucinepeltus* sp. Ameghino. We did not record *St. tessellatum* in Segundas Barrancas Blancas and *St. tessellatum*, *P. pumilus* and *Eucinepeltus* sp. in Yaten Huageno. The comparative analysis between the faunal composition of the Santa Cruz Formation in the Río Santa Cruz and other areas to the west and the east reveals minor differences that, preliminarily, suggest environmental differences between the analyzed regions.

Key words. Santacrucian. Armadillos. Glyptodonts. Taxonomy. Carlos and Florentino Ameghino.

Resumen. CINGULADOS (MAMMALIA, XENARTHRA) DE LA FORMACIÓN SANTA CRUZ (MIOCENO TEMPRANO–MEDIO) DEL RÍO SANTA CRUZ, PATAGONIA ARGENTINA. En 1887 Carlos Ameghino llevó a cabo la expedición más importante que prospectó las localidades ubicadas a lo largo del Río Santa Cruz. Los fósiles recolectados le permitieron a su hermano Florentino erigir más de 100 especies de vertebrados. Este conjunto faunístico sería reconocido mundialmente como la Edad Mamífero Santacrucense (Mioceno Temprano–Medio). En los últimos años un grupo interdisciplinario del Museo de La Plata, el Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Argentina) y la Duke University (USA) realizó expediciones a las localidades del Río Santa Cruz incluyendo Barrancas Blancas, Segundas Barrancas Blancas y Yaten Huageno. En esta contribución presentamos una lista taxonómica de los cingulados sustentada en la gran cantidad de especímenes recolectados en las expediciones arriba mencionadas. En Barrancas Blancas registramos los armadillos *Peltephilus pumilus* Ameghino, *Stenotatus patagonicus* Ameghino, *Proeutatus oenophorus* Ameghino, *Prozaedyus proximus* Ameghino y *Stegotherium tessellatum* Ameghino y los glyptodontes *Cochlops muricatus* Ameghino y *Eucinepeltus* sp. Ameghino. En Segundas Barrancas Blancas no registramos *St. tessellatum* y en Yaten Huageno no se registraron *St. tessellatum*, *P. pumilus* y *Eucinepeltus* sp. El análisis comparativo entre esta composición faunística y las registradas para la Formación Santa Cruz en otras áreas ubicadas al oeste y al este del Río Santa Cruz, permite reconocer pequeñas diferencias faunísticas que, en forma preliminar, sugieren diferencias ambientales entre las regiones evaluadas.

Palabras clave. Santacrucense. Armadillos. Gliptodontes. Taxonomía. Carlos y Florentino Ameghino.

CINGULATES (armadillos, including the specialized glyptodonts) are grouped with anteaters and sloths as Xenarthra, a group of mammals with only a modest current representation in the Americas, but that was much more diverse during the Cenozoic. Their most conspicuous feature is the presence of armor composed of osteoderms covered with epidermal scales protecting the head, body, and tail. Extant cingulates include 10 genera of armadillos (Wetzel, 1985; Aguiar and

Fonseca, 2008; Castro *et al.*, 2015), whereas more than 65 extinct genera, including specialized armadillos such as peltephilids, pampatheres, and glyptodonts, have been described (Mones, 1986; McKenna and Bell, 1997). Except for the pampatheres, they were common during the Early–Middle Miocene, particularly as part of the Santacrucian South American Land Mammal Age (SALMA) faunas of the Santa Cruz Formation (SCF; Burdigalian–early Langhian).

The SCF is a continental sedimentary succession distributed over a large area of southern Patagonia, within the Austral-Magallanes Basin (Fosdick *et al.*, 2013; Cuitiño *et al.*, 2016; Ghiglione *et al.*, 2016; Parras and Cuitiño, 2018). The unit is composed of mudstones, tuffaceous sandstones, and tuffs deposited in fluvial environments under the influence of intense explosive pyroclastic input (Matheos and Raigemborn, 2012; Raigemborn *et al.*, 2015; Cuitiño *et al.*, 2016). In the Province of Santa Cruz, it is exposed in the northwest area (Cuitiño *et al.*, 2019a), in the central region along the Ríos Santa Cruz (Fernicola *et al.*, 2014; Cuitiño *et al.*, 2016) and Chalía (= Sehuén; Vizcaíno *et al.*, 2018), and in the southeastern area along the Atlantic coast (Vizcaíno *et al.*, 2012a,b). This unit contains the richest pre-Pleistocene assemblage of mammalian skulls and articulated skeletons on the continent (Kay *et al.*, 2008; Vizcaíno *et al.*, 2010, 2012a) and was seminal for the construction of the South American Land Mammal Age scheme in Patagonia (Pascual *et al.*, 1965; Vizcaíno *et al.*, 2012a). The Río Santa Cruz (RSC) extends from Lago Argentino and flows from west to east through a broad and deeply incised valley stretching 230 km from west to east. Along the RSC two Miocene sedimentary units of the Austral-Magallanes Basin can be recognized: (1) the shallow marine to deltaic Early Miocene Monte León Formation (Sacomani and Panza, 2011; Parras and Cuitiño, 2018), and (2) the terrestrial Early–Middle Miocene SCF (Tauber *et al.*, 2008; Sacomani and Panza, 2011; Cobos *et al.*, 2014; Fernicola *et al.*, 2014; Cuitiño *et al.*, 2016). The outcrops of the SCF along the southern margin of the RSC were described by Cuitiño *et al.* (2016, 2019b) and three fossil localities were recognized by Fernicola *et al.* (2014, 2019); from east to west they are: Barrancas Blancas (BB), Segundas Barrancas Blancas (SBB), and Yaten Huageno (YH; Fig. 1). Based on radiometric ages, the entire SCF represents a span of ~18.0 to ~15.6 Ma; the localities along the Atlantic coast range between ~18.0 to ~16.0 Ma (Fleagle *et al.*, 2012; Perkins *et al.*, 2012; Trayler *et al.*, 2019), and between ~18.20 to ~15.6 Ma in the Río Bote and Río Santa Cruz localities (Cuitiño *et al.*, 2016).

Moreno (1882) provided the first mention of cingulates from the SFC in a brief list of terrestrial fossil mammals from the RSC. Among them, he included the glyptodont *Hoplophorus australis* Moreno, 1882, which is currently recognized as a *nomen nudum* (Ameghino, 1889). Florentino Ameghino (1887) studied the remains (osteoderms) noted by Moreno together with an assemblage of exo- and en-

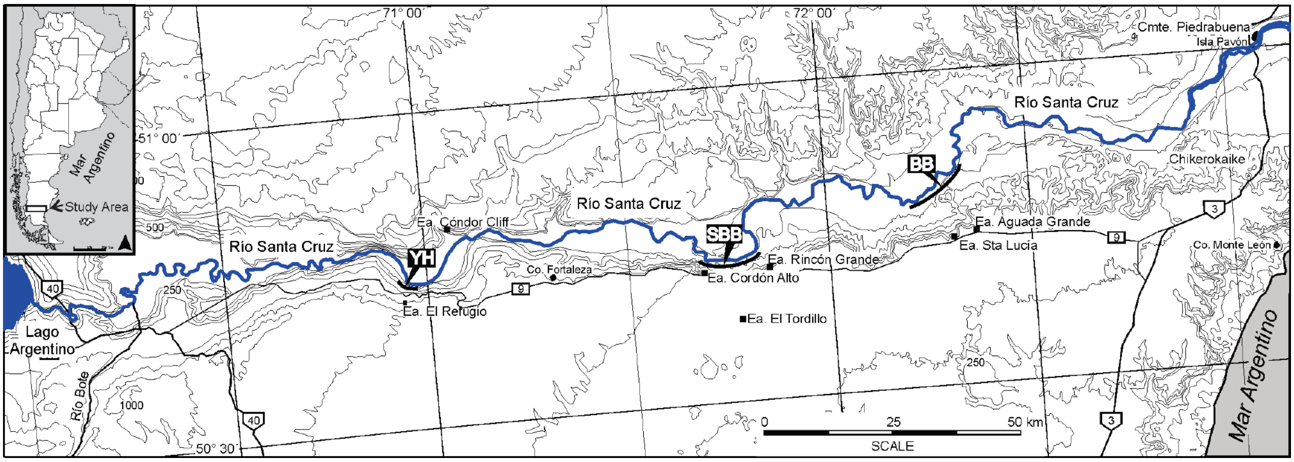

Figure 1. Map of the Río Santa Cruz with the prospected localities and estancias mentioned in the text. **BB,** Barrancas Blancas; **SBB,** Segundas Barrancas Blancas; **YH,** Yaten Huageno; **Ea.,** Estancia. Modified from Fernicola *et al.* (2014).

doskeletal remains collected from the same outcrops by Carlos Ameghino, and provided the first formal descriptions of Santacrucian cingulates. He named 11 species of armadillos, currently assigned to *Peltephilus* Ameghino, 1887, *Stegotherium* Ameghino, 1887, *Prozaedyus* Ameghino, 1891a, *Proeutatus* Ameghino, 1891a, and *Stenotatus* Ameghino, 1891a, and two species of the glyptodont *Propalaehoplophorus* Ameghino, 1887. Later, Ameghino (1889, 1891a, 1894, 1898, 1900–02) erected other genera of Santacrucian cingulates, three armadillos and four glyptodonts, based on specimens collected from other regions. Moreno and Mercerat (1891) and Mercerat (1890, 1891) named different taxa that Ameghino (1891b, 1894) did not accept. Lydekker (1894) synonymized most of the Santacrucian taxa proposed by Ameghino and Mercerat. In an extensive work, the first part of which was published in 1895 and the second posthumously, Ameghino (1895, 1920) rejected, sometimes without providing evidence, nearly all the synonymies proposed by Lydekker (1894). Scott (1903) validated most of the taxa originally erected by Florentino Ameghino. Subsequently published taxonomic revisions have dealt with only a very few taxa (see below).

Recent exhaustive fieldwork (Fernicola *et al.*, 2019) has provided new material of cingulates from Santacrucian localities along the RSC, allowing, after over a century, new views on the taxonomic richness of this group of mammals. These new remains were recovered by collaborative expeditions involving the Museo de La Plata (MLP) and Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN; Argentina), and Duke University (USA). This contribution reviews the taxonomic richness of Santacrucian cingulates collected by the MLP-MACN-Duke expeditions along the RSC and evaluates it with regard to that recorded from other Santacrucian localities.

SANTACRUCIAN CINGULATES

The taxonomy of the Santacrucian Cingulata proposed during the late 19th century was highly controversial until Scott’s (1903) revisions. In addition to the thorough descriptions and extensive taxonomic breadth, quality, and abundance of figured specimens, Scott’s contribution gained wide acceptance also because he studied all of the most important collections of Santacrucian cingulates then available. His work described, for the first time, the specimens collected by John B. Hatcher and Barnum Brown between the years 1886 and 1890, housed in Princeton University and the American Museum of Natural History, and compared them with the type and reference specimens in the MLP and Ameghino’s personal collection (the latter currently housed in the MACN) (Vizcaíno *et al.*, 2012a).

A century would pass before González Ruiz (2010) performed the next, albeit unpublished, comprehensive taxonomic revision of the Santacrucian cingulates. Other revisions were limited to peltephilids (Bordas, 1936, 1938) and *Stegotherium* (Fernicola and Vizcaíno, 2008; González Ruiz and Scillato-Yané, 2008, 2009).

The current taxonomic scheme, according to the published literature (Scott, 1903; Bordas, 1936, 1938; Fernicola and Vizcaíno, 2008; González Ruiz and Scillato-Yané, 2008, 2009; Vizcaíno *et al.*, 2012c) and followed here, of Santacrucian cingulates recognizes six genera of armadillos: *Peltephilus*, *Proeutatus*, *Prozaedyus*, *Stegotherium*, *Stenotatus*, and *Vetelia* Ameghino, 1891c. The species level systematics, which has not been considered since Scott (1903), is less certain, and we do not agree with several of this author’s taxonomic actions. These species are considered in the Systematic Paleontology section. Three other genera have been erected based on remains from Santacrucian deposits, *Anatiosodon* Ameghino, 1891a, *Eodasypus* Ameghino, 1894, and *Pareutatus* Scott, 1903. The status of these genera is controversial due largely and variably to the limited material on which the taxon was erected, poor original descriptions, unsupported by proper illustrations, and the type specimen is either of ambiguous identity or lost. *Anatiosodon* is represented by *Anantiosodon rarus* Ameghino, 1891a. Scott (1903) assigned this species, with reservation, to *Peltephilus*, but Bordas (1938) did not accept this taxonomic decision and retained the species in *Anatiosodon*. Vizcaíno and Fariña (1997) suggested that the type specimen, a mandibular fragment, may represent a juvenile individual, and Vizcaíno *et al.* (2012c) agreed (although without providing supporting evidence) with Scott’s (1903) assignment to *Peltephilus*. The possible juvenile condition of the specimen prevents considering its status beyond *Peltephilus* sp. The second genus, *Eodasypus*, was considered by Scott (1903) and Scillato-Yané (1980) as *incertae sedis*. Further, as the type specimens of the two species assigned to *Eodasypus*, *E. nanus* (Ameghino, 1891b) and *E. limus* (Ameghino, 1891b), cannot be located in the Ameghino collection and they are poorly described (Ameghino 1891b), this genus will not be considered in this study. Finally, the specimen used by Scott (1903) to support the taxonomic identity of *Pareutatus distans* (Ameghino, 1887) includes osteoderms and a skull and mandible (MACN-A 7972-7974). A perfunctory examination of the cranial features provided by Scott (1903) might allow its recognition as a different genus from the remaining Santacrucian taxa, but a more thorough analysis reveals many similarities with the skull of *Stenotatus* and the osteoderms purportedly associated with the skull are very similar to those of *Proeutatus*. Although Ameghino's catalog at the MACN notes that all the remains cataloged as MACN-A 7972-7974 belong to the same individual, their association according to Scott (1903, p. 68) is doubtful. Given the ambiguous status of *Pareutatus distans*, and doubts about the association of the fossil remains it is not considered in this study.

Scott (1903) recognized five glyptodont genera, *Propalaehoplophorus*, *Eucinepeltus* Ameghino, 1891a, *Cochlops* Ameghino, 1889, *Asterostemma* Ameghino, 1889 and *Metopotoxus* Ameghino, 1898. The last two genera were based on small fragments of osteoderms that do not allow identification beyond Propalaehoplophoridae (*sensu* Fernicola, 2008). Again, at the species level we disagree with some taxa proposed by Scott (1903), and treat them in the Systematic Paleontology.

MATERIALS AND METHODS

The approximately 370 specimens of cingulates studied here were collected between 2013–2014 by the MLP-MACN-Duke Univeristy expeditions (Fernicola *et al.*, 2019), and belong to the Museo Regional Provincial "Padre M. Jesús Molina" of Río Gallegos (Province of Santa Cruz, Argentina) (Appendix 1). These specimens were identified through comparison with the type specimens and with more complete remains of specimens housed in the institutions mentioned below. Quotation marks indicate that there is a lack of consensus on the monophyly of a suprageneric group.

Osteoderms were measured with manual calipers; the descriptive terminology follows Fernicola and Vizcaíno (2008), Krmpotic *et al.* (2009), Ciancio *et al.* (2013), and Francia and Ciancio (2013) (Fig. 2).

The geographic references for the localities reported for the SCF are grouped as follows: 1) eastern area, including the Atlantic coast, 2) central area, including RSC and Río Chalía (= Sehuen), 3) western area, including the Lago Argentino and Lago Posadas regions (see Fernicola *et al.*, 2019, fig. 1). The localities along the RSC are BB (~17.45 to ~16.49 Ma; S 50° 9’ 38.31” W 69° 40’ 23.40” to S 50° 12’ 31.70” W 69° 43’ 10.66”), SBB (~16.43 to ~15.63 Ma; S 50° 16’ 12.48” W 70° 22’ 23.21” to S 50° 16’ 51.90” W 70° 17’ 54.76”) and YH (~17.22 to ~16.67 Ma; S 50° 15’ 17.48” W 71° 4’ 9.56” to S 50° 15’ 17.48” W 71° 4’ 9.56”) (Fernicola *et al.*, 2014, 2019; Cuitiño *et al.*, 2016, 2019b).

The comparative study on the taxonomic richness of the RSC cingulates includes three levels of analysis. The first considers the taxonomic richness referred to the RSC by Ameghino (1887, 1889) with that obtained based on the new remains. The second considers the richness among the three localities BB, SBB, and YH, based only on the new remains, as previous works that provided faunal lists from the RSC did not discriminate among the three localities (*e.g.*, Ameghino, 1887). The third level of analysis includes com-

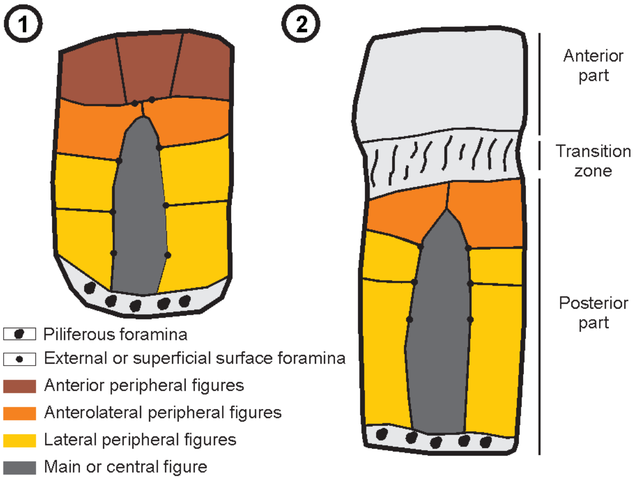

Figure 2. Terminology of the osteoderm features mentioned in the text**. 1,** fixed osteoderm; **2,** moveable osteoderm.

parison of the taxonomic richness of the RSC with that recognized for the remaining SCF locations in the eastern, central and western regions. This last level includes information related to the geographical distribution of the Santacrucian cingulates as compiled from Ameghino (1887, 1889, 1891a–d, 1894, 1900–02, 1906), Scott (1903), Tauber (1999), González Ruiz and Scillato-Yané (2008, 2009), and Vizcaíno *et al.* (2012c). Comparison of the taxonomic richness in each level of analysis is based on the presence or absence of each taxon listed in each locality.

Institutional abbreviations. **MPM-PV,** Museo Regional Provincial "Padre M. Jesús Molina", Río Gallegos, Argentina. **MACN-A,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Nacional Ameghino, Buenos Aires, Argentina. **MACN-Ma,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Nacional de Mastozoología, Buenos Aires, Argentina. **YPM-VPPU,** Yale Peabody Museum, Vertebrate Paleontology, New Haven, USA.

SYSTEMATIC PALEONTOLOGY

Order XENARTHRA Cope, 1889
Suborder CINGULATA Illiger, 1811
Family PELTEPHILIDAE Ameghino, 1894

Genus ***Peltephilus*** Ameghino, 1887

Type species. *Peltephilus strepens* Ameghino, 1887. Santa Cruz Formation, Barrancas del Río Santa Cruz, Province of Santa Cruz, Argentina.

Species recognized in the Santa Cruz Formation in this paper. *P. strepens*, *P. pumilus* Ameghino, 1887, *P. giganteus* Ameghino, 1894, *P. nanus* Ameghino, 1898, and *P. ferox* Ameghino 1891a.

Peltephilus pumilus Ameghino, 1887
Figure 3.1

Type specimen. MACN-A 866-870 (Mones, 1986).

Referred material. See Appendix 1.

Geographic distribution. BB and SBB.

Description. The osteoderms collected are approximately intermediate in size compared to those of the *Peltephilus* species considered. Those of the movable bands vary from 9.03–11.45 mm in width, and 11.46–15.12 mm in length (Fig. 3.1). The osteoderms of *P. nanus* are *ca.* 30 % smaller; those of *P. ferox* and *P. giganteus* are at least 20 % larger, whereas those of *P. strepens* are 40 to 50 % larger. The superficial surface is rough; there is a row of moderately developed tubercles in the anterior part, and posterior to it two pair of large and oval foramina (1.2 to 1.7 mm × 1.3 to 1.8 mm), separated from each other by a narrow septum.

Peltephilus sp.

Referred material. See Appendix 1.

Geographic distribution. BB and SBB.

Family "DASYPODIDAE" Gray, 1821
Subfamily "DASYPODINAE" Gray, 1821
Tribe STEGOTHERIINI Ameghino, 1889

Genus ***Stegotherium*** Ameghino, 1887

Type species. *Stegotherium tessellatum* Ameghino, 1887. Santa Cruz Formation, Barrancas del Río Santa Cruz, Province of Santa Cruz, Argentina.

Species recognized in the Santa Cruz Formation in this paper. *St. tessellatum*, *St. simplex* (Ameghino, 1887), *St. notohippidensis* González Ruiz and Scillato-Yané, 2009, *St. tauberi* González and Scillato-Yané, 2008.

Comments. The holotype of *Stegotherium simplex* is a mandibular portion with only two teeth and it is lost (Mones 1986, p. 231). Scott's photographic album of fossil specimens that this researcher examined in Argentina (Vizcaíno *et al.*, 2017, suppl. files, appendix 1, p. 1b, figs. 168 and 169) illustrates a mandibular fragment labeled as the type of *St. simplex* that broadly coincides with the original description of Ameghino (1887). Unfortunately, the image is insufficiently clear to allow determination of whether the condition of its anterior part is due to loss of its teeth or corresponds to the presence of predental ridges described by Vizcaíno (1994) in the skulls and mandibles of *St. tessellatum*. According to Fernicola and Vizcaíno (2008), if the latter were the case, then the presence of two teeth in *St. simplex vs.* six in *St. tessellatum* would support the recognition of two different genera.

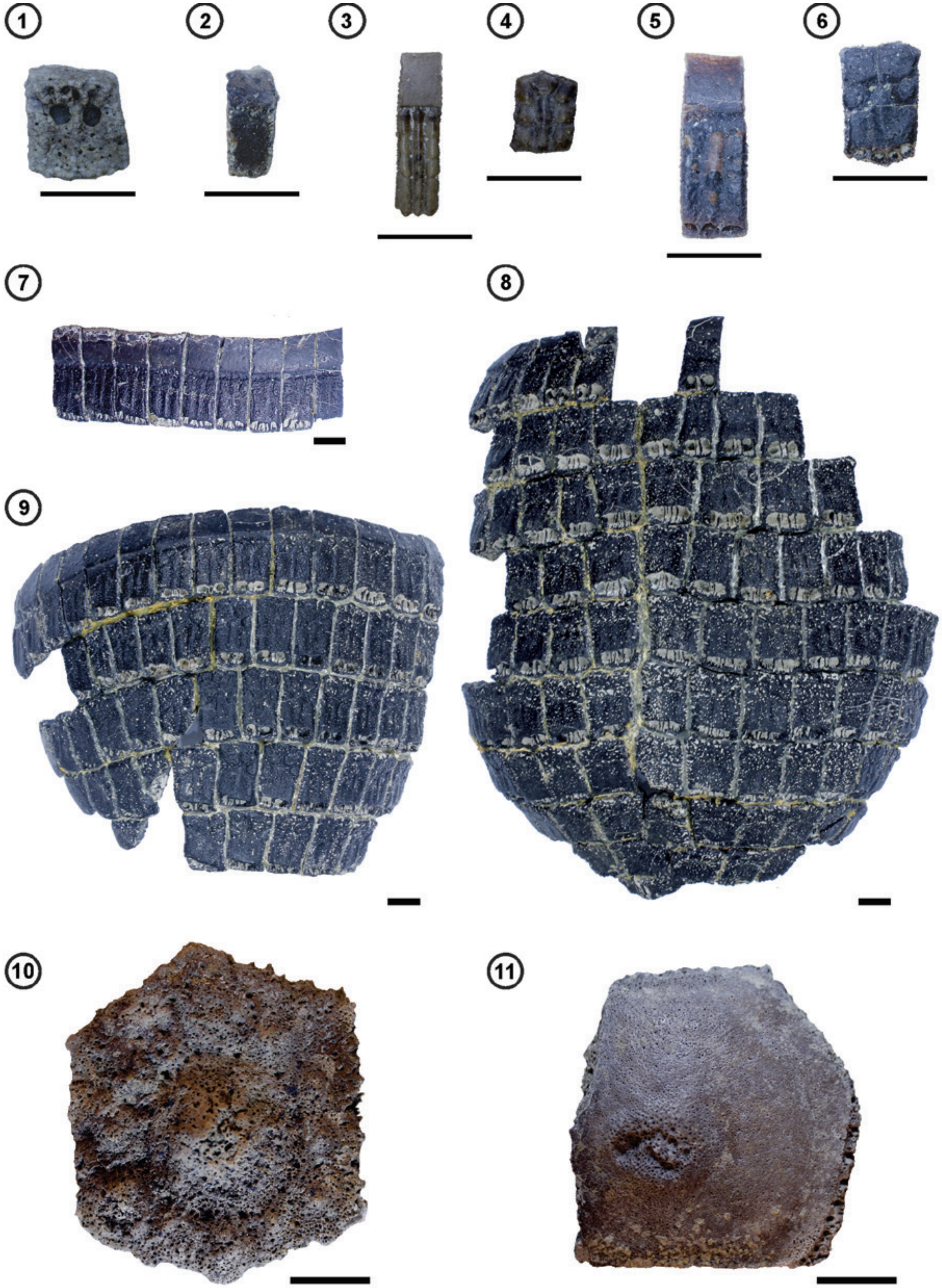

Figure 3. 1, ***Peltephilus pumilus***, **MPM-PV 20832**, osteoderm of the moveable band; **2,** ***Stegotherium tessellatum***, **MPM-PV 20832**, osteoderm of the moveable band**; 3–4,** ***Prozaedyus proximus***, **MPM-PV 20859**; **3,** osteoderm of the moveable band; **4,** fixed osteoderm; **5–6,** ***Stenotatus patagonicus***, **MPM-PV 20946**; **5,** osteoderm of the moveable band; **6,** fixed osteoderm; **7–9,** ***Proeutatus oenophorus***, **MPM-PV 21023**; **7,** portion of the moveable band; **8–9,** pelvic shield; **10,** ***Cochlops muricatus***, **MPM-PV 21071**, osteoderm; **11,** ***Eucinepeltus*** sp., **MPM-PV 21091** cephalic shield osteoderm. Scale bars= 10 mm.

Stegotherium tessellatum Ameghino, 1887
Figure 3.2

Lectotype. MACN-A 781 (Fernicola and Vizcaíno, 2008).
Paralectotype. MACN-A 782-785 (Fernicola and Vizcaíno, 2008).
Referred material. See Appendix 1.
Geographic distribution. BB.
Description. The three osteoderms assigned to this species are similar in size compared to those of the *Stegotherium* considered here. Those of the moveable bands vary from 4.48 to 5.53 mm in width, and from 9.13 to 12.28 mm in length (Fig. 3.2). These osteoderms have a rough superficial surface that lacks the pronounced longitudinal ridge (YPM-VPPU 15565) surrounded by a large number of foramina present in *St. tauberi*. In the anterior part, there is a large foramen, whereas in *St. notohippidensis* (MLP 84-III-5-10) there are at least two.

Subfamily "EUPHRACTINAE" Winge, 1923
Tribe "EUPHRACTINI" Winge, 1923

Genus ***Prozaedyus*** Ameghino, 1891a

Type species. *Prozaedyus proximus* (Ameghino, 1887). Santa Cruz Formation, Barrancas del Río Santa Cruz, Province of Santa Cruz, Patagonia, Argentina.

Species recognized in the Santa Cruz Formation in this paper. *Pr. proximus*.
Comments. Based on size, Scott (1903) recognized, with reservation, two species of *Prozaedyus*: *Pr. proximus* and *Pr. exilis* (Ameghino, 1887). However, several of the metric differences noted by Scott (1903) do not support specific distinction; for example, the "skull length on medial basal line" is 55 mm in *Pr. exilis* and 56 mm in *Pr. proximus*, whereas the "skull extreme length" is 66 mm in *Pr. exilis* and 70 mm in *Pr. proximus* (Scott, 1903, p. 77, 79 respectively). Concerning this last feature, in *Chaetophractus vellerosus* (Gray, 1865) the value measured in MACN-Ma 50.39 is 60 mm and in MACN-Ma 14.821 is 67.2 mm. With respect to the mandible, Scott (1903) mentioned that the toothless portion of the mandible in *Pr. exilis* is 6 mm, while it is about 5.3 mm in *Pr. proximus*. Once again, these differences are minimal and this feature may vary within an individual. For example, in *Chaetophractus vellerosus* (MACN-Ma 48.360) it length is 3.1 mm in the left dentary and 4.1 mm in the right one. Finally, with regard to the superficial morphology of the osteoderms, Scott (1903, p. 77) considered the differences between *Pr. proximus* and *Pr. exilus* as only minor and, probably, inconsistent. According to Scott (1903) a moveable band osteoderm of *Pr. exilis* is 4 mm in width by 15 mm in length, while in *Pr. proximus* it is 5.5 mm in width by 20 mm length (Scott, 1903, p. 77, 78 respectively). In *Zaedyus pichiy* (Desmarest, 1804) the osteoderms of the moveable bands vary from 4.47 to 5.87 mm in width and from 16.45 to 22.00 mm in length. With respect to the fixed osteoderms, the measurements provided by Scott (1903, p. 77, 78, respectively) for *Pr. exilis* are 6 mm in width by 8 mm in length, and 6 mm in width by 9 mm in length for *Pr. proximus*. In *Zaedyus pichiy* (MACN-Ma 25295) the fixed osteoderms vary from 4.99 to 7.73 mm in width and from 7.90 to 9.60 mm in length. Indeed, the metric and morphological differences provided by Scott (1903) for these two species are slight and within the range of variation of different species of other cingulates such as the extant *Chaetophractus vellerosus* and *Zaedyus pichiy*. Thus, only the type species, *Prozaedyus proximus*, is recognized here.

Prozaedyus proximus (Ameghino, 1887)
Figure 3.3–4

Type specimen. Lost (Mones, 1986).
Referred material. See Appendix 1.
Geographic distribution. BB, SBB, and YH.
Description. The collected osteoderms assigned to this species are smaller than in *Stenotatus* and their overall morphology coincides with the description of the osteoderms of *Pr. proximus* provided by Ameghino (1887, 1889) and Scott (1903). The osteoderms of the moveable bands vary from 4.02 to 4.89 mm in width and from 12.98 to 18.89 mm in length (Fig. 3.3). The superficial surface of the moveable band osteoderms bears three convex longitudinal figures of similar width, separated by two longitudinal sulci, which extend posteriorly to reach its posterior border. The sulci are parallel along their anterior two-thirds but tend to converge toward each other posteriorly. The lateral figures are divided by two to four transverse sulci each, resulting in three to

five pairs of small lateral figures. Generally, a very small foramen is present at each intersection between the main and the transverse sulci. Along the posterior border there are two foramina, larger than those on the superficial surface, that are usually aligned with the main sulci. Some osteoderms have three posterior foramina. The fixed osteoderms vary from 4.73 to 6.58 mm in width, and from 8.46 to 8.93 mm in length (Fig. 3.4). Each fixed osteoderm bears an elongated main figure surrounded by four to eight markedly convex peripheral figures. An external foramen is generally present at the intersection between the main figure and each radial sulcus. Along the posterior margin are two piliferous foramina, each aligned with the one of the sulci that define the main figure; a third foramen may be present.

Family "Dasypodidae" Gray, 1821
Subfamily "Euphractinae" Winge, 1923
Tribe "Eutatini" Bordas, 1933

Genus ***Stenotatus*** Ameghino, 1891a

Type species. *Stenotatus patagonicus* (Ameghino, 1887). Santa Cruz Formation, Barrancas del Río Santa Cruz, Province of Santa Cruz, Argentina.

Species recognized in the Santa Cruz Formation in this paper. *S. patagonicus* and *S. hesternus* (Ameghino, 1889).

Stenotatus patagonicus (Ameghino, 1887)
Figure 3.5–6

Type specimen. Lost (Mones, 1986).

Referred material. See Appendix 1.

Geographic distribution. BB, SBB, and YH.

Description. The collected osteoderms assigned to this species are larger than *Prozaedyus* and smaller than *Proeutatus*. The osteoderms of the moveable bands vary from 5.29 to 7.33 mm in width and from 17.63 to 21.05 mm in length (Fig. 3.5). The superficial surface of the moveable band osteoderms bears three convex longitudinal figures that are defined by two longitudinal sulci, which extend posteriorly to reach the posterior border. The main figure is somewhat wider than the two figures, one on either side, that flank it. The main figure is undivided, while the two lateral figures may be divided by one or two transverse sulci into two or three smaller figures, respectively. The posterior border of the moveable band osteoderms bears two types of piliferous foramina, differing in size and position and alternating with each other. The three or four large posterior foramina are located less peripherally than the small foramina, each of which lies midway between two large foramina. Small piliferous foramina are present at the intersection between the main and the radial sulci. By contrast, in *S. hesternus* these foramina are conspicuous. The fixed osteoderms vary from 7.20 to 8.69 mm in width and from 11.54 to 12.99 mm in length (Fig. 3.6). They bear an elongated main figure, which does not reach the posterior border and may be anteriorly wider or of constant width. The anterior and lateral regions are divided by three to five radial sulci that delimit four to six peripheral figures surrounding the main figures. The posterior two peripheral figures on each side contact each other at the midline of the osteoderm, forming a larger U-shaped figure. In some osteoderms this contact is narrow, whereas it is wide in others. The pattern of the foramina at the posterior border is similar to that of the moveable osteoderms, but there may be as many as six large and five small foramina. The latter are present at the intersection between the main and the radial sulci.

Genus ***Proeutatus*** Ameghino, 1891a

Type species. *Proeutatus oenophorus* (Ameghino, 1887). Santa Cruz Formation, Barrancas del Río Santa Cruz, Province of Santa Cruz, Patagonia, Argentina.

Species recognized in the Santa Cruz Formation in this paper. *Pro. oenophorus*, *Pro. deleo* (Ameghino, 1891b), and *Pro. carinatus* (Ameghino, 1891b).

Comments. Scott (1903) recognized five species, *Pro. oenophorus*, *Pro. lagena* (Ameghino, 1887), *Pro. carinatus*, *Pro. deleo*, and *Pro. robustus* Scott, 1903. This author considered the morphology of the osteoderms of *Pro. oenophorus* and *Pro. lagena* identical (Scott, 1903, p. 65), and that neither species exhibits marked differences compared with *Pro. robustus* (Scott, 1903, p. 43). Scott (1903) noted that the feature that best differentiates *Pro. lagena* from *Pro. oenophorus* is the presence, in the former, of an elongated and tubular rostrum that widens anteriorly but without achieving the spatulate condition present in the latter. However, the value of this difference for specific distinction is unreliable, as both conditions occur in adult specimens of the extant *Euphractus sexcintus* (Linnaeus, 1758) (MACN-Ma 50.121, MACN-Ma 34.592). Another difference noted by Scott (1903) refers to the presence of a longer mandibular symphysis in *Pro. lagena* (22 mm) with respect to *Pro. oenophorus* (15 mm). However, in *E. sexcinctus* the symphysis ranges between 17 (MACN-Ma 42.104) and 25 mm in length (MACN-Ma 31.88). Scott (1903) also reported that *Pro. robustus* is characterized by a larger size and notably heavier proportions compared to *Pro. oenophorus*. The tables of measurements of the femur provided by Scott (1903) for these two species reveals that the difference in size of these two species is approximately 10–15 %. This difference is within the range of variation of several other cingulates species (*e.g., E. sexcinctus* ~12 %, Fernicola pers. obs.). The status of *Pro. lagena* and *Pro. robustus* with respect to each other and whether either is distinguishable specifically from *Pro. oenophorus* is uncertain. In the context of the present report, a decision cannot be taken, because the type specimen of *Pro. lagena* is lost (Mones, 1986) and the authors were unable to access part of the holotype of *Pro. robustus* (YPM-VPPU 15214). Clearly, the metric and morphological differences noted by Scott (1903) in differentiating among the species are within the range of variation of at least one species of living armadillos, *Euphractus sexcinctus* (see above), and their taxonomic utility is doubtful. As well, the osteoderms of these three species, as described by Scott (1903), cannot be distinguished by the current authors. It is worth noting, in this regard, that the carapace of *Pro. robustus* on which Scott (1903, p. VIII; YPM-VPPU 15957) based his description was assigned to this species with a question mark by the author himself. In this context, we have only compared the superficial morphology of the osteoderms among *Pro. oenophorus*, *Pro. deleo* and *Pro. carinatus*, which morphology is in fact different (see below).

Proeutatus oenophorus (Ameghino, 1887)

Figure 3.7–9

Type specimen. Lost (Mones, 1986).

Referred material. See Appendix 1.

Geographic distribution. BB, SBB, and YH.

Description. The osteoderms assigned to *Proeutatus oenophorus* are similar in size to other species of this genus. Those of the moveable bands vary from 9.22 to10.44 mm in width and 27.80 to 32.5 mm in length (Fig. 3.7). The superficial surface of the moveable band osteoderms is rugose and bears a main lageniform figure, narrow on the middle part of the osteoderm and widening posteriorly. The main figure bears a prominent keel along its midline and lateral figure lies on either side of the narrowed part of the main figure. The external surface of the osteoderms is pierced posteriorly by three or four large foramina, separated from each other and from the posterior margin of the osteoderms by a thin bony septum. The fixed osteoderms vary from 10.84 to 15.26 mm in width and from 18.87 to 19.34 mm in length (Figs. 3.8–9). They are rectangular with a distinctly lageniform main figure. By contrast in the fixed osteoderm of *Pro. deleo* (MACN-A 4800-4802; see Vizcaíno *et al.*, 2017, suppl. files, appendix 1, p. 34, fig. 71c) this main figure is much less marked. The midline of the lageniform main figure of *Pro. oenophorus* shows a well-developed keel, but the keel in *Pro. carinatus* (MACN-A 561; see Vizcaíno *et al.*, 2017, suppl. files, appendix 1, p. 34, fig. 70) is even more prominent. Anteriorly, there are one or two well-developed figures, and a lateral figure is present on either side of the narrow part of the main figure. The posterior part of the osteoderm is similar to that described for the moveable osteoderms.

Family PROPALAEHOPLOPHORIDAE Ameghino, 1891c

Genus ***Cochlops*** Ameghino, 1889

Type species. *Cochlops muricatus* Ameghino, 1889. Santa Cruz Formation, Río Chico, Province of Santa Cruz, Argentina.

Species recognized in the Santa Cruz Formation in this paper. *Cochlops muricatus*.

Comments. Scott (1903) recognized two species, *Cochlops muricatus* and *Cochlops debilis* Ameghino, 1891a. *Cochlops muricatus* was based on osteoderms of the carapace with the central figure raised into a high cone, while the peripheral figures form a ring of lower conical tubercles around it (Ameghino, 1889). *Cochlops debilis* was based on a mandible (Ameghino, 1891a), but Scott (1903) assigned a skull with a cephalic shield to this species; in other words, based on nonhomologous elements. The specimens assigned by Ameghino (1891a) and Scott (1903) to *Cochlops debilis* lack carapace osteoderms, and it is not therefore possible to confirm this taxonomic assignment. In this context, we have only recognized *Cochlops muricatus*.

Cochlops muricatus Ameghino, 1889
Figure 3.10

Type specimen. Lost. According to Mones (1986) the type is MACN-A 4751, but this specimen is a mandible and Ameghino (1889) only described osteoderms. These osteoderms, despite extensive searches, have not been found in the Ameghino collection.
Referred material. See Appendix 1.
Geographic distribution. BB and YH.
Description. The osteoderms bear marked central and peripheral figures; in some cases, the central figure raised into a high cone reaching 20 mm in height (Fig. 3.10). This kind of osteoderm is located in the posterodorsal region of the carapace.

Genus ***Eucinepeltus*** Ameghino, 1891a

Type species. *Eucinepeltus petesatus* Ameghino, 1891a. Santa Cruz Formation, Cerro Observatorio, Province of Santa Cruz, Argentina.
Species recognized in the Santa Cruz Formation in this paper. *Eu. petesatus*, *Eu. crassus* Scott, 1903, and *Eu. complicatus* Brown, 1903.
Comments. Scott (1903) recognized three species, *Eu. petesatus*, *Eu. crassus*, and *Eu. complicatus*. The shape and number of osteoderms of the cephalic shield were used to diagnose these species. Unfortunately, only isolated cephalic shield osteoderms were collected by the MLP-MACN-Duke expeditions, so it is not possible to evaluate the number of osteoderms and shape of the cephalic shield.

Eucinepeltus sp.
Figure 3.11

Referred material. See Appendix 1.
Geographic distribution. BB and SBB.
Description. The osteoderms of the cephalic shield recovered by us show the typical fossa in middle of the superficial surface, which is a diagnostic feature of this genus (Ameghino, 1891a; Scott, 1903; Brown, 1903) (Fig. 3.11).

PROPALAEHOPLOPHORIDAE indet.

Referred material. See Appendix 1.
Geographic distribution. BB, SBB, and YH.

TAXONOMIC RICHNESS

According to the taxonomic assignments presented here of the new specimens from the SCR, five species of armadillos are recognized in BB, *Peltephilus pumilus*, *Stegotherium tessellatum*, *Stenotatus patagonicus*, *Proeutatus oenophorus*, and *Prozaedyus proximus*, and two glyptodonts, *Cochlops muricatus* and *Eucinepeltus* sp. In SBB we recognized four armadillos, *Peltephilus pumilus*, *Stenotatus patagonicus*, *Proeutatus oenophorus*, and *Prozaedyus proximus*, and one glyptodont *Eucinepeltus* sp., while in YH the armadillos *Stenotatus patagonicus*, *Proeutatus oenophorus*, and *Prozaedyus proximus*, and the glyptodont *Cochlops muricatus* (Tab. 1) are present.

The first level comparison, that between the taxa reported from the RSC by Ameghino (1887, 1889) with those based on the new specimens reported here, reveals the presence of the same five genera of armadillos initially reported by Ameghino (1887): *Stegotherium*, *Peltephilus*, *Proeutatus*, *Prozaedyus*, and *Stenotatus*. Remains assignable to the glyptodont *Propalaehoplophorus*, noted by Ameghino (1887), were not recovered during the course of the recent expeditions to the RSC; however, the first record from this area of *Eucinepeltus* and *Cochlops* are reported. At the specific level, the taxonomic richness of the armadillos is similar to that mentioned by Ameghino (1887, 1889), five species, with *Peltephilus strepens* being the only species not recorded. Regarding the glyptodonts, the species richness increased from one to at least three taxa (Tab. 2).

In the second level of comparison, the richness among BB, SBB, and YH based only on the new remains, seven cingulate species of (Tab. 1) are recognized from BB. The difference between BB and SBB is the absence in the latter of *Stegotherium tessellatum* and *Cochlops muricatus*. The differ-

TABLE 1 – **Distribution of cingulates in Barrancas Blancas, Segunda Barrancas Blancas, and Yaten Huageno recorded in this contribution**

Taxa	*Barrancas Blancas*	*Segundas Barrancas Blancas*	*Yaten Huageno*
Peltephilus pumilus	*X*	*X*	
Stegotherium tessellatum	*X*		
Stenotatus patagonicus	*X*	*X*	*X*
Proeutatus oenophorus	*X*	*X*	*X*
Prozaedyus proximus	*X*	*X*	*X*
Cochlops muricatus	*X*		*X*
Eucinepeltus *sp.*	*X*	*X*	
Total number of species	7	5	4

ence between BB and YH is the absence in YH of *Peltephilus pumilus*, *Stegotherium tessellatum*, and *Eucinepeltus* sp. Finally, SBB and YH shared the following taxa: *Stenotatus patagonicus*, *Proeutatus oenophorus*, and *Prozaedyus proximus*, while *Peltephilus pumilus* and *Eucinepeltus* sp. are in SBB, and *Cohlops muricatus* in YH (Tab. 1).

The third level of analysis, excluding the taxa that we considered doubtful (see above), reveals that the seven genera recorded along the RSC have been recorded in other areas (Tab. 2). The only difference is the absence of *Vetelia* and *Propalaehoplophorus* from the outcrops along the RSC. *Vetelia* was recorded by Ameghino (1891c) based on material collected from exposures northwest of the RSC, and assigned by (Ameghino, 1902) to the "Notohippidian" —the oldest Santacrucian faunal assemblage according to Marshall *et al.* (1983)—. Fernicola *et al.* (2009) reported this genus from the SCF in the Atlantic coast. At the specific level, only seven species were recorded of the 21 recognized from the SCF (Tabs. 1, 2). Among peltephilines, this report records *Peltephilus pumilus* and *Peltephilus strepens*, which were mentioned by Ameghino (1887) for the RSC. In addition to these two species, *P. ferox* and *P. nanus* have also been recorded from the Atlantic coast (see Vizcaíno *et al.*, 2012c). From the western area, Ameghino (1900–02) listed the peltephilines *P. giganteus* and *P. pumilus*. The first species and *P. ferox* have also been reported from the central area (see Vizcaíno *et al.*, 2012c). Regarding *Stegotherium*, the only recorded species in the RSC is *Stegotherium tessellatum*, which is also present in the western (Ameghino, 1887, 1900-02, 1906). González Ruiz and Scillato-Yané (2008, 2009) identified two new stegotherines: *Stegotherium tauberi* form the eastern and *Stegotherium notohippidensis* from the western areas. Among eutatines *Stenotatus patagonicus* is recorded all along the SCF from the eastern to the western areas (Ameghino, 1887, 1900–02, 1906), whereas *S. herternus* has only been reported from the Atlantic coast (Vizcaino *et al.*, 2012c). With regard to *Proeutatus*, *Pro. oenophorus* has been reported throughout the SCF, *Pro. deleo* from the western region and the Atlantic coast, and *Proeutatus carinatus* only from the latter region (Vizcaíno *et al.*, 2012c). The euphractine *Prozaedyus proximus* has been recorded from all outcrops of the SCF. With respect to glyptodonts, *Propalaeohoplophorus australis* and *Cochlops muricatus* have been noted from all three areas, while *Eucinepeltus* was reported in the RSC and the Atlantic coast (Vizcaíno *et al.*, 2012c).

DISCUSSION AND CONCLUSION

The new specimens collected with precise geographic provenance allowed evaluation of the taxonomic richness of the cingulates of the SCF outcropping along the southern banks of the RSC. In total, seven species, each belonging to different genera, were recognized here (Tab. 1).

All the genera of armadillos reported by Ameghino (1887) and six of the seven species of this group were recovered by the MLP-MACN-Duke expeditions. Among glyptodonts, the presence of *Eucinepeltus* and *Cochlops* is novel, but remains of *Propalaehoplophorus*, reported by Ameghino (1887), were not recovered. Indeed, at the species level, the difference between the composition and taxonomic richness between the remains noted by Ameghino (1887) and those reported here are very few, and is likely due to sampling. The presumed absence of *Propalaehoplophorus* remains may be an artifact due to the lack of diagnostic features in the material collected by us. The osteoderms that we assigned to *Eucinepetus* and *Cochlops* correspond to two small parts of the exoskeleton: the cephalic shield and a small portion located in the posterior region of the carapace, respectively. The osteoderms that were not assigned to

Table 2 – Distribution of cingulates of the Santa Cruz Formation in different areas of the Province of Santa Cruz (see Systematic Paleontology)

Taxa	*Eastern*	*Central*	*Western*
Peltephilus strepens	X^3	X^1	
Peltephilus pumilus	X^1	X^1	X^2
Peltephilus giganteus		X^3	X^2
Peltephilus nanus	X^3		
Peltephilus ferox	X^3	X^3	
Stegotherium tessellatum		X^1	X^2
Stegotherium tauberi	X^4		
Stegotherium notohippidensis			X^5
Stenotatus patagonicus	X^3	X^1	X^2
Stenotatus hesternus	X^3		
Proeutatus oenophorus	X^3	X^1	X^2
Proeutatus deleo	X^3		X^2
Proeutatus carinatus	X^3		
Prozaedyus proximus	X^3	X^1	X^2
Vetelia puncta	X^6		X^2
Propalaehoplophorus australis	X^3	X^1	X^2
Propalaehoplophorus minor	X^8		
Cochlops muricatus	X^3	X^9	X^2
Eucinepeltus petesatus	X^3	X^9	
Eucinepeltus crassus	X^7		
Eucinepeltus complicatus	X^8		
Total number of species	*18*	*12*	*11*

X^1: Ameghino (1887); X^2: Ameghino (1900-02); X^3: Vizcaíno et al. (2012); X^4: González Ruiz and Scillato-Yané (2009); X^5: González Ruiz and Scillato-Yané (2008); X^6: Fernicola et al. (2009); X^7: Scott (1903); X^8 Brown (1903); X^9: Fernicola and Vizcaíno, this work

Eucinepeltus or *Cochlops* can only be assigned to Propalaehoplophoridae due to the similarity among the three genera in osteoderm morphology over a large part of the carapace.

The second level of analysis considers the taxonomic richness among the localities of the RSC (Tab. 1) based on the new remains recovered. The only difference between BB and SBB is the presence of the armadillo *Stegotherium tessellatum* and the glyptodont *Cochlops muricatus* in the former. *Stegotherium tessellatum* is represented by only three osteoderms, suggesting that this species may not have been particularly abundant, thus reducing the probability of recovering its remains in other localities, which have yielded fewer specimens. The absence of *Cochlops muricatus* in SBB may, as in the case of *Propalaehoplophorus*, be attributable to sampling, given that this taxon has been reported in the other regions of the SCF (see below). The lower taxonomic richness registered in YH, three armadillos and one glyptodont species, could be a due to sampling size, given that this locality is the smallest of the three. Although Carlos Ameghino claimed that this was the richest fossiliferous site in the area (letter 166 in Torcelli, 1935; Vizcaíno, 2011), in 1889 Clemente Onelli had the opposite impression, recovering only a few armadillo osteoderms and a toxodont skull over several days (Vizcaíno *et al.*, 2013; Brinkman and Vizcaíno, 2014). The new collections in YH confirm Onelli's view.

The third level of analysis considers the taxonomic richness of cingulates recognized from the SCF in the RSC and other central areas, such as Río Chalía, compared with that previously recognized in the western and eastern localities of the SCF (Tab. 2). All the genera recorded in the western and eastern areas are also known from the central area, with the exception of *Vetelia*; indeed, this cingulate is scarce in the SCF. Fernicola *et al.* (2009) reported the first and only record of this genus from the coast of the Province of Santa Cruz, 3 km south of the mouth of the Río Coyle, based on a single osteoderm. Given this circumstance, evaluation of its absence in the central areas is not particularly meaningful. At the specific level, the taxonomic differences compared with other regions of the SCF are more pronounced. In the three areas defined for the SCF there are at least 21 species of cingulates, of which six are glyptodonts (Tab. 2). The highest taxonomic richness is recorded in the eastern region (Atlantic coast), while in the other two regions it is approximately one third lower (Tab. 2), a difference that may be due to the much more intensive collecting efforts along the Atlantic coast (Vizcaíno *et al.*, 2013).

The number of shared species among the three areas decreases from east to west (east-center: ten spp.; center-west: eight spp.; east-west: six spp.). This taxonomic gradient may coincide with an environmental gradient produced by the elevation of the Andes. Evaluation of this hypothesis requires analyses of specific climatically or environmentally sensitive morphological features such as, for example, piliferous foramina size (Ciancio *et al.*, 2017), and of exhaustive abiotic and biotic evidence, as by Kay *et al.* (2012).

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REFERENCES

Aguiar, J.M., and Fonseca, G.A.B. 2008. Conservation status of Xenarthra. In: S.F. Vizcaíno, and W.J. Loughry (Eds.), *The Biology of the Xenarthra.* University Press of Florida, Gainesville, p. 215–231.

Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de la Patagonia y depositados en el Museo de La Plata. *Boletín del Museo de La Plata* 1: 1–26.

Ameghino, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas de la Academia Nacional de Ciencias de Córdoba* 6: 1–1027.

Ameghino, F. 1891a. Nuevos restos de mamíferos fósiles descubiertos por Carlos Ameghino en el Eoceno inferior de la Patagonia Austral. Especies nuevas, adiciones y correcciones. *Revista Argentina de Historia Natural* 1: 286–328.

Ameghino, F. 1891b. Mamíferos y aves fósiles argentinas. Especies nuevas, adiciones y correcciones. *Revista Argentina de Historia Natural* 1: 240–259.

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

Ameghino, F. 1891d. Observaciones críticas sobre los mamíferos eocenos de la Patagonia austral. *Revista Argentina de Historia Natural* 1: 328–382.

Ameghino, F. 1894. *Énumération synoptique des espèces de mammifères fossiles des formations éocènes de Patagonie.* Coni é hijos, Buenos Aires, 196 p.

Ameghino, F. 1895. Sur les édentés fossiles de l'Argentine: Examen critique, revision et correction de l'ouvrage de R. Lydekker: The extint edentates of Argentina. *Revista del Jardín Zoológico de Buenos Aires* 3: 97–192.

Ameghino, F. 1898. Primera sinopsis geológico-paleontológica. *2º Censo de la República Argentina* 1: 111–255.

Ameghino, F. 1900–1902. L'âge des formations sédimentaires de Patagonie. *Anales de la Sociedad Científica Argentina* 50: 109–130, 145–165,209–229; 51: 20–39, 65–91; 52: 189–197, 244–250; 54: 161–180, 220–249, 283–342.

Ameghino, F. 1906. Les formations sédimentaires du Créetacé Superieur et du Tertaire de Patagonie avec un parallele entre leurs faunes mammalogiques et celles de l'ancien continent. *Anales del Museo Nacional de Buenos Aires* 15: 1–568.

Ameghino, F. 1920. Sur les édentés fossiles de l'Argentine: Examen critique, revision et correction de l'ouvrage de R. Lydekker: The extint edentates of Argentina. Revista del Jardín Zoológico de Buenos Aires. In: A.J. Torcelli (Ed.), *Obras completas y correspondencia científica de Florentino Ameghino.* Taller de Impresiones Oficiales del Gobierno de la Provincia de Buenos Aires, La Plata, Volumen 11, p. 603–909.

Bordas, A.F. 1936. Los Peltateloidea de la colección Ameghino. Peltephiloda. (Infraorden de los Xenarthra). *Physis* 12: 1–18.

Bordas, A.F. 1938. Sobre un nuevo Peltephiloda del Trelewense. *Physis* 12: 267–277.

Brinkman, P.D., and Vizcaíno, S.F. 2014. Clemente Onelli's sketch map and his first-hand, retrospective account of an early fossil-hunting expedition along the Río Santa Cruz, southern-Patagonia, 1888–1889. *Society for the Bibliography of Natural History; Archives of natural history* 41: 326–337.

Brown, B. 1903. A new Species of fossil Edentate from the Santa Cruz Formation of Patagonia. *Bulletin of the American Museum of Natural History* 19: 453–457.

Castro, M.C., Ciancio, M.R., Pacheco, V., Salas-Gismondi, R.M., Bostelmann, J.E., and Carlini, A.A. 2015. Reassessment of the hairy long-nosed armadillo "*Dasypus*" *pilosus* (Xenarthra, Dasypodidae) and revalidation of the genus *Cryptophractus* Fitzinger, 1856. *Zootaxa* 3947: 30–48.

Ciancio, M.R., Carlini, A.A., Campbell, K.E. Jr., and Scillato-Yané, G.J. 2013. New Paleogene cingulates (Mammalia, Xenarthra) from Santa Rosa, Peru, and their importance in the context of South American faunas. *Journal of Systematic Paleontology* 11: 727–741.

Ciancio, M.R., Krmpotic, C.M., Scarano, A.C., and Epele, M.B. 2017. Internal morphology of osteoderms of extinct armadillos and its relationship with environmental conditions. *Journal of Mammalian Evolution* 26: 71–83.

Cobos, J.C., Rodríguez, M.F., and Panza, J.L. 2014. Hoja Geológica 5172-II, Paso Río Bote, Provincia de Santa Cruz. *Boletín del Instituto de Geología y Recursos Minerales, Servicio Geológico Minero Argentino* 405: 1–99.

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

Cuitiño, J.I., Fernicola, J.C., Raigemborn, M.S., and Krapovickas, V. 2019b. 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: 14–33.

Cuitiño, J.I., Vizcaíno, S.F., Bargo, M.S., and Aramendía, I. 2019a. Sedimentology and fossil vertebrates of the Santa Cruz Formation (early Miocene) in Lago Posadas, a sub-Andean locality of southwestern Patagonia. *Andean Geology* 46: 383–420.

Desmarest, A. 1804. *Nouveau Dictionnaire d'Histoire Naturelle, appliquée aux arts, principalement à l'agriculture, à l'économie rurale et domestique: Par une société de naturalistes et d'agriculteurs: Avec des figures tirées des trois règnes de la nature*. Vol. 24. Chez Deterville, Paris, 538 p.

Fernicola, J.C. 2008. Nuevos aportes para la sistemática de los Glyptodontia Ameghino, 1889 (Mammalia, Xenarthra, Cingulata). *Ameghiniana* 45: 553–574.

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.

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 Notohippidian. *Journal of South American Earth Sciences* 52: 94–107.

Fernicola, J.C., and Vizcaíno, S.F. 2008. Revisión del género *Stegotherium* Ameghino, 1887 (Mammalia, Xenarthra, Dasypodidae). *Ameghinana* 45: 321–332.

Fernicola, J.C., Vizcaíno, S.F., and Bargo, M.S. 2009. Primer registro de *Vetelia puncta* Ameghino (Xenarthra, Cingulata) en la Formación Santa Cruz (Mioceno temprano) de la costa atlántica de la provincia de Santa Cruz, Argentina. *Ameghiniana* 46: 77R.

Francia, A., and Ciancio, M.R. 2013. First record of *Chaetophractus villosus* (Mammalia, Dasypodidae) in the late Pleistocene of Corrientes Province (Argentina). *Revista del Museo de La Plata* 13: 1–9.

Fleagle, J.H., Perkins, M.E., Heizler, M.T., Nash, B., Bown, T.M., Tauber, A.A., Dozo, M.T., and Tejedor, M.F. 2012. Absolute and relative ages of fossil localities in the Santa Cruz and Pinturas Formations. 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. 41–58.

Fosdick, J.C., Grove, M., Hourigan, J.K., and Calderón, M. 2013. Retroarc deformation and exhumation near the end of the Andes, southern Patagonia. *Earth and Planetary Science Letters* 361: 504–517.

Ghiglione, M.C., Ramos, V.A., Cuitiño, J.I., and Varberón, V. 2016. Growth of the Southern Patagonian Andes (46–53°S) and their Relation to Subduction Processes. In: A. Folguera, M. Naipauer, L. Sagripanti, M. Ghiglione, D. Orts, and L. Giambiagi (Eds.), *Growth of the Southern Andes*. Springer Earth System Sciences. Springer International Publishing, Switzerland doi 10.1007/978-3-319-23060-3_10.

González Ruiz, L.R. 2010. [*Los Cingulata (Mammalia, Xenarthra) del Mioceno temprano y medio de Patagonia (edades Santacrucense y "Friasense") revisión sistemática y consideraciones bioestratigráficas*. PhD Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, 471 p. Unpublished.].

González Ruiz, L.R., and Scillato-Yané, G.J. 2008. Una nueva especie de *Stegotherium* (Xenarthra, Dasypodidae, Stegotheriini) del Mioceno de la provincia de Santa Cruz. *Ameghinana* 45: 641–648.

González Ruiz, L.R., and Scillato-Yané, G.J. 2009. A new Stegotheriini (Mammalia, Xenarthra, Dasypodidae) from the "Notohippidian" (early Miocene) of Patagonia. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 252: 81–90.

Gray, J.E. 1865. Revision of the genera and species of entomophagous Edentata, founded on the examination of the specimens in the British Museum. *Proceedings of the Zoological Society of London* 1865: 359–386.

Kay, R.F., Vizcaíno, S.F., and Bargo, M.S. 2012. A review of the paleoenvironment and paleoecology of the Miocene Santa Cruz Formation. 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. 331–365.

Kay, R.F., Vizcaíno, S.F., Bargo, M.S., Perry, J.M.G., Prevosti, F.J., and Fernicola, J.C. 2008. Two new fossil vertebrate localities in the

Santa Cruz Formation (late early Miocene, Argentina), 51 degrees South latitude. *Journal of South American Earth Sciences* 25: 187–195.

Krmpotic, C.M., Ciancio, M.R., Barbeito, C., and Carlini, A.A. 2009. Osteoderm morphology in recent and fossil Euphractinae Xenarthrans. *Acta Zoologica* 90: 339–351.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentis, synonymis, locis*. Tomus I. Edito Decima, Reformata. Holmiae, Impensis Direct. Laurentii Salvii, 824 p.

Lydekker, R. 1894. Contribuciones al conocimiento de los vertebrados fósiles de la Argentina. Observaciones adicionales sobre los ungulados argentinos. *Anales del Museo de La Plata* 2: 1–248.

Marshall, L.G., Hoffstetter, R., and Pascual, R. 1983. Mammals and stratigraphy: Geochronology of the continental mammal-bearing Tertiary of South America. *Paleovertebrata, Mémoire Extraordinaire* 1–93.

Matheos, S.D., and Raigemborn, M.S. 2012. Sedimentology and paleoenvironment of the Santa Cruz Formation. 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. 59–82.

McKenna, M.C., and Bell, S.K. 1997. *Classification of Mammals above the Species Level*. Columbia University Press, New York, 640 p.

Mercerat, A. 1890. Sinopsis de la familia de los Astrapotheridae (Eoceno de Patagonia). *Revista del Museo de La Plata* 1: 241–255.

Mercerat, A. 1891. Notas sobre la paleontología de la República Argentina. II. Sinopsis de la familia de los Proxotodontidae conservados en el Museo de La Plata (Eoceno de Patagonia). *Revista del Museo de La Plata* 1: 381–444.

Mones, A. 1986. Palaeovertebrata Sudamericana. Catálogo sistemático de los vertebrados fósiles de América del Sur. Parte I. Lista Preliminar y Bibliografía. *Courier Forschungsinstitut Senckenberg* 82: 1–625.

Moreno, F.P. 1882. Patagonia. Resto de un antiguo continente sumergido. *Anales de la Sociedad Científica Argentina* 14: 97–131.

Moreno, F.P., and Mercerat, A. 1891. Notas sobre algunas especies de un género aberrante de los Dasypoda (eoceno de Patagonia) conservadas en el Museo de La Plata. *Revista del Museo de La Plata* 2: 57–63.

Pascual, R., Ortega Hinojosa, E.J., Gondar, D., and Tonni, E. 1965. Las edades del Cenozoico mamalífero de la Argentina, con especial atención a aquellas del territorio Bonaerense. *Anales de la Comisión de Investigaciones Científicas* 6: 165–193.

Parras, A.M., and Cuitiño, J.I. 2018.The stratigraphic and paleoenvironmental significance of the regressive Monte Observación Member, early Miocene of the Austral Basin, Patagonia. *Latin American Journal of Sedimentology and Basin Analysis* 25: 25–47.

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.

Raigemborn, M.S., Matheos, S.D., Krapovickas, V., Vizcaíno, S.F., Bargo, M.S., Kay, R.F., Fernicola, J.C., and Zapata, L. 2015. Paleoenvironmental reconstruction of the coastal Monte León and Santa Cruz formations (Early Miocene) at Rincón del Buque, Southern Patagonia: A revisited locality. *Journal of South American Earth Sciences* 60: 31–55.

Sacomani, L.E., and Panza, J.L. 2011. Hojas Geológicas 5169-I y 5169-II, Puerto Coig y Puerto Santa Cruz, Provincia de Santa Cruz. *Instituto de Geología y Recursos Minerales, Servicio Geológico Minero Argentino, Boletín* 392: 1–133.

Scillato-Yané, G.J. 1980. Catálogo de los Dasypodidae fósiles (Mammalia, Edentata) de la República Argentina. *2° Congreso Argentino de Paleontología y Bioestratigrafía y 1° Congreso Latinoamericano de Paleontología* (Buenos Aires), *Actas* 3: 7–36.

Scott, W.B. 1903. Mammalia of the Santa Cruz beds. Part I. Edentata. In: W.B. Scott (Ed.), *Reports of the Princeton University Expeditions to Patagonia 1896–1899*. Vol. 5, Paleontology 2, Princeton. Princeton University Press, New Jersey, p. 1–226.

Tauber, A.A. 1999. Los Vertebrados de la Formación Santa Cruz (Mioceno inferior-medio) en el extremo sureste de la Patagonia y su significado paleoecológico. *Revista Española de Paleontología* 14: 173–182.

Tauber, A.A., Palacios, M.E., Krapovickas, J., and Rodríguez, P. 2008. La Formación Santa Cruz (Mioceno temprano-medio) en la mitad occidental del Río Santa Cruz, Patagonia, Argentina. *17° Congreso Geológico Argentino* (Jujuy), *Actas*: 1500–1501.

Torcelli, A.J. 1935. Correspondencia científica. In: A.J. Torcelli (Ed.), *Obras completas y correspondencia científica de Florentino Ameghino. Volumen 20.* Taller de Impresiones Oficiales del Gobierno de la Provincia de Buenos Aires, La Plata, 621 p.

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

Vizcaíno, S.F. 1994. Mecánica masticatoria de *Stegotherium tessellatum* Ameghino (Mammalia, Xenarthra) del Mioceno de Santa Cruz (Argentina). Algunos aspectos paleoecológicos relacionados. *Ameghiniana* 31: 283–290.

Vizcaíno, S.F. 2011. Cartas para Florentino desde la Patagonia. Crónica de la correspondencia édita entre los hermanos Ameghino (1887-1902). *Publicación Especial de la Asociación Paleontológica Argentin*a 12: 51–67.

Vizcaíno, S.F., Bargo, M.S., Cuitiño, J.I., Pérez, M.E., Muñoz, N.A., Aramendía, I., Tomassini, R.L., and Kay, R.F. 2018. The outstanding Río Chalía (= Sehuén) outcrops of the Santa Cruz Formation (Early Miocene, Burdigalian) and its fossil vertebrate content. *Publicación Electrónica de la Asociación Paleontológica Argentina* 19: 85R.

Vizcaíno, S.F., Bargo M.S., and Fernicola, J.C. 2013. Expediciones paleontológicas durante los Siglos XIX y XX A la Formación Santa Cruz (Mioceno Inferior, Patagonia) y destino de los fósiles. *3° Congreso Argentino de Historia de la Geología* (Salta), *Actas*: 231–246.

Vizcaíno, S.F., Bargo, M.S., Kay, R.F., Fariña, R.A., Di Giacomo, M., Perry, J.M.G., Prevosti, F.J., Toledo, N., Cassini, G.H., and Fernicola, J.C. 2010. A baseline paleoecological study for the Santa Cruz Formation (late–early Miocene) at the Atlantic coast of Patagonia, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* 292: 507–519.

Vizcaíno, S.F., De Iuliis, G., Brinkman, P.D., Kay, R., and Brinkman, D.L. 2017. On an album of photographs recording fossils in the "Old Collections" of the Museo de La Plata and Ameghino's private collection at the beginning of the XX^th^ century. *Publicación Electrónica de la Asociación Paleontológica Argentina* 17: 14–23.

Vizcaíno, S.F., and Fariña, R.A. 1997. Diet and locomotion of the armadillo *Peltephilus*: a new view. *Lethaia* 30: 79–86.

Vizcaíno, S.F., Fernicola, J.C., and Bargo, M.S. 2012c. Paleobiology of

Santacrucian glyptodonts and armadillos (Xenarthra, Cingulata). 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. 194–215.

Vizcaíno, S.F., Kay, R.F., and Bargo, M.S. 2012a. 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.

Vizcaíno, S.F., Kay, R.F., and Bargo, M.S. 2012b. *Early Miocene Paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, 370 p.

Wetzel, R.M. 1985. Taxonomy and distribution of armadillos, Dasypodidae. *The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas*. Smithsonian Institution Press, Washington, 2346 p.

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Appendix 1. List of the cingulates recorded in Barrancas Blancas (Estancia Aguada Grande and Estancia Santa Lucía), Segundas Barrancas Blancas (Estancia Cordón Alto and Estancia El Tordillo) and Yaten Huageno (Estancia El Refugio).

BARRANCAS BLANCAS (170 specimens)

Peltephilus pumilus. MPM-PV 20818, osteoderm of the cephalic shield and carapace; MPM-PV 20816, MPM-PV 20819, MPM-PV 20821, and MPM-PV 20822, carapace osteoderms.

Peltephilus sp. MPM-PV 20820, fragment of cephalic shield osteoderm, MPM-PV 20817, fragment of cephalic shield osteoderm.

Stegotherium tessellatum. MPM-PV 20832, three osteoderms.

Prozaedyus proximus. MPM-PV 20844, small carapace fragment; MPM-PV 20845, small carapace fragment; MPM-PV 20848, osteoderms and small carapace fragment; MPM-PV 20833, MPM-PV 20834, MPM-PV 20835, MPM-PV 20836, MPM-PV 20837, MPM-PV 20838, MPM-PV 20839, MPM-PV 20840, MPM-PV 20841; MPM-PV 20842, MPM-PV 20843, MPM-PV 20846, MPM-PV 20847, MPM-PV 20849, MPM-PV 20850, MPM-PV 20851, MPM-PV 20852, MPM-PV 20853, MPM-PV 20854, MPM-PV 20855, MPM-PV 20856, MPM-PV 20857, MPM-PV 20858, MPM-PV 20859, MPM-PV 20860, MPM-PV 20861, MPM-PV 20862, MPM-PV 20863, MPM-PV 20864, MPM-PV 20865, MPM-PV 20866, MPM-PV 20867, MPM-PV 20868, MPM-PV 20869, MPM-PV 20870, MPM-PV 20871, MPM-PV 20872, MPM-PV 20873, MPM-PV 20874, MPM-PV 20875, MPM-PV 20876, MPM-PV 20877, MPM-PV 20878, and MPM-PV 20879, carapace osteoderms.

Stenotatus patagonicus. MPM-PV 20932, MPM-PV 20933, MPM-PV 20934, MPM-PV 20935, MPM-PV 20936, MPM-PV 20937, MPM-PV 20938, MPM-PV 20939, MPM-PV 20940, MPM-PV 20941, MPM-PV 20942, MPM-PV 20943, MPM-PV 20944, MPM-PV 20945, MPM-PV 20946, MPM-PV 20947, MPM-PV 20948, MPM-PV 20949, MPM-PV 20950, MPM-PV 20951, MPM-PV 20952, MPM-PV 20953, MPM-PV 20954, MPM-PV 20955, MPM-PV 20956, and MPM-PV 20957, carapace osteoderms.

Proeutatus oenophorus. MPM-PV 20981, osteoderms and postcranial elements; MPM-PV 21006, osteoderms and postcranial elements; MPM-PV 20982, MPM-PV 20983, MPM-PV 20984, MPM-PV 20985, MPM-PV 20986, MPM-PV 20987, MPM-PV 20988, MPM-PV 20989, MPM-PV 20990, MPM-PV 20991, MPM-PV 20992, MPM-PV 20993, MPM-PV 20994, MPM-PV 20995, MPM-PV 20996, MPM-PV 20997, MPM-PV 20998, MPM-PV 20999, MPM-PV 21000, MPM-PV 21001, MPM-PV 21002, MPM-PV 21003, MPM-PV 21004, MPM-PV 21005, MPM-PV 21007, MPM-PV 21008, MPM-PV 21009, MPM-PV 21010, MPM-PV 21011, MPM-PV 21012, MPM-PV 21013, MPM-PV 21014, MPM-PV 21015, MPM-PV 21016, MPM-PV 21017, MPM-PV 21018, MPM-PV 21019, MPM-PV 21020, MPM-PV 21021, and MPM-PV 21022, carapace osteoderms.

Cochlops muricatus. MPM-PV 21070, MPM-PV 21071, MPM-PV 21072, MPM-PV 21073, MPM-PV 21074, MPM-PV 21075, MPM-PV 21076, MPM-PV 21077, MPM-PV 21078, MPM-PV 21079, MPM-PV 21080, and MPM-PV 21081, carapace osteoderms.

Eucinepeltus sp. MPM-PV 21084, cephalic shield osteoderm; MPM-PV 21085, cephalic shield osteoderm.

Propalaehoplophoridae. MPM-PV 21111, osteoderms and postcranial elements; MPM-PV 21116, osteoderms and postcranium; MPM-PV 21123, osteoderms and postcranial elements; MPM-PV 21096, MPM-PV 21097, MPM-PV 21098, MPM-PV 21099, MPM-PV 21100, MPM-PV 21101, MPM-PV 21102, MPM-PV 21103, MPM-PV 21104, MPM-PV 21105, MPM-PV 21106, MPM-PV 21107, MPM-PV 21108, MPM-PV 21109, MPM-PV 21110, MPM-PV 21112, MPM-PV 21113, MPM-PV 21114, MPM-PV 21115, MPM-PV 21117, MPM-PV 21118, MPM-PV 21119, MPM-PV 21120, MPM-PV 21121, MPM-PV 21122, MPM-PV 21124, MPM-PV 21125, MPM-PV 21126, MPM-PV 21127, MPM-PV 21128, and MPM-PV 21129, carapace osteoderms.

SEGUNDAS BARRANCAS BLANCAS (186 specimens)

Peltephilus pumilus. MPM-PV 20823, fragment of mandible and osteoderms; MPM-PV 20824, osteoderms and postcranial elements; MPM-PV 20828, MPM-PV 20830, MPM-PV 20825, MPM-PV 20831, and MPM-PV 20826, carapace osteoderms.

Peltephilus sp. MPM-PV 20827, cephalic shield osteoderm; MPM-PV 20829, fragment of mandible.

Prozaedyus proximus. MPM-PV 20882, osteoderms and postcranial elements; MPM-PV 20880, MPM-PV 20881, MPM-PV 20883, MPM-PV 20884, MPM-PV 20885, MPM-PV 20886, MPM-PV 20887, MPM-PV 20888, MPM-PV 20889, MPM-PV 20890, MPM-PV 20891, MPM-PV 20892, MPM-PV 20893, MPM-PV 20894, MPM-PV 20895, MPM-PV 20896, MPM-PV 20897, MPM-PV 20898, MPM-PV 20899, MPM-PV 20900, MPM-PV 20901, MPM-PV 20902, MPM-PV 20903, MPM-PV 20904, MPM-PV 20905, MPM-PV 20906, MPM-PV 20907, MPM-PV 20908, MPM-PV 20909, MPM-PV 20910, MPM-PV 20911, MPM-PV 20912, MPM-PV 20913, MPM-PV 20914, MPM-PV 20915, MPM-PV 20916, MPM-PV 20917, MPM-PV 20918, MPM-PV 20919, MPM-PV 20920, MPM-PV 20921, MPM-PV 20922, MPM-PV 20923, MPM-PV 20924, MPM-PV 20925, MPM-PV 20926, MPM-PV 20927, MPM-PV 20928, MPM-PV 20929, MPM-PV 20930, and MPM-PV

21185, carapace osteoderms.

Stenotatus patagonicus. MPM-PV 20958, MPM-PV 20959, MPM-PV 20960, MPM-PV 20961, MPM-PV 20962, MPM-PV 20963, MPM-PV 20964, MPM-PV 20965, MPM-PV 20966, MPM-PV 20967, MPM-PV 20968, MPM-PV 20969, MPM-PV 20970, MPM-PV 20971, MPM-PV 20972, MPM-PV 20973, MPM-PV 20974, MPM-PV 20975, MPM-PV 20976, MPM-PV 20977, MPM-PV 20978, and MPM-PV 20979, carapace osteoderms.

Proeutatus oenophorus. MPM-PV 21037, osteoderms and postcranial elements; MPM-PV 21044, osteoderms and postcranial elements; MPM-PV 21053, fragment of mandible; MPM-PV 21049, fragment of maxilar; MPM-PV 21023, MPM-PV 21024, MPM-PV 21025, MPM-PV 21026, MPM-PV 21027, MPM-PV 21028, MPM-PV 21029, MPM-PV 21030, MPM-PV 21031, MPM-PV 21032, MPM-PV 21033, MPM-PV 21034, MPM-PV 21035, MPM-PV 21036, MPM-PV 21038, MPM-PV 21039, MPM-PV 21040, MPM-PV 21041, MPM-PV 21042, MPM-PV 21043, MPM-PV 21045, MPM-PV 21046, MPM-PV 21047, MPM-PV 21048, MPM-PV 21050, MPM-PV 21051, MPM-PV 21052, MPM-PV 21054, MPM-PV 21055, MPM-PV 21056, MPM-PV 21057, MPM-PV 21058, MPM-PV 21059, MPM-PV 21060, MPM-PV 21061, MPM-PV 21062, MPM-PV 21063, MPM-PV 21064, and MPM-PV 21065, carapace osteoderms.

Eucinepeltus sp. MPM-PV 21086, cephalic shield osteoderm; MPM-PV 21087, MPM-PV 21088, MPM-PV 21089, MPM-PV 21090, MPM-PV 21091, MPM-PV 21092, MPM-PV 21093, MPM-PV 21094, and MPM-PV 21095, carapace osteoderms, and a cephalic shield osteoderm; and MPM-PV 21169, carapace osteoderms.

Propalaehoplophoridae. MPM-PV 21139, fragment of mandible; MPM-PV 21140, osteoderms, fragment of skull, and postcranial elements; MPM-PV 21165, osteoderms and a molariform; MPM-PV 21130, MPM-PV 21131, MPM-PV 21132, MPM-PV 21133, MPM-PV 21134, MPM-PV 21135, MPM-PV 21136, MPM-PV 21137, MPM-PV 21138, MPM-PV 21141, MPM-PV 21142, MPM-PV 21143, MPM-PV 21144, MPM-PV 21145, MPM-PV 21146, MPM-PV 21147, MPM-PV 21148, MPM-PV 21149, MPM-PV 21150, MPM-PV 21151, MPM-PV 21152, MPM-PV 21153, MPM-PV 21154, MPM-PV 21155, MPM-PV 21156, MPM-PV 21157, MPM-PV 21158, MPM-PV 21159, MPM-PV 21160, MPM-PV 21161, MPM-PV 21162, MPM-PV 21163, MPM-PV 21164, MPM-PV 21166, MPM-PV 21167, MPM-PV 21168, MPM-PV 21170, MPM-PV 21171, MPM-PV 21172, MPM-PV 21173,; MPM-PV 21174, MPM-PV 21175, MPM-PV 21176, MPM-PV 21177, MPM-PV 21178, and MPM-PV 21179, carapace osteoderms.

YATEN HUAGENO (12 specimens)

Prozaedyus proximus. MPM-PV 20931, carapace osteoderms.

Stenotatus patagonicus. MPM-PV 20980, carapace osteoderms.

Proeutatus oenophorus. MPM-PV 21066, MPM-PV 21067, MPM-PV 21068, and MPM-PV 21069, carapace osteoderm.

Cochlops muricatus. MPM-PV 21082, and MPM-PV 21083, carapace osteoderms.

Propalaehoplophoridae. MPM-PV 21181, ungual phalanx; MPM-PV 21183, osteoderms and postcraneal elements; MPM-PV 21182, and MPM-PV 21180, carapace osteoderms.

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EARLY MIOCENE SLOTHS (XENARTHRA, FOLIVORA) FROM THE RÍO SANTA CRUZ VALLEY (SOUTHERN PATAGONIA, ARGENTINA). AMEGHINO, 1887 REVISITED

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Abstract. The first detailed geological and paleontological survey of the Santa Cruz Formation (Early–Middle Miocene; Burdigalian–early Langhian) along the Río Santa Cruz was carried out in 1887 by Carlos Ameghino, who recovered more than 2000 fossil remains. In that same year, his brother Florentino studied and reported these remains, recognizing 122 taxa, of which 110 were new species. Fourteen of these new species were of sloths (Xenarthra, Folivora). In this contribution we report and describe new fossil sloth remains recovered in recent expeditions (between 2013 and 2014) along the southern banks of the Río Santa Cruz. The new specimens were recovered from two localities: Barrancas Blancas and Segundas Barrancas Blancas. We review the taxonomic richness of fossil sloths, in comparison with other Santacrucian localities recently studied, *e.g*, from the Atlantic coast and from the Andean region. An analysis of the original taxa erected by Ameghino is also included. As several of the original fossils on which these taxa are based are no longer available, we explore the value of the new collection in helping resolve systematic issues, as well as considering the specimens that formed the basis for the species erected by Ameghino in 1887. Further, the degree to which W.B. Scott's systematic decisions on the Santacrucian sloths, published in 1903 and 1904, should continue to be recognized is also assessed.

Key words. Burdigalian. Santacrucian. Phyllophaga. Taxonomy. Holotype. Ameghino.

Resumen. LOS PEREZOSOS (XENARTHRA, FOLIVORA) DEL MIOCENO TEMPRANO DEL VALLE DEL RÍO SANTA CRUZ (PATAGONIA AUSTRAL, ARGENTINA). REEXAMINANDO AMEGHINO, 1887. La primera exploración geológica y paleontológica de la Formación Santa Cruz (Mioceno Temprano–Medio; Burdigaliense–Langhiense temprano) a lo largo del Río Santa Cruz fue llevada a cabo en 1887 por Carlos Ameghino, quien recuperó más de 2.000 restos fósiles. Ese mismo año, su hermano Florentino estudió y reportó estos restos fósiles; reconoció 122 taxones de los cuales 110 eran nuevas especies. De estas últimas, resultaron 14 nuevas especies de perezosos (Xenarthra, Folivora). En esta contribución se reportan y describen nuevos restos fósiles de perezosos recuperados en trabajos de campo recientes (entre 2013 y 2014) en la margen sur del Río Santa Cruz. Los nuevos especímenes provienen de dos localidades: Barrancas Blancas y Segundas Barrancas Blancas. Se analizó la riqueza taxonómica del grupo en comparación con otras localidades santacrucenses estudiadas recientemente, *e.g.*, de la costa atlántica y de la región andina. Se incluye además un análisis de los taxones originales erigidos por Ameghino. Debido a que muchos de los especímenes originales sobre los que se han basado estos taxones ya no están disponibles, se analiza la importancia de las nuevas colecciones para resolver cuestiones sistemáticas y se consideran los especímenes sobre los que Ameghino erigió las primeras especies en 1887. Asimismo, se evalúa el grado en que las decisiones sistemáticas sobre perezosos santacrucenses realizadas por W.B. Scott, en 1903 y 1904, deben continuar siendo reconocidas.

Palabras clave. Burdigaliense. Santacrucense. Phyllophaga. Taxonomía. Holotipo. Ameghino.

SLOTHS or Folivora belong to Xenarthra, one of the four major clades of placental mammals, although a consensus on their relationships has not been achieved (see Asher and Helgen, 2010; Meredith *et al.*, 2011; O'Leary *et al.*, 2013; Delsuc *et al.*, 2019; Presslee *et al.*, 2019). The fossil history of sloths is extremely rich and diverse, constituting one of the largest and most distinctive elements of the South American Cenozoic fauna. The long standing consensus on phylogenetic relationships, based on osteological characters, recognizes five main sloth clades (Gaudin, 2004; Pujos *et al.*, 2007;

Amson *et al*., 2016): Bradypodidae (the sister clade to all remaining sloths and including only the extant *Bradypus*), Megalonychidae (including one extant genus, *Choloepus*, and several extinct genera), Nothrotheriidae, Megatheriidae, and Mylodontidae (with numerous extinct genera; see McDonald and De Iuliis, 2008 for a review). Megalonychidae, Nothrotheriidae, and Megatheriidae form a monophyletic clade, Megatherioidea (Gaudin, 2004). However, recent molecular based analyses by Delsuc *et al.* (2019) and Presslee *et al.* (2019) proposed a marked departure from this arrangement, with *Bradypus* being closely related to Nothrotheriidae and Megatheriidae (*i.e.*, Megatherioidea) and *Choloepus* to Mylodontidae. Living sloths are small sized (from ~3 to 8 kg), and almost exclusively arboreal and folivorous. Fossil sloths include a wide range of body sizes (from tens of kg to almost five tons), and a variety of dietary and locomotory habits (*e.g.*, Bargo, 2001; Pujos *et al*., 2007; Bargo and Vizcaíno, 2008; McDonald and De Iuliis, 2008; Vizcaíno *et al*., 2008; Bargo *et al*., 2009, 2012; Amson *et al*., 2014).

This contribution focuses on the sloths of the Santa Cruz Formation (SCF; Early–Middle Miocene; Burdigalian–early Langhian) of southern Patagonia, recovered from exposures along the Río Santa Cruz valley (Cuitiño *et al*., 2019a; Fernicola *et al*., 2019). The SCF is one of the most relevant stratigraphic units of southern South America in terms of the Miocene terrestrial stratigraphic record, upon which Pascual *et al.* (1965) based the South American Land Mammal Ages (SALMAs; Vizcaíno *et al*., 2012a). The SCF is widely distributed in the Austral (= Magallanes) Basin in the Province of Santa Cruz (Argentina). It crops out in the northwest area of the province, the central region along the Río Santa Cruz (Fernicola *et al*., 2014; Cuitiño *et al*., 2016) and Chalía (= Sehuen; Vizcaíno *et al*., 2018), and in the southeastern area along the Atlantic coast (Vizcaíno *et al*., 2012b). This continental sedimentary unit is composed of mudstones, tuffaceous sandstones, and tuffs deposited in fluvial environments under the influence of intense explosive pyroclastic input (Matheos and Raigemborn, 2012; Raigemborn *et al*., 2015 and Cuitiño *et al*., 2016 for extensive geological descriptions). The SCF along the Río Santa Cruz is part of extra-Andean Patagonia and crops out in both margins of the river; the exposed unit below the SCF is the marine Early Miocene Monte León Formation (Parras *et al*., 2012). The SCF was recently studied and described in three locations (see below) along the river by Cuitiño *et al.* (2016; see also Cuitiño *et al*., 2019a). Radiometric ages for the entire SCF span the interval ~18 to 15.60 Ma, being ~18–16 Ma for the Atlantic coastal localities (Perkins *et al*., 2012; Fleagle *et al*., 2012); ~18.20–15.60 Ma for the Río Bote and Río Santa Cruz localities (Cuitiño *et al*., 2016), and ~18–14 Ma for the Lago Posadas region (Perkins *et al*., 2012).

The Río Santa Cruz valley was first geographically explored in 1877 by F. P. Moreno (1879). Carlos Ameghino made the first detailed geological and paleontological exploration in 1887 collecting more than 2000 fossil remains. Many of these fossils were promptly studied and reported by his brother Florentino in a concise paper that recognized 122 taxa, 110 of which were new species (Ameghino, 1887). None of the taxa was figured nor were the localities indicated (see Fernicola *et al*., 2019). In a later contribution, Ameghino (1889) expanded the descriptions of the taxa, upon which he based the *Formación Santacruceña* and *Piso Santacruceño* (Santacrucian Stage), and figured many of them (see Fernicola, 2011). Over the subsequent years, more widely exposed and highly fossiliferous outcrops of the SCF, such as those located to the southeast along the Atlantic coast, took such priority in the paleontological literature (see Vizcaíno *et al*., 2012a and references therein) that C. Ameghino's Río Santa Cruz discoveries were largely forgotten. Recently, Fernicola *et al.* (2014) provided the precise geographic location of C. Ameghino's (1887) fossiliferous localities, formalized their names, and evaluated the stratigraphic position of the mammal-bearing levels (see Fernicola *et al*., 2019 for a review of the historical context). The fossil localities prospected by C. Ameghino along the Río Santa Cruz, and recognized by Fernicola *et al.* (2014) are, from east to west: Barrancas Blancas (= Estancias Santa Lucía and Aguada Grande), Segundas Barrancas Blancas (= Estancias Cordón Alto, El Tordillo, and Rincón Grande), and Yaten Huageno (= Estancia El Refugio) (Fig. 1). C. Ameghino also prospected in the nearby area of Lago Argentino in a fourth locality named Río Bote (= Estancia María Elisa).

The goal of this contribution is to describe new sloth remains recently recovered from fossiliferous localities along the Río Santa Cruz, and to review the taxonomic richness of

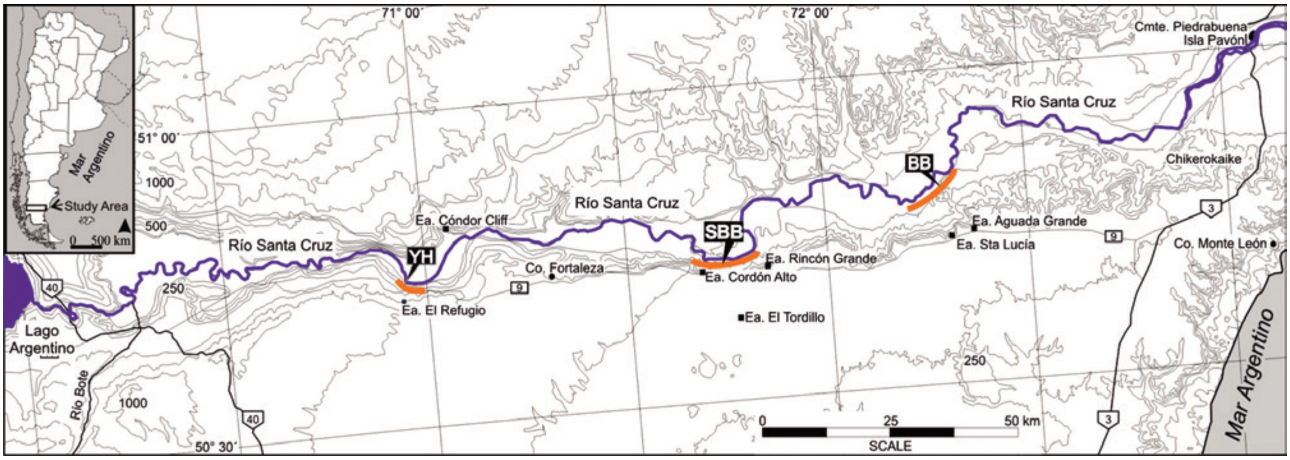

Figure 1. Map of the Río Santa Cruz indicating the prospected localities and estancias mentioned in the text. **SBB,** Segundas Barrancas Blancas; **BB,** Barrancas Blancas; **Co.,** Cerro; **Ea.,** Estancia; **YH,** Yaten Huageno. Modified from Fernicola *et al.* (2014).

sloths in comparison with other Santacrucian localities. A review of the original taxa of the Río Santa Cruz erected by Ameghino (1887) is also included.

TAXONOMIC AND PHYLOGENETIC BACKGROUND

Our current understanding of the systematics of the Santacrucian sloths (but see below for *Eucholoeops* Ameghino, 1887 and *Schismotherium* Ameghino,1887) is based mainly on the work of Ameghino (*e.g.*, 1887, 1891a, 1894), as interpreted and revised by Scott (1903, 1904). Indeed, our concept of these sloths has remained largely static since Scott's efforts more than a century ago, and it has long been appreciated that they are in dire need of revision (see De Iuliis *et al.*, 2014). Although Scott's efforts clarified aspects of F. Ameghino's work, there remained a good deal of ambiguity over Santacrucian sloth systematics: the number of valid species and genera, what precisely they represent, how they are distinguished from each other, and the lower-level relationships among them remain as uncertain as when Scott last dealt with them. As noted in De Iuliis *et al.* (2014; see also McDonald and De Iuliis, 2008), the numerous taxa erected by earlier workers (*e.g.*, Ameghino 1887, 1891a, 1894, 1897; Mercerat, 1891; Lydekker, 1894) were based largely on fragmentary remains, and there are many more published taxa than can be justified on the available material.

Scott's (1903, 1904) extensive work attempted to synthesize the then known material and reconcile it with the taxonomic impasse that had developed, due mainly to the multiplication of taxa largely through Ameghino's (*e.g.*, 1887, 1891a, 1894) creation of new species and genera based often on inadequate material. De Iuliis *et al.* (2014) outlined this situation with regard to *Eucholoeops*, but it is also true for other taxa, particularly *Hapalops* Ameghino, 1887: even Scott's attempts could not resolve the taxonomic situation, with this author admitting that the 22 *Hapalops* species that he recognized (reduced from the many more named mainly by F. Ameghino) were probably too many (Scott, 1904, p. 261), despite the fact that this list includes, ironically, several new *Hapalops* species that Scott himself erected. In addition to the 22 species that Scott (1903, 1904, p. 258) considered "as more or less well defined", he listed another 15 for which he "could arrive at no definite conclusion".

Nevertheless, making headway into resolving taxonomic issues must begin with consideration, as much as possible, of the original specimens, and the work of Scott, who is considered first reviser of Ameghino's work (see De Iuliis *et al.*, 2014). Scott was the only researcher who examined (during his visit to Argentina in 1901; Vizcaíno *et al.*, 2017) nearly all the material that had entered into the decisions by F. Ameghino, A. Mercerat, and R. Lydekker, and he also had access to considerable new material resulting from expeditions to Patagonia by Princeton University (the Princeton Material, except for a composite mounted skeleton, is currently housed in Yale's Peabody Museum, New Haven, USA) and the American Museum of Natural History (New York, USA). As noted below, however, strict adherence to Scott's decisions is among the factors that hinder an enhanced understanding of the Santacrucian sloths.

De Iuliis *et al.* (2014) and Racco *et al.* (2018) provided partial clarification of the systematics of *Eucholoeops ingens* Ameghino, 1887, and *Schismotherium fractum* Ameghino, 1887, respectively. These recent efforts made use of material recovered after Scott's work, including the largely unpublished remains recovered by H.T. Martin (Kansas University Natural History Museum, Kansas, USA; Vizcaíno *et al.*, 2016) and E. Riggs (Field Museum of Natural History, Chicago, USA; see Marshall, 1975, 1976), as well as those resulting from expeditions led by researchers of the Museo de La Plata (La Plata, Argentina), Museo Argentino de Ciencias Naturales "B. Rivadavia" (Buenos Aires, Argentina) and Duke University (Durham, USA). This collaboration began in 2003 and has continued to the present, with earlier efforts concentrated on costal localities between Monte León and Río Gallegos, and more recently on localities along the Río Santa Cruz and Río Chalía. The localities along the Río Santa Cruz and their fossils are the main focus of the current contribution. They are particularly relevant because the fossils recovered along the Río Santa Cruz by C. Ameghino formed the basis for F. Ameghino's (1887) initial descriptions of Santacrucian sloths (as well as other mammals; see Fernicola, 2011), and thus they are the type localities of many Santacrucian taxa. As several of the original fossils on which the 1887 taxa are based are no longer available (see below), the remains recovered by the joint expeditions mentioned above (housed at Museo Regional Provincial Padre M.J. Molina, Río Gallegos, Argentina) are potentially meaningful in helping resolve systematic issues. The present contribution explores their value in this regard, as well as considering the specimens that formed the basis for the species erected by Ameghino (1887). Further, the degree to which Scott's (1903, 1904) taxonomic and systematic actions should continue to be recognized is also assessed.

Of the numerous sloth genera erected on Santacrucian remains, only some half dozen –*Schismotherium* (with *Pelecyodon* Ameghino, 1891a, which probably cannot be distinguished from it; Racco *et al.*, 2018), *Eucholoeops*, *Hapalops*, *Nematherium*, *Planops* (these five erected on material from Río Santa Cruz localities), and *Analcimorphus*– have been considered sufficiently well represented for inclusion in the phylogenetic analyses. Gaudin (2004) and Amson *et al.* (2016) considered all six, whereas Pujos *et al.* (2007) included only *Schismotherium*, *Hapalops*, and *Planops*. The relationships of these genera among sloths are not entirely resolved. All three studies agree on the position of *Eucholoeops* as a basal Megalonychidae. The analysis by Pujos *et al.* (2007) was unable to resolve the positions of *Hapalops* and *Planops*. Gaudin (2004) and Amson *et al.* (2016) recognized *Planops* as a basal Megatheriidae (although the latter authors proposed the novel placement of Thalassocninae within this clade); *Schismotherium*, with *Pelecyodon*, as basal Megatherioidea; and *Nematherium* as among basal Mylodontidae. Gaudin (2004) hypothesized *Analcimorphus* and *Hapalops* as successive sister taxa to the clade including Megatheriidae and Nothrotheriidae, but noted that they could also be considered as successive sister taxa to Megalonychidae under different character weighting schemes. Amson *et al.* (2016) viewed *Analcimorphus* and *Hapalops* as successive sister taxa to Megalonychidae (all within an unnamed clade B), although the authors expressed reservation in noting that some of their arrangements are not particularly well supported. *Prepotherium* and *Planops* are regarded as Megatheriidae, as by, for example, De Iuliis (1994) and Gaudin (2004), respectively. Given the current understanding of these sloths, we recognize *Eucholoeops* as a basal megalonychid, *Schismotherium*, *Analcimorphus*, *Hapalops*, and *Xyophorus* as megatherioids, *Planops* and *Prepotherium* as megatheriids, and *Nematherium* as a mylodontid.

Ameghino's collection from the Río Santa Cruz

Ameghino (1887, p. 21–24) erected 110 taxa from the Río Santa Cruz, 14 of which were new sloth genera and species. He provided only species descriptions, without generic diagnoses. These taxa are, in order of publication, *Schismotherium fractum*, *Eucholoeops ingens*, *E. infernalis*, *E. adteger*, *Hapalops rectangularis*, *H. indifferens*, *H. ellipticus*, *Trematherium intermixtum*, *Nematherium angulatum*, *N. sinuatum*, *Planops longirostratus*, *Xyophorus rostratus*, *X. simus*, and *Entelops dispar*. In Figures 2 and 3 we provide images of the

Figure 2. Type specimens of Ameghino's (1887) sloths housed at MLP. **1–2,** ***Eucholoeops infernalis*** **MLP 4-7**, palatal view, and right lateral view of partial skull. **3–4,** ***E. adteger*** **MLP 4-63**, palatal view, and left lateral view of a maxillary portion. **5–6,** ***Hapalops ellipticus*** **MLP 4-44**, occlusal view, and left lateral view of a partial dentary. **7–8,** ***H. indifferens*** **MLP 4-33**, occlusal view, and right lateral view of a mandibular ramus. **9–10,** ***Trematherium intermixtum*** **MLP 4-45**, occlusal view, and left lateral view of a partial dentary. Scale bars= 1 cm.

few original types of Ameghino (1887) that are currently available in the Museo de La Plata.

In addition to these, Ameghino (*e.g.*, 1889, 1891a, b, 1894, 1897) subsequently named numerous additional sloth genera and species (as well as other mammalian taxa) based mainly on specimens recovered from coastal localities of the SCF. Fernicola (2011) provided a detailed description of the historical context related to the collection made by C. Ameghino at the Río Santa Cruz and the destiny of the fossils. This author reviewed all specimens listed in Ameghino (1887) that were later figured in Ameghino (1889), and/or were located recently in the Colección Nacional Ameghino at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". Fernicola (2011) also indicated that Ameghino (1889) figured 64 of the 110 new species published in 1887; of these new taxa figured, 19 were collected at the Río Santa Cruz, 15 of which were recovered by his brother Carlos. Vizcaíno *et al.* (2013a, b) went a step further in the history of Santacrucian collections, and reviewed the fate of the "Old Collections" of the Museo de La Plata that may have included specimens sent abroad during the 20th century.

MATERIAL AND METHODS

Acronyms. AMNH, American Museum of Natural History, New York, USA; **FMNH,** Field Museum of Natural History, Chicago, USA; **KUNHM,** Kansas University Natural History Museum, Lawrence, USA; **MACN-A,** Museo Argentino de

Figure 3. Figure 125 of Scott's album (from Vizcaíno *et al.*, 2017, Suppl. files, Appendix 1, p. 66), including photographs in occlusal view of several of the sloth type specimens of Ameghino (1887). **1,** ***Hapalops rectangularis*** (lost); **2,** ***H. ellipticus***; **3,** ***Eucholoeops adteger***; **4,** ***Schismotherium fractum*** (lost and never figured); **5,** ***Planops longirostratus*** (lost and never figured); **6,** ***H. indifferens***. Scott's album is archived in the Department of Paleontology of KUNHM.

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.J. Molina, Río Gallegos, Argentina; **NHMUK,** Natural History Museum, London, United Kingdom; **YPM-VPPU,** Yale Peabody Museum, Vertebrate Paleontology, Princeton University Collection, New Haven, USA.

Other abbreviations. cf, lower caniniform; **Cf,** upper caniniform; **Ea.,** Estancia; **L,** left; **mf,** lower molariform; **Mf,** upper molariform; **R,** right.

Recent fieldwork carried out between 2013 and 2014 by joint expeditions of the MLP, MACN, and Duke University recovered 69 remains of fossil sloths. This collection belongs to the MPM-PV and is listed in Appendix 1. The specimens collected include mostly postcranial elements (fragmentary long bones, several pes and manus elements, for example) and some skull and mandibular fragments. They were recovered from two fossiliferous localities: Barrancas Blancas (BB; 20 specimens) and Segundas Barrancas Blancas (SBB; 49 specimens). No sloth remains were recovered from Yaten Huageno (YH). The list of specimens studied and used for comparison is provided in Appendix 2.

SYSTEMATIC PALEONTOLOGY

XENARTHRA Cope, 1889
FOLIVORA Delsuc, Catzeflis, Stanhope, and Douzery, 2001
MEGATHERIOIDEA Gray, 1821

Genus *Hapalops* Ameghino, 1887

Type species. *H. rectangularis* Ameghino, 1887. Santa Cruz Formation, Barrancas del Río Santa Cruz, Province of Santa Cruz, Argentina.

Hapalops cf. *elongatus* Ameghino, 1891a

Figures 4, 5.1–3, Table 1

Referred material. MPM-PV 19353 (Fig. 4), anterior portion of skull preserving palate with all teeth; molariforms are set in their alveoli, whereas the Cf1s are isolated and only the distal portion of their alveolus is preserved; distal portion of R humerus, R and L humeral heads, central humeral diaphysis, R radius, proximal R ulna; several podial elements; L distal femur and partial R diaphysis, several fragments of vertebrae and of ribs; several sternebrae. MPM-PV 19352 (Fig. 5.1), portion of R dentary preserving cf1-mf3, with cf1 broken above level of alveolar margin. MPM-PV 19317 (Fig. 5.2), portion of R dentary preserving distal part of cf1 alveolus, mf1 and mf2 completely, and all but distolingual portion of mf3. MPM-PV 19318 (Fig. 5.3), anterior portion of skull, preserving L Cf1, Mf1-Mf3, Mf4 broken, and R Mf1-Mf3 (Mf1 broken vestibularly and Mf2 lacking its occlusal surface), and a small portion of Mf4.

Geographic occurrence. MPM-PV 19352 and 19353, Segundas Barrancas Blancas (Ea. Cordón Alto); MPM-PV 19317 and 19318, Barrancas Blancas (Ea. Santa Lucía), Río Santa Cruz, Province of Santa Cruz, Argentina.

Stratigraphic occurrence. Santa Cruz Formation (Early–Middle Miocene).

Description. In MPM-PV 19353 (Fig. 4) and 19318 (Fig. 5.3) the Cf1 is cylindrical to oval, slightly vestibulolingually compressed, with major axis oblique to the long axis of the tooth row, and separated from the cheek teeth by a diastema. The molariforms are rectangular in section (that is, mesiodistally compressed), with Mf2 being the largest and Mf4 being the smallest. The mesial tooth, cf1, of MPM-PV 19352 (Fig. 5.1) is nearly cylindrical in section and the smallest tooth. A diastema separates it from mf1. The mesial molariforms, mf1 and mf2, are rectangular, with the surfaces of each tooth meeting angularly. They are more nearly squared in section, particularly mf2, compared to those in some other *Hapalops* species, owing to their increased mesiodistal length (see below). The distal cheek tooth, mf3, is nearly cylindrical in section and with its major axis set obliquely to the long axis of the tooth row. The occlusal surfaces of the teeth are not preserved, as the teeth are broken near the level of their alveolar margin. In MPM-PV 19317 (Fig. 5.2) the diastema is slightly shorter than in MPM-PV 19352. Of the molariform teeth, mf1 and mf2 are nearly squared, similar to those of MPM-PV 19352, and mf3 is nearly cylindrical in shape, with major axis set obliquely to the long axis of the tooth row.

Comments. In MPM-PV 19353 and 19318 the molariforms are similar in form, with the former being larger. These teeth appear more mesiodistally compressed than in the type of *Eucholoeops adteger* (MLP 4-63; Fig. 2.3–4, 3.3) although the latter is approximately intermediate in size. MLP 4-63, how-

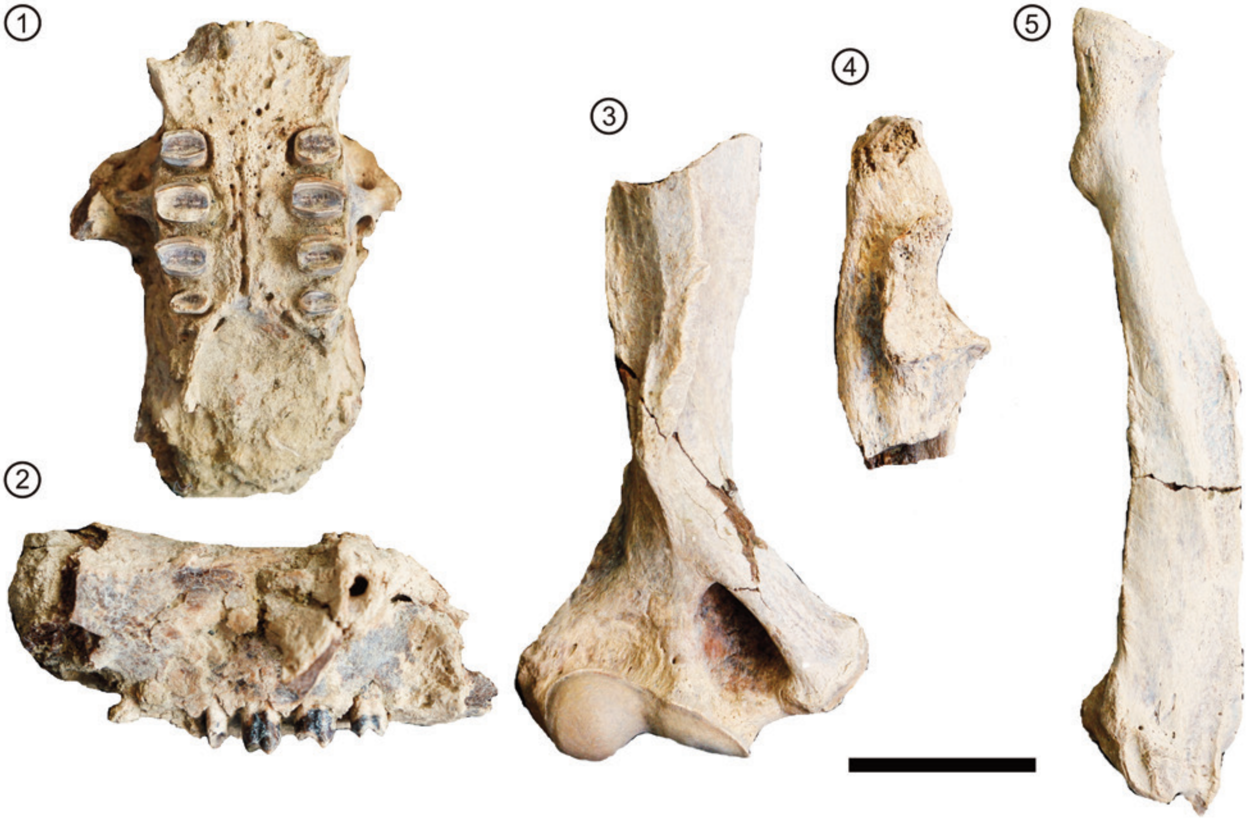

Figure 4. ***Hapalops*** **cf.** ***elongatus*** **MPM-PV 19353**. **1,** anterior portion of skull in palatal view; **2,** anterior portion ofskull in right lateral view; **3,** right humerus, anterior view; **4,** proximal portion of right ulna, lateral view; **5,** right radius, lateral view. Scale bar= 3 cm.

ever, belongs to a very young individual, as judged by the open intermaxillary suture, and may thus represent a larger species with more square molariforms, such as *E. infernalis* (MLP 4-7; Fig. 2.1–2). The palatal width of MPM-PV 19353 and 19318 is narrower than in *Hapalops platycephalus* (YPM-VPPU 15564) and more similar to the condition in *H. elongatus* (*e.g.*, YPM-VPPU 15011, 15597, 15545, and 15160) and *H. ruetimeyeri* (*e.g.*, AMNH 9250 and 9293, the latter as *H. ruetimeyeri*? by Scott, 1904). Confident assignment of both MPM-PV specimens to species is not possible, but as they are closer in size to the remains that Scott (1903, 1904) assigned to *H. elongatus* rather than *H. ruetimeyeri*, they are tentatively assigned to the former.

The nearly cylindrical mf3 of MPM-PV 19352 is the usual form of this tooth in *Hapalops* species, as well as in *Eucholoeops* and *Schismotherium*; as noted below, this morphology is diagnostic neither specifically not generically. MPM-PV 19352 is most similar morphologically and metrically to several specimens that Scott (1903, 1904: pl. 40, figs. 2–4) assigned to and illustrated as *H. elongatus*; hence its tentative assignment here to this species. The form of its molariform teeth are similar to that of YPM-PU 15110, assigned by Scott (1903: pl. 34, figs. 4, 5) to *H. indifferens*, but the latter is larger. *Hapalops elongatus* and *H. indifferens* are closely similar in dental morphology, but judging by the preserved portion of the mandibular spout of *H. indifferens*, it appears that the spout would have been longer than that of *H. elongatus*. It is considerably smaller than the remains assigned by Scott (1903) to *H. longiceps*, in which mf1 and mf2 are also rectangular rather than more nearly squared. The specimen, AMNH 9222, that Scott (1904: pl. 40, fig. 1, 1a) assigned to and figured as *H. rectangularis* is similar in size to MPM-PV 19352 and the *H. elongatus* remains, but mf1 and mf2 are more transversely expanded and thus more rectangular in the AMNH specimen.

MPM-PV 19317 strongly resembles MPM-PV 19352 in size and morphology of the molariforms, although the diastema appears slightly shorter. Although cf1 is not preserved, the homologous portions of MPM-PV 19317, as with MPM-PV 19352, sufficiently resemble in size and form those of remains assigned by Scott (1903, 1904) to *H. elongatus* to permit tentative assignment of MPM-PV 19317 to this species.

Genus ***Schismotherium*** Ameghino, 1887

Type species. *Schismotherium fractum* Ameghino, 1887. Santa Cruz Formation, Barrancas del Río Santa Cruz, Province of Santa Cruz, Argentina.

Schismotherium* cf. *fractum Ameghino, 1887

Figure 5.4, Table 1

Referred material. MPM-PV 19328, portion of L dentary with mf1-2 alveoli, and alveoli of cf1 and mf3 incomplete, and two ungual phalanges (one complete and one partial).

Geographic occurrence. Segundas Barrancas Blancas (Ea. Cordón Alto), Río Santa Cruz, Province of Santa Cruz, Argentina.

Stratigraphic occurrence. Santa Cruz Formation (Early-Middle Miocene).

Description. Although the specimen MPM-PV 19328 is incomplete (Fig. 5.4), there is clearly no diastema between the first and second alveoli. The preserved portion of the first alveolus suggest that the tooth was approximately cylindrical or oval and thus caniniform. The mf1 and mf2 alveoli suggest that the molariform teeth were oval and transversely expanded.

Comments. The lack of a diastema of MPM-PV 19328 excludes, among similarly sized specimens, remains assigned to *Hapalops*, *Eucholoeops*, and *Xyophorus*. The molariform teeth, oval and transversely expanded, also rules out *Nematherium*. Among reasonably well-known Santacrucian sloths, MPM-PV19328 most closely resembles the mandible

Figure 5. 1–3, *Hapalops* cf. *elongatus*. 1, MPM-PV 19352, right dentary, oclusal (upper) and right lateral view (lower); **2, MPM-PV 19317**, right dentary, occlusal (upper) and right lateral view (lower). **3, MPM-PV 19318**, anterior portion of skull in palatal view. **4, *Schismotherium* cf. *fractum* MPM-PV 19328**, portion of left dentary, occlusal view. Scale bars= 1 cm.

TABLE 1 – **Skull and mandible measurements (in mm) of the new specimens reported, as in De Iuliis *et al.* (2014)**

Skull	**Hapalops** *cf.* **elongatus**		*Mandible*	**Hapalops** *cf.* **elongatus**		**Schismotherium** *cf.* **fractum**	**Xyophorus atlanticus**	**Nematherium longirostris**
	MPM-PV 19353	*MPM-PV 19318*		*MPM-PV 19352*	*MPM-PV 19317*	*MPM-PV 19328*	*MPM-PV 19337*	*MPM-PV 19326*
Cf1	—	*4.50 / 5.25*	*cf1*	*4.77 / 5.49*	—	—	—	—
Mf1	*7.28 / 5.88*	*7.12 / 4.92*	*mf1*	*9.83 / 7.13*	*7.26 / 6.17*	*8.33 / 6.71*	*8.75 / 5.61*	*5.72 / 7.29*
Mf2	*8.44 / 6.42*	*9.02 / 5.28*	*mf2*	*9.45 / 7.25*	*7.10 / 6.40*	*8.63 / 6.37*	*8.80 / 6.15*	*7.03 / 7.88*
Mf3	*8.26 / 6.56*	*7.44 / 5.06*	*mf3*	*8.16 / 7.38*	*7.58 / 6.81*	—	*8.35 / 8.15*	*6.98 / 6.05*
Mf4	*6.54 / 3.98*	*~5.62 / ~4.17*	*H Ramus*	—	—	*21.62*	*18.25*	*5.46 / 7.28*
L Cf1-OC	—	—	*L cf1-mf3*	*35.80*	—	—	—	—
L Cf1-Mf4	—	*39.92*	*L Dias Mand*	*6.40*	*~4.06*	—	—	—
L Dias	*10.73*	*11.19*	*L Mand*	—	—	—	—	—
L Mf1-Mf4	*29.04*	*24.36*	*L mf1-mf3*	*25.79*	*21.58*	—	*21.76*	—
W Cf1	*~33.26*	—	*L Spout*	—	—	—	—	—
W Dias	*10.92*	—						
W Mast	—	—						
W Mf3	*26.61*	*~26.38*						
W Pal	*11.22 at M2*	*10.40 at M2*						
W Pal Cf1	*21.64*	—						
W Postorb	—	—						
W Preorb	—	*~27.50*						
W Temp	—	—						

Skull and upper teeth: ***Cf1,*** *transverse/mesiodistal diameters of caniniformor its alveolus;* ***Mf1-Mf4,*** *transverse/mesiodistal diameters of molariform teeth or their alveoli;* ***L Cf1-OC,*** *length from the mesial margin of Cf1 or of its alveolus to the posterior margin of the occipital condyles;* ***L Cf1-Mf4,*** *length from the mesial margin of Cf1 to the distal margin of Mf4 or of their alveoli;* ***L Dias,*** *diastema length;* ***L Mf1-Mf4,*** *length from the mesial margin of Mf1 to the distal margin of Mf4 or of their alveoli;* ***W Cf1,*** *maximum width across maxillae at level of Cf1s;* ***W Dias,*** *maximum width across maxillae at level of diastemata;* ***W Mast,*** *skull width across mastoid processes;* ***W Mf3,*** *maximum width between lateral borders of M3 alveoli;* ***W Pal,*** *minimum palatal diameter at M- (see Table);* ***W Pal Cf1,*** *palatal width between Cf1s or their alveoli;* ***W Postorb,*** *width at postorbital constriction;* ***W Preorb,*** *dorsal width at preorbital constriction;* ***W Temp,*** *width between temporal lines;* ***~,*** *estimated measurement. Mandible and lower teeth:* ***cf1,*** *transverse/mesiodistal diameters of caniniform or its alveolus;* ***mf1-mf3,*** *transverse/mesiodistal diameters of molariform teeth or their alveoli;* ***H Ramus,*** *maximal height of horizontal ramus at m3.* ***L cf1-mf3,*** *length from the mesial margin of c1 to the distal margin of mf3 or of their alveoli;* ***L Dias Mand,*** *length of mandibular diastema;* ***L Mand,*** *maximal mandibular length from anterior margin of spout to posterior margin of mandibular condyle;* ***L mf1-mf3,*** *length from the mesial margin of m1 to distal margin of m3 or of their alveoli;* ***L Spout,*** *length of the spout from anterior to posterior margins of mandibular symphysis;* ***~,*** *estimated measurement.*

(MACN-A 6446) of *Schismotherium fractum*. The specimen is therefore tentatively assigned to this species. This decision reflects the suggestion by Racco *et al.* (2018) that *Pelecyodon* may not be distinguishable from *Schismotherium*.

Genus ***Xyophorus*** Ameghino, 1887

Type species. *Xyophorus rostratus* Ameghino, 1887. Santa Cruz Formation, Barrancas del Río Santa Cruz, Province of Santa Cruz, Argentina.

Xyophorus atlanticus Ameghino, 1891a

Figure 6, Table 1

Referred material. MPM-PV 19337, partial L and R dentaries; L dentary preserving mf1-mf3 completely (occlusal surface of mf2 and mf3 broken); R dentary preserving mf2-mf3 completely, incomplete alveolus of mf1 with a tooth fragment; several incomplete vertebrae; proximal portions of R radius and L and R ulnae; nearly complete L femur; distal part of R femur; proximal portion of L tibia; R astragalus; several skeletal fragments.

Geographic occurrence. Segundas Barrancas Blancas (Ea. Cordón Alto), Río Santa Cruz, Province of Santa Cruz, Argentina.

Stratigraphic occurrence. Santa Cruz Formation (Early–Middle Miocene).

Description. The mf1 and mf2 of MPM-PV 19337 (Fig. 6.1) are compressed mesiodistally, particularly mf1, which is rectangular with slightly rounded corners, whereas mf2 is nearly rectangular. The mf3 is approximately cylindrical, with major axis set obliquely to the long axis of the tooth row. The radius bears an elliptical head, with a nearly flat ulnar facet, and a prominent bicipital tuber. The ulna (Fig. 6.2) possesses a well-developed olecranon process, aligned with the long axis of the diaphysis, and the semilunar notch is wide and triangular in anterior view. The radial notch is wide and flat. The femur (Fig. 6.3) has a gracile and nearly rectilinear diaphysis (bearing only a slight diaphyseal deflection); its head is spherical, with a distinct neck, and is flanked by a low greater trochanter and a pyramidal lesser trochanter. The well developed and distinct third trochanter projects laterally from midshaft. Distally the femur bears a wide and shallow patellar groove that is contiguous with both the medial and lateral condyles, of which the former is larger. The tibial plateau (Fig. 6.4) bears a flat medial condyle, with a proximally projected lateral margin that forms a sharp intercondyloid eminence and a convex lateral margin that descends to contact the fibular facet posteriorly. The tibial tuberosity is rugose and flat, and projects laterally. The astragalus (Fig. 6.5–7) possess a triangular trochlea tali, almost as wide as long, with gently convex condyles. The fibular facet is orthogonal to the trochlea, and the head, which bears a long and well defined neck, is triangular in anterior view, with an anteriorly protruding lateral lip and a smooth and rounded medial one. The navicular facet is concave and triangular. The cuboidal facet is flat and well defined and the sustentacular facet is convex and medially inclined. The ectal facet contacts the fibular facet only anteriorly.

Comments. In size and form the dentary portions, including the teeth, of MPM-PV 19337 are closely similar to those of the type of *Xyophorus atlanticus* (MACN-A 4631). Characteristic of the latter, and MPM-PV 19337, is that mf1 and mf2 are strongly compressed mesiodistally, with mf2 being rectangular and mf1 nearly so (the corners of this tooth are slightly rounded). The postcranial remains are quite representative of most Santacrucian sloths. The elliptical head of the radius is similar to that of *Hapalops longiceps* (YPM-VPPU 15523) and *Eucholoeops ingens* (MPM-PV 3451). The wide, triangular semilunar notch is similar to that of *Schismotherium fractum* (MACN-A 6445–6470) and differs from the narrow notch of *Hapalops longiceps* (YPM-VPPU 15523). The anconeal process is deflected laterally and the coronoid process is deflected medially. The femur is typical of stem megatherioid Santacrucian sloths, differing from the massive femur of *Prepotherium potens* (YPM-VPPU 15345). The well-developed third trochanter, projects laterally from midshaft, in contrast to the robust and proximodistally elongated third trochanter of *Prepotherium potens*. The morphology of the femur distally is characteristic of most Santacrucian sloths (see, for example, *Hapalops longiceps* YPM-VPPU 15523), as does that of the tibia proximally. The astragalus bears a general overall similarity to that of other Santacrucian sloths. The ectal facet contacts the fibular facet only anteriorly, leaving a posteriorly wide opening for the ligamentary fovea as in *Xyophorus simus* (MACN-A 4617-4618 and an unnumbered astragalus), while in other similarly-sized Santacrucian sloths (*i.e.*, not *Prepotherium*, see below) the facets contact each other both anteriorly and posteriorly (*e.g.*, *S. fractum* FMNH 13137), or the posterior isthmus is narrower (*e.g.*, *H. longiceps* YPM-VPPU 15523). Besides the features described above, the astragalus of MPM-PV 19337 shows several peculiarities that differentiate it. For example, the trochlea tali in dorsal view (Fig. 6.5) is shorter and more regularly triangular; the concave ectal facet is more rectangular (rather than crescent-shaped), is laterally inclined, and meets the fibular facet at an obtuse angle (rather than orthogonal, as in, *e.g.*, *Hapalops* species, and *S. fractum*); in plantar view (Fig. 6.6), the ectal facet diverges more markedly posteriorly from the fibular facet, adopting a more oblique condition than occurs in *H. longiceps*; and the sulcus tali is wider.

MEGATHERIIDAE Gray, 1821
PLANOPINAE Simpson, 1945

Planopinae indet.
Figure 7. 1–6

Referred material. MPM-PV 19323 (Fig. 7.1–3), R astragalus.

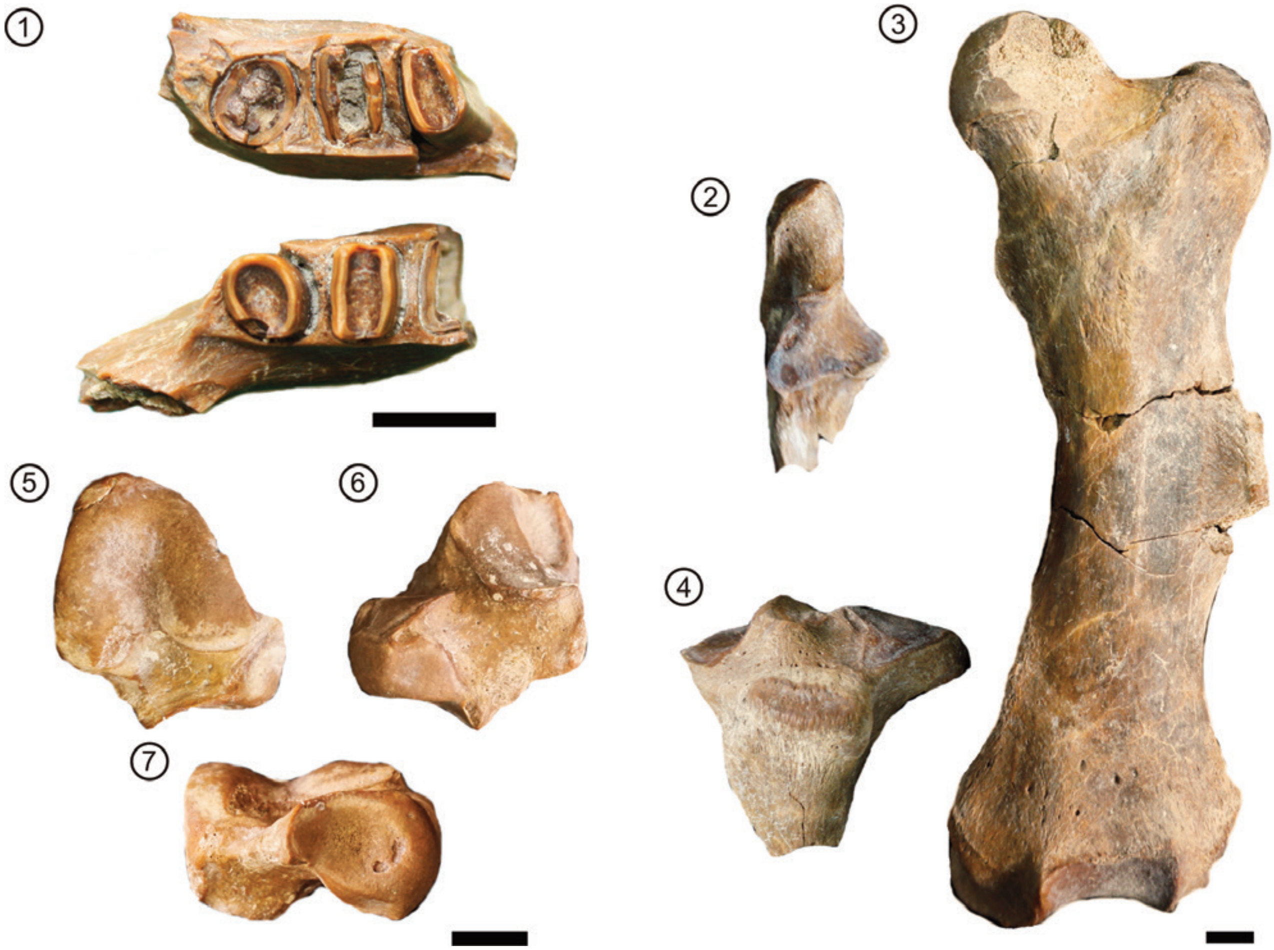

Figure 6. ***Xyophorus atlanticus*** **MPM-PV 19337**. **1,** left (upper) and right (lower) partial dentaries in occlusal view; **2,** proximal portion of right ulna, anterior view; **3,** left femur in anterior view; **4,** proximal portion of left tibia in anterior view; **5–7,** right astragalus in **5,** dorsal, **6,** plantar, and **7,** anterior views. Scale bars= 1 cm.

MPM-PV 19358 (Fig. 7.4–6), proximal two-thirds and distal epiphysis of a R humerus; proximal portion, patellar trochlea, and lateral distal condyle of a L femur; proximal epiphysis, nearly complete, and distal half of a R tibia; distal portion of a R fibula, including articular surfaces.

Geographic occurrence. Segundas Barrancas Blancas (Ea. Cordón Alto), Río Santa Cruz, Province of Santa Cruz, Argentina.

Stratigraphic occurrence. Santa Cruz Formation (Early–Middle Miocene).

Description. The astragalus, MPM-PV 19323 (Fig. 7.1–3), is short and massive. Its trochlea tali is wide and comparatively short, bearing a deep trochlear sulcus. The medial trochlear condyle (odontoid process) is rounded and short. The lateral trochlear condyle, gently convex, bears the discoid facet and is longer than the medial trochlear condyle. The fibular facet is flat, with its proximal margin contacting the lateral trochlear condyle. In anterior view it meets the trochlear plane at a right angle. The head is wide and bulky, with a very short neck, and hence the navicular facet is coincident with the anterior most margin of the lateral trochlear condyle. The facet for the navicular is composed of a concave, elliptical, mediolaterally elongated, and anteriorly-facing lateral portion and a smaller, convex, medially-facing portion. Ventrally the head bears a convex and smooth cuboidal facet. The elliptical and convex sustentacular facet is inclined medially. The ectal facet is crescentic and concave, and closely approaches the fibular facet anteriorly, leaving a ligamentary lateral fovea that is widely opened posteriorly. A wide and deep sulcus tali opens between sustentacular and ectal facets.

MPM-PV 19358 (Fig. 7.4–6) comprises partially preserved long bones and several fragmentary remains of other elements. Their large size is notable. The humerus shows a round head, projecting more proximally than the tuberosities, and a well-developed and elongated deltopectoral shelf (Fig. 7.4). The distal epiphysis is wide, with a round capitulum and a medially elongated trochlea (Fig. 7.5). The cochlea tibiae is wider than long, with clear and distinct grooves for the astragalar odontoid and discoid facets (Fig. 7.6). The process for the flexor tendons is conspicuous. The distal portion of the fibula bears a robust malleolus, with a flat tibial facet, a triangular to crescentic facet for the astragalus, and a posterior isthmus for ligaments.

Comments. MPM-PV19323 strongly resembles the holotype of *Prepotherium potens* MACN-A 4694 and the astragali of the holotype of *Planops martini* (NHMUK PV M 43404) in the features described above, including size. In this sense, the astragalus of this specimen, as well as of *Prepotherium potens* and *Planops martini*, is at least 20% larger than in the next largest Santacrucian sloths (*e.g.*, *Analcimorphus giganteus*, YPM-VPPU 15561, and *Hapalops longiceps*, YPM-VPPU 15523). The peg-shaped medial trochlear condyle resembles the peg-shaped morphology present in later megatheriines and mylodontids, and differs from the condition in other species such as *H. longiceps*, *A. giganteus,* and *Schismotherium fractum* (FMNH 13137), while the lateral trochlear condyle is more elongated. The trochlear sulcus is also deeper. The short-necked head is similar to that of both *Prepotherium* and *Planops* while, conversely, in the other above-mentioned sloths the neck is conspicuous, and the same is true for an astragalus assigned dubiously to *Nematherium* (YPM-VPPU 15965, see Scott, 1904). The sustentacular facet differs from that described for *Nematherium*, where it is divided into two flat and orthogonally disposed facets; a similar morphology is described by Hoffstetter (1961) for *Planops martini*. This appears to be the only difference with *Planops*. In other Santacrucian sloths the posterior portions of the fibular and ectal facets approach each other closely, conversely to the condition in this specimen and in *Prepotherium*. The fibular facet of *Prepotherium* is more extensive anteriorly and is contiguous with the ectal facet, rendering the fovea much shorter; and the two facets are widely separated posteriorly, so that the fovea is also taller. These details, along with a less posteriorly positioned odontoid process, are the only differences with *Prepotherium*. The astragalus also strong resembles that of the Early Miocene Planopinae *Prepoplanops boleadorensis* (MLP 97-XI-3-1) from Cerro Boleadoras Formation (Northwestern of the Province of Santa Cruz) as described in Carlini *et al.* (2013).

Summarizing, the large size of this specimen and the development of its medial trochlear condyle align it to the Santacrucian sloths described as *Prepotherium* and *Planops*, which have been variably assigned, within Megatheriidae, to Planopinae (see Mones, 1986) or Prepotheriina (see McKenna and Bell, 1997), although Planopinae appears to be more current. However, the differences of MPM-PV 19323 from one or the other genus preclude confident generic assignment. Therefore, it is assigned only to Planopinae.

In addition to the elements listed above for MPM-PV 19358, this specimen includes several additional partial elements of a single individual. The listed remains are those that are sufficiently preserved to permit comparisons. They are relatively massive compared to the sloth remains typically recovered from the SCF, and thus compare closely in size with the homologous portions of elements of *Planops martini* (Hoffstetter, 1961: NHMUK PV M 43404), *Prepotherium potens* (YPM-VPPU 15345), and *Prepoplanops boleadorensis* (MLP 97-XI-3-1; Carlini *et al.*, 2013). Examples of such dimensions are the width across the humeral deltopectoral shelf and distal humeral articular surface, and width of the cochlea tibiae of the tibia. MPM-PV 19358 also closely resembles morphologically the remains of these two species in such features as the shape of the humeral head and tuberosities and their relative positions, shape and extent of the humeral deltopectoral shelf, shape of the greater trochanter of the femur, and size and shape of the cochlea tibiae. The shape of the medial portion of the cochlea tibiae suggests that the medial astragalar condyle was peg shaped, as occurs in *Planops* and *Prepotherium*. Other large humeri recovered from Santacrucian levels have been recognized as mylodontid (*e.g.*, YPM-VPPU 15374), but that of MPM-PV 19358 does not possess as expanded a del-

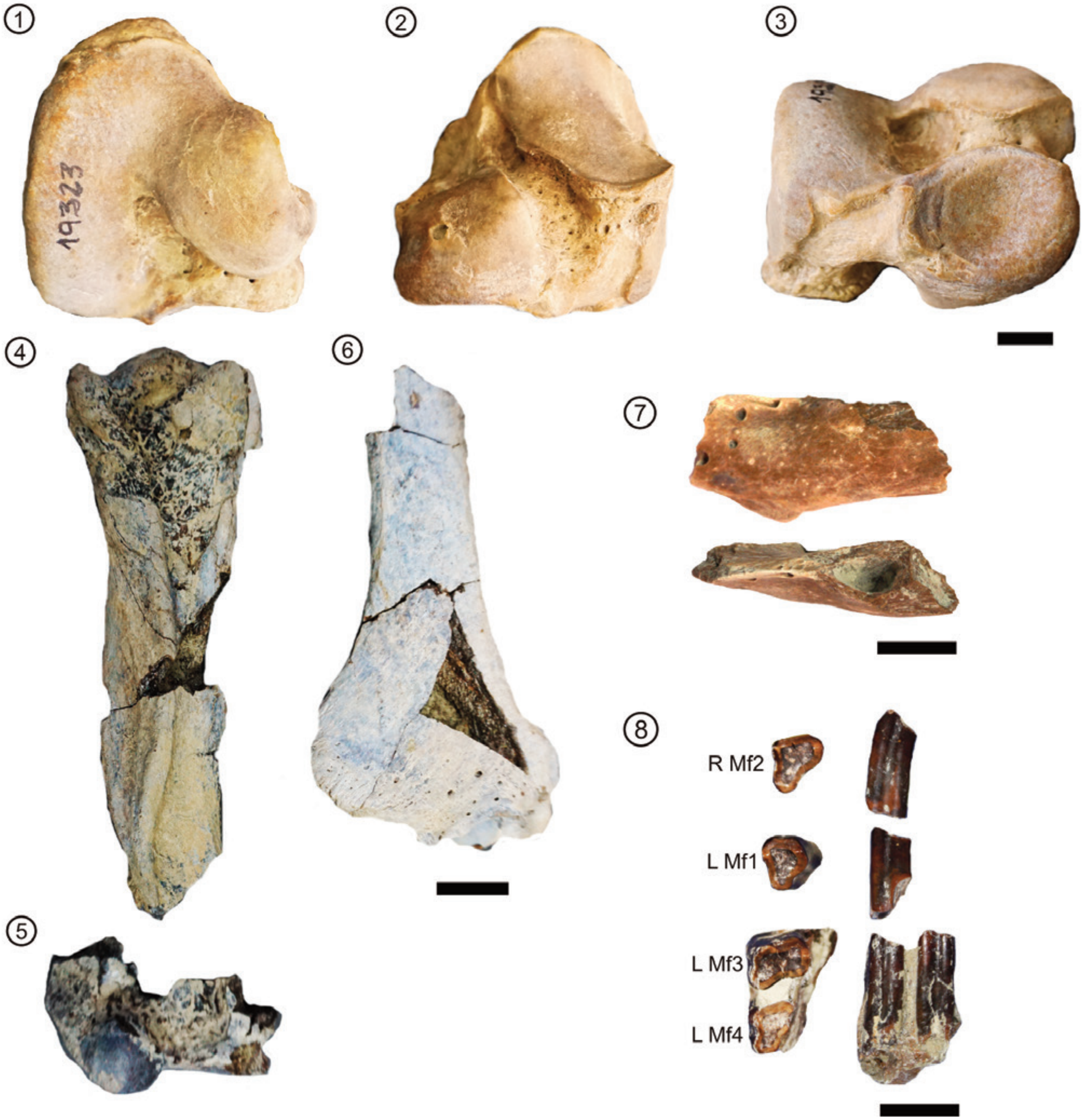

Figure 7. Planopinae indet. MPM-PV 19323, right astragalus. **1,** dorsal view; **2,** plantar view; **3,** anterior view. Scale bar= 1 cm. **MPM-PV 19358**. **4,** proximal portion of right humerus in anterior view; **5,** distal epiphysis of right humerus in anterior view; **6,** distal half of right tibia in anterior view. Scale bar= 3 cm.**7-8,** ***Nematherium longirostris*** **MPM-PV 19326**. **7,** anterior fragment of left dentary in lateral view (above) and oclusal view (below); **8,** upper molariforms in oclusal view (to the left) and lateral view (to the right). Scale bar= 1 cm

topectoral shelf as observed in mylodontids, or the overall robustness typical of these sloths. The size and morphology of MPM-PV 19358 allow confident assignment to Planopinae, but its remains are not sufficiently well preserved for a more precise identification.

MYLODONTIDAE Gill, 1872

Genus ***Nematherium*** Ameghino, 1887

Type species. *Nematherium angulatum* Ameghino, 1887. Santa Cruz Formation, Barrancas del Río Santa Cruz, Province of Santa Cruz, Argentina.

Nematherium longirostris Ameghino, 1891a

Figure 7.7–8, Table 1

Referred material. MPM-PV 19326, L dentary portion with mf1 alveolus, isolated upper teeth, and several skull fragments.
Geographic occurrence. Segundas Barrancas Blancas (Ea. Cordón Alto), Río Santa Cruz, Province of Santa Cruz, Argentina.
Stratigraphic occurrence. Santa Cruz Formation (Early-Middle Miocene).
Description. MPM-PV 19326 is an anterior portion of a L dentary, with part of the symphysis, the mf1 alveolus, and the mesial part of the mf2 alveolus (Fig. 7.7), four upper molariforms, L Mf1 and Mf3–4 connected by bone, and R Mf2 (Fig. 7.8). The skull fragments are very small and not identifiable.
Comments. The upper teeth of MPM-PV 19326 more closely resemble in form and size those of the type of *Nematherium longirostris*, MACN-A 4660 (a nearly complete skull for which Scott, 1904: pl. 63, fig. 3, illustrated only the palatal portion), than the type specimens of *Analcitherium antarcticum* (Scott, 1904: pl. 63, fig. 1a), *Ammotherium aculeatum* Ameghino, 1894 (see Scott, 1904: pl. 62, fig. 2a), *Ammotherium declivum* Ameghino, 1891a (see Scott, 1904: pl. 62, fig. 4a), and *Lymodon perfectus* Ameghino, 1891a (see Scott, 1904: pl. 62, fig. 1a). The dentary portion of MPM-PV 19326 is fragmentary and preserves the alveolus of cf1. It is probably of a young individual because the symphyseal suture is open. MPM-PV 19326 is assigned to *N. longirostris* for the reasons explained below.

COMMENTARY ON AMEGHINO'S 1887 TAXA

This section provides a brief account of Ameghino's (1887) taxa (type specimens) recorded from the Río Santa Cruz, including their descriptions, current taxonomic status, and figures when possible (Table 2). In the Discussion, we provide a historical and critical review of their taxonomy, focusing on the taxa for which the remains reported here allow critical observations on taxonomic and systematic issues regarding them.

Schismotherium fractum *Ameghino, 1887, p. 21*

The type specimen (an incomplete dentary, no record of the catalogue number) on which Ameghino (1887) erected this species was never figured, and Mones (1986, p. 250) indicated that it was lost. However, the specimen appears in Scott's album (Vizcaíno *et al.*, 2017: Suppl. files, Appendix 1, p. 64, fig. 125d; Fig. 3.4), but it does not match Ameghino's (1887, 1889) descriptions. Recent efforts to find the holotype at the MLP collection were unsuccessful, so designation of a neotype was required to permit further systematic analyses. Racco *et al.* (2018) provided an extensive description of the events that occurred during the years that followed C. Ameghino's expedition to the Río Santa Cruz, including the destiny of the fossils collected. These authors designated MACN-A 6445–6470 as the neotype for the species *Schismotherium fractum*, a specimen that was recognized by Ameghino (1894, 1898) and illustrated by Scott (1904), and includes a complete skull and mandible, several vertebrae, and elements of the forelimb and hind limb.

Eucholoeops ingens *Ameghino, 1887, p. 21*

The designation of *Eucholoeops ingens* was based on a complete skull and mandible, largely covered by hard matrix, that was never figured, and for which there is no record of the catalogue number. Mones (1986, p. 248) indicated that it was housed at the MLP, but lost. Exhaustive searches for the original type specimen failed. New well-preserved remains of *Eucholoeops* recovered in the last 15 years by MLP-MACN-Duke University expeditions allowed De Iuliis *et al.* (2014) to provide a revision of the status of several species erected for *Eucholoeops*, focusing on *E. ingens*, and designated a neotype for the latter, MPM-PV 3401.

Eucholoeops infernalis *Ameghino, 1887, p. 21*

The type of *E. infernalis* (MLP 4-7; Fig. 2.1–2) had not been previously figured, although it appears in Scott's album (Vizcaíno *et al.*, 2017: Suppl. files, Appendix 1, p. 61, fig. 120), and identified as the type. It consists of the anterior part of a skull with left and right molariforms present but with their occlusal surface broken, and only the basal portion of the right Cf1, broken deeply within its alveolus, preserved. Ameghino's original diagnosis mentioned a cf1, but there are no associated mandibular remains. Fernicola (2011) noted that MLP 4-7 could not be located, but it has since been recovered. MACN-A 2095 is identified in MACN records as the type of *E. infernalis*, but this is incorrect as explained below in the Discussion.

Eucholoeops adteger *Ameghino, 1887, p. 21–22*

The type specimen of *E. adteger* (MLP 4-63; Fig. 2.3–4) is a left maxillary portion preserving Mf1-3, the mesial part of the Mf4 alveolus, and the distal part of the Cf1 alveolus of a very young individual, as evidenced by the open intermaxillary suture. The specimen had not been previously figured in the literature, but appears in Scott's album as the type of *Hapalops adteger* (Vizcaíno *et al.*, 2017: Suppl. files, Appendix 1, p. 64, fig. 125c; Fig. 3.3). Ameghino (1891a) transferred the species to *Hapalops*, whereas Mercerat (1891) moved it to *Eurysodon*, based on the same specimen. Scott (1904, p. 258) synonymized it with *Hapalops*. MACN records indicate that MACN-A 4509, a right mandibular ramus, and MACN-A 4510, a left mandibular ramus, from the same individual comprise the type of this species (as *Hapalops adteger*), but this is not correct (see Table 2).

Hapalops rectangularis *Ameghino, 1887, p. 22*

The type specimen of *H. rectangularis* is lost (no record of the catalogue number at MLP). Ameghino (1889) noted that it included the posterior part of a left dentary, with a complete mf3 and the distal part of mf2, but missing the coronoid and angular processes. He described this specimen, as well another, as the two specimens that represented this species. The second specimen was described as the posterior portion of the right dentary with mf2–3 and part of mf1 (see Ameghino, 1889) The left dentary was figured by Scott (1903, p. 206, fig. 29) and appears (albeit as a poor image) in Scott's album (Vizcaíno *et al.*, 2017: Suppl. files, Appendix 1, p. 64, fig. 125a; Fig. 3.1); it is identified as the type of *H. rectangularis* in both sources. MACN-A 2089 and MACN-A 2091 are identified as the type specimens of *H. rectangularis* in the MACN catalogue and in Mones (1986, p. 249).These remains, considered in more detail below, are clearly not so (see Table 2), and are among the remains that Ameghino came to consider as alternate types for several of the species he erected on material to which he no longer had access.

Hapalops indifferens *Ameghino, 1887, p. 22*

The type specimen (MLP 4-33, Fig. 2.7–8) is a right mandibular ramus preserving cf1 broken below the level of the alveolar margin, the alveoli of mf1-mf2, and the partial alveolus of mf3. It is figured in Scott (1903, p. 208, fig. 31) and appears in his album (Vizcaíno *et al.*, 2017: Suppl. files, Appendix 1, p. 64, fig.125f; Fig. 3.6). It is indicated as the type of this species in both sources. MACN records indicate that MACN-A 2093, a nearly complete skull, and MACN-A 2094, a right mandibular ramus belonging to the same individual as MACN-A 2093, comprise the type of this species; however, it is clear that this is incorrect (see Table 2).

Hapalops ellipticus *Ameghino, 1887, p. 22*

The type specimen (MLP 4-44; Fig. 2.5–6), is a partial left dentary preserving mf1–3, poorly preserved but with the section of these teeth intact. The specimen was figured by Scott (1903, p. 206, fig. 30) and appears in his album (Vizcaíno *et al.*, 2017: Suppl. files, Appendix 1, p. 64, fig. 125b; Fig. 3.2), and indicated as the type in both sources. Scott (1903) synonymized this species with *H. rectangularis*. MACN records indicates that MACN-A 1089, a right mandibular ramus, is the type of *H. ellipticus*, but it is clearly not the original type (see Table 2).

Trematherium intermixtum *Ameghino, 1887, p. 22*

The type specimen (MLP 4-45; Fig. 2.9–10) is a partial left dentary preserving the alveolus of mf2, all but the lingual wall of the mf3 alveolus, and the distal part of the mf1 alveolus. It has never been figured, but appears in Scott's album and is noted as the type (Vizcaíno *et al.*, 2017: Suppl.

TABLE 2 – Taxonomic synopsis of Ameghino's (1887) sloth species[1]

Species	*Type specimen*	*Invalid types in MACN-A catalogue*	*Current status and references*
Schismotherium fractum	*Lost. No catalogue number at MLP. Figured in Scott's album (Vizcaíno* et al., *2017; see Fig. 3.4, this work).*	—	**Schismotherium fractum**, *Neotype MACN-A 6445-70, Racco* et al. *(2018)*
Eucholoeops ingens	*Lost. No catalogue number at MLP. Not figured.*	—	**Eucholoeops ingens**, *Neotype MPM-PV 3401, De Iuliis* et al. *(2014)*
Eucholoeops infernalis	*MLP 4-7, Fig. 2.1–2. Figured in Scott's album (Vizcaíno* et al., *2017).*	*MACN-A 2095*	**Hapalops infernalis** *Scott (1904)*
Eucholoeops adteger	*MLP 4-63, Fig. 2.3–4. Figured in Scott's album (Vizcaíno* et al., *2017; see Fig. 3.3, this work).*	*MACN-A 4509-10 [2]*	**Hapalops adteger** *Scott (1904)*
Hapalops rectangularis	*Lost. No catalogue number at MLP. Figured by Scott (1903), in Scott's album (Vizcaíno* et al., *2017; see Fig. 3.1, this work).*	*MACN-A 2089, 2091[3]*	**Hapalops rectangularis** *Scott (1903)*
Hapalops indifferens	*MLP 4-33, Fig. 2.7–8. Figured in Scott's album (Vizcaíno* et al., *2017; see Fig. 3.6, this work).*	*MACN-A 2093-94[2]*	**Hapalops indifferens** *Scott (1903)*
Hapalops ellipticus	*MLP 4-44, Fig. 2.5–6. Figured by Scott (1903) and in Scott's album (Vizcaíno* et al., *2017; see Fig. 3.2, this work).*	*MACN-A 1089*	**Hapalops rectangularis** *Scott (1903)*
Trematherium intermixtum	*MLP 4-45, Fig. 2.9–10. Figured in Scott's album (Vizcaíno* et al., *2017).*	—	*Edentata* incertae sedis *Scott (1904)*
Nematherium angulatum	*Lost. No catalogue number at MLP. Not figured.*	—	**Nematherium angulatum** *Scott (1904)*
Nematherium sinuatum	*Lost. No catalogue number at MLP. Not figured.*	—	**Nematherium angulatum** *Scott (1904)*
Planops longirostratus	*Lost. No catalogue number at MLP. Figured in Scott's album (Vizcaíno* et al., *2017; see Fig. 3.5, this work).*	*MACN-A 4637*	**Planops longirostratus** *Scott (1904)*
Xyophorus rostratus	*Lost. No catalogue number at MLP. Figured in Scott's album (Vizcaíno* et al., *2017).*	—	**Hapalops rostratus** *Scott (1904)*
Xyophorus simus	*Lost. No catalogue number at MLP. Figured in Scott's album (Vizcaíno* et al., *2017).*	*MACN-A 6417,* *MACN-A 4636*	**Hapalops rostratus** *Scott (1904)*
Entelops dispar	*Lost. No catalogue number at MLP. Not figured.*	—	*Edentata* incertae sedis *Scott (1904)*

[1]See text for further information. [2]MACN records indicate that these specimens belong to the same individual. [3]MACN records indicate that these specimens are probably from the same individual, as are MACN-A 2090 and 2092 (which, however, are not indicated as types).

files, Appendix 1, p. 66, fig.131e, and Appendix 2: p. 62, respectively). Mercerat (1891) considered it as *Schismotherium intermixtum*, which Scott (1904, p. 326) in part synonymized with *Trematherium intermixtum*. Scott (op. cit., p. 358–359) considered this species as Edentata *incertae sedis*.

Nematherium angulatum *and* N. sinuatum *Ameghino, 1887, p. 22–23*

The type specimens of *N. angulatum* and *N. sinuatum* are lost, as indicated by Mones (1986, p. 257), and there is no record of the catalogue numbers at MLP. They were never figured, and do not appear in Scott's album (Vizcaíno *et al.*, 2017: Suppl. files, Appendix 1, 2). Ameghino's (1887) description of *N. angulatum* recognized a greater resemblance of its molarifoms to those of *Mylodon* than to those of the genera he had previously described; *i.e.*, that at least some molariforms were lobated. Mf2 was considered "elipticocilíndrica;" Mf3–4 triangular; and mf4 bilobate, with the mesial lobe smaller than the distal. *Nematherium sinuatum* was described as slightly larger than *N. angulatum*, and with mf4 large, angular, and bilobate on its vestibular surface (*i.e.*, its vestibular surface bore an apicobasal sulcus), and the mesial lobe shorter but wider than the distal.

In addition to *Nematherium angulatum* and *N. sinuatum*, two other species were erected, *N. longirostris* Ameghino (1891a, p. 324) and *N. lavagnanum* Mercerat (1891, p. 26). Scott (1904) synonymized these last three species with *N. angulatum*. Further, this author also recognized additional species of *Nematherium* (*e.g.*, *N. auca* Ameghino, 1891a, *N. profundatum*, *N. declivum*; these species were originally described under *Ammotherium* and *Lymodon*) and provisionally recognized *Analcitherium*. Given that the remains of these taxa have not been critically revised since Scott's (1904) work (the efforts of Simpson, 1941, and Bordas, 1939, resulted only to further increase the number of *Nematherium* species) and that the original type of *Nematherium* is lost and was never figured, we retain *N. longirostris* pending a systematic revision.

Planops longirostratus *Ameghino, 1887, p. 23*

The type specimen of *P. longirostratus* is lost, as indicated by Mones (1986, p. 253), and there is no record of the catalogue number at MLP. It has been never figured, but it appears in Scott's album as the type (Vizcaíno *et al.* 2017: Suppl. files, Appendix 1, page 64, fig.125e; Fig. 3.5). Ameghino's (1887) description of the specimen indicates that Mf1, separated from Mf2 by a short diastema, was elliptical, with its major axis aligned with the long axis of the tooth row, and obliquely worn. The palate extended well beyond Mf1, producing an elongated rostrum. Ameghino (1889) noted that the species was known only from a fragment of a right maxilla, including the Cf1 and part of the Mf1 alveolus, which coincides precisely with the image in Scott's album, noted above. Carlini *et al.* (2013: fig. 7C) provided an illustration of a specimen, claiming that is was the "holotype of *Planops longirostratus* (no catalogue number)." Their illustration, however, is of an anterior part of a skull in palatal view, with a complete dentition, that does not match Ameghino's (1887) original description and, therefore, it is not the type specimen. The specimen illustrated in Carlini *et al.* (2013: fig. 7C) is AMNH 9302, which was illustrated by Scott (1904: pl. 59, fig. 1a).

MACN-A 4637 is catalogued as the type of *Planops longirostratus*. This specimen is a right maxilla of a juvenile individual and preserves Cf1, Mf1, the alveolus of Mf2, and Mf2–4. It does not match the descriptions of Ameghino (1887, 1889), and was recovered by C. Ameghino from Killik-Aike, a coastal locality along the Río Gallegos, in 1890–1891; it is thus not the original type and MACN records should be altered to reflect this.

Xyophorus rostratus *and* X. simus *Ameghino, 1887, p. 23*

The type specimens of *X. rostratus* and *X. simus* are lost, as indicated by Mones (1986, p. 251), and there is no record of the catalogue numbers at MLP. They have been never figured, but appear in Scott's album, *X. rostratus* as the type (Vizcaíno *et al.*, 2017: Suppl. files, Appendix 1, p. 66, fig. 131c), and *X. simus* not indicated as the type (Vizcaíno *et al.*, 2017: Suppl. files, Appendix 1, p. 9, fig. 14a, and p. 66, fig. 131d). *Xyophorus rostratus* appears as a mandibular fragment with one tooth, but the fragmentary nature of the specimen and poor quality of the image preclude any interpretation; *X. simus* is represented by the anterior portion of a skull (p. 9, fig. 14a) and a small mandibular fragment (p. 66, fig. 131d). They are not identified as types and do not match Ameghino's original description. MACN records indicate MACN-A 6417 and MACN-A 4636 as type specimens of *X. simus*, but this is incorrect (see Table 2), as explained in more detail below.

Entelops dispar *Ameghino, 1887, p. 23*

The type specimen of *E. dispar* is lost, as indicated by Mones (1986, p. 245), and there is no record of the catalogue number at MLP. Ameghino (1889, p. 654) described but did not figure it. Scott (1904, p. 360) did not describe it and only listed it under Edentata *incertae sedis*. This enigmatic taxon has received scant attention, but only in part due to the early loss of its type and only specimen and the absence of any visual reference: Ameghino's (1887, 1889) descriptions presented characteristics that were decidedly odd for a sloth. Pascual's (1961) description of *Entelops parodii*, based on MLP 58-V-21-1, verified these odd characteristics. The dentary of the latter carried ten teeth arranged to form a closed dental arcade. The distal three were bilobate in section, whereas those nearer the front of the dentary were apparently peg shaped and some possibly incisiform (see Hoffstetter, 1982; Pujos and De Iuliis, 2007). However, the status of *Entelops* as a sloth was and remains uncertain. It has been considered both a possible candidate as a basal sloth (see Pujos and De Iuliis, 2007) and dubiously a sloth at all (Hautier *et al.*, 2016). On a positive note, the concern expressed by Pujos and De Iuliis (2007) over the possible loss as well of the type of *E. parodii* was premature – the specimen has recently been rediscovered in MLP.

DISCUSSION

TAXONOMIC RICHNESS OF SANTACRUCIAN SLOTHS

In order to review the taxonomic richness of Santacrucian sloths, we evaluate the new remains reported here with those described by Ameghino (1887), and then compare them with other remains recently recovered from localities from the eastern coastal area of the Province of Santa Cruz (*e.g.*, between Ríos Coyle and Gallegos; Bargo *et al.*, 2012; Kay *et al.*, 2012) and from the western region (*e.g.*, Lago Posadas= Pueyrredón; Cuitiño *et al.*, 2019b).

Ameghino (1887) described 14 species from Río Santa Cruz localities (see above), of which only *Schismotherium fractum* and *Eucholoeops ingens* were recently reviewed and considered valid (Racco *et al.*, 2018 and De Iuliis *et al.*, 2014, respectively). The remaining species have not been critically reviewed since Scott (1903, 1904), as noted above (and see the discussions below). Whereas we are able to

Table 3 – Taxonomic richness of Santacrucian sloths: comparison of the Río Santa Cruz taxa with other localities recently studied

Taxa		*Río Santa Cruz (this article)*		*Eastern coastal localities*[1]	*Lago Posadas*[2]
		BB	*SBB*		
Megalonychidae	**Eucholoeops fronto**			x	
	Eucholoeops ingens			x	
Megatherioidea	**Hapalops** *sp.*	x	x	x	x
	cf. **Hapalops**	x	x		x
	Hapalops *cf.* **elongatus**	x	x		
	Hapalops platycephalus				x
	Hapalops gracilidens				x
	Pelecyodon cristatus			x	
	Hyperleptus garzonianus			x	
	Schismotherium *cf.* **fractum**		x		
	Xyophorus atlanticus		x		
	Megatherioidea indet.	x	x		x
Megatheriidae	*Planopinae indet.*		x		
	Megatheriidae indet.		x		
Mylodontidae	**Nematherium longirostris**		x		
	Nematherium *sp.*			x	
	Mylodontidae indet.	x			

[1] *Bargo* et al. *(2012), and Kay* et al. *(2012).* [2] *Cuitiño* et al. *(2019b)*

assign with some degree of confidence the remains reported here to only one, *Schismotherium* cf. *fractum* (MPM-PV 19328; Fig. 5.4), of Ameghino's (1887) species, our generic level assignments are broader. Of Ameghino's (op. cit.) eight described genera (*Schismotherium, Eucholoeops*, *Hapalops*, *Trematherium*, *Nematherium*, *Planops*, *Xyophorus*, and *Entelops*) we are able to recognize four: *Schismotherium, Hapalops*, *Nematherium*, and *Xyophorus*. As will become clear from the descriptions and discussions below, the inability for providing more confident and complete identifications at both the generic and species levels is due largely to the unstable taxonomy and systematics of these sloths. We report here remains of *Xyophorus atlanticus* (MPM-PV 19337; Fig. 6), based on near-identical morphologic and metric resemblance to the type of this species, MACN-A 4631. Similarly, we also report *Nematherium longirostris* (MPM-PV 19326; Fig. 7.6). These species were not described from Río Santa Cruz by Ameghino (1887). At a higher level, we record the presence of Planopinae, although we are unable to verify whether the remains belong to *Planops*.

Table 3 lists the taxa recovered from the Río Santa Cruz localities, as well as those reported by Bargo *et al.* (2012) and Kay *et al.* (2012) from four Atlantic coastal localities: Anfiteatro, Estancia La Costa, Cañadón Silva, and Puesto Estancia La Costa; and by Cuitiño *et al.* (2019b) from Lago Posadas (see Fernicola *et al*., 2019: figs. 1 and 5). The coastal localities (although these contain additional remains that have not yet been analyzed) yielded three genera and four species (*Eucholoeops ingens*, *E. fronto*, *Pelecyodon cristatus* and *Hyperleptus garzonianus*) not present in our collection, although *Eucholoeops* is recorded from the Río Santa Cruz, as reported by Ameghino (1887). The two regions (coastal localities and Río Santa Cruz) do share the presence of *Hapalops* and *Nematherium*. A notable difference is the presence of megatheriids (that is, large-sized sloths) from the Río Santa Cruz.

Our Río Santa Cruz localities and Lago Posadas share the presence of *Hapalops*. Likewise notable is the absence of large-sized sloths in Lago Posadas, although the total sample is much smaller.

CRITICAL TAXONOMIC REVIEW AND FURTHER CONSIDERATIONS

Scott's (1903, 1904) decisions largely suggest that he broadly accepted Ameghino's (1887, 1889) concepts of the genera as initially established from the fossil remains that Ameghino (1887, see Tab. 2) described and reinforced by material subsequently recovered from the Santa Cruz Formation by his brother C. Ameghino. The inclusion of these additional remains and F. Ameghino's lack of access to his original specimens introduced confusion over which specimens were being considered as he continued to develop and refine his concepts of the taxa first established in 1887, as explained in the following paragraphs.

As is well known, F. Ameghino's relationship with the MLP deteriorated to such an extent that he was denied access to many of the remains on which he had established the taxa under consideration (as well as of other taxa; see Fernicola, 2011). Because of these circumstances, Ameghino's (*e.g.*, 1889, 1891a, 1894) subsequent work, including the further development of his concepts of *H. rectangularis* and other Santacrucian sloths, relied on additional specimens collected by Carlos. Several of them were considered by Florentino (as recorded in the MACN catalogue) as alternate types for species based on material that he could no longer access (an example is noted above). Although these remains were important to Ameghino's further understanding of the Santacrucian sloths erected in 1887, it is worth keeping in mind that they were collected from different localities; that is, not from localities along the Río Santa Cruz, but from coastal localities. In addition to this, a large proportion (9 out of 14) of the 1887 type specimens are currently lost (Table 2), as explained below.

Scott's (1903, 1904) decisions with regard to the sloths erected by Ameghino (1887; 1891a, b; 1894) have come to represent the modern concept of the Santacrucian sloths, but it was clear then and remains so today that there are many more taxa than can be justified based on the available remains. Without improved resolution of the taxonomic issues, other aspects of the paleobiology (for example, the paleoecological context) of these sloths (and indeed of the Santacrucian fauna) cannot be reliably considered at the species and, albeit to a lesser degree, generic levels. However, Scott's taxonomic and systematic actions have largely been accepted uncritically (in stark contrast, we might add, to Ameghino's actions), and this, we suggest, has contributed in no small degree to the unsatisfactory understanding of these sloths. Given this state of affairs, it is worth considering whether Scott's actions should be laxly maintained or rigorously reconsidered.

While resolving the taxonomic and systematic issues is beyond the scope of this paper (this would require considerable morphological and metric analyses of the many specimens beyond those that were initially used to erect the taxa), we offer paths towards resolution for several of the genera first established by Ameghino (1887) by identifying contentious taxonomic and systematic issues, and by framing the questions that need to be addressed in order to reach robust decisions. Certainly, several of the taxonomic actions that must be made will involve arbitrary decisions (for example, on choice of neotypes; there is no other way out of the impasse), but this is acceptable provided that the decisions are justified based on rigorous argumentation and analyses.

Hapalops *and* Eucholoeops

These genera are discussed together because the taxonomic history of several of their species is intertwined, and it becomes difficult to discuss the one without numerous references to the other.

Ameghino (1887) erected *Hapalops rectangularis*, and described it as possessing four lower teeth, with the first tooth being small and caniniform in shape. Ameghino (1889, p. 686, translated from the original by the authors) noted that this species "is represented by two mandibular fragments, the posterior part from the left side, preserving the two last molars, and the posterior part from the right side, preserving the last two molars and part of the antepenultimate molar." From this, it is evident that neither specimen preserved the first (or most mesial) tooth. The left dentary was recognized as the type and as housed in MLP by Scott (1903: fig. 29; Vizcaíno *et al.*, 2017; Fig. 3.1), and is considered lost; this specimen matches Ameghino's (1889) description of the partial left dentary. The identity of the right side dentary is unknown, and to our knowledge has not been mentioned since. The type specimen, however, did not match Ameghino's (1887) original description, in the sense that it was insufficiently preserved to have served this purpose, as was noted by Mercerat (1891); Ameghino (1887) could not have determined the form of the anteriormost tooth, which was described as caniniform in shape, from the type specimen. Indeed, Ameghino (1889) made no mention of a caniniform tooth in the description of *H. rectangularis*, but his generic description of *Hapalops* indicates the presence of a small, more or less cylindrical first tooth, separated from the remaining teeth (*i.e.*, a diastema was present, Ameghino, op. cit.).

Even though *H. rectangularis* is the type species of *Hapalops*, Scott (1903, p. 206) clearly recognized the inadequate nature of the type specimen of the species: "unfortunately, this fragment is uncharacteristic and might belong to any one of several species" of *Hapalops*. Nonetheless, Scott (1903, p. 206) saw fit to use AMNH 9222 as a proxy for this specimen, noting that it "is an excellently preserved mandible... with all the teeth in place, which agrees very clearly with the corresponding portion of the type and is probably referable to the same species." Scott (1903) then described this species based on AMNH 9222, and further noted that *H. rectangularis* is also distinguished on astragalar morphology, based on the astragalus of AMNH 9222. However, as this author himself noted, this depends on the correct association of the astragalus (and calcaneum) with the mandibular remains, and this association is not certain.

Ameghino (1887) erected two other *Hapalops* species, *H. indifferens* (MLP 4-33; Fig. 2.7–8) and *H. ellipticus* (MLP 4-44, Fig. 2.5–6). Given the similarity among the homologous portions of the three type specimens, it becomes evident that Ameghino (1887) likely proceeded by recognizing them as congeneric but as specifically distinct, and generically distinct from other sloth remains recovered from localities along the Río Santa Cruz. This would explain Ameghino's (1887) reference to a caniniform-like tooth in *H. rectangularis* despite the lack of appropriate material for this characterization to have been made (*i.e.*, based on Ameghino's 1889 descriptions, neither specimen known for *H. rectangularis* preserved a caniniform tooth or its alveolus), and Ameghino's (1889) formal presentation of a generic diagnosis for *Hapalops*. That is, Ameghino (1887) deduced the presence of a caniniform tooth in *H. rectangularis* (and *H. ellipticus*) based on its presence in a species, *H. indifferens*, which he considered congeneric with it.

Scott (1903, p. 206) synonymized *H. ellipticus* (as well as Mercerat's, 1891, *Schismotherium rectangularis* and Lydekker's, 1894, *Eucholoeops ingens*, in part) with *H. rectangularis*, although he offered no rigorous justification for this synonymy. As noted above, he supplemented the description of the species with AMNH 9222. Conversely, Scott (1903) maintained *H. indifferens* as a distinct species, but he did not provide justification for this decision based on the original type of this species: there is no attempt at comparison with the type of *H. rectangularis* or, for that matter, of *H. ellipticus*. Instead, he noted that the nearly complete mandible of YPM-VPPU 15110 (which also includes the anterior half of a skull with dentition preserved) is assignable to *H. indifferens*, and then proceeded to characterize the species based entirely on this specimen.

Ameghino (1887) erected three species of *Eucholoeops*: *E. ingens*, *E. infernalis*, and *E. adteger*. As noted above in Commentary on Ameghino's 1887 Taxa, *E. ingens* and several related species of *Eucholoeops* subsequently named by Ameghino (1891a, 1894) were treated by De Iuliis *et al.* (2014). The other two, *E. infernalis* and *E. adteger*, were subsequently transferred to *Hapalops* (Scott, 1904). Ameghino (1889, p. 694) considered *E. infernalis* as slightly smaller than *E. ingens*, based on the anterior part of a skull, with palate and dentition, "bastante destrozada [considerably destroyed or damaged]" and several maxillary fragments and isolated teeth. The partial skull is MLP 4-7 (Fig. 2.1–2), but the identity of the other remains is not known. Mf1 to Mf3 of MLP 4-7 are mesiodistally elongated, producing a nearly squared section.

Ameghino (1889, p. 694, pl. 34, figs. 9) illustrated MACN-A1061, the anterior part of a skull that closely resembles MLP 4-7, as *E. infernalis*. Although poorly preserved, its molariform alveolar sections are nearly squared, as in MLP 4-7. Ameghino (1894) maintained this species in *Eucholoeops*, but this decision may have been based on a different specimen, MACN-A2095 (see below). Mercerat (1891, p. 23) transferred it to *Eurysodon infernalis*. Lydekker (1894, pl. 59, figs. 1, 1a) illustrated a partial skull as *Pseudhapalops infernalis*, but this is not any of those noted here. Scott (1904) transferred Ameghino's (1887) *E. infernalis* (and Lydekker's 1894 *Pseudhapalops infernalis*) to *Hapalops*. Scott (op. cit., p. 238–239) noted that the type specimen "is in a much damaged condition, but apparently indicates a species different from any of the preceding representatives of *Hapalops*," but the only features explicitly noted are that the molariform teeth were relatively long mesiodistally and the "preorbital fossae of the maxillaries are unusually deep." MACN-A 2095 is identified in MACN records as the type of *E. infernalis*. This specimen is another of those that Ameghino selected as an alternate type for one of his species, but has not been considered in the literature (see below).

The remains on which *E. adteger* is based include at least a partial left maxilla (MLP 4-63; Fig. 2.2–3). Ameghino (1887) did not identify these remains explicitly but provided characters from these elements. Ameghino (1889) indicated that the species was known from a left partial maxilla, preserving the first three molariforms and partial Cf1 and Mf4 alveoli, a fragment of a right maxilla, preserving mf1 and mf2, and the anterior portion of a left dentary, preserving cf1 and part of the mf1 alveolus. Ameghino (1889: pl. 34, fig. 7) illustrated the left mandibular fragment, and retained the species in *Eucholoeops*, but considered that it might belong to a distinct genus. Ameghino (1891a, p. 317) transferred it to *Hapalops* (although the former genus is misspelled: "*Hapalops adteger*. = *Encholoeops adteger*, Amegh., 1887"). Mercerat (1891, p. 18) transferred Ameghino's species to his new genus *Eurysodon*. The latter author in effect followed Ameghino's (1889) opinion, but created a new genus to receive, in part, Ameghino's *Eucholoeops adteger*, in contrast to Ameghino's (1891a) transfer of the species to *Hapalops*. However, it may be conjectured that Mercerat (1891) was likely unaware of Ameghino's (1891a) action in time to have addressed it in his own publication: Ameghino (1891c; 1894) noted that Ameghino (1891a) and Mercerat (1891) appeared and were distributed as offprints during the first half of August, 1891, and second half of August, 1891, respectively. Mercerat (1891) only considered the left maxilla (the type, MLP 4-63; see above) as belonging to the species, and erected the new species *Eurysodon boulei* for reception of Ameghino's two other specimens.

A start to resolving the issues regarding *Hapalops* requires an understanding of the main differences that are apparent among Santacrucian sloths. Among those in which the most mesial tooth is caniniform and separated by a distinct diastema from the remaining molariform cheek teeth (that is, none of these are relatively simple, slender, and apicobasally curved), three dental patterns are apparent. These patterns are recognizable based on subsequently recovered and more complete remains than those reported on by Ameghino (1887, 1889). In one pattern, present in *Eucholoeops*, the caniniform tooth is large and tends to be triangular in section, and the molariform teeth, except for the distal lower, tend to be transversely expanded and elliptical; that is, the corners of the teeth are rounded. The other two patterns typically occur in species that have been attributed to *Hapalops*. These two patterns are similar in that the caniniform tooth is smaller and tends to be circular or oval in section and the molariform teeth tend to have angular corners, again except for the distal lower cheek tooth. In one pattern the teeth are more nearly squared (*e.g.*, *H*. *infernalis*) and in the other the teeth appear more rectangular (that is, somewhat transversely expanded, as in *e.g.*, *H*. *elongatus* and *H*. *longiceps*). Within this last group (*i.e.*, with rectangular molariforms) a distinction is apparent in the length of the symphyseal spout: in the type of *H*. *longiceps* (YPM-VPPU 15523) the spout, about equal to the length of the lower tooth row, is decidedly longer than in *H*. *elongatus* (*e.g.*, YPM-VPPU 15597), in which the spout is shorter than the lower tooth row length. These differences suggest the existence of two dental morphotypes, more nearly squared *vs.* rectangular cheek teeth, and within the latter a difference in symphyseal spout length. It should be noted that this difference is exaggerated in Scott (1903: pl. 32, fig. 1) because the illustration of the mandible of *H*. *longiceps* is inaccurate with regard to the length of the symphyseal spout: it is depicted as longer (decidedly more so than the lower tooth row length) than it actually is.

The remains from the Río Santa Cruz localities provide evidence that supports the presence of the two dental *Hapalops* morphotypes. In one the molariforms are relatively squared (the type of *E*. *infernalis*) and in the other relatively rectangular (MPM-PV 19318, *H.* cf. *elongatus*). The relatively squared morphotype also occurs in the type of *H*. *ponderosus* (YPM-VPPU 15520), and the rectangular morphotype in the type of *H*. *longiceps* (YPM-VPPU 15523). The significance of such differences has not been assessed. It may be that many of the specimens subsequently attributed to *Hapalops* (as by Scott, 1903, 1904) all represent a single species, but this conclusion would ignore the demonstrable difference of the *Hapalops* morphotypes based on dentition and mandibular spout length, as just noted.

Given the degree of confusion that persists over the taxonomy and systematics of *Hapalops*, we suggest that Scott's actions require rigorous reassessment. Three such actions are related to the nature of the type specimen of *H*. *rectangularis*: 1) recognition of *H*. *rectangularis* as a valid zoological (as opposed to nomenclatural) entity; 2) assignment of AMNH 9222 to *H*. *rectangularis*; and 3) synonymy of *H*. *ellipticus* with *H*. *rectangularis*.

It is clear that the type specimen of *H*. *rectangularis* is inadequate for diagnosis, but *H*. *rectangularis* is a valid name and cannot be easily dismissed (see below). Scott's (1903) comment, noted above, that it could belong to several species, was presumably meant to include other species of *Hapalops*. However, the only clearly identifiable portion is m4, which is nearly circular (though slightly deformed) with its major axis set obliquely to the long axis of the tooth row, a morphology that is essentially identical with that of other species identified as *Hapalops*, as well as that of *Eucholoeops ingens* (see De Iuliis *et al*., 2014: fig. 6A) and *Schismotherium fractum* (see Racco *et al*., 2018: fig. 2.1). Indeed, Mercerat (1891) made this very observation and considered *H*. *rectangularis* as a synonym of *S*. *fractum*. It is a vexing question indeed as to why Scott (1903), who so obviously considered the original type of *H*. *rectangularis* inadequate for diagnosing the species, let alone the genus, would have chosen to maintain this species with the aim of retaining and assigning other (including new) species to the same genus. An adequate diagnosis has not, to our knowledge, ever been published for *Hapalops*, and based on the utterly inadequate nature of the type specimen of the type species, it would be most unlikely that a diagnosis could be provided. For this reason, it is critical that a reasonable solution be found that promotes stability in nomenclature. As the type specimen cannot stand as an objective standard of reference, Scott's (1903, 1904) assignment of AMNH 9222 and synonymy of *H*. *ellipticus* cannot be readily maintained based on this author's reasoning. Given the ambiguity of the type and concept of *H*. *rectangularis*, retention of this species does not appear to offer any taxonomic or systematic advantages, barring perhaps the possibility that at least many of the numerous subsequently recovered remains (*i.e.*, species) recognized currently as *Hapalops* based on Scott (1903, 1904) are conspecific. However, this seems highly unlikely, given the differences in *Hapalops* morphotypes noted above. If conspecificity were the case, it would render the matter trivial, and the justification for retaining the name could then indeed be that it is the type species of *Hapalops*, effectively following Scott (1903). However, the decision is not straightforward, given Scott's (1903, 1904) actions. The appropriate (we might even say, correct) action, in 1903, would have been to restrict the genus *Hapalops* to *H. rectangularis* (thus recognizing that it was a valid name) but, given its inadequate type, refer other species to other known or new genera. This would have had the advantage of isolating *H. rectangularis*. However, we are now more than 100 years beyond this, and *Hapalops* has become well known and accepted, and there is advantage in retaining it for stability in nomenclature.

A possible solution is to retain *H. rectangularis*, in acknowledgement of Scott's role as first reviser (see De Iuliis *et al.*, 2014). The chain of procedure would then be to designate a neotype. There are at least two possible candidates: AMNH 9222 (a complete mandible), and MACN-A 2089–2092 (including the remains attributed by MACN records as probably belonging to the same individual, but only 2089, a right mandibular ramus, and 2091, a complete skull that cannot be located, are listed as type specimens; 2090 is a left mandibular ramus and 2092 includes postcranial remains (*e.g.*, atlas, phalanges)). In choosing between them, a decision would need to consider the degree to which 1) Scott's role as first reviser should be maintained (the species is currently known on Scott's (1903) description of AMNH 9222), and 2) Ameghino's influence on the concept of the species should be considered, as this author choose the MACN remains as alternate types for his concept of the species. If the first consideration is deemed more appropriate, then the neotype would be AMNH 9222; if the second, then MACN-A 2089–2092. Once a decision is reached the second specimen must be compared with the first to evaluate whether the former is conspecific with the latter. A cursory comparison suggests that they are not. In AMNH 9222 the lower molariforms tend to be transversely wide, whereas in MACN-A 2089 and 2090 they tend to be more squared, strongly resembling the specimens that Scott (1904, pl. 40, figs. 2–4) assigned to *H. elongatus* (YPM-VPPU 15155, 15597, and 15531). A complicating issue is that MACN-A 2089 and 2090 strongly resemble MLP 4-33, the type of *H. indifferens*, in size, section of the teeth, and the oval and obliquely oriented alveolus of cf1; it would appear that these two sets of remains are almost certainly conspecific.

There is also the question of Scott's (1903) synonymy of *H. ellipticus* with *H. rectangularis*. Although there may be little reason to doubt this synonymy, given the minor metric and morphological differences apparent between the two specimens, neither is there reason to accept it –there is no objective way of evaluating this decision due to the insufficient preservation of the type of *H. rectangularis*. Further, it is not clear that the type of *H. ellipticus* represents *Hapalops*, as mf2 is oval in section.

Scott's methods of reasoning in his recognition of *H. indifferens*, in contrast to his synonymy of *H. ellipticus* with *H. rectangularis*, requires scrutiny. It is clear, on the one hand, that this author was willing to accept individual variation, but his application of this criterion was inconsistent. For example, there was no hesitation in synonymizing *H. ellipticus* with *H. rectangularis* despite minor metric differences; on the other hand, he was willing to assign YPM-VPPU 15110 to *H. indifferens* despite a "remarkable" difference in position of the mental foramen, a difference that Scott (1903, p. 208; pl. 34, figs. 1–5) regarded as "doubtless individual merely."

However, the solution of recognizing and retaining *H. rectangularis* as the type species of *Hapalops* is problematic for the following reasons. The description of the species given by Ameghino (1887) cannot have been based on the type –it was simply not sufficiently complete for Ameghino to have drawn the characters indicated from it; the "diagnostic" features were drawn from other specimens that Ameghino erected as species that he considered congeneric with the type of *H. rectangularis* (as alluded to above, this is the most plausible explanation for Ameghino's actions, although it is not demonstrable). However, Ameghino's actions (for whatever reasons) were inappropriate: he could not have made this decision on sufficient information, given the nature of the type specimen. If we choose to accept *H. rectangularis* (and therefore *Hapalops*), our decision would be based ultimately on Scott's willingness to recognize it, based in turn on his acceptance of Ameghino's decision to recognize it as congeneric with remains assigned to other species of *Hapalops*. While a possibility, we maintain that this choice requires ignoring or overlooking the fact that it can never be objectively demonstrated –in other words, as we cannot test its accuracy (because we cannot know what *H. rectangularis* is), acceptance of *H. rectangularis* would undermine accuracy and objectivity in science.

In our opinion, we would do better to reject *H. rectangularis*, but attempt to salvage *Hapalops* –this would maintain a very well-known genus, thus promoting nomenclatural stability. There are several avenues for rejection that may be explored, including considering *H. rectangularis* a *nomen dubium*, *species inquirenda*, or *nomen vanum*. A *nomen dubium* is defined by the International Code of Zoological Nomenclature (ICZN, 1999) as a name of unknown or doubtful application. Although this applies to *H. rectangularis* (a name of doubtful application), Mones (1989) noted that the scope of this term allows for the possibility or even probability that its status will be elucidated. However, it should be clear from the preceding discussion that this would be highly unlikely for this species. *Species inquirenda* is defined by the Code as a species of doubtful identity needing further investigation. Similar to the argument just made for *nomen dubium*, it is highly unlikely that further investigation could be expected to elucidate the identity of *H. rectangularis*. *Nomen vanum* ("empty name") is not included in the ICZN but is one of many terms used by zoologists (see, for example, Mones, 1989; Dubois, 2010). Simpson (1945) applied this term to names for which the proper application cannot be determined, although they otherwise fulfill the requirements of the rules of nomenclature. As explained more fully by Simpson (1948), such names are not known to be valid and cannot be applied to any specimens besides the type or syntypes; in this sense they may have a standing in nomenclature, but not in zoology, and it is unlikely (even though it may be conceivable) that such names can be validated by future work. Mones (1989) noted that a component of a *nomen vanum* is poorness of the type specimen.

A designation of *nomen vanum* would seem to best fit the circumstances of *H. rectangularis*, particularly as the type, besides being a poor specimen, is lost. We suggest that this proposal be elevated to the Commission for rejection of *H. rectangularis* as the type species, and another species, preferably one of the others originally assigned by Ameghino (1887) to *Hapalops*, be designated as the type species of the genus. Of the two other species, *H. indifferens* and *H. ellipticus* (the type specimens of which are still available at MLP), it should be clear from the discussions above that *H. indifferens* is by far the better choice in serving for formulating a diagnosis of *Hapalops*, as its type is more complete and its features are those that have come to be recognized as characteristic of *Hapalops*. This proposal would "solve" the problem of *H. rectangularis*, while saving *Hapalops*, thereby stabilizing nomenclature. This would be preferable to, for example, reviving a junior synonym or naming a new genus.

The type of *E. infernalis* is MLP 4-7, as indicated above. Scott (1904) noted the relatively long mesiodistal dimension of the molariform teeth, but did not mention MACN-A1061, the specimen that Ameghino (1889) illustrated, which resembles the type in molariform shape. Neither did Scott (1904) mention MACN-A 2095, which appears in MACN records as the type of *E. infernalis*. This specimen, also the anterior part of a skull, is presumably the specimen on which Ameghino settled on as a basis for his concept of *E. infernalis*. However, the molariforms, mesiodistally compressed, are approximately oval in section and the caniniform is approximately triangular. These are features characteristic of *Eucholoeops*. Indeed, it may offer an explanation for Ameghino's (1889, 1894) continued retention of this species in *Eucholoeops*, whereas Scott (1904), likely based on the original type MLP 4-7, transferred the species to *Hapalops*. In any event, it is clear that MLP 4-7 is the type of the species and MACN records should be corrected in this regard.

Xyophorus

Ameghino (1887) erected *Xyophorus rostratus* and *X. simus*. This author described the former as possessing a horizontally worn, small, and approximately cylindrical ("elíptico cilíndrica") first lower tooth, separated from the remaining teeth by a diastema (although Ameghino did not consider it caniniform), and a short symphysis. These features were considered by Scott (1904, p. 239) as indicative of individuals of *Hapalops*. *Xyophorus simus* was distinguished by Ameghino (1887) as being twice the size of *X. rostratus*, with a shorter and stronger (more steeply tapered) symphyseal spout, and a completely cylindrical first lower tooth, which was also identified as a "muela" (cheek tooth or molariform) rather than a caniniform. It is unclear why Ameghino (1887) did not consider the first tooth as caniniform, but presumably he was influenced by aspects of its wear pattern as noted in Ameghino (1889).

Ameghino (1889) expanded the descriptions of these species. *Xyophorus rostratus* was represented by the anterior part of a left dentary, preserving the first tooth and symphyseal spout and part of the alveolus of the second tooth. The diastema was very short, very nearly the same length as the mesiodistal length of the first tooth. Of the second tooth, Ameghino (op. cit.) was only able to note that it was much larger than the first, but that its form could not be discerned. The type of *X. simus*, the anterior part of a right dentary, preserved the first tooth and part of the alveolus of the second. Both species were similar morphologically, except that the first tooth of *X. simus* was cylindrical (this appears to contradict the description of this tooth in *X. rostratus* as cylindrical in his 1887 description); the diastema, however, was about as long as the diameter of this tooth, as in the first species.

The type specimens of these two species are lost and were never figured, although that of *X. rostratus* (but not *X. simus*) appears in Scott's album (Vizcaíno *et al.*, 2017: see above, Commentary on Ameghino's 1887 Taxa). The anterior portion of the skull illustrated in Scott's album is MACN-A 6417 and is listed in MACN records as the type of *X. simus*. Associated with this skull portion is the nearly complete horizontal ramus of a left dentary, MACN-A 6418, and an unnumbered right astragalus. These remains clearly do not constitute the original type, as the horizontal ramus of the dentary (including cf1, mf3, and the alveoli of mf1 and mf2) is almost entirely preserved. Further, they were collected by C. Ameghino during 1892–1893. Confusingly, MACN records identify a second specimen as the type of *X. simus*. This is MACN-A 4636, the anterior end of a left dentary preserving the first lower tooth and the partial alveolus of the second. This specimen, although it has a diastema nearly equal in length to the diameter of the cylindrical first tooth, is not the original type either. The latter was a portion of a right dentary, rather than of a left, and MACN-A 4636 was collected by C. Ameghino during 1890–1891.

Ameghino (1891a) provided a generic description of *Xyophorus* and erected three more species, *X. sulcatus*, *X. atlanticus*, and *X. andinus*. Of the generic characteristics that are somewhat distinct from those typically ascribed to *Hapalops* are that the first upper and lower teeth are small and worn approximately horizontally and the symphyseal spout is short and strongly tapered ("puntiaguda"; Ameghino, 1891a, p. 320). Ameghino (op. cit.) characterized *X. sulcatus* as twice as large as *X. simus*. Mf2 to Mf4 were described as rectangular, with the vestibular surface of Mf1 and Mf2 bearing a marked apicobasal sulcus on their vestibular surface, but with the vestibular and lingual margins of Mf3 and Mf4 being rounded. In the dentary, mf1 and mf2 were rectangular, bearing a pronounced apicobasal sulcus on the lingual surface, and mf3 was cylindrical.

Scott's album illustrates a right maxilla as *X. sulcatus* (Vizcaíno *et al.*, 2017: Suppl. files, Appendix 1, p. 9, fig. 14b). This specimen is MACN-A 4629, clearly of a young individual given the open sutures, and identified by MACN records as the type of the species. The description and measurements given by Ameghino (1891a) for *X. sulcatus* leave no doubt that MACN-A 4629 is the maxillar portion on which this species is based. Similarly, MACN-A 4633, a nearly complete horizontal ramus of a left dentary preserving cf1-mf3, is almost surely the dentary discussed by Ameghino (1891a). A third specimen, MACN-A 4632, a portion of a right dentary, preserving mf1-mf3, is assigned by MACN records to *X. sulcatus*. The dentition is similar morphologically and nearly identical in size to that of MACN-A 4633, but in addition to the apicobasal sulcus on the lingual surface of mf1 and mf2, as in the latter specimen, the vestibular surface of mf1 and mf2 of MACN-A 4632 also bears an apicobasal sulcus. MACN-A 4629, 4632, and 4633 were recovered from Monte Observación by C. Ameghino during 1890–1891.

Xyophorus atlanticus is represented by several specimens in MACN. The type is MACN-A 4631, a mandible preserving nearly all of the left dentary (missing the tip of the coronoid and angular processes), including cf1-mf3, and the anterior part of the right dentary, preserving cf1 and the alveolus of mf1. It was collected by C. Ameghino from Corriguen-Kaik during 1890–1891. Ameghino (1891a) pointed out its salient features, among which are that it is larger and more robust than *X. sulcatus*, cf1 is small and followed by a long diastema, and, most notably, mf1 and, in particular, mf2 are strongly rectangular, and mesiodistally compressed. Also noteworthy is that cf1 is nearly triangular rather than cylindrical. This specimen appears in Scott's album (Vizcaíno *et al.*, 2017: Suppl. files, Appendix 1, p. 9, fig. 14c) and is indicated as the type, but its condition at that time differed from its current condition. For example, matrix was present between the dentaries, the right mf2 was within its alveolus, and more of the right dentary was preserved. Despite these differences, there is no doubt that MACN-A 4631 is the same specimen as in fig. 14c of Scott's album. A second specimen assigned to *X. atlanticus*, MACN-A 4630, was recovered from Sehuen, Province of Santa Cruz, by C. Ameghino during 1890–1891. It is not particularly well preserved, but the form of the molariform teeth strongly resembles that of MACN-A 4631. A third specimen, MACN-A6435, collected by C. Ameghino during 1891–1892 from Corriguen-Kaik, is also assigned in MACN records to *X. atlanticus*. It preserves the better part of both dentaries, including left cf1-mf3 and right cf1-mf2. The mf1 and mf2, however, are not as strongly rectangular and compressed as in the other specimens assigned to *X. atlanticus*.

Xyophorus andinus was described as being of similar size to but somewhat more robust than *X. atlanticus*. Judging by Ameghino's (1891a) description, the specimen on which this species is based preserved the four lower teeth. The specimen was not illustrated, but MACN-A 4634, preserving the left cf1-mf3 and right cf1 and most of mf1 is identified as the type of this species. It was recovered by C. Ameghino during 1890–1891 from Sehuen. The cf1 is triangular, as in the type of *X. atlanticus*; mf1 and mf2 are mesiodistally compressed, but they are not rectangular, particularly mf1, which is elliptical. In this regard the molariform teeth resemble those of the type of *H. ellipticus*, MLP 4-44.

Ameghino (1894) erected *X. crassissimus*, based on MACN-A 6436, recovered by C. Ameghino from Corriguen-Kaik during 1892–1893. This author noted that the specimen represented a species larger than *X. andinus* and possessed a short, high, and thick mandible. The specimen preserves the right cf1, left mf3, mesial half of mf2, and complete alveoli of the remaining teeth, except for the right mf3, for which only the mesial half of the alveolus is preserved. The mf1 and mf2 are mesiodistally compressed, but seem rather more elliptical than rectangular, although this is unclear owing to deformation.

The taxonomic confusion created by Mercerat (1891), who, as noted earlier, erected several genera and species without, in most cases, providing any diagnostic characters, extends to *Xyophorus*. Several species that Mercerat (1891) erected for *Eurysodon*, such as *E. nasutus*, *E. boulei*, and *E. rostratus*, were considered by Ameghino (1891c) as likely synonyms of *X. rostratus*, *X. sulcatus*, and *X. altanticus*, respectively. Ameghino (1894) formally synonymized *E. boulei* with *X. sulcatus*.

Scott (1903) included *Xyophorus* as a synonym of *Hapalops*. Specifically, Scott (op. cit., p. 217) considered both Ameghino's (1891a) *X. sulcatus* and Mercerat's (1891) *Eurysodon nasutus* as synonyms of *Hapalops elongatus*. Scott (1904, p. 239) transferred *X. rostratus* to *Hapalops*, as *H. rostratus*, and synonymized, with reservation, *X. simus* with it. Scott (1904: pl. 43, fig.1, 1a) considered the type of *X. rostratus* (noted above as now lost and never illustrated) as an unsatisfactory fragment of a very young animal (explaining its small size) and instead based his description on YPM-VPPU 15342, illustrated by him in the cited figure. This author reasoned that the type of *X. simus* represented an older and therefore larger individual of the same species. Scott (1904, p. 241; 260, respectively) transferred *X. atlanticus* to *H. atlanticus* and synonymized *X. andinus* with it, and transferred *X. crassissimus* to *Hapalops* as *H. crassissimus*. Scott (1904, p. 260) transferred Mercerat's *Eurysodon boulei* to *Hapalops* and included *X. sulcatus* in its synonymy list, as "*X. sulcatus* Amegh., in part; Enum. Synopt. Des Mamm. Foss. de Patagonie; 1894, p. 155." This likely refers to Ameghino's (1891c; 1894) synonymy of *E. boulei* with *X. sulcatus*. Many of Scott's (1903, 1904) actions were not accompanied by justification. In the case of *H. crassissimus* and *H. boulei*, Scott (1904, p. 258) listed them as among the species "concerning which I could arrive at no definite conclusions." Adding to the confusion, Scott (1904) transferred Mercerat's

(1891) *Eurysodon rostratus* to *Hapalops* as *H. rostratus*, not to be confused with *H. rostratus* (Ameghino, 1887); that is, *X. rostratus*, which (as noted above) was transferred by Scott (1904) to *Hapalops*.

Clearly, the taxonomic and systematic issues with many of the above mentioned taxa require careful and rigorous analyses, but such efforts are impeded by the confusion over which specimens Ameghino, Mercerat, and Scott used in their decisions, compounded by the fact that the original types of several taxa are no longer available. In the case of *Xyophorus*, the type specimen of the type species, *X. rostratus*, is lost and was never illustrated, as is the case as well for the second-named species, *X. simus*, which Scott (1904) considered as a synonym of *X. rostratus*. Given that *X. rostratus* is a valid name, one might accept Scott's (1904) decision as first reviewer to recognize YPM-VPPU 15342, designate it the neotype of *X. rostratus*, and base the concept of the species on this specimen. Alternatively, should the concept of *X. rostratus* not be reconcilable with these specimens, then the Commission may be petitioned to suppress the name and designate *X. simus* as the type species of the genus, perhaps with MACN-A 4617 and MACN-A 4618, the remains that Ameghino came to regard as the type of his species *X. simus*, as neotypes. In MACN-A 4618 mf1 and mf2 are not preserved but their alveoli suggest the typical (*i.e.*, mesiodistally uncompressed) form present in *Hapalops*. In any event, while it might be allowed that YPM-VPPU 15342 and MACN-A 4618 do represent *Hapalops*, it is not clear that *X. atlanticus*, *X. andinus*, and *X. crassissimus* do, given the striking mesiodistal compression of mf1 and mf2 in the type specimens of these species.

Despite Scott's (1903, 1904) synonymy of *Xyophorus* with *Hapalops*, subsequent workers have largely maintained *Xyophorus* (but see Perea, 1999), as manifest in the erection of *X. bondesioi* Scillato-Yané, 1979 and *X. villarroeli* Saint-André, 1996, and their recognition by, for example, Pujos *et al.* (2007) and Croft *et al.* (2009). The position of *Xyophorus* among other sloths has varied, as noted by Brandoni (2014). Croft *et al.* (2009) recognized *X.* cf. *bondesioi* as a nothrotheriid, whereas *Xyophorus* was considered as a basal megatherioid by De Iuliis *et al.* (2011), and as a megatherioid of uncertain position by Pujos *et al.* (2011). Brandoni (2014; see also Brandoni *et al.*, 2017) attempted to clarify the position of *Xyophorus* by recognizing two groups within *Xyophorus*. One included the classically known species with affinities to basal megatherioids from the Early–Middle Miocene SCF of Argentine Patagonia, for which this author retained *Xyophorus*. The second group, including species recorded from the Middle–Late Miocene of Argentina and Bolivia, were designated as '*Xyophorus*' and considered as nothrotheriids. In other words, *Xyophorus* was retained for Ameghino's (1887, 1891a, 1894) species, whereas those erected by Scillato-Yané (1979) and Saint-André (1996) were designated '*Xyophorus*,' '*X.*' *bondesioi* and '*X.*' *villarroeli*, respectively. Brandoni *et al.* (2017, p. 6) explained that erection of a new genus for '*Xyophorus*' could be justified on several features, but that "the scarcity of materials and their poor state of preservation prevents us from making a nearly complete diagnosis for a new genus".

Among the distinguishing features identified by Brandoni (2014) and Brandoni *et al.* (2017) are that the molariforms, at least mf1 and mf2, are nearly rectangular and mesiodistally compressed and apicobasal sulci are present on the lingual and vestibular surface of at least the mf1 and mf2 of '*Xypohorus*' but absent in *Xyophorus*. However, Brandoni (2014) and Brandoni *et al.* (2017) considered only *X. atlanticus*, *X. simus*, and *X. crassissimus*. The first two *Xyophorus* species erected by Ameghino (1887) were not considered, which is justified given that the original types are lost and were never figured, and the MACN specimens recorded as the types are clearly not so. However, the features present in Ameghino's (1891a) *X. sulcatus*, for which the type is available (see above), do not agree with some of the distinguishing characters outlined by Brandoni (2014) and Brandoni *et al.* (2017). Ameghino (1891a) noted the presence of an apicobasal sulcus on the lingual surface of mf1 and mf2, clearly visible on MACN-A 4633. Interestingly, an apicobasal sulcus is present on the lingual and vestibular surfaces of mf1 and mf2 in MACN-A 4632. Thus, the presence of such sulci in the molariforms of at least some basal Santacrucian megatherioids predates their appearance in the Middle to Late Miocene '*Xyophorus*' species. Also, the teeth of *X. sulcatus* are not mesiodistally compressed.

It is not clear how consideration of such features reflect the relationships and status of the Santacrucian megatherioids. *Xyophorus atlanticus*, *X. andinus*, and *X. crassissimus* seem to form a group, based on the marked mesiodistal compression of at least mf1 and mf2 and absence of apicobasal sulci. The dentition of *X. sulcatus* sets it apart from this group of species. In *X. sulcatus* mf1 and mf2 are uncompressed, resembling the condition present in remains that have typically been assigned to *Hapalops*, but these teeth bear apicobasal sulci on at least their lingual surface and possibly also on their vestibular surface if MACN-A 4632 is correctly assigned to *X. sulcatus*. Regardless, the evidence suggests that lingual and vestibular apicobasal sulci on mf1 and mf2 arose among Santacrucian megatherioid sloths.

Trematherium

Ameghino (1887, p. 22) described *Trematherium intermixtum* as possessing a small and cylindrical cf1, followed by "eliptico-cilíndricas"mf1-mf3, as in *Hapalops*. The distinguishing feature emphasized by this author was the extremely small posterolateral opening of the mandibular canal. It is unclear how Ameghino (1887) was able to note the presence and condition of cf1, given that this tooth is not preserved in the type. This may be a situation similar to that noted above for *Hapalops rectangularis*; that is, Ameghino considered *Trematherium* to be morphologically very similar to *Hapalops* (and thus deduced the form and size of an unpreserved cf1), but differing in possessing an extremely small opening of the mandibular canal. This is a reasonable assumption, for had a *Hapalops*-like morphology been preserved, it is likely that Ameghino (1887) would have reported the length of the diastema. Another possibility is that a more anterior portion was present but has since become lost. This suggestion seems less likely, based on Ameghino´s (1889) contradictory description, which noted the presence of only the base of the cf1 alveolus that indicated little separation between cf1 and mf1, but that only the distal part of the mf1 alveolus was preserved, and the image in Scott´s album (Vizcaíno *et al.*, 2017), which presents the condition of this specimen as it currently remains.

The type specimen of *T. intermixtum* is MLP 4-45 (Fig. 2.9–10). A second specimen is indicated in MACN records for this species, MACN-A 2097, a right mandibular ramus lacking teeth that also appears in Scott´s album (Vizcaíno *et al.* 2017: Suppl. files, Appendix 1, p. 30, fig. 62.2). This specimen preserves most of the cf1 alveolus, which is separated by a narrow gap from the mf1 alveolus, but this specimen was recovered by C. Ameghino in 1889–1890 and could not have been available for, at least, Ameghino´s (1887) publication. Further, the alveoli of mf1 and mf2 are transversely compressed and slightly oval compared to those of the type MLP 4-45, suggesting that the specimens are unlikely conspecific. On the other hand, the homologous elements of MLP 4-45 and MLP 4-33, the type of *Hapalops indifferens*, are nearly identical in size and form, suggesting that they are conspecific. Ameghino (1889) named a second species, *T. nanum*, drawing attention to its smaller size and, particularly, very small openings for the posterolateral opening of the mandibular canal. Mones (1986) indicated this specimen as lost, but MACN records indicate that MACN-A 4617 is the type of this species. It differs from MACN-A 2097 at least in possessing a diastema, but the two portions of the left mandibular ramus of this specimen do not belong to the same individual.

CONCLUDING THOUGHTS

The recovery of new remains from localities along the Río Santa Cruz provides an opportunity to revisit the taxa established by Ameghino (1887) on fossils recovered by his brother Carlos from localities along this river. These latter remains are the types of numerous Santacrucian mammalian taxa erected by Ameghino (1887), although several are lost. The new specimens reported here, along with other recently recovered collections from the SCF, are potentially useful in verifying Ameghino's original descriptions and revision of the Santacrucian taxa. With particular regard to Santacrucian sloths, these fossils provide a window for reconsideration of Scott's (1903, 1904) taxonomic and systematic decisions, which have been largely and uncritically accepted for more than a century. Although the latter author's efforts were monumental in scope, they require analyses by modern methods.

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REFERENCES

Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de Patagonia Austral y depositados en el Museo de La Plata. *Boletín del Museo de La Plata,* p. 1–26.

Ameghino, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas de la Academia Nacional de Ciencias en Córdoba* 6: 1–1027 + Atlas: [xi], 98 pls. Buenos Aires.

Ameghino, F. 1891a. Nuevos restos de mamíferos fósiles descubiertos por Cárlos 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. 1891c. Observaciones críticas sobre los mamíferos eocenos de la Patagonia austral. *Revista Argentina de Historia Natural* 1: 328–380.

Ameghino, F. 1894. Énumération synoptique des espèces de mammifères fossiles des formations éocènes de Patagonie. *Boletín de la Academia Nacional de Ciencias en Córdoba* 13: 259–455.

Ameghino, F. 1897. Mammifères crétacés de l'Argentine. Deuxième contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium*. *Boletín del Instituto Geográfico Argentino*18: 406–429; 431–521.

Ameghino, F. 1898. Sinopsis geológica-paleontológica de la Argentina. In: De La Fuente (Ed.), *Segundo Censo de la República Argentina Tomo I (Territorio).* Taller Tipográfico de la Penitenciaría Nacional, Buenos Aires, p. 111–255.

Amson, E., Muizon, C., and Gaudin, T.J. 2016. A reappraisal of the phylogeny of the Megatheria (Mammalia: Tardigrada), with an emphasis on the relationships of the Thalassocninae, the marine sloths. *Zoological Journal of the Linnean Society* 179: 217–236.

Amson, E., de Muizon, C., Laurin, M., Argot, C., and de Buffrénil, V. 2014. Gradual adaptation of bone structure to aquatic lifestyle in extinct sloths from Peru. *Proceedings of the Royal Society B-Biological Sciences* 281: 1–6.

Asher, R.J., and Helgen, K.M. 2010. Nomenclature and placental mammal phylogeny. *BMC Evolutionary Biology* 10: 1–9.

Bargo, M.S. 2001. The ground sloth *Megatherium americanum*: skull shape, bite forces, and diet. *Acta Paleontologica Polonica, Special Issue* 46: 41–60.

Bargo, M.S., and Vizcaíno, S.F. 2008. Paleobiology of Pleistocene ground sloths (Xenarthra, Tardigrada): biomechanics, morphogeometry and ecomorphology applied to the masticatory apparatus. *Ameghiniana* 45: 175–196.

Bargo, M.S., Toledo N., and Vizcaíno, S.F. 2012. Paleobiology of the Santacrucian sloths and anteaters (Xenarthra, Pilosa). 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. 216–242.

Bargo, M.S., Vizcaíno, S.F., and Kay, R.F. 2009. Predominance of orthal masticatory movements in the early Miocene *Eucholaeops* (Mammalia, Xenarthra, Tardigrada, Megalonychidae) and other megatherioid sloths. *Journal of Vertebrate Paleontology* 29: 870–880.

Bordas, A.F. 1939. Los restos de mamíferos de la serie continental postpatagoniana de la Meseta del Castillo. *Physis* 14: 435–446.

Brandoni, D. 2014. "*Xyophorus*" sp. en el Mioceno Medio de Chubut: implicancias sistemáticas, biogeográficas y biocronológicas del registro de un Nothrotheriinae en el Neógeno de la Argentina. *Ameghiniana* 51: 94–105.

Brandoni, D., González Ruiz, L., Reato, A., and Martin, G. 2017. Chronological implications of the nothrotheriid '*Xyophorus*' (Mammalia, Xenarthra) from the Collón Curá Formation (Miocene of Patagonia, Argentina). *Historical Biology* doi: 10.1080/08912963.2017.1398748

Carlini, A.A., Brandoni, D., and Dal Molin, C.N. 2013. A new genus and species of Planopinae (Xenarthra: Tardigrada) from the Miocene of Santa Cruz Province, Argentina. *Zootaxa* 3694: 565–578.

Croft, D.A., Anaya, F., Auerbach, D., Garzione, C., and MacFadden, B.J. 2009. New data on Miocene Neotropical provinciality from Cerdas, Bolivia. *Journal of Mammalian Evolution* 16: 175–198.

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

Cuitiño, J.I., Fernicola, J.C., Raigemborn, M.S., and Krapovickas, V. 2019a. 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: 14–33.

Cuitiño, J.I., Vizcaíno, S.F., Bargo, M.S., and Aramendía, I. 2019b. Sedimentology and fossil vertebrates of the Santa Cruz Formation (early Miocene) in Lago Posadas, a sub-Andean locality of southwestern Patagonia. *Andean Geology* 46: 383–420.

De Iuliis, G. 1994. Relationships of the Megatheriinae, Nothrotheriinae, and Planopsinae: some skeletal characteristics and their importance for phylogeny. *Journal of Vertebrate Paleontology* 14: 577–591.

De Iuliis, G., Gaudin, T.J., and Vicars, M. 2011. A new genus and species of nothrotheriid sloth (Xenarthra, Tardigrada, Nothrotheriidae) from the late Miocene (Huayquerian) of Peru. *Palaeontology* 54: 171–205.

De Iuliis, G., Pujos, F., Toledo, N., Bargo, M.S., and Vizcaíno, S.F. 2014. *Eucholoeops* Ameghino, 1887 (Xenarthra, Pilosa, Megalonychidae) from the Santa Cruz Formation, Argentine Patagonia: implications for revising the systematics of Santacrucian sloths. *Geodiversitas* 36: 209–255.

Delsuc, F., Martínez, J.G., Poinar. H.N., Kuch, M., Mead, J.I., Gibb, G.C., McDonald, H.G., Karpinski, E., Hackenberger, D., MacPhee, R.D.E., Szpak, P., Billet, G., and Hautier, L. 2019. Ancient mitogenomes reveal the evolutionary history and biogeography of sloths. *Current Biology* doi: 10.1016/j.cub.2019.05.043

Dubois, A. 2010. Retroactive changes should be introduced in the Code only with great care: problems related to the spellings of nomina. *Zootaxa* 2426: 1–42

Fernicola, J.C. 2011. Implicancias del conflicto Ameghino-Moreno sobre la colección de mamíferos fósiles realizada por Carlos Ameghino en su primera exploración al río Santa Cruz, Argentina. *Revista del Museo Argentino de Ciencias Naturales*, *nueva serie* 13: 41–57.

Fernicola, J.C., Cuitiño, J., 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 Notohippidian. *Journal of South America Earth Sciences* 52: 9–107.

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.H., Perkins, M. E., Heizler, M.T., Nash, B., Bown, T.M., Tauber, A.A., Dozo, M.T., and Tejedor M.F. 2012. Absolute and relative ages of fossil localities in the Santa Cruz and Pinturas Formations. 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. 41–58.

Gaudin, T.J. 2004. Phylogenetic relationships among sloths (Mammalia, Xenarthra, tardigrada): the craniodental evidence. *Zoological Journal of the Linnean Society, London* 140: 255–305.

Hautier, L., Gomes Rodrigues, H., Billet, G., and Asher, R.J. 2016.The hidden teeth of sloths: evolutionary vestiges and the development of a simplified dentition. *Scientific Reports* 6: 27763.

Hoffstetter, R. 1961. Description d'un squelette de *Planops* (Gravigrade du Miocène de Patagonie). *Mammalia* 25: 57–96.

Hoffstetter, R. 1982. Les Edentés Xénarthres, un groupe singulier de la faune néotropicale (origine, affinités, radiation adaptative, migrations et extinctions). In: E. Montanaro Gallitelli (Ed.), *Palaeontology, Essential of Historical Geology. Proccedings First International Meeting of Paleontology*. S.T.E.M. Mucchi, Modena, p. 385–443.

International Commission on Zoological Nomenclature, 1999. *International Code of Zoological Nomenclature.* Fourth ed., online version at: http://www.iczn.org/iczn/index.jsp.

Kay, R.F., Vizcaíno, S.F., and Bargo, M.S. 2012. A review of the paleoenvironment and paleoecology of the Miocene Santa Cruz Formation. 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. 331–365.

Lydekker, R. 1894. Contributions to the knowledge of the fossil vertebrates of Argentina.The extinct edentates of Argentina/Contribuciones al conocimiento de los vertebrados fósiles de la Argentina. Los edentados extinctos de la Argentina. Part II. *Anales del Museo de La Plata, Paleontología Argentina* 1: 1–118.

Marshall, L.G. 1975. The Handel T. Martin paleontological expedition to Patagonia in 1903. *Ameghiniana* 12: 109–111.

Marshall, L.G. 1976. Fossil localities for Santacrucian (Early Miocene) mammals, Santa Cruz Province, Southern Patagonia, Argentina. *Journal of Paleontology* 50: 1129–1142.

McDonald, H.G., and De Iuliis, G. 2008. Fossil history of sloths. In: S.F. Vizcaíno and W.J. Loughry (Eds), *The Biology of the Xenarthra*. The University of Florida Press, Gainesville, p. 39–55.

McKenna, M.C., and Bell, S.K. 1997. *Classification of Mammals above the Species Level*. Columbia University Press, New York, p. 631.

Matheos, S.D., and Raigemborn, M.S. 2012. Sedimentology and paleoenvironment of the Santa Cruz Formation. 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. 59–82.

Mercerat, A. 1891. Datos sobre restos de mamíferos fósiles pertenecientes a los Bruta conservados en el Museo de La Plata y procedentes de los terrenos eocenos de Patagonia. *Revista del Museo de La Plata* 2: 5–46.

Meredith, R.W., JaneČka, J.E., Gatesy, J., Ryder, O.A., Fisher, C.A., Teeling, E.C., Goodbla, A., Eizirik, E., Simão, T.L.L., Stadler, T., Rabosky, D.L., Honeycutt, R.L., Flynn, J.J., Ingram, C.M., Steiner, C., Williams, T.L., Robinson, T.J., Burk-Herrik, A., Westerman, M., Ayoub, N.A., Springer, M.S., and Murphy, W.J. 2011. Impacts of the Cretaceous Terrestrial Revolution and KPg extinction on mammal diversification. *Science* 334: 521–524.

Mones, A. 1986. Palaeovertebrata Sudamericana. Catálogo Sistemático de los Vertebrados fósiles de América del Sur. Parte I. Lista Preliminar y Bibliografía. *Courier Forschungsinstitut Senckenberg* 82: 1–625.

Mones, A. 1989. Nomen dubium *vs.* Nomen vanum. *Journal of Vertebrate Palentology* 9: 232–234.

Moreno, F.P. 1879. Viaje a la Patagonia Austral, emprendido bajo los auspicios del Gobierno Nacional, 1876-1877. Imprenta de La Nación, Buenos Aires, 460 p.

O'Leary, M.A., Giallombardo, A., Luo, Zhe-Xi, Meng, J., Bloch, J.I., Giannini, N.P., Ni, X., Flynn, J.J., Gaudin, T.J., Goldberg, S.L., Novacek, M.J., Kraatz, B.P., Perini, F.A., Randall, Z.S., Simmons, N.B., Rougier, G.W., Spaulding, M., Sargis, E.J., Velazco, P.M., Silcox, M.T., Weksler, M., Wible, J.R., and Cirranello, A.L. 2013. The placental mammal ancestor and the post–K-Pg radiation of placentals. *Science* 662: 339.

Parras, A., Dix, G.R., and Griffin, M. 2012. Sr-isotope chronostratigraphy of Paleogene/Neogene marine deposits: Austral Basin, southern Patagonia (Argentina). *Journal of South American Earth Sciences* 37: 122–135.

Pascual, R. 1961. Una nueva superfamilia 'Entelopsoidea' descripción de la nueva especie '*Entelops parodii*'. *Acta Geológica Lilloana* 3: 127–146.

Pascual, R., Ortega Hinojosa, E.J., Gondar, D., and Tonni, E.P. 1965. Las Edades del Cenozoico mamalífero de la Argentina, con especial atención a aquellas del territorio bonaerense. *Anales de la Comisión de Investigaciones Científicas de la Provincia de Buenos Aires* 6: 165–193.

Perea, D. 1999. Un singular grupo de perezosos, los 'Nothrotheriinae' (Xenarthra). *Boletín de la Sociedad Zoológica del Uruguay,* 2 época 10: 1–8.

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.

Presslee, S., Slater, G.J., Pujos, F.R., Forasiepi, A.M., Fischer, R., Molloy, K., Mackie, M., Olsen, J.V., Kramarz, A., Taglioretti, M., Scaglia, F., Lezcano, M., Lanata, J.L., Southon, J., Feranec, R., Bloch, J., Hadjuk, A., Martin, F.M., Gismondi, R.S., Reguero, M., de Muizom, C., Greenwood, A., Chait, B.T., Penkman, K., Collins, M., and MacPhee, R.D. 2019. Palaeoproteomics resolves sloth relationships. *Nature Ecology and Evolution* doi: 10.1038/s41559-019-0909-z

Pujos, F., and De Iuliis, G. 2007. Late Oligocene Megatherioidea fauna (Mammalia: Xenarthra) from Salla-Luribay (Bolivia): new data on basal sloth radiation and Cingulata–Tardigrada split. *Journal of Vertebrate Paleontology* 27: 132–144.

Pujos, F., De Iuliis, G., Argot, C., and Werdelin, L. 2007. A peculiar climbing Megalonychidae from the Pleistocene of Peru and its implication for sloth history. *Zoological Journal of the Linnean Society* 149: 179–235.

Pujos, F., De Iuliis, G., and Mamani Quispe, B. 2011. *Hiskatherium saintandrei* gen. et sp. nov.: an unusual sloth from the Laventan of Quebrada Honda (Bolivia) and an overview of middle Miocene, small megatherioids. *Journal of Vertebrate Paleontology* 31: 1131–1149.

Racco, A., Fernicola, J.C., Bargo, M.S., Vizcaíno, S.F., and De Iuliis, G. 2018. On the type of *Schismotherium fractum* Ameghino, 1887 (Xenarthra, Folivora, Megatherioidea) from the Early Miocene Santa Cruz Formation (Santa Cruz province, Argentina). *Ameghiniana* 55: 117–125.

Raigemborn, M.S., Matheos, S.D., Krapovickas, V., Vizcaíno, S.F., Bargo, M.S., Kay, R.F., Fernicola, J.C., and Zapata, L. 2015. Paleoenvironmental reconstruction of the coastal Monte Léon and Santa Cruz formations (early Miocene) at Rincón del Buque, southern Patagonia: A revisited locality. *Journal of South American Earth Sciences* 60: 31–55.

Saint-André, P.A. 1996. Deux nouveaux Édentés (Mammalia, Xenarthra) *Trachycalyptoides achirense* nov. gen. et nov. sp. (Glyptodontidae, Sclerocalyptinae) et *Xyophorus villarroeli* nov. sp. (Megatheriidae, Nothrotheriinae) du Huayquérien (Miocène supérieur) de l'Altiplano bolivien. *Bulletin du Museum National d'Histoire Naturelle*, 4° Serie 18: 79–106.

Scillato-Yané, G.J. 1979. Nuevo Nothrotheriinae (Edentata, Tardigrada) de Edad Chasiquense (Plioceno temprano) del sur de la Prov. de Buenos Aires (Argentina). Su importancia bioestratigráfica, filogenética y paleobiogeográfica. *7° Congreso Geológico Argentino* (*Neuquén), Actas* 2: 449–457.

Scott, W.B. 1903. Mammalia of the Santa Cruz beds. Part I. Edentata. In: W.B. Scott (Ed.), *Reports of the Princeton University Expeditions to Patagonia 1896–1899*. Vol. 5, Paleontology 2, Princeton University Press, Princeton, p. 1–226.

Scott, W.B. 1904. Mammalia of the Santa Cruz beds. Part I. Edentata. In: W.B. Scott (Ed.), *Reports of the Princeton University Expeditions to Patagonia 1896–1899*. Vol. 5, Paleontology 2, Princeton University Press, Princeton, p. 227–364.

Simpson, G.G. 1941. A Miocene sloth from Southern Chile. *American Museum Novitates* 1156: 1–6.

Simpson, G.G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* 85: 1–350.

Simpson, G.G. 1948. The beginning of the age of mammals in South America, 1. *Bulletin of the American Museum of Natural History* 91: 1–232.

Vizcaíno, S.F., Bargo M.S., and Fariña, R.A. 2008. Form, function and paleobiology in xenarthrans. In: S.F. Vizcaíno, and W.L. Loughry (Eds.), *The Biology of the Xenarthra*. University Press of Florida, Florida, p. 86–99.

Vizcaíno, S.F., Kay, R.F., and Bargo, M.S. 2012a. *Early Miocene Paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, 370 pp.

Vizcaíno, S.F., Kay R.F., and Bargo M.S. 2012b. 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.

Vizcaíno, S.F., and Bargo, M.S. 2013b. De Patagonia a Budapest: caminos europeos de fósiles santacrucenses (1845-1956). *Museo* 26: 36–42.

Vizcaíno, S.F., Bargo M.S., and Fernicola, J.C. 2013a. Expediciones paleontológicas durante los siglos XIX y XX a la Formación Santa Cruz (Mioceno Inferior, Patagonia) y destino de los fósiles. *3° Congreso Argentino de Historia de la Geología (Salta), Actas*: 231–246.

Vizcaíno, S.F., Brinkman, P.D., and Kay, R.F. 2016. On the objectives and results of the Handel T. Martin paleontological expedition (1903-04) to the Santa Cruz Formation in southern Patagonia. *Revista del Museo de La Plata* 1: 316–333.

Vizcaíno, S.F., De Iuliis, G., Brinkman, P.D., Kay, R.F., and Brinkman, D.L. 2017. On an album of photographs recording fossils in the "Old Collections" of the Museo de La Plata and Ameghino's private collection at the beginning of the XX^th^ Century. *Publicación Electrónica de la Asociación Paleontológica Argentina* 17: 14–23.

Vizcaíno, S.F., Bargo, M.S., Cuitiño, J.I., Pérez, M.E., Muñoz, N.A., Aramendía, I., Tomassini, R.L., and Kay, R.F. 2018. The outstanding Río Chalía (= Sehuen) outcrops of the Santa Cruz Formation (Early Miocene, Burdigalian) and its fossil vertebrate content. *Publicación Electrónica de la Asociación Paleontológica Argentina* 19, Suplemento de resúmenes, p. R85.

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Appendix 1 - List of new sloths remains recovered from the Santa Cruz Formation along the Río Santa Cruz

Barrancas Blancas (Estancias Aguada Grande and Santa Lucía)

MPM-PV	*Taxa*	*Description*
19303	*Mylodontidae indet.*	*Ungual phalanx and right astragalus*
19304	*Megatherioidea indet.*	*Ungual phalanx*
19305	*Megatherioidea indet.*	*Several tooth, mandibular, and palatal fragments, ungual phalanx, and several unidentifiable fragments*
19306	*Megatherioidea indet.*	*Left astragalus*
19307	*Megatherioidea indet.*	*Small anterior portion of right dentary, preserving cf1, posterior part of spout and partial region of diastema. Isolated teeth fragment, proximal humerus*
19308	*Megatherioidea indet.*	*Two tooth fragments*
19309	*Megatherioidea indet.*	*Ungual phalanx*
19310	*Megatherioidea indet.*	*Right astragalus*
19311	*Megatherioidea indet.*	*Right astragalus*
19312	*Megatherioidea indet.*	*Tooth fragments*
19313	*Megatherioidea indet.*	*Ungual phalanx*
19314	*Megatherioidea indet.*	*Metatarsal IV*
19315	*Megatherioidea indet.*	*Metatarsal III*
19316	*cf.* **Hapalops**	*Distal and proximal humerus, left astragalus, ungual phalanx, and several fragments*
19317	**Hapalops** *cf.* **elongatus**	*Portion of right dentary preserving distal part of cf1 alveolus, mf1 and mf2 completely, and all but distolingual portion of mf3*
19318	**Hapalops** *cf.* **elongatus**	*Anterior portion of skull, preserving left Cf1, Mf1-Mf3, Mf4 broken, and right Mf1-Mf3 (Mf2 broken vestibularly, and Mf3 broken, lacking its occlusal surface)*
19319	*Megatherioidea indet.*	*Ungual phalanges*
19320	*Megatherioidea indet.*	*Ungual phalanx*
19321	*Megatherioidea indet.*	*Tooth fragments and fragmented skull*
19322	*Megatherioidea indet.*	*Mandibular fragment: portion of the spout with cf1 broken*

Segundas Barrancas Blancas (Estancias Cordón Alto and El Tordillo)

19323	*Planopinae indet.*	*Right astragalus*
19324	**Hapalops** *sp.*	*Astragalus, ungual phalanx and several fragments*
19325	*Megatheriidae indet.*	*Tooth fragments of a large-sized sloth*
19326	**Nematherium longirostris**	*Left mandibular fragment with mf1 alveolus, isolated teeth, and several skull fragments*
19327	*Megatherioidea indet.*	*Ungual phalanx*
19328	**Schismotherium** *cf.* **fractum**	*Portion of left dentary with mf1-2 alveoli, alveoli of cf1 and mf3 incomplete, and ungual phalanx*
19329	*Megatherioidea indet.*	*Mandibular fragment with two broken teeth*
19330	*Megatherioidea indet.*	*Teeth and ungual phalanx*
19331	*Megatherioidea indet.*	*Postcranial fragments, probably of the same individual; one tooth*
19332	**Hapalops** *sp.*	*Right astragalus*
19333	*Megatheriidae indet.*	*Broken teeth of a large-sized sloth*
19334	*Megatherioidea indet.*	*Distal tibia*
19335	*Megatherioidea indet.*	*Fragment of humeral diaphysis*
19336	*Megatherioidea indet.*	*Distal tibia, incomplete astragalus, phalanx and ungual phalanx*
19337	**Xyophorus atlanticus**	*Partial left and right dentaries. Left dentary preserving mf1-mf3 completely; right dentary preserving mf2-mf3 completely, mf1 partially. Some postcranial elements: femur, ulna, astragalus*
19338	*Megatherioidea indet.*	*Petrosal and several postcranial elements, including trapezium + metacarpal I*
19339	**Hapalops** *sp.*	*Right tibia and astragalus*
19340	*cf.* **Hapalops**	*Anterior fragment of mandible, with cf1 and mf1 broken, and an isolated molariform. Astragalus, three metapodials and three ungual phalanges*
19341	*Megatherioidea indet.*	*Postcranial elements*

Appendix 1 - Continued

Segundas Barrancas Blancas (Estancias Cordón Alto and El Tordillo)

MPM-PV	*Taxa*	*Description*
19342	*Megatherioidea indet.*	*Ungual phalanx*
19343	*Megatheriidae indet.*	*Isolated large-sized teeth*
19344	*Megatherioidea indet.*	*Ungual phalanges*
19345	*Megatheriidae indet*	*Ungual phalanges and several fragmentary postcranial remains of a large-sized sloth*
19346	*Megatherioidea indet.*	*Very fragmented mandible, with few teeth*
19347	*Megatherioidea indet.*	*Caniniform teeth*
19348	*Megatherioidea indet.*	*Partial mandible with two teeth, and proximal portion of an ungual phalanx*
19349	*Megatherioidea indet.*	*Radius and ungual phalanx*
19350	*Megatherioidea indet.*	*Isolated teeth (molariforms)*
19351	*Megatherioidea indet.*	*Several teeth, two ungual phalanges (one very large), fragment of left maxilla with the last three teeth. Not associated, different individuals*
19352	**Hapalops** *cf.* **elongatus**	*Portion of right dentary preserving cf1-mf3, with cf1 broken above level of alveolar margin*
19353	**Hapalops** *cf.* **elongatus**	*Partial skull, with palate and teeth; several postcranial elements (humerus, radius, proximal ulna, vertebrae, ribs, manus and pes elements, among others. Same individual*
19354	*Megatherioidea indet.*	*Two tooth fragments*
19355	*Nematheriinae?* *Planopinae?*	*Ungual phalanx and distal fibula*
19356	*Megatherioidea indet.*	*Mandibular fragment, teeth fragments and postcrania: fragments of femora, distal tibiae, both patellas, proximal and distal humeri, proximal ulna, proximal and distal radii, carpal/tarsal bones, ungual phalanges*
19357	*Megatherioidea indet.*	*calcaneum and ungual phalanx fragments*
19358	*Planopinae indet.*	*Distal tibia, proximal and distal humerus, femoral fragments, digit*
19359	*Planopinae?* *Nematheriinae?*	*Several podial elements*
19360	*Megatherioidea indet.*	*Maxillary fragment with broken Mf1-3*
19361	*Megatherioidea indet.*	*Mandibular fragment, very poorly preserved*
19362	*Megatherioidea indet.*	*Digits and ungual phalanx*
19363	*Megatherioidea indet.*	*Two tooth fragments*
19364	*Megatherioidea indet.*	*Left astragalus*
19365	*Megatherioidea indet.*	*Right astragalus*
19366	*Megatherioidea indet.*	*Left astragalus*
19367	*Megatherioidea indet.*	*Two phalanges*
19368	*Megatherioidea indet*	*Tooth fragment*
19369	*Megatherioidea indet*	*Postcrania fragmentary*
19370	*Megatherioidea indet*	*Teeth and postcranial elements*
19371	*Megatherioidea indet*	*Two astragali, associated*

Appendix 2 - List of the specimens of Folivora studied

Megatherioidea

AMNH 9222, **Hapalops rectangularis**. *Locality: Río Gallegos, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation Collector: AMNH expedition 1899*

AMNH 9250, **H. ruetimeyeri**. *Locality: Río Gallegos, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation. Collector: Brown*

AMNH 9293, **H. ruetimeyeri***? Locality: Halliday Estancia, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation. Collector: AMNH expedition 1899*

MACN-A 6445-6470, **Schismotherium fractum**, *neotype (Racco* et al., *2018). Locality: La Cueva, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation. Collector: C. Ameghino*

MACN-A 2089-2092, **Hapalops rectangularis**, *identified as the type in MACN catalogue (see text). Locality: Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation. Collector: C. Ameghino 1889-1890*

MACN-A 4630, **Xyophorus atlanticus**. *Locality: Río Sehuen, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: C. Ameghino, 1890-91*

MACN-A 4631, **X. atlanticus**, *holotype. Locality: Corriguen Kaik, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: C. Ameghino, 1890-91*

MACN-A 6435, **X. atlanticus**. *Locality: Corriguen Kaik, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: C. Ameghino, 1890-91*

MACN-A 4629, **X. sulcatus**, *identified as the type in MACN catalogue (see text). Locality: Monte Observación, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: Ameghino 1890-91*

MACN-A 4632, **X. sulcatus**. *Locality: Monte Observación, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: Ameghino 1890-91*

MACN-A 4633, **X. sulcatus**. *Locality: Monte Observación, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: Ameghino 1890-91*

MACN-A 4634, **X. andinus**, *holotype. Locality: Río Sehuen, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: C. Ameghino, 1890-91*

MACN-A 6417-18, **X. simus**, *identified as the type in MACN catalogue (see text). Locality: La Cueva, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: C. Ameghino 1892-93*

MACN-A 4636, **X. simus**, *identified as the type in MACN catalogue (see text). Locality: Monte Observación, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: Ameghino 1890-91*

MACN-A 6436, **X. crassissimus**. *Locality: Corriguen Kaik, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: C. Ameghino, 1892-93*

MACN-A 2097, **Trematherium intermixtum**. *Locality: Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: C. Ameghino, 1899-90*

FMNH 13137, **Schismotherium fractum**. *Locality: Killik Aike, Río Gallegos, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation*

YPM-VPPU 15110, **Hapalops indfferens**. *Locality: 10 miles south of Coy Inlet, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation. Collector: J.B. Hatcher*

YPM-VPPU 15011, **H. elongatus**. *Locality: Guer Aike Department, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation. Collector: O.A. Peterson*

YPM-VPPU 15155, **H. elongatus**. *Locality: 10 miles south of Coy Inlet, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation. Collector: O.A. Peterson*

YPM-VPPU 15160, **H. elongatus**. *Locality: 10 miles south of Coy Inlet, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation. Collector: J.B. Hatcher*

YPM-VPPU15545, **H. elongatus**. *Locality: Guer Aike Department, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation. Collector: J. B. Hatcher*

YPM-VPPU 15597, **H. elongatus**. *Locality: Killik Aike (Felton's Estancia), Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation. Collector: J.B. Hatcher*

YPM-VPPU 15531, **H. elongatus**. *Locality: Killik Aike, Santa Cruz, Argentina Stratigraphy: Santa Cruz Formation. Collector: O.A. Peterson 1899*

YPM-VPPU 15523, **H. longiceps**, *holotype. Locality: 8 miles South of Coy Inlet, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation. Collector: O.A. Peterson 1896-97*

YPM-VPPU 15564, **H. platycephalus**, *holotype. Locality: Lago Pueyrredón, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation. Collector: J. B. Hatcher, 1899*

YPM-VPPU 15520, **H. ponderosus**, *holotype. Locality: Guer Aike Department, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation. Collector: J. Hatcher*

YPM-VPPU 15561, **Analcimorphus giganteus**. *Locality: Guer Aike Department, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation. Collector: O. Peterson*

YPM-VPPU 15342, **Xyophorus rostratus**. *Locality: Coy Inlet, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation. Collector: J.B. Hatcher and O. Peterson*

Megalonychidae

MACN-A 1061, **Eucholoeops infernalis**. *Locality: Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: C. Ameghino*

MACN-A 2095, **E. infernalis**, *identified as the type in MACN catalogue (see text). Locality: Corriguen-Kaik, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: C. Ameghino 1890-91*

MPM-PV 3401, **E. ingens**, *neotype. Locality: Puesto Ea. La Costa, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Fossiliferous level: 7.2. Collector: MLP-Duke expeditions 2003*

Appendix 2 - Continued

Mylodontidae, Nematheriinae

MACN-A 4660, **Nematherium longirostris***, type. Locality: Monte Observación, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: Ameghino 1890-91*

YPM-VPPU 15965, **Nematherium** *sp. Locality: Coy Inlet, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation. Collector: J.B. Hatcher and O.A. Peterson*

YPM-VPPU 15374, **Nematherium***? sp. Locality: Killik Aike, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation. Collector: O.A. Peterson*

Megatheriidae, Planopinae

MACN-A 4637, **Planops longirostratus***, identified as the type in MACN catalogue (see text). Locality: Killik Aike, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: Ameghino 1890-91*

MACN-A 4691-4694, **Prepotherium potens***, holotype. Locality: Río Sehuen, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: C. Ameghino*

MLP 97-XI-3-1, **Prepoplanops boleadorensis***, holotype. Locality; Cerro Boleadoras, Santa Cruz, Argentina. Stratigraphy: Cerro Boleadoras Formation, Grupo Zeballos, Early Miocene*

NHMUK PV M 43404, **Planops martini***, holotype. Locality: Cabo Buen Tiempo, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: H.T. Martin 1905*

YPM-VPPU 15345, **Prepotherium potens***. Locality: Killik Aike, Santa Cruz, Argentina. Stratigraphy: Santa Cruz Formation, Santacrucian. Collector: O.A. Peterson, 1899*

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ARTÍCULO

NOTOUNGULATA AND ASTRAPOTHERIA (MAMMALIA, MERIDIUNGULATA) OF THE SANTA CRUZ FORMATION (EARLY–MIDDLE MIOCENE) ALONG THE RÍO SANTA CRUZ, ARGENTINE PATAGONIA

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Abstract. This contribution details new records of Notoungulata and Astrapotheria from the exposures of the Santa Cruz Formation in the Río Santa Cruz (Early–Middle Miocene; Province of Santa Cruz). The astrapothere *Astrapotherium* sp. Burmeister, the notoungulate toxodonts *Homalodotherium* sp. Flower, *Nesodon* sp. Owen and *Adinotherium* sp. Ameghino, and the typotheres *Hegetotherium mirabile* Ameghino, *Interatherium* sp. Ameghino, *Protypotherium* sp. Ameghino, *P. attenuatum* Ameghino, *P. australe* Ameghino and *P. praerutilum* Ameghino are recognized in the localities Barrancas Blancas and Segundas Barrancas Blancas. *Nesodon imbricatus* Owen was recorded in the former and *Adinotherium ovinum* (Owen) in the latter locality. The typothere *Pachyrukhos moyani* Ameghino was identified only in Segundas Barrancas Blancas, but with numerous specimens. Only the large ungulates *Astrapotherium magnum* (Owen) and *Adinotherium* sp. were recorded in Yaten Huageno. At a generic level, Barrancas Blancas and Segundas Barrancas Blancas only differ by the presence of *Pachyrukhos* Ameghino in the latter; at Yaten Huageno the Typotheria, Homalodotheriidae and *Nesodon* have not been recorded. The general faunal composition, including the larger samples from Barrancas Blancas and Segundas Barrancas Blancas, matches the record from the better-known Santacrucian localities from the Atlantic coast. This faunal similarity implies that similar environmental conditions prevailed in the two areas, indicating that the localities from Río Santa Cruz, as the Atlantic coastal localities, would have constituted a complex mosaic of open and closed habitats.

Key words. Notoungulates. Astrapotheres. Typotheria. Toxodontia. Ameghino. Santacrucian.

Resumen. NOTOUNGULATA Y ASTRAPOTHERIA (MAMMALIA, MERIDIUNGULATA) DE LA FORMACION SANTA CRUZ (MIOCENO TEMPRANO–MEDIO) A LO LARGO DEL RÍO SANTA CRUZ, PATAGONIA ARGENTINA. Esta contribución involucra un reporte faunístico de los nuevos registros de Notoungulata y Astrapotheria provenientes de los yacimientos de la Formación Santa Cruz del Río Santa Cruz (Mioceno Temprano–Medio; provincia de Santa Cruz). El astrapoterio *Astrapotherium* sp., los notoungulados toxodontes *Homalodotherium* sp. Flower, *Nesodon* sp. Owen y *Adinotherium* sp. Ameghino, y los tipoterios *Hegetotherium mirabile* Ameghino, *Interatherium* sp. Ameghino, *Protypotherium* sp. Ameghino, *P. attenuatum* Ameghino, *P. australe* Ameghino y *P. praerutilum* Ameghino fueron reconocidos en Barrancas Blancas y Segunda Barrancas Blancas. Las especies *Nesodon imbricatus* Owen y *Adinotherium ovinum* (Owen) fueron identificados en la primera y en la segunda localidad, respectivamente. El tipoterio *Pachyrukhos moyani* Ameghino fue identificado únicamente en Segundas Barrancas Blancas, pero a través de numerosos ejemplares. Solo los ungulados de gran talla *Astrapotherium magnum* (Owen) y *Adinotherium* sp. fueron reconocidos en Yaten Huageno. A un nivel supraespecífico, Barrancas Blancas y Segundas Barrancas Blancas difieren por la presencia de *Pachyrukhos* Ameghino en la segunda, mientras que en Yaten Huageno los Typotheria, Homalodotheriidae y *Nesodon* no han sido identificados. La composición faunística general, incluyendo las grandes muestras provenientes de Barrancas Blancas y Segundas Barrancas Blancas, coincide con la registrada en las localidades Santacrucenses más conocidas de la costa Atlántica. Esta similitud faunística permite inferir, preliminarmente, similares condiciones ambientales, indicando que las localidades del Río Santa Cruz podrían haber constituido un complejo mosaico de ambientes abiertos y cerrados.

Palabras clave. Notoungulados. Astrapoterios. Typotheria. Toxodontia. Ameghino. Santacrucense.

THE EXTINCT South American native ungulates (SANUs) constitute a remarkable widespread and highly diverse group of mammals. They consist of five orders: Astrapotheria, Litopterna, Notoungulata, Pyrotheria, and Xenungulata

(Patterson and Pascual, 1968; Simpson, 1980; Cifelli, 1993; Bond *et al.*, 1995). Their phylogenetic relationships have been little explored, and although there has been progress in the last few years, they are still not resolved (*e.g.*, Cifelli, 1985, 1993; Gelfo *et al.*, 2008; Billet, 2010, 2011; Buckley, 2015; Welker *et al.*, 2015; Fig. 1).

Among the SANUs, only notoungulates, astrapotheres and litopterns survived until the Miocene, or later. The order Notoungulata is by far the most diverse and abundant clade within the SANUs at a morphological, taxonomic and ecological level (Simpson, 1936; Patterson and Pascual, 1972; Cifelli, 1993; Croft, 1999; Cassini *et al.*, 2012). They are united by features of the ear region (Patterson, 1934; Simpson, 1948, 1967, 1980) and cheek teeth, including a structure on the upper molars known as the "*crochet*" (Patterson, 1934; Simpson, 1948, 1967, 1980). Notoungulates are divided into

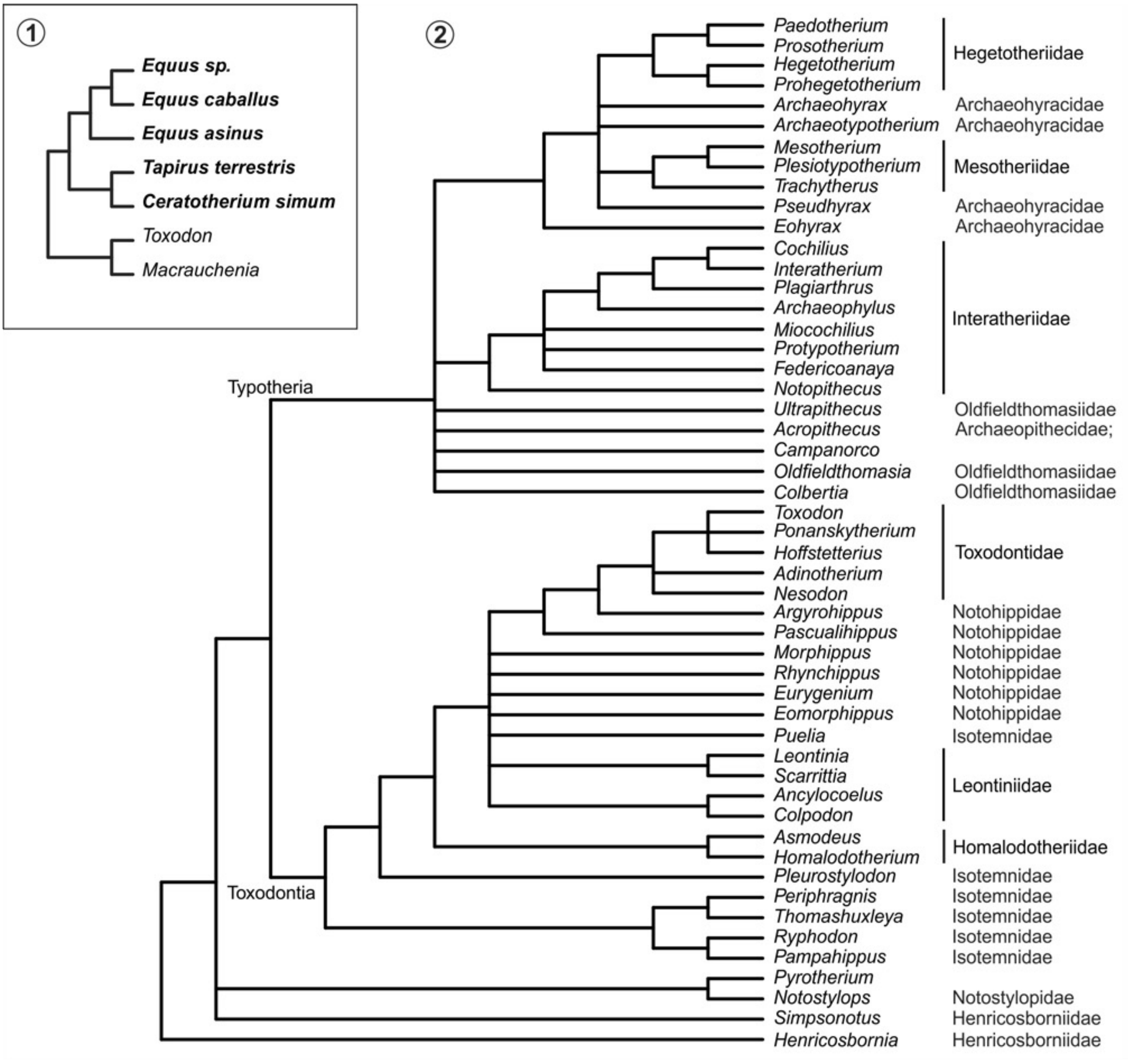

Figure 1. Phylogenetic hypothesis. **1,** Clade Panperissodactyla, modified from Welker *et al.* (2015); **2,** Clade Notoungulata, modified from Billet (2011).

two basal (and unnatural) families (Notostylopidae and Henricosborniidae) plus two monophyletic suborders, Toxodontia and Typotheria (Cifelli, 1993; Billet, 2011). The toxodonts include large to very large herbivores that share some convergent features with horses, bisons, hippos or rhinos (Ameghino, 1907; Scott, 1912; Bond, 1999), whereas the typotheres were small to medium-sized herbivores (Patterson and Pascual, 1968; Bond, 1986; Croft *et al.*, 2004; Billet *et al.*, 2008; Elissamburu, 2011) many of which exhibit rodent or rabbit-like cranial and/or postcranial characteristics.

Astrapotheria are among the most peculiar and largest mammals among the Tertiary native faunas of South America (Kramarz and Bond, 2009), being the only Miocene taxon with dental enamel distributed in vertically oriented Hunter-Schreger bands. Many astrapothere taxa exhibit strongly retracted nasals that suggest the presence of a proboscis; they have a reduced dental series, enlarged canines and brachydont rhino-like cheek teeth (Ameghino, 1894; Scott, 1937; Kramarz and Bond, 2009). The third order within the Miocene SANUs, Litopterna, includes large to very large animals similar to small horses and camelids, which are reviewed by Schmidt *et al.* (2019).

Notoungulates and astrapotheres are common in the Santa Cruz Formation (SCF; Burdigalian–early Langhian) in Patagonia. The unit is one of the most widespread continental formations in South America, and contains the richest pre-Pleistocene assemblage of mammal skulls and articulated skeletons in the continent (Kay *et al.*, 2008; Vizcaíno *et al.*, 2010, 2012a). The SCF is part of the infill of the Austral (= Magallanes) Basin of the Province of Santa Cruz, and it crops out in the northwest, the central area along the Río Santa Cruz (Fernicola *et al.*, 2014; Cuitiño *et al.*, 2016) and Río Chalía (Vizcaíno *et al.*, 2018), and in the southeast along the Atlantic coast (Vizcaíno *et al.*, 2012b). The unit is composed of mudstones, tuffaceous sandstones, and tuffs deposited in fluvial environments under the influence of intense explosive pyroclastic input (see Cuitiño *et al.*, 2019 for the geological background). The outcrops of SCF along the southern margin of the Río Santa Cruz (RSC) are concentrated in three localities (Fernicola *et al.*, 2014, 2019): Barrancas Blancas (S 50° 9′ 38.31″ - W 69° 40′ 23.40″ to S 50° 12′ 31.70″ - W 69° 43′ 10.66″), Segundas Barrancas Blancas (S 50° 16′ 12.48″ - W 70° 22′ 23.21″ to S 50° 16′ 51.90″ - W 70° 17′ 54.76″), and Yaten Huageno (S 50° 15′ 17.48″ - W 71° 4′ 9.56″ to S 50° 15′ 17.48″ - W 71° 4′ 9.56″; Fig. 2). Based on radiometric ages, the entire SCF represents a span of ~18.0 to 15.6 Ma; the localities along the Atlantic coast range between ~18.0 to 16.0 Ma (Fleagle *et al.*, 2012; Perkins *et al.,* 2012; Trayler *et al.*, 2019), and between ~18.2 to 15.6 Ma in Río Bote and Río Santa Cruz localities (Cuitiño *et al.*, 2016).

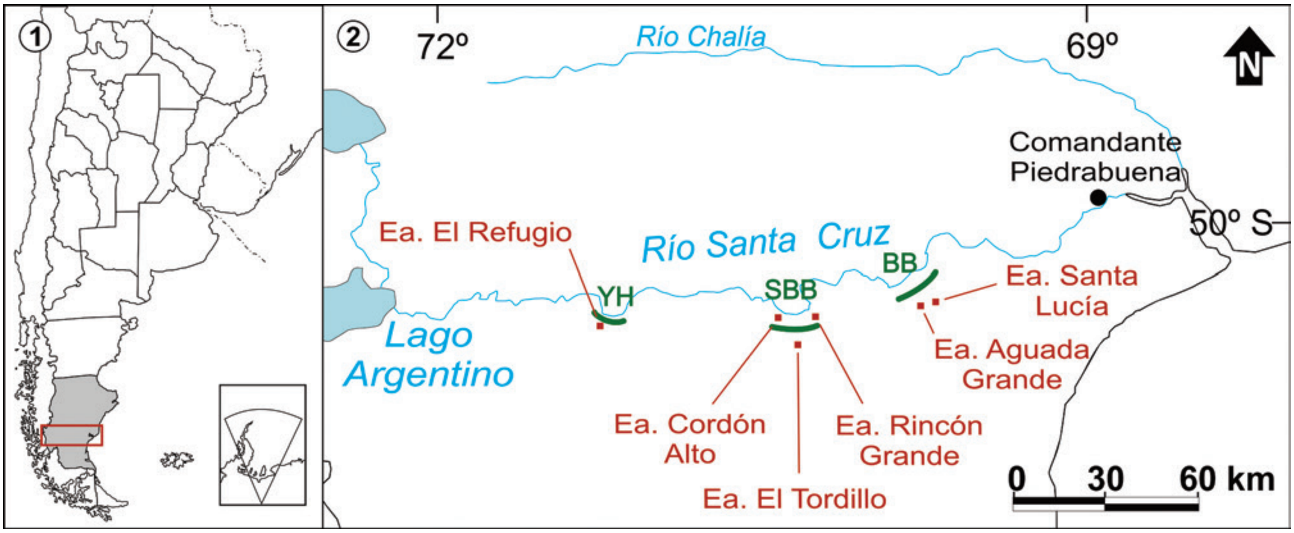

Figure 2. Map of the study area. **1,** Argentina, emphasizing the Province of Santa Cruz; **2,** Río Santa Cruz with the prospected localities and estancias mentioned in the text. **BB,** Barrancas Blancas; **SBB,** Segundas Barrancas Blancas; **YH,** Yaten Huageno; **Ea.,** Estancia. Modified from Fernicola *et al.* (2014).

The fossil remains collected by Carlos Ameghino from the exposures of the SCF along the Río Santa Cruz valley were described by his older brother Florentino Ameghino (1887a,b, 1889) and produced the data on which he based his *Formación Santacruceña* and *Piso Santacruceño* (Ameghino, 1889; currently the SCF). Ameghino (1900–1902) divided the former into two stages, naming the older as the *Notohippidien* and the younger as the *Santacruzienne*, which was later formalized as the Santacrucian SALMA by Pascual *et al.* (1965). Despite the historical importance of the material from the Río Santa Cruz in characterizing Santacrucian fauna, these localities passed into obscurity (Vizcaíno *et al.*, 2012a, 2013; Fernicola *et al.*, 2014), overshadowed by the rich faunas from extensive exposures of the SCF in the southeast of the Province of Santa Cruz along the Atlantic coast (Marshall and Pascual, 1976; Tauber, 1994, 1997a,b, 1999; Vizcaíno *et al.*, 2012a,b; Fernicola *et al.*, 2014, 2019). The Río Santa Cruz localities were so neglected that even the type locality of the Santacrucian SALMA was proposed to be Monte León in the coastal region (Marshall *et al.*, 1983).

This contribution focuses on the Notoungulata and Astrapotheria recovered from the exposures of the SCF along the Río Santa Cruz valley at three localities: Barrancas Blancas, Segundas Barrancas Blancas, and Yaten Huageno, which recent extensive fieldwork has provided new material after a lapse of more than a century since the explorations of C. Ameghino. We report the astrapothere and notoungulate specimens recovered from these three localities along the Río Santa Cruz in the last few years, compare them with those from the Atlantic Coast localities, and propose a paleoecological scenario for these RSC localities based on the recovered astrapothere and notoungulate content.

Historical and taxonomic background

The exposures of the SCF at the Río Santa Cruz valley were first explored in 1876–1877 by Francisco Moreno (1879), who collected a few, but remarkable fossil mammals. Based on these materials, Burmeister (1879) used a well-preserved skull to describe the new taxon *Astrapotherium patagonicum* Burmeister,1879 (Astrapotheria) (without Moreno's permission; Moreno, 1882, p. 114), and Florentino Ameghino (1887a) named the notoungulates *Interatherium rodens* Ameghino, 1887a, *Protypotherium australe* Ameghino, 1887a and *Protoxodon patagonensis* Ameghino, 1887a. Also from the RSC, Ameghino (1885) had already founded the notoungulate *Pachyrukhos moyani* Ameghino, 1885 based on several specimens given to him in 1885 by Carlos Moyano, who was governor of the Territory of Santa Cruz.

In 1887, Carlos Ameghino, who was the fossil preparator of the Museo de La Plata (MLP) explored the Río Santa Cruz, as part of his first collecting trip to Patagonia on behalf of that institution (Farro, 2009; Podgorny, 2009; Fernicola, 2011a,b; Vizcaíno, 2010; Vizcaíno *et al.*, 2012a,b, 2013). He returned with more than 2000 fossil specimens (Ameghino, 1887b; Ameghino, 1890), initially deposited at the MLP (Ameghino, 1887b; Fernicola, 2011a,b). Many of them were quickly studied and published by Florentino in a brief paper, in which he recognized 122 taxa, of which 110 were new species (Ameghino, 1887b). Among them were the astrapothere *Astrapotherium patagonicum* and 27 notoungulates (including 22 new species; see Appendix 1).

Two years after, and subsequent to his leaving from the MLP, F. Ameghino (1889) published "*Contribución al Conocimiento de los Mamíferos Fósiles de la Argentina*", in which he described and figured all known fossil mammals of Argentina, including approximately 40 astrapotheres and notoungulates from the RSC, and founded ten new notoungulate species (see Appendix 1). Among these taxa, Ameghino (1889) erected *Patriarchus* Ameghino, 1889 with *P. palmidens* Ameghino, 1889, but Fernández *et al.* (2019a) proved that the holotype of *P. palmidens* did not come from the RSC, but from the SCF in Río Bote, a western locality in the Province of Santa Cruz. Almost all of the specimens figured in Ameghino's Atlas (1889), many of which were type specimens collected by Carlos that should be housed at the MLP, remained in Florentino's private collection when he left the institution (see Fernicola, 2011a,b; Fernández *et al.*, 2018, 2019b). Currently, the collection forms part of the Ameghino Collection housed at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". This collection also includes specimens collected by Carlos in other exposures of the SCF, which were latter used by Florentino (Ameghino, 1891a,b,c,d, 1894, 1899) to erect almost 50 new species within Astrapotheria and Notoungulata.

Mercerat (1890, 1891) revised the astrapotheres and the toxodonts from the SCF housed at the MLP. He recognized two new astrapotheres from the exposures in the RSC and six from other localities (Mercerat, 1890), which were later synonymized with *Astrapotherium magnum* (Owen, 1853) by Ameghino (1891b) and Lydekker (1894). Within the Toxodontia, Mercerat (1891) erected almost 30 species from the RSC and nine from other exposures of the SCF. All of these species were later considered as synonyms of many of Ameghino's toxodontid nesodontines by Lydekker (1894) and, mainly, by Ameghino (1891a,b, 1894).

Santacrucian Astrapotheria and Notoungulata were revised during the beginning of the 20th century by several American naturalists, who reduced by ~45 % Ameghino's (1894) Santacrucian astrapothere and notoungulate richness. Sinclair (1909) studied the Typotheria and Scott (1912, 1928, 1937) the Toxodontia and the Astrapotheria. These taxonomic revisions are currently the most accepted taxonomic schemes due to its deep analyses and the quality of the specimens studied by these authors (in person by Scott and by means of photographs by Sinclair) that were also part of the most important collections of Santacrucian ungulates. Nevertheless, as highlighted by Cassini *et al.* (2012) and Kay *et al.* (2012), of a full and exhaustive systematic revision of Santacrucian native ungulates is needed. In this context, Kramarz *et al.* (2019) and Seoane and Cerdeño (2019) recently studied the Astrapotheria and the hegetotheriid Typotheria, respectively, and Hernández del Pino (2018) reviewed the Toxodontia in his doctoral thesis. One of the authors of this contribution (MF) is currently reviewing the interatheriid Typotheria.

A summary of the present status of the notoungulates and astrapotheres from the RSC is given in Appendix 1.

MATERIALS AND METHODS

The new specimens studied here were collected in Barrancas Blancas (BB= Estancia Santa Lucía and Estancia Aguada Grande), Segundas Barrancas Blancas (SBB= Estancia Cordón Alto, Estancia El Tordillo and Estancia Rincón Grande) and Yaten Huageno (YH= Estancia El Refugio) (see Fernicola *et al.*, 2014; Cuitiño *et al.*, 2019), deposited in the Museo Regional Provincial "Padre Jesús Molina" of Río Gallegos (MPM-PV; Province of Santa Cruz). They were compared with type specimens and more complete materials from the old collections housed at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Museo de La Plata (MLP), American Museum of Natural History (New York, USA), Field Museum of Natural History (Chicago, USA), and Yale Peabody Museum (New Have, USA). This contribution builds upon the taxonomic arrangements of Kramarz *et al.* (2019) for the astrapotheres; Scott (1912) for the toxodonts, with the exception of some species (see the systematic paleontological section); Sinclair (1909) for the interatheres, and this last author and Seoane and Cerdeño (2019) for the hegetotheres. These schemes recognize one genus (*Astrapotherium* Burmeister, 1879) within Astrapotheria, and nine genera within Notoungulata: *Nesodon* Owen, 1846; *Homalodotherium* Flower, 1873; *Pachyrukhos* Ameghino, 1885; *Protypotherium* Ameghino, 1885; *Interatherium* Ameghino, 1887a; *Adinotherium* Ameghino, 1887b; *Phobereotherium* Ameghino, 1887b; *Hyperoxotodon* (Ameghino, 1887b) and *Hegetotherium* Ameghino, 1887b. In the case of *Phobereotherium* (with *P. silvaticum* Ameghino, 1887b), it is not included in the present analysis because its status is considered here as doubtful. Unfortunately, the type specimen of *P. silvaticum* is lost and there is no other recognized material in the MACN and MLP, so its diagnostic features could not be directly evaluated. There is a photograph of an assigned juvenile specimen (Vizcaíno *et al.*, 2017, Suppl. files, Appendix 1, p. 139, fig. 343; p. 140, figs. 344, 467) that exhibits a poorly preserved premaxilla. The incisor region is broken and the photograph is not clear enough to establish the absence of the median incisors, which is the diagnostic feature used to distinguish the genus and species; moreover, the lack of a scale in the photograph do not allow us to compare the length of P3–M3 with the one given for the species by Ameghino (1887b).

Institutional abbreviations. **MACN,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad Autónoma de Buenos Aires, Argentina; **MACN-A,** Colección Nacional Ameghino at the MACN, Ciudad Autónoma de Buenos Aires, Argentina; **MPM-PV,** Colección Paleontología de Vertebrados at the Museo Padre Molina, Santa Cruz, Argentina.

Anatomical abbreviations. **C/c,** upper/lower canine; **I/i,** upper/lower incisor; **M/m,** upper/lower molar; **P/p,** upper/lower premolar.

Other abbreviations. **L,** length; **LLL,** labio-lingual length of the teeth; **MDL,** mesio-distal length of the teeth; **SALMA,** South America Land Mammal Age.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Astrapotheria Lydekker, 1894
Family Astrapotheriidae Ameghino, 1887
Subfamily Astrapotheriinae Ameghino, 1887

Genus ***Astrapotherium*** Burmeister, 1879

Type species. *Astrapotherium magnum* (Owen, 1853). Santa Cruz Formation, Barrancas del Río Santa Cruz, Province of Santa Cruz, Argentina.

Species recognized in the Santa Cruz Formation. The type and *A. burmeisteri* Mercerat, 1890.

Comments. Following Kramarz *et al.* (2019), *A. magnum* is the smallest species and *A. burmeisteri* could reach up to 20 % of the former's length.

Astrapotherium magnum
Figure 3.1

Referred material. MPM-PV 19927, left mandibular fragment with m1–2, talonid of right m2, and broken tusk, all from the same individual (see Appendix 2).

Geographic distribution. YH (Estancia El Refugio).

Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene).

Comments. MPM-PV 19927 has an m1 and m2 with the Hunter-Schreger enamel bands; there is a well-developed (but broken) isolated tusk-like canine. The specific identification of MPM-PV 19927 is associated to its size ($MDL_{m1} \approx$ 3.9 cm, LLL_{m1}= 2.1 cm; MDL_{m2}= 4.8 cm, LLL_{m2}= 2.4 cm) because its dimension falls within the range of measurements given by Scott (1928) and Kramarz *et al.* (2019) for *A. magnum* ($MDL_{m1} \approx$ 3.5–5.0 cm, $LLL_{m1} \approx$ 2.0–3.0 cm; $MDL_{m2} \approx$ 4.8–6.2 cm, $LLL_{m2} \approx$ 2.2–3.4 cm).

Astrapotherium sp.

Referred material. See Appendix 2.

Geographic distribution. BB (Estancia Aguada Grande and Estancia Santa Lucia) and SBB (Estancia Cordón Alto and Estancia El Tordillo).

Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene).

Comments. The referred materials are very fragmentary in order to establish a specific identification.

Order Notoungulata Roth, 1903
Suborder Toxodontia Owen, 1853
Family Homalodotheriidae (Ameghino, 1889) Gregory, 1910

Genus ***Homalodotherium*** Flower, 1873

Type species. *Homalodotherium cunninghami* Flower, 1873. Santa Cruz Formation, Río Gallegos, Province of Santa Cruz, Argentina.

Species recognized in the Santa Cruz Formation. The type, *H. segoviae* Ameghino, 1891a (with reservations; see Scott, 1912), *H. excursum* Ameghino, 1894 and *H. crassum* Ameghino, 1894.

Comments. Scott (1912) contrasted *H. cunninghami* and *H. segoviae* by the presence of smaller incisors, reduced P1, and a narrower muzzle in the latter. The remaining species of *Homalodotherium*, *H. crassum* and *H. excursum*, only known by a few postcranial remains —astragalus and tibia, and foot-bones, respectively— were differentiated by Scott (1912) by their size, *H. crassum* being the largest and *H. excursum*, the smallest.

Homalodotherium sp.
Figure 3.2–3

Referred material. See Appendix 2.

Geographic distribution. BB (Estancia Santa Lucia) and SBB (Estancia Cordón Alto).

Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene).

Description and comments. The cheek teeth of the referred specimens exhibit roots and labial and lingual cingula, features that, among others, characterize *Homalodotherium*. Their size resembles that of both *H. cunninghami* and *H. segoviae*, but a further specific taxonomic identification was not possible due to the fragmentary condition of the specimens that do not allow us to evaluate the differential development of upper incisors and P1.

Family Toxodontidae Owen, 1845

Subfamily Nesodontinae Murray, 1866

Genus ***Nesodon*** Owen, 1847

Type species. *Nesodon imbricatus* Owen, 1847. Santa Cruz Formation, Río Gallegos, Province of Santa Cruz, Argentina.

Species recognized in the Santa Cruz Formation. The type species, *N. conspurcatus* (Ameghino, 1887b) and *N. cornutus* Scott, 1912.

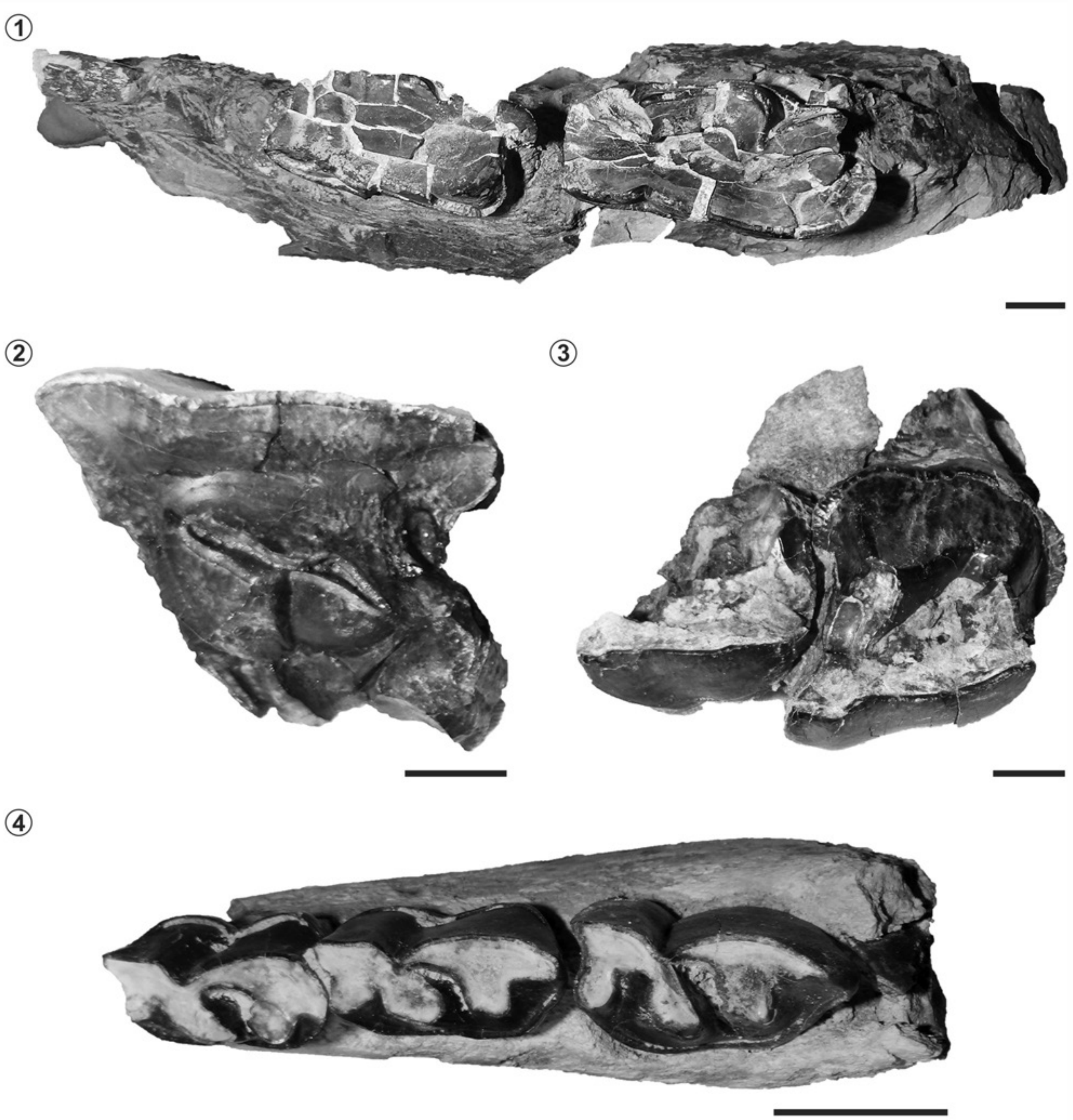

Figure 3. In oclusal view. **1,** ***Astrapotherium magnum***, left mandibular fragment with m1–2 of **MPM-PV 19927**; **2–4,** ***Homalodotherium*** sp., **2,** broken left M3 of **MPM-PV 19629**; **3, MPM-PV 19802**, right maxillary fragment with P4–M1?; **4,** right mandibular fragment with p4–m2 of **MPM-PV 19725**. Scale bars= 10 mm.

Comments. According to Scott (1912), *N. imbricatus* is the largest species, whereas *N. conspurcatus* is the smallest (at least 15 % smaller than *N. imbricatus*). *Nesodon cornutus*, only known by its holotype, exhibits an intermediate size and is characterized by a higher cranium, a higher sagittal crest and the presence of a bulge in the frontal bone located in front of the temporal lines, probably associated to a dermal horn (Scott, 1912; Croft *et al.*, 2003).

Nesodon imbricatus Owen, 1847

Figure 4.1–2; Appendix 3; Table 1

Referred material. MPM-PV 19560, almost complete mandible and lower dentition.

Geographic distribution. BB (Estancia Santa Lucia).

Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene).

Description and comments. MPM-PV 19560 is assigned to *Nesodon imbricatus* due its morphology (*e.g.*, well-developed p1) and its size (MDL_{m1}= 31.0 mm; LLL_{m1}= 17.8 mm; see Appendix 3 for the remaining teeth), which falls within the range established by Scott (1912) for the species (*e.g.*, $MDL_{m1}\approx$ 25.0–35.0 mm; $LLL_{m1}\approx$ 15.0–20.0 mm).

Nesodon sp.

Figure 4.3

Referred material. See Appendix 2.

Geographic distribution. BB (Estancia Santa Lucia) and SBB (Estancia Cordón Alto).

Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene).

Comments. Mostly all of the assigned specimens are fragments of upper and lower cheek teeth in different ontogenetic stages, but its fragmentary nature does not allow a determination below the genus level.

Genus ***Adinotherium*** Ameghino, 1887b

Type species. *Adinotherium magister* Ameghino, 1887b. Santa Cruz Formation, Barrancas del Río Santa Cruz, Province of Santa Cruz, Argentina.

Species recognized in the Santa Cruz Formation. *A. ovinum* (Owen, 1853), *A. nitidum* Ameghino, 1887b, *A. splendidum* Ameghino, 1887b, *A. robustum* Ameghino, 1891a and *A. karaikense* Ameghino, 1891c.

Comments. Scott (1912) used *A. ovinum* to characterize the genus, and differentiated *A. splendidum* by its high cranium and the presence of extremely broad and massive postorbital processes, which exhibit an unusual anterior position. Scott (1912) validated *A. robustum* with reservations and described the species as being the largest and heaviest species, which presents a protuberance on the occipital region due to the development of the epitympanic sinus, greatly expanded zygomatic arches and a well-developed sagittal crest that is markedly high and descends quite abruptly to the forehead. Scott (1912) differentiated *A. nitidum* by its size mentioning that it was the smallest *Adinotherium*, but, as recognized by the author, the species was erected based on a juvenile specimen, a reason why *A. nitidium* is not included in our analysis. *A. karaikense* is only known from its type specimen that is currently lost in the collection at MACN-A, it is characterized by its long and narrow skull, anteriorly narrow rostrum and the presence of a slight curvature of the zygomatic arches. Fortunately, there there is a photograph of this skull in Scott's album in Vizcaíno *et al.* (2017, Suppl. files, Appendix 1, p. 137, fig. 461), a fact that allowed us to question the diagnostic characteristics mentioned by Scott (1912), because the zygomatic arches are not preserved in the type and the narrowing of the rostrum falls within the range observed in specimens of *Adinotherium ovinum* (M. Fernández pers. obs.). For this reason, *A. karaikense* is also omitted from the present analysis.

Adinotherium ovinum (Owen, 1853)

Figure 5.1–2; Appendix 3; Tables 2–3

Referred material. MPM-PV 19717, almost complete skull with associated dentition.

Geographic distribution. SBB (Estancia Cordón Alto).

Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene).

Description and comments. MPM-PV 19717 is a well-preserved skull of a young adult which features that allows its identification as *Adinotherium* (*e.g.*, reduced I3, C and P1; I1–2 more transversely positioned than in *Nesodon*; presence of a conspicuous narrowing of the skull at the level of the

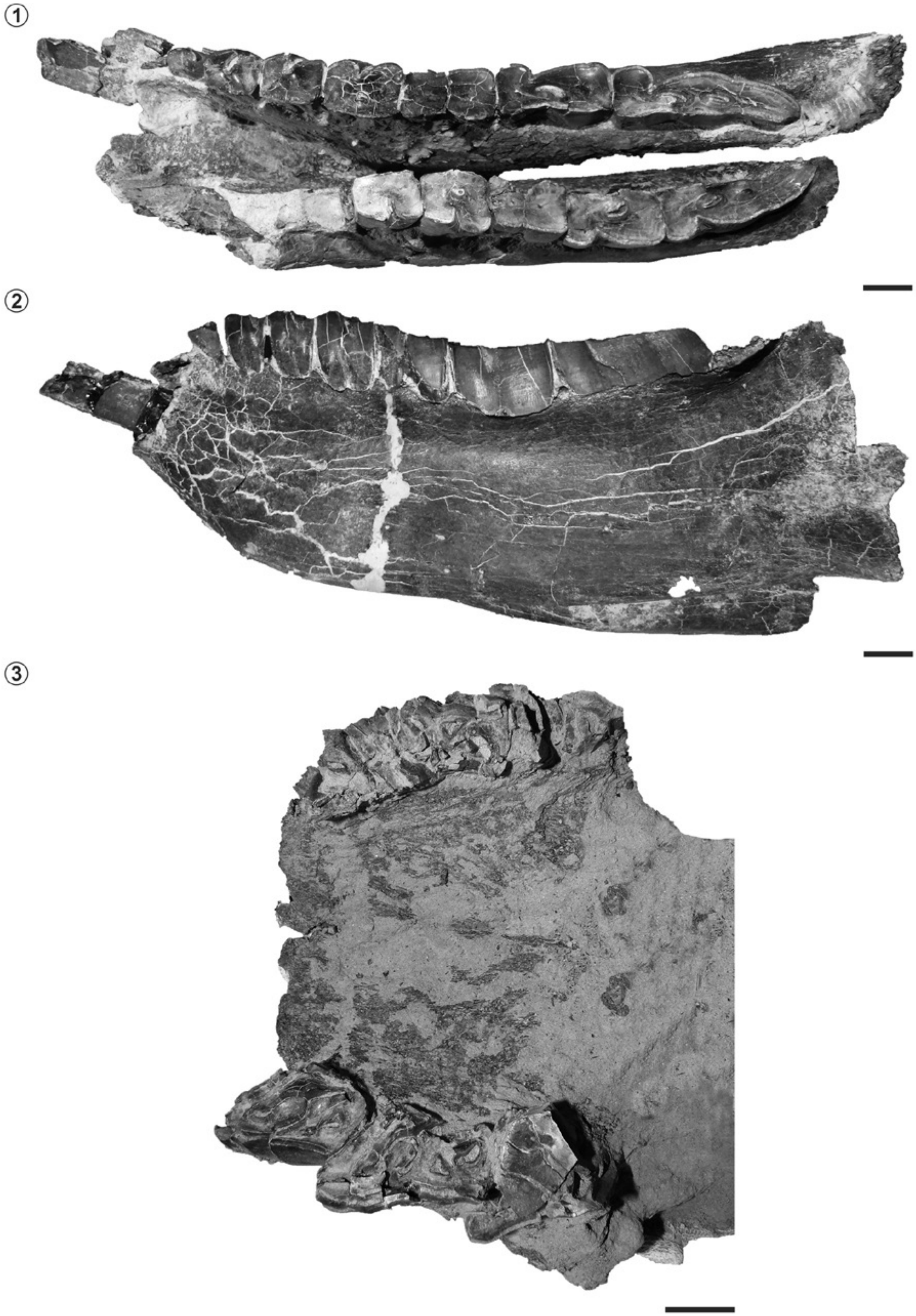

Figure 4. ***Nesodon*. 1–2, *N. imbricatus*, MPM-PV 19560**, almost complete mandible with its dentition; **1,** oclusal view; **2,** right lateral view (reversed); **3, *Nesodon*** sp., **MPM-PV 19568**, maxillary fragment with both broken M1–3, oclusal view; Scale bars= 20 mm.

premaxillary-maxillary suture). Regarding the allocation to *A. ovinum*, the postorbital processes, which are incomplete, do not show the conspicuous development described for *A. splendidum* and both are located posterior to the level of M3, in contrast to the unusually anterior position of *A. splendidum* (Scott, 1912). The sagittal crest is long and with a similar height throughout its length, the zygomatic arches are well-developed, but not massive nor greatly expanded as described for *A. robustus* (Scott, 1912). In addition, the skull does not exhibit the large size nor the robustness described for the last species.

Adinotherium sp.

Referred material. See Appendix 2.
Geographic distribution. BB (Estancia Aguada Grande and Estancia Santa Lucia), SBB (Estancia Cordón Alto) and YH.
Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene).
Comments. All the referred specimens involve fragments of upper and lower cheek teeth in different ontogenetic stages, which are too incomplete to establish the species.

Suborder TYPOTHERIA Zittel, 1893
Family HEGETOTHERIIDAE Ameghino, 1894
Subfamily HEGETOTHERIINAE Ameghino, 1894

Genus ***Hegetotherium*** Ameghino, 1887b

Type species. *Hegetotherium mirabile* Ameghino, 1887b. Santa Cruz Formation, Barrancas del Río Santa Cruz, Province of Santa Cruz, Argentina.
Species recognized in the Santa Cruz Formation. The type species according to Seoane and Cerdeño (2019).

Hegetotherium mirabile Ameghino, 1887b
Figure 6.1–4; Appendix 3; Tables 4–5

Referred material. See Appendix 2.
Geographic distribution. BB (Estancia Aguada Grande and Estancia Santa Lucia) and SBB (Estancia Cordón Alto).
Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene).
Description and comments. All the referred specimens involve euhypsodont cheek teeth, which identification as *Hegetotherium mirabile* is associated to both its morphology (*e.g.*, upper teeth sub-elliptical in outline, with simple oclusal surfaces that lack fossettes and prominent folds; lower cheek teeth with straight lingual faces and prominent labial sulci) and size (*e.g.*, $MDL_{M1} \approx 7.5–8.0$ mm, $LLL_{M1} \approx 4.0–4.5$ mm; $MDL_{m1} \approx 6.0–7.0$ mm, $LLL_{m1} \approx 3.0–4.0$ mm; see Appendix 3, Tables 4–5 for other dimensions) that falls within the range given by Sinclair (1909) and Seoane and Cerdeño (2019) for the species (*e.g.*, $MDL_{M1} \geq 7$ mm, $LLL_{M1} \geq 3.8$ mm; $MDL_{m1} \geq 5$ mm, LLL_{m1} is ≥ 3 mm).

Genus ***Pachyrukhos*** Ameghino, 1885

Type species. *Pachyrukhos moyani* Ameghino, 1885. Santa Cruz Formation, Barrancas del Río Santa Cruz, Province of Santa Cruz, Argentina.
Species recognized in the Santa Cruz Formation. The type species according to Seoane and Cerdeño (2019).

Pachyrukhos moyani Ameghino, 1885
Figure 6.5–8; Appendix 3; Tables 6–7

Referred material. See Appendix 2.
Geographic distribution. SBB (Estancia Cordón Alto and Estancia El Tordillo).
Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene).
Description and comments. The referred specimens involve incomplete skulls and maxillary and mandibular fragments for which the identification as *Pachyrukhos moyani* is related to both its morphology (*e.g.*, rodent-like skulls with lower rostrum; absence of I2–P1 that is replaced in a conspicuous upper diastema; upper teeth sub-elliptical in outline without fossettes and marked folds; i3–p1 absent and replaced by a pronounced lower diastema; lower cheek teeth with straight lingual faces and conspicuous labial sulci) and small size compared with other typotheres (*e.g.*, $MDL_{M1} \approx 4.0–4.6$ mm, $LLL_{M1} \approx 2.5–3.5$ mm; $MDL_{m1} \approx 3.0–4.0$ mm, $LLL_{m1} \approx 2.0–2.5$ mm; see Appendix 3, Tables 6–7 for other dimensions) that falls within the range of measurements given by Sinclair (1909) and Seoane and Cerdeño (2019) for the species (*e.g.*, $MDL_{M1} \approx 4.0–5.2$ mm, $LLL_{M1} \approx 2.5–3.5$ mm; $MDL_{m1} \approx 3.5–4.6$ mm, $LLL_{m1} \approx 1.8–2.5$ mm).

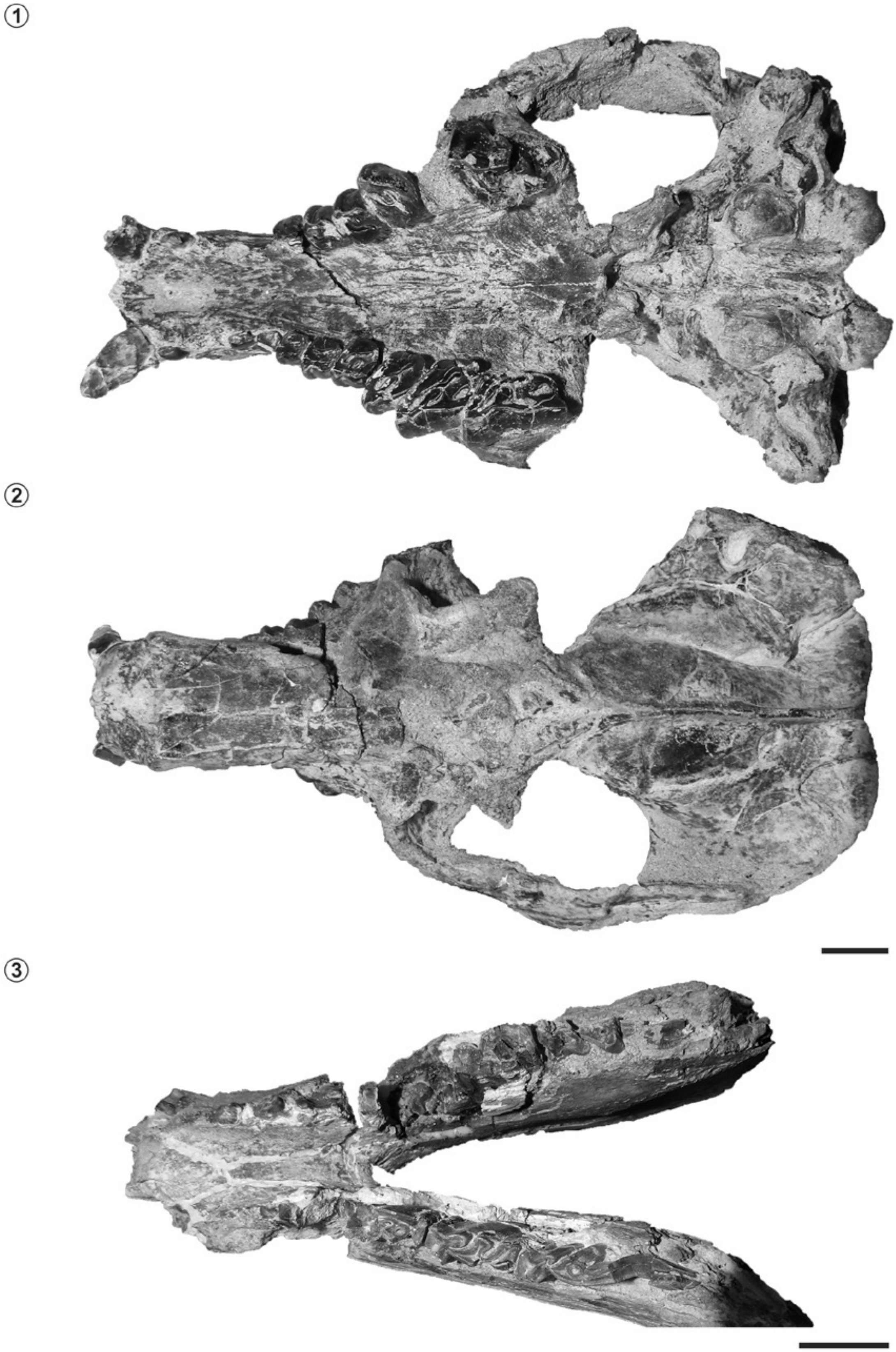

Figure 5. ***Adinotherium*. 1–2, *A. ovinum*, MPM-PV 19717**, almost complete skull with associated dentition; **1,** ventral view; **2,** dorsal view; **3,** ***Adinotherium*** sp., **MPM-PV 19567**, incomplete mandible with associated broken dentition, oclusal view. Scale bars= 20 mm.

Family Interatheriidae Ameghino, 1887a

Subfamily Interatheriinae Ameghino, 1887a

Genus *Protypotherium* Ameghino, 1885

Type species. *Protypotherium antiquum* Ameghino, 1885. Formación Ituzaingó, Barrancas del Río Paraná, Province of Entre Ríos, Argentina.

Species recognized in the Santa Cruz Formation. *Protypotherium australe* Ameghino, 1887a, *Protypotherium praerutilum* Ameghino, 1887b, and *Protypotherium attenuatum* Ameghino, 1887b.

Comments. *Protypotherium* presents continuous and complete dental series, I1–C mesiodistally expanded, labiolingually compressed and equally developed; P/p2–4 not molarized; P2–4 sub-triangular in outline and with shallow lingual and labial folds; M1–3 with deep and long entoflexus and very shallow –or even absent– parastilar sulcus and ectoflexus; bifid i1–2, with a cylindrical section shape; i3–c mesiodistally expanded with lingual sulcus, and p1 completely caniniform with no differentiated talonid; p3–4 with the trigonid larger than the talonid, with the opposite condition observed in the molars. Within the species of *Protypotherium* validated by Sinclair (1909), *P. australe* is characterized by its wider molars and larger size; *P. praerutilum* by its relatively narrower molars and intermediate size (at least 15 % smaller than *P. australe*; Sinclair, 1909), and *P. attenuatum* distinguished only by its smaller size (30 % smaller than *P. australe*; Sinclair, 1909). Tauber

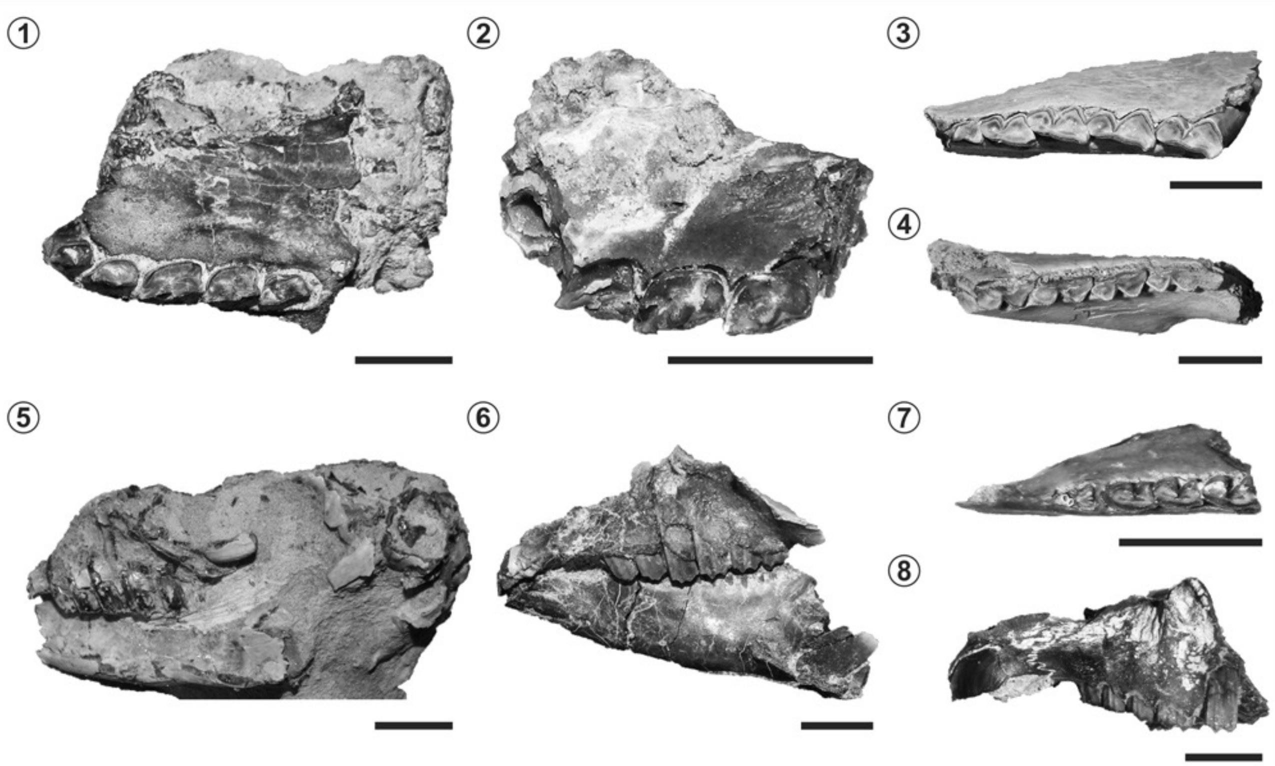

Figure 6. Hegetotheriidae. **1–4,** ***Hegetotherium mirabile***; **1, MPM-PV 19513**, right maxillary fragment with P3 (erupting)–M3, oclusal view; **2, MPM-PV 19626**, right maxillary fragment with broken P2 (alveolus)–4 and M1, oclusal view; **3, MPM-PV 19487**, right mandibular fragment with p2–m2, oclusal view, oclusal view; **4, MPM-PV 19658**, left mandibular fragment with p4–m3, oclusal view; **5–8,** ***Pachyrukhos moyani***; **5, MPM-PV 19800**, articulated incomplete skull and mandible, left lateral view; **6, MPM-PV 19905**, articulated incomplete skull and mandible, left lateral view; **7, MPM-PV 19917**, right mandibular fragment with p2–m1, oclusal view; **8, MPM-PV 19917**, incomplete skull, right lateral view (reversed). Scale bars= 10 mm.

(1996) supported this taxonomic arrangement and emended their diagnoses; nevertheless, a preliminary analysis developed in the doctoral thesis in progress of one of the authors (MF) indicates that some characteristics mentioned by Tauber (1996) are variable, reason why we focus mainly on Sinclair (1909), particularly on the size, in order to establish the specific determination.

Protypotherium australe Ameghino, 1887a

Figure 7.1–4; Appendix 3; Tables 8–9

Referred material. See Appendix 2.
Geographic distribution. BB (Estancia Santa Lucia) and SBB (Estancia Cordón Alto and Estancia El Tordillo).
Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene).
Description and comments. The identification as *P. australe* is related to both its morphology (*e.g.*, I1 is highly curved and well expanded and cheek teeth are generally wider than those observed in *P. praerutilum* and *P. attenuatum*) and, particularly, its size (*e.g.*, $MDL_{M1} \approx$ 7.0–9.5 mm, $LLL_{M1} \approx$ 4.0–6.5 mm; $MDL_{m1} \approx$ 7.0–9.0 mm, $LLL_{m1} \approx$ 4.0–5.0 mm; see Appendix 3, Tables 8–9 for other dimensions) that fall within the range of size mentioned by Sinclair (1909) for this species (*e.g.*, $MDL_{M1} \approx$ 7.0–9.0 mm, $LLL_{M1} \approx$ 5.0–6.0 mm; $MDL_{m1} \approx$ 7.0–9.0 mm, $LLL_{m1} \approx$ 3.5–4.5 mm).

Protypotherium praerutilum Ameghino, 1887b

Figure 7.5–6; Appendix 3; Tables 10–11

Referred material. See Appendix 2.
Geographic distribution in Río Santa Cruz. BB (Estancia Aguada Grande and Estancia Santa Lucia) and SBB (Estancia Cordón Alto and Estancia El Tordillo).
Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene).
Description and comments. The identification as *P. praerutilum* is based on its teeth morphology (*e.g.*, upper incisors sub-equally developed and cheek teeth narrower than in *P. australe*; m3 lacks of labial sulcus in the talonid as observed in the holotype MACN-A 1082 that is present on *P. australe* and *P. attenuatum*) and teeth size (*e.g.*, $MDL_{M1} \approx$ 6.3–6.7 mm, $LLL_{M1} \approx$ 4.5 mm; $MDL_{m1} \approx$ 6.0–6.5 mm, $LLL_{m1} \approx$ 3.0–3.5 mm; see Appendix 3, Tables 10–11 for other dimensions) that matches the range of dimensions given by Sinclair (1909) for the species (*e.g.*, $MDL_{M1} \approx$ 6.2–6.6 mm, $LLL_{M1} \approx$ 4.5 mm; $MDL_{m1} \approx$ 6.0 mm, $LLL_{m1} \approx$ 3.0 mm).

Protypotherium attenuatum Ameghino, 1887b

Figure 7.7–8; Appendix 3; Tables 12–13

Referred material. See Appendix 2.
Geographic distribution. BB (Estancia Aguada Grande and Estancia Santa Lucia) and SBB (Estancia Cordón Alto and Estancia El Tordillo).
Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene).
Description and comments. The assignation to *P. attenuatum* is based on both its teeth morphology (*e.g.*, more pronounced curvature on the upper cheek tooth row as seen in the syntype MACN-A 524 compared with *P. australe* and *P. praerutilum*) and its teeth size (*e.g.*, $MDL_{M1} \approx$ 6.0–6.2 mm, $LLL_{M1} \approx$ 4.0 mm; $MDL_{m1} \approx$ 4.5–6.0 mm, $LLL_{m1} \approx$ 2.0–3.0 mm; see Appendix 3, Tables 12–13 for other dimensions) that falls within the range of size mentioned by Sinclair (1909) for the species (*e.g.*, $MDL_{M1} \leq$ 6.2 mm, $LLL_{M1} \approx$ 4.5 mm; $MDL_{m1} \approx$ 5.0–5.5 mm, $LLL_{m1} \leq$ 3.0 mm).

Protypotherium sp.

Referred material. See Appendix 2.
Geographic distribution. BB (Estancia Santa Lucia) and SBB (Estancia Cordón Alto and Estancia El Tordillo).
Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene).
Comments. All the referred specimens are too fragmented in order to establish a specific identification.

Genus ***Interatherium*** Ameghino, 1887a

Type species. *Interatherium rodens* Ameghino, 1887a. Santa Cruz Formation, Barrancas del Río Santa Cruz, Province of Santa Cruz, Argentina.

Species recognized in the Santa Cruz Formation. The type species, *Interatherium extensum* Ameghino, 1889, *I. excavatum* Ameghino, 1889 and *I. robustum* Ameghino, 1891a.
Comments. *Interatherium* is characterized, among other fea-

tures, by exhibiting a well-developed descending maxillary process of the zygomatic arch; I1 more developed than I2–C, with the latter two reduced or even missing; P/p3–4 completely molarized; P3–4 sub-rectangular in outline; M1–3 with deep and continuous entoflexus and parastylar sulcus, with well-developed folds, but less than the pre-

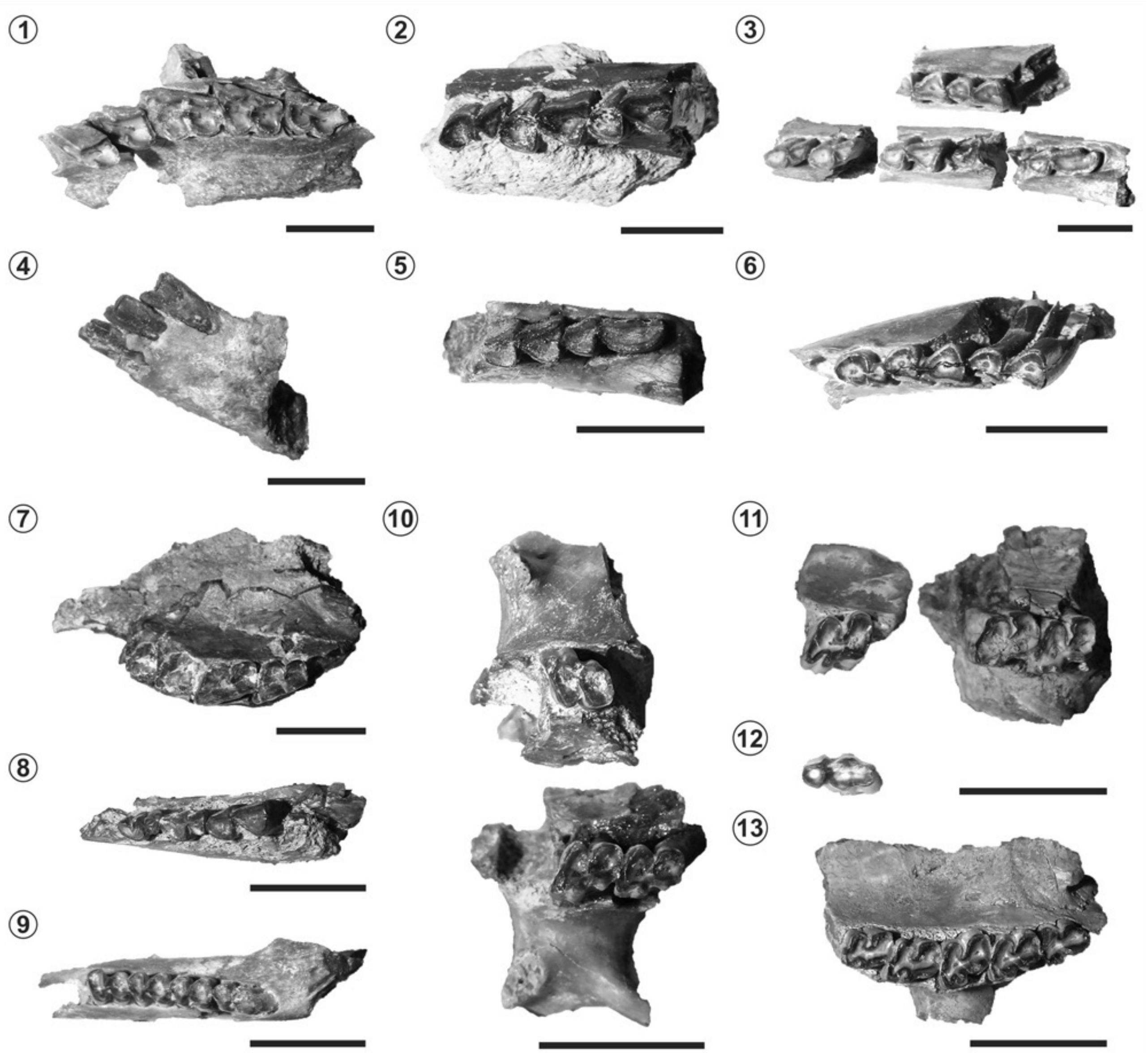

Figure 7. Interatheriinae. **1–4,** ***Protypotherium australe***; **1–3, MPM-PV 19921**; **1,** left maxillary fragment with P3–M3, oclusal view; **2,** right mandibular fragment with m1 (broken)–2 (above) and left mandibular fragments with p3–m2 (trigonid)–3 (below), oclusal view; **3,** mandibular symphysis, right lateral view (reversed); **4, MPM-PV 19925**, left mandibular fragment with p4–m2, oclusal view; **5–6,** ***Protypotherium praerutilum***; **5, MPM-PV 19911**, left mandibular fragment with m2–3, oclusal view; **6, MPM-PV 19526**, right mandibular fragment with p4–m2, oclusal view; **7–8,** ***Protypotherium attenuatum***; **7, MPM-PV 19534**, right maxillary fragment with alveoli of P3–4 and complete M1–2, oclusal view; **8, MPM-PV 19525**, left mandibular fragment with p3–m1, oclusal view; **9–13,** ***Interatherium*** sp.; **9,** right mandibular fragment with dp4–m3 of **MPM-PV 19770**, oclusal view; **10,** fragmented palate with left M1 and right M1–2 of **MPM-PV 19770**, oclusal view; **11,** fragmented maxilla with right P4 (isolated) and M1–2 of **MPM-PV 19729**, oclusal view; **12,** left m3 of **MPM-PV 19729**, oclusal view; **13, MPM-PV 19825**, right maxillary fragment with P3–M3, oclusal view. Scale bars= 10 mm.

molars; i1–p1 slightly mesiodistally expanded and very procumbent; in p3–4 the trigonid and talonid exhibit a similar development. Following Sinclair (1909), *I. extensum* is distinguished from *I. robustum* by a smaller I3 and the presence of a straight fronto-nasal suture in the former, but the author himself expressed doubt about whether these differences are specific or interindividual in nature. Likewise, Sinclair (1909) distinguished *I. excavatum* by its lyre-shaped temporal ridges, but the taxonomic value of this feature needs to be re-evaluated (Cassini *et al.*, 2012).

Interatherium sp.

Figure 7.9–17

Referred material. See Appendix 2.
Geographic distribution. BB (Estancia Aguada Grande and Estancia Santa Lucia) and SBB (Estancia Cordón Alto and Estancia El Tordillo).
Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene).
Comments. No referred specimens exhibit any of the bony structures (*e.g.*, cranial sutures, premaxilla and anterior region of the maxilla) and dental elements (*e.g.*, I3 and C) described by Sinclair (1909) that permit a specific identification.

DISCUSSION AND CONCLUSIONS

Taxonomic richness from the Río Santa Cruz and comparison with the coastal localities

Based on the new specimens collected in the exposures of the SCF in Barrancas Blancas, Segundas Barrancas Blancas and Yaten Huageno at the RSC, and following the current taxonomic schemes, with the observations already made throughout this work, this contribution recognizes one genus (*Astrapotherium*) and a single species (*A. magnum*) within Astrapotheria, and seven genera (*Pachyrukhos*, *Hegetotherium*, *Protypotherium*, *Interatherium, Homalodotherium*, *Nesodon* and *Adinotherium*) and eight species (*Pachyrukhos moyani*, *Hegetotherium mirabile*, *Protypotherium attenuatum*, *P. australe*, *P. praerutilum*, *Interatherium* sp., *Nesodon imbricatus* and *Adinotherium ovinum*) among the Notoungulates.

The generic richness of the astrapotheres and notoungulates recorded in BB, SBB and YH only differs from the one presented by Scott (1912, 1927, 1937) and Sinclair (1909) for the RSC in the absence of *Hyperoxotodon* in our sample. In a specific level, our ungulate richness is lower than the one presented by these authors. This could be associated to the fragmentary state of many of the collected materials that prevent us from providing identifications at the species level (*e.g.*, *Homalodotherium* sp., *Nesodon* sp., *Adinotherium* sp., *Protypotherium* sp., *Interatherium* sp. and *Adinotherium* sp.)

According to the dates in Cuitiño *et al.* (2016), the sedimentary succession from BB extends from ~17.45 to ~16.49 Ma, which is likely older than SBB (~16.32 to ~15.63 Ma), but it is synchronous with the succession at YH (~17.22 to ~16.67 Ma). In BB and SBB, we were able to identify almost the same faunal content regarding astrapotheres and notoungulates. Notably, the two localities differ by the presence of *Pachyrukhos* at SBB, which has been abundantly identified in the entire stratigraphic column. This genus has also been recognized (M. Fernández, pers. obs.) in the coastal localities Cerro Observatorio (= Monte Observación; Vizcaíno *et al.*, 2012b) (~17.80 to ~16.30 Ma; Cuitiño *et al.*, 2016) from materials housed at MACN-A, Killik Aike Norte (Sinclair, 1909) (~17.0 to ~15.9 Ma; Cuitiño *et al.*, 2016), and Puesto Estancia La Costa (*e.g.*, left mandibular fragment with four cheek teeth MPM-PV 17489) (~17.50 to ~16.70 Ma; Cuitiño *et al.*, 2016). Cerro Observatorio is synchronous with BB, whereas the fossils recovered from Killik Aike Norte (~17.0 to ~16.9 Ma; Cuitiño *et al.*, 2016) and Puesto Estancia La Costa (~17.5 to ~17.4 Ma; Cuitiño *et al.*, 2016) are younger than those collected from BB (~17.0 to ~16.5 Ma; Cuitiño *et al.*, 2016). Therefore, the absence of *Pachyrukhos* in BB could be associated with a regional difference or a population movement event (a hypothesis that cannot be tested at the moment). YH differs from BB and SBB in the absence of all the Typotheria, Homalodotheriidae and *Nesodon*; the sample obtained in YH is by far the smallest so the observed differences could be associated with the incomplete sampling obtained in YH, and do not represent a real difference in the ungulate diversity.

At the species level, the main differences observed between BB, SBB and YH are the exclusive presence of *Nesodon* *imbricatus* in BB, *Adinotherium ovinum* and *Pachyrukhos moyani* in SBB, and *Astrapotherium magnum* in YH. However, in those localities in which these species have not been identified, a large number of specimens are assigned to *Nesodon* sp., *Adinotherium* sp. and, to a lesser extent, *Astrapotherium* sp. In his recent unpublished revision, Hernández del Pino (2018) concludes that *Nesodon imbricatus* and *Adinotherium ovinum* are the only valid species of each respective genus. If so, all *Nesodon* sp. and *Adinotherium* sp. should be allocated to *N. imbricatus* and *A. ovinum*, respectively. Only in this context, *Nesodon imbricatus* would be present in BB and SBB, whereas *Adinotherium ovinum* would be also present in YH, and, as a result, these differences are equal to those mentioned for the generic level.

The astrapothere and notoungulate generic richness already described for BB, SBB and YH matches the one registered in the well-known coastal localities when comparing to the information given by Scott (1912, 1927, 1938), Sinclair (1909), Tauber (1997a,b), Tauber *et al.* (2004, 2008) and Cassini *et al.* (2012). But differs from Tauber (1999) since this author recognized the Interatheriinae *Cochilius* –a genus known from the Deseadan (Late Oligocene) to the Colhuehuapian (Early Miocene) SALMAs of Patagonia (Reguero *et al.*, 2003)– at the Estancia La Costa locality. Tauber (1999) did not make any further comment nor publish any details in support of this unusual occurrence, nor does this taxon appear in the large samples collected at this locality over the past twenty years, so we have reservations about the identification. On the other hand, when comparing the specific richness among BB, SBB and YH, and the eastern localities, the one from the RSC is reduced since only *Nesodon imbricatus*, *Adinotherium ovinum*, *Protypotherium australe*, *P. attenuatum*, *P. praerutilum*, *Hegetotherium mirabile*, *Pachyrukhos moyani* and *Astrapotherium magnum* have been identified in the area. All these species are also recorded for the coastal localities, associated to several species not present at the RSC: *Interatherium robustum*, *I. extensum*, *I. excavatum*, *Adinotherium robustum*, *Homalodotherium segoviae*, *H. cunnighami*, *H. crassum*, *Astrapotherium nanum*? and *Nesodon conspurcatus*. Tauber (1999) identified *Homalodotherium rutimeyeri*, but we follow Scott (1912) in placing *H. rutimeyeri* in synonymy with *N. conspurcatus*.

Paleoenvironmental inferences

The paleoecological interpretations and comparisons were made at a genus level following most of the inferences in the studies performed with the coastal materials both in the taxa analysed here and in other clades (*e.g.*, Cassini *et al.*, 2012; Cassini, 2013; Toledo *et al.*, 2013, 2015; Muñoz *et al.*, 2017, 2019).

As stated above, the sample of YH is considerably smaller than the one from the other localities and only two of the three largest ungulates have been found (*Astrapotherium* and *Adinotherium*). If this is not due to sampling error, it would mean the absence of small body mass ungulates and a deeper analysis would be necessary to find some explanation. This could be related to ecological reasons (the temporary span is similar to BB) or to taphonomic reasons (the environment on the west would have been one with more energy than the one towards the east; Fernicola *et al.*, 2014).

The other two localities present virtually the same richness of the ungulates treated in this contribution. The only difference is the presence of *Pachyrukhos* in SBB and its absence in BB. As mentioned above, this discrepancy is not related with the differences in temporality (*e.g.*, *Pachyrukhos* is present in Monte Observación, Killik Aike Norte and Puesto Estancia La Costa). The absence of this genus in the easternmost locality treated here is lacking the smallest Santacrucian ungulate. *Pachyrukhos* was probably a rapid runner and the most agile among the typotheres and would have been a grazer of open environments (Cassini *et al.*, 2012). Its absence could be interpreted as indicative of less open areas in BB than in SBB. Overall, the similarity between the ungulate fauna of Río Santa Cruz and the one in the coastal localities (all the same genera), except for the presence of *Hyperoxotodon* in the former (Ameghino, 1887b), could lead to interpret the environment in a similar way, a complex mosaic of open and closed habitats (Cassini *et al.*, 2012; Kay *et al.*, 2012; Vizcaíno *et al.*, 2012a). This inference should be contrasted with the remaining taxa and sedimentological evidences.

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REFERENCES

Ameghino, C. 1890. Exploraciones geológicas en la Patagonia. *Boletín del Instituto Geográfico Argentino* 11: 3–46.

Ameghino, F. 1885. Nuevos restos de mamíferos fósiles oligocenos, recogidos por el profesor Pedro Scalabrini y pertenecientes al Museo Provincial de la Ciudad del Paraná. *Boletín de la Academia Nacional de Ciencias de Córdoba* 8: 5–207.

Ameghino, F. 1887a. Observaciones generales sobre el orden de mamíferos extinguidos sub-americanos llamados Toxodontes (Toxodontia) y sinopsis de los géneros y especies hasta ahora conocidos. *Anales del Museo de La Plata* 1: 1–66.

Ameghino, F. 1887b. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de la Patagonia austral y depositados en el Museo La Plata. *Boletín del Museo de La Plata* 1: 1–26.

Ameghino, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas de la Academia Nacional de Ciencias de Córdoba*, 6: i–xxxii, 1–1027, atlas of 98 pls.

Ameghino, F. 1891a. Nuevos restos de mamíferos fósiles descubiertos por Carlos Ameghino en el Eoceno inferior de la Patagonia Austral. Especies nuevas, adiciones y correcciones. *Revista Argentina de Historia Natural* 1: 286–328.

Ameghino, F. 1891b. Observaciones críticas sobre los mamíferos eocenos de la Patagonia austral. *Revista Argentina de Historia Natural* 1: 328–382.

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

Ameghino, F. 1891d. Los monos fósiles del Eoceno de la República Argentina. *Revista Argentina de Historia Natural* 1: 383–395.

Ameghino, F. 1894. *Énumération synoptique des espèces de mammifères fossiles des formations éocènes de Patagonie*. Coni e hijos, Buenos Aires, 196 p.

Ameghino, F. 1899. Sinopsis geológico-paleontológica de la Argentina, Correspondencia científica. In: A.J. Torcelli (Ed.), *Obras Completas y Correspondencia Científica de Florentino Ameghino*. Taller de Impresiones Oficiales del Gobierno de la Provincia de Buenos Aires, La Plata, p. 485–734.

Ameghino, F. 1900–1902. L'âge des formations sédimentaires de Patagonie. *Anales de la Sociedad Científica Argentina* 50: 109–130, 145–165, 209–229; 51: 20–39; 52: 65–91, 189–197, 244–250; 54: 161–180, 220–249, 283–342.

Ameghino, F. 1907. Les toxodontes a'cornes. *Anales del Museo Nacional de Historia Natural de Buenos Aires* 16: 49–91.

Billet, G. 2010. New Observations on the Skull of *Pyrotherium* (Pyrotheria, Mammalia) and New Phylogenetic Hypotheses on South American Ungulates. *Journal of Mammalian Evolution* 17: 21–59.

Billet, G. 2011. Phylogeny of the Notoungulata (Mammalia) based on cranial and dental characters. *Journal of Systematic Palaeontology* 9: 481–497.

Billet, G., De Muizon, C., and Mamani Quispe, B. 2008. Late Oligocene mesotheriids (Mammalia, Notoungulata) from Salla and Lacayani (Bolivia): implications for basal mesotheriid phylogeny and distribution. *Zoological Journal of the Linnean Society* 152: 153–200.

Bond, M. 1986. Los ungulados fósiles de Argentina: evolución y paleoambientes. *4° Congreso Argentino de Paleontología y Bioestratigrafía* (Mendoza), *Actas* 2: 173–185.

Bond, M. 1999. Quaternary native ungulates of Southern South America. A synthesis. In: J. Rabassa, and M. Salemme (Eds.), *Quaternary of South America and Antarctic Peninsula*. Centro Austral de Investigaciones Científicas and Universidad Nacional de la Patagonia, Ushuaia, p. 177–205.

Bond, M., Cerdeño, E., and López, G. 1995. Los ungulados nativos de América del Sur. In: M.T. Alberdi, G. Leone, and E.P. Tonni (Eds.), *Evolución biológica y climática de la región Pampeana durante los últimos cinco millones de años. Un ensayo de correlación con el Mediterráneo occidental*. Monografías del Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, Madrid, p. 259–275.

Buckley, M. 2015. Ancient collagen reveals evolutionary history of the endemic South American 'ungulates'. *Proceedings of the Royal Society B* 282: 1806 doi: 10.1098/rspb.2014.2671

Burmeister, G. 1879. *Description physique de la République Argentine. D'après des observations personnelles et étrangères.* Imprenta Paul-Émile Coni, Buenos Aires, Argentina, 553 p.

Cassini, G.H. 2013. Skull geometric morphometrics and paleoecology of Santacrucian (late early Miocene; Patagonia) native ungulates (Astrapotheria, Litopterna, and Notoungulata). *Ameghiniana* 50: 193–217.

Cassini, G.H., Cerdeño, E., Villafañe, A., and Muñoz, N.A. 2012. Paleobiology of Santacrucian native ungulates (Meridiungulata; Astrapotheria, 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.

Cifelli, R.L. 1985. South American ungulate evolution and extinction. In: F.G. Stehli, and S.D. Webb (Eds.), *The Great American Biotic Interchange*. Plenum Press, New York, p. 249–266.

Cifelli, R.L. 1993. The phylogeny of the native South American ungulates. In: F.S. Szalay, M.J. Novacek, and M.C. Mckenna (Eds.), *Mammals Phylogeny: Placentals*. Springer-Verlag, New York and London, p. 195–216.

Croft, D.A. 1999. Placentals: endemic South American ungulates. In: R. Singer (Ed.), *The Encyclopedia of Paleontology.* Fitzroy-Dearborn, Chicago, p. 890–906.

Croft, D.A., Flynn, J.J., and Wyss, A.R. 2004. Notoungulata and Litopterna of the early Miocene Chucal Fauna, northern Chile. *Fieldiana: Geology (New Series)* 50: 1–49.

Croft, D.A., Radic, J.P., Zurita, E., Charrier, R., Flynn, J.J., and Wyss, A.R. 2003. A Miocene toxodontid (Mammalia: Notoungulata) from the sedimentary series of the Cura-Mallín Formation, Loquimay, Chile. *Revista Geológica de Chile* 30: 285–298.

Cuitiño, J.I., Fernicola, J.C., Kohn, M.J., Trayler, R., Naipauer, M., Bargo, M.S., Kay, R.F., and Vizcaíno, S.F. 2016. U-Pb geochronology of the Santa Cruz Formation (early Miocene) at the Río Bote and Río Santa Cruz (southernmost Patagonia, Argentina): Implications for the correlation of fossil vertebrate localities. *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: 14–33.

Elissamburu, A. 2011. Estimación de la masa corporal en géneros del Orden Notoungulata. *Estudios Geológicos* 68: 91–11 doi:10.3989/egeol.40336.133

Farro, M.E. 2009. *La formación del Museo de La Plata. Coleccionistas, comerciantes y naturalistas viajeros a fines del Siglo XIX.* Prohistoria ediciones, Rosario, Argentina, 230 p.

Fernández, M., Fernicola, J.C., and Cerdeño, E. 2019a. The genus *Patriarchus* Ameghino, 1889 (Mammalia, Notoungulata, Typotheria), from the Santa Cruz Formation, Santa Cruz Province, Argentina. *Journal of Vertebrate Paleontology* doi: 10.1080/02724634.2019.1613416

Fernández, M., Fernicola, J.C., and Cerdeño, E. 2019b. On the type materials of the genera *Interatherium* Ameghino, 1887 and *Icochilus* Ameghino, 1889 (Interatheriidae, Notoungulata, Mammalia) from early Miocene of the Santa Cruz Province, Argentina. *Zootaxa* 4543: 195–220.

Fernández, M., Fernicola, J.C., Cerdeño, E., and Reguero, M.A. 2018. Identification of type materials of the species of *Protypotherium* Ameghino, 1885 and *Patriarchus* Ameghino, 1889 (Notoungulata: Interatheriidae) erected by Florentino Ameghino. *Zootaxa* 4387: 473–498.

Fernicola, J.C. 2011a. 1886–1888: Ascenso, auge y caída de la sociedad entre Florentino Ameghino y Francisco P. Moreno. *Publicación Electrónica de la Asociación Paleontológica Argentina* 12: 35–49.

Fernicola, J.C. 2011b. Implicancias del conflicto Ameghino-Moreno sobre la colección de mamíferos fósiles realizada por Carlos Ameghino en su primera exploración al río Santa Cruz, Argentina. *Revista del Museo Argentino de Ciencias Naturales nueva serie* 13: 41–57.

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.

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 Notohippidian. *Journal of South American Earth Sciences* 52: 94–107.

Fleagle, J.H., Perkins, M.E., Heizler, M.T., Nash, B., Bown, T.M., Tauber, A.A., Dozo, M.T., and Tejedor, M.F. 2012. Absolute and relative ages of fossil localities in the Santa Cruz and Pinturas Formations. 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. 41–58.

Flower, W.H. 1873. On a newly discovered extinct ungulate mammal from Patagonia, *Homalodontotherium cunninghami. Philosophical Transactions of the Royal Society of London* 164: 173–182.

Gelfo, J.N., López, G.M., and Bond, M. 2008. A new Xenungulata (Mammalia) from the Paleocene of Patagonia, Argentina. *Journal of Paleontology* 82: 329–335.

Hernández Del Pino, S. 2018. [*Anatomía y sistemática de los Toxodontidae (Notoungulata) de la Formación Santa Cruz, Mioceno temprano, Argentina*. Doctoral thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, 432 p. Unpublished.].

Kay, R.F., Vizcaíno, S.F., and Bargo, M.S. 2012. A review of the paleoenvironment and paleoecology of the Miocene Santa Cruz Formation. 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. 331–365.

Kay, R.F., Vizcaíno, S.F., Bargo, M.S., Perry, J.M.G., Prevosti, F.J., and Fernicola, J.C. 2008. Two new fossil vertebrate localities in the Santa Cruz Formation (late early Miocene, Argentina), 51 degrees South latitude. *Journal of South American Earth Sciences* 25: 187–195.

Kramarz, A.G., and Bond, M. 2009. A new Oligocene astrapothere (Mammalia, Meridiungulata) from Patagonia and a new appraisal of astrapothere phylogeny. *Journal of Systematic Palaeontology* 7: 117–128.

Kramarz, A.G., Garrido, A., and Bond, M. 2019. *Astrapotherium* from the middle Miocene Collón Cura Formation and the decline of astrapotheres in Southern South America. *Ameghiniana* doi: 10.5710/AMGH.15.07.2019.3258

Lydekker, R. 1894. Contribuciones al conocimiento de los vertebrados fósiles de la Argentina. Observaciones adicionales sobre los ungulados argentinos. *Anales del Museo de La Plata* 2: 1–248.

Marshall, L.G., Hoffstetter, R., and Pascual, R. 1983. Mammals and stratigraphy: Geochronology of the continental mammal-bearing Tertiary of South America. *Paleovertebrata, Mémoires Extraordinaires* 1–93.

Marshall, L.G., and Pascual, R. 1976. Fossil localities for Santacrucian (Early Miocene) mammals, Santa Cruz Province, Southern Patagonia, Argentina. *Journal of Paleontology* 50: 1129–1142.

Mercerat, A. 1890. Sinopsis de la familia de los Astrapotheridae (Eoceno de Patagonia). *Revista del Museo de La Plata* 1: 241–255.

Mercerat, A. 1891. Notas sobre la paleontología de la República Argentina. II. Sinopsis de la familia de los Proxotodontidae conservados en el Museo de La Plata (Eoceno de Patagonia). *Revista del Museo de La Plata* 1: 381–444.

Mercerat, A. 1895. Contributions a l'étude systématique des Toxodontia (Haplodontheridae, Toxodontidae et Xotodontidae). *Anales del Museo Argentino de Ciencias Naturales* 4: 257–306.

Moreno, F.P. 1879. *Viaje á la Patagonia austral: emprendido bajo los auspicios del gobierno nacional, 1876–1877.* Imprenta de La Nación, Buenos Aires, 498 p.

Moreno, F.P. 1882. Patagonia. Resto de un antiguo continente sumergido. *Anales de la Sociedad Científica Argentina* 14: 97–131.

Muñoz, N.A., Cassini, G.H., Candela, A.M., and Vizcaíno, S.F. 2017. Ulnar articular surface 3-D landmarks and ecomorphology of small mammals: a case study of two early Miocene typotheres (Notoungulata) from Patagonia. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 106: 315–323.

Muñoz, N.A., Toledo, N., Candela, A.M., and Vizcaíno, S.F. 2019. Functional morphology of the forelimb of Early Miocene caviomorph rodents from Patagonia. *Lethaia* 52: 91–106.

Owen, R. 1847. Notices of some fossil mammalia of South America.

Reports of the British Association of Advancements in Science (Southampton) 16: 65–67.

Owen R. 1853. Description of some species of the extinct genus *Nesodon*, with remarks on the primary group (Toxodontia) of hoofed quadrupeds, to which that genus is referable. *Philosophical Transactions of the Royal Society of London* 143: 291–310.

Pascual, R., Ortega Hinojosa, E.J., Gondar, D., and Tonni, E. 1965. Las edades del Cenozoico mamalífero de la Argentina, con especial atención a aquellas del territorio Bonaerense. *Anales de la Comisión de Investigaciones Científicas* 6: 165–193.

Patterson, B. 1934. Upper premolar-molar structure in the Notoungulata with notes on taxonomy. *Fieldiana: Geological Series, Field Museum of Natural History* 6: 91–111.

Patterson, B., and Pascual, R. 1968. The fossil mammal fauna of South America. *The Quarterly Review of Biology* 43: 409–451.

Patterson, B., and Pascual, R. 1972. The fossil mammal fauna of South America. In: A. Keast, F.C. Erk, and B. Glass (Eds.), *Evolution, Mammals and Southern Continents*. State University of New York Press, New York, p. 274–309.

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.

Podgorny, I. 2009. *El sendero del tiempo y de las causas accidentales. Los espacios de la prehistoria en la Argentina, 1850–1910*. Prohistoria ediciones, Rosario, 331 p.

Reguero, M.A., Ubilla, M., and Perea, D. 2003. A new species of *Eopachyrucos* (Mammalia, Notoungulata, Interatheriidae) from the late Oligocene of Uruguay. *Journal of Vertebrate Paleontology* 23: 445–457.

Schmidt, G.I., Hernández del Pino, S., Muñoz, N.A., and Fernández, M. 2019. Litopterna (Mammalia) from the Santa Cruz Formation (Early–Middle Miocene) at the Río Santa Cruz, southern 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: 170–192.

Scott, W.B. 1912. Mammalia of the Santa Cruz beds. Part II, Toxodonta of the Santa Cruz beds and Part III, Entelonychia of the Santa Cruz beds. In: W.B. Scott (Ed.), *Reports of the Princeton University Expeditions to Patagonia, 1896–1899.* Princeton, Princeton University, New Jersey, p. 111–300.

Scott, W.B. 1928. Mammalia of the Santa Cruz beds. Part IV. Astrapotheria. In: W.B. Scott (Ed.), *Reports of the Princeton University Expeditions to Patagonia, 1896–1899*. Princeton, Princeton University, New Jersey, p. 301–352.

Scott, W.B. 1937. The Astrapotheria. *Proceedings of the American Philosophical Society* 77: 309–393.

Seoane, F.D., and Cerdeño, E. 2019. Systematic revision of *Hegetotherium* and *Pachyrukhos* (Hegetotheriidae, Notoungulata) and a new phylogenetic analysis of Hegetotheriidae. *Journal of Systematic Palaeontology* 19: 1635–1663.

Simpson, G.G. 1936. Structure of a primitive Notoungulate cranium. *American Museum Novitiates* 824: 1–31.

Simpson, G.G. 1948. The beginning of the age of mammals in South America. Part I. *Bulletin of the American Museum of Natural History* 91: 1–232.

Simpson, G.G. 1967. The beginning of the age of mammals in South America. Part II. *Bulletin of the American Museum of Natural History* 137: 1–260.

Simpson, G.G. 1980. *Splendid Isolation, the Curious History of South American Mammals.* Yale University Press, New Haven, 266 p.

Sinclair, W.J. 1909. Mammalia of the Santa Cruz beds. Part I. Typotheria. In: W.B. Scott (Ed.), *Reports of the Princeton University Expeditions to Patagonia, 1896–1899.* Princeton University, New Jersey, p. 1–110.

Tauber, A.A. 1994. [*Estratigrafía y vertebrados fósiles de la Formación Santa Cruz (Mioceno inferior) en la costa atlántica entre las rías del Coyle y Río Gallegos, Provincia de Santa Cruz, República Argentina*. Doctoral thesis, Universidad Nacional de Córdoba, Córdoba, 422 p. Unpublished.].

Tauber, A.A. 1996. Los representantes del género *Protypotherium* (Mammalia, Notoungulata, Interatheridae) del Mioceno Temprano del sudoeste de la Provincia de Santa Cruz, República Argentina. *Academia Nacional de Ciencias* (Córdoba), 95: 1–29.

Tauber, A.A. 1997a. Biostratigraphy of the Santa Cruz Formation (Lower Miocene) in southeastern Patagonia. *Ameghiniana* 34: 413–426.

Tauber, A.A. 1997b. Palaeoecology of the Santa Cruz Formation (Lower Miocene) in the southeast border of Patagonia. *Ameghiniana* 34: 517–529.

Tauber, A.A. 1999. Los vertebrados de la Formación Santa cruz (Mioceno inferior–medio) en el extremo sureste de la Patagonia y su significado paleoecológico. *Revista Española de Paleontología* 14: 173–182.

Tauber, A.A., Kay, R.F., and Luna, C. 2004. Killik Aike Norte, una localidad clásica de la Formación Santa Cruz (Mioceno temprano–medio), Patagonia, Argentina. *Ameghiniana* 41 Suplemento Resúmenes: 63R–64R.

Tauber, A.A., Palacios, M.A., Krapovickas, J., and Rodríguez, P. 2008. La Formación Santa Cruz (Mioceno Temprano–Medio) en la mitad occidental del río homónimo, Patagonia, Argentina. *17º Congreso Geológico Argentino* (Jujuy)*, Actas* 2: 1500–1501.

Toledo, N., Bargo, M.S., and Vizcaíno, S.F. 2013. Muscular Reconstruction and Functional Morphology of the Forelimb of Early Miocene Sloths (Xenarthra, Folivora) of Patagonia. *The Anatomical Record* 296: 305–325.

Toledo, N., Bargo, M.S., and Vizcaíno, S.F. 2015. Muscular reconstruction and functional morphology of the hind limb of santacrucian (Early Miocene) sloths (Xenarthra, Folivora) of Patagonia. *The Anatomical Record* 298: 842–864.

Trayler, R.B., Schmitz, M.D., Cuitiño, J.I., 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:10.1130/B35203.1

Vizcaíno, S.F., Bargo, M.S., Cuitiño, J.I., Pérez, M.E., Muñoz, N.A., Aramendía, I., Tomassini R.L., and Kay, R.F. 2018. The outstanding Río Chalía (= Sehuén) outcrops of the Santa Cruz Formation (Early Miocene, Burdigalian) and its fossil vertebrate content. *Publicación Electrónica de la Asociación Paleontológica Argentina* 19 Suplemento de Resúmenes: 85 R.

Vizcaíno, S.F., Bargo, M.S., and Fernicola, J.C. 2013. Expediciones paleontológicas durante los Siglos XIX y XX A la Formación Santa Cruz (Mioceno Inferior, Patagonia) y destino de los fósiles. *3º Congreso Argentino de Historia de la Geología* (Salta)*, Actas* 231–246.

Vizcaíno, S.F., Bargo, M.S., Kay, R.F., Fariña, R.A., Di Giacomo, M., Perry, J.M.G., Prevosti, F.J., Toledo, N., Cassini, G.H., and

Fernicola, J.C. 2010. A baseline paleoecological study for the Santa Cruz Formation (late–early Miocene) at the Atlantic coast of Patagonia, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* 292: 507–519.

Vizcaíno, S.F., De Iullis, G., Brinkman, P.D., Kay, R., and Brinkman, D.L. 2017. On an album of photographs recording fossils in the Old Collections of the Museo de La Plata and Ameghino's private collection at the beginning of the XXth century. *Publicación Electrónica de la Asociación Paleontológica Argentina* 17: 14–23.

Vizcaíno, S.F., Kay, R.F., Bargo, M.S. 2012a. *Early Miocene Paleobiology in Patagonia: High-latitude Paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, 370 p.

Vizcaíno, S.F., Kay, R.F., Bargo, M.S. 2012b. 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.

Welker, F., Collins, M.J., Thomas, J.A., Wadsley, M., Brace, S., Cappellini, E., Turvey, S.T., Reguero, M., Gelfo, J.N., Kramarz, A.G., Burger, J., Thomas-Oates, J., Ashford, D.A., Ashton, P.D., Rowsell, K., Porter, D.M., Kessler, B., Fischer, R., Baessmann, C., Kaspar, S., Olsen, J.V., Kiley, P., Elliott, J.A., Kelstrup, C.D., Mullin, V., Hofreiter, M., Willerslev, E., Hublin, J.J., Orlando, L., Barnes, I., and MacPhee, R. 2015. Ancient proteins resolve the evolutionary history of Darwin's South American ungulates. *Nature* 522: 81–84. Doi:10.1038/nature14249

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APPENDIX 1 – Summary of the taxa identified in the localities from Río Santa Cruz by Ameghino (1887a,b, 1889) and Mercerat (1890, 1891) and its current nomenclatural status

Taxa	*Current nomenclatural status*
Astrapotheria	
Nesodon magnum *Owen, 1853*	**Astrapotherium magnum** *according to Ameghino (1889), Lydekker (1894), Scott (1928) and Kramarz* et al. *(2019)*
Astrapotherium patagonicum *Burmeister,1879*	**A. magnum** *according to Ameghino (1889), Lydekker (1894), Scott (1928) and Kramarz* et al. *(2019)*
Astrapotherium burmeisteri *Mercerat, 1890*	*Valid name according to Kramarz* et al. *(2019)*
Listriotherium filholi *Mercerat, 1890*	**A. magnum** *according to Ameghino (1894) and Scott (1928)*
Notoungulata	
Toxodontia	
Nesodon imbricatus *Owen, 1847*	*Valid name according to Scott (1912)*
Nesodon sulivani *Owen, 1847*	**Nesodon imbricatus** *according to Ameghino (1891b, 1894), Lydekker (1894) and Scott (1912)*
Nesodon ovinum *Owen, 1853*	**Adinotherium ovinum** *according to Ameghino (1891b, 1894, 1907) and Scott (1912)*
Homalodotherium cunnighami *Flower, 1873*	*Valid name according to Scott (1912)*
Protoxodon patagonensis *Ameghino, 1887a*	**N. imbricatus** *according to Ameghino (1894) and Scott (1912)*
Stenotephanos speciosus Ameghino, 1887b	**Hyperoxotodon speciosus** *according to Mercerat (1895) and Madden (1990)*
Lithops praevius *Ameghino, 1887b*	*Toxodontia* incertae sedis *according to Scott (1912)*
Protoxodon conspurcatus *Ameghino, 1887b*	**N. conspurcatus** *according to Ameghino (1894) and Scott (1912), but Lydekker (1894) synonimised it with* **N. imbricatus**
Protoxodon marmoratus *Ameghino, 1887b*	**N. imbricatus** *according to Lydekker (1894) and Scott (1912)*
Protoxodon obliteratus *Ameghino, 1887b*	**N. imbricatus** *according to Lydekker (1894) and Scott (1912)*
Adelphotherium ligatum *Ameghino 1887b*	**N. imbricatus** *according to Ameghino (1894), Lydekker (1894) and Scott (1912)*
Acrotherium rusticum *Ameghino, 1887b*	**N. imbricatus** *according to Lydekker (1894) and Scott (1912)*
Gronotherium decrepitum *Ameghino, 1887b*	**N. imbricatus** *according to Scott (1912)*
Adinotherium magister *Ameghino, 1887b*	**A. ovinum** *according to Scott (1912)*
Adinotherium splendidum *Ameghino, 1887b*	*Valid name according to Scott (1912)*
Adinotherium proximum *Ameghino, 1887b*	**A. ovinum** *according to Ameghino (1904) and Scott (1912)*
Adinotherium ferum *Ameghino, 1887b*	**A. ovinum** *according to Scott (1912)*
Adinotherium nitidum *Ameghino, 1887b*	*Valid name according to Scott (1912)*
Phobereotherium sylvaticum *Ameghino, 1887b*	**Adinotherium sylvaticum** *according to Mercerat (1891),* **Nesodon sylvaticum** *following Lydakker (1893), but valid name according to Scott (1912)*
Atryptherium bifurcatum *Ameghino, 1887b*	**N. imbricatus** *according to Ameghino (1894), but Scott (1912) established the synonym with* **N. conspurcatus**
Scophotherium cyclops *Ameghino, 1887b*	**N. imbricatus** *according to Ameghino (1894) and Scott (1912)*
Rhadinotherium limitatum *Ameghino, 1887b*	*Toxodontia* incertae sedis *according to Scott (1912)*
Nesodon oweni *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1894) and Scott (1912)*
Nesodon rutimeyeri *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1894), but Scott (1912) established the synonym with* **N. conspurcatus**.
Nesodon typicus *Mercerat, 1891*	**N. imbricatus** *according to Scott (1912)*
Adinotherium pulchrum *Mercerat, 1891*	**A. splendidum** *according to Ameghino (1894) and Scott (1912)*
Adinotherium antiquum *Mercerat, 1891*	**A. splendidum** *according to Scott (1912)*
Nesotherium carinatum *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1891b, 1894), but Scott (1912) established the synonym with* **N. conspurcatus**.

APPENDIX 1 – Continued

Taxa	*Current nomenclatural status*
Nesotherium studeri *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1891b, 1894) and Scott (1912)*
Nesotherium elegans *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1891b, 1894), but Scott (1912) established the synonym with* **N. conspurcatus**.
Nesotherium rufum *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1891b, 1894) and Scott (1912)*
Nesotherium nehringi *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1891b, 1894) and Scott (1912)*
Nesotherium argentinum *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1891b, 1894), Lydekker (1894) and Scott (1912)*
Protoxodon evidens *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1891b, 1894), but Scott (1912) established the synonym with* **N. conspurcatus**
Protoxodon americanus *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1891b, 1894) and Scott (1912)*
Protoxodon clemens *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1891b, 1894) and Scott (1912)*
Protoxodon henseli *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1891b, 1894) and Scott (1912)*
Protoxodon speciosus *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1891b, 1894) and Scott (1912)*
Adelphotherium lutarium *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1894) and Scott (1912)*
Adelphotherium repandum *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1894), Lydekker (1894) and Scott (1912)*
Adelphotherium trivium *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1894), Lydekker (1894) and Scott (1912)*
Adelphotherium rothi *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1894) and Scott (1912)*
Adelphotherium pumilum *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1894) and Scott (1912)*
Acrotherium intermedium *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1894) and Scott (1912)*
Acrotherium mutabile *Mercerat, 1891*	**A. ovinum** *according to Scott (1912)*
Acrotherium patagonicum *Mercerat, 1891*	**N. imbricatus** *according to Ameghino (1894), but Scott (1912) established the synonym with* **N. conspurcatus**
Acrotherium variegatum *Mercerat, 1891*	**N. imbricatus** *according to Scott (1912)*
Typotheria	
Pachyrukhos moyani *Ameghino, 1885*	*Valid name according to Sinclair (1909)*
Interatherium rodens *Ameghino, 1887a*	*Typotheria* incertae sedis *according to Sinclair (1909)*
Protypotherium australe *Ameghino, 1887a*	*Valid name according to Sinclair (1909)*
Interatherium supernum *Ameghino, 1887b*	*Typotheria* incertae sedis *according to Sinclair (1909)*
Hegetotherium mirabile *Ameghino, 1887b*	*Valid name according to Sinclair (1909)*
Hegetotherium strigatum *Ameghino, 1887b*	**H. mirabile** *according to Sinclair (1909) and Seoane and Cerdeño (2019)*
Protypotherium praerutilum *Ameghino, 1887b*	*Valid name according to Sinclair (1909)*
Protypotherium attenuatum *Ameghino, 1887b*	*Valid name according to Sinclair (1909)*
Pachyrukhos teres *Ameghino, 1889*	**P. moyani** *according to Seoane and Cerdeño (2019)*
Pachyrukhos trivius *Ameghino, 1889*	**P. moyani** *according to Seoane and Cerdeño (2019)*
Pachyrukhos absis *Ameghino, 1889*	**P. moyani** *according to Sinclair (1909) and Seoane and Cerdeño (2019)*
Pachyrukhos naevius *Ameghino, 1889*	**P. moyani** *according to Sinclair (1909) and Seoane and Cerdeño (2019)*
Icochilus extensus *Ameghino, 1889*	**Interatherium extensum** *according to Sinclair (1909)*
Icochilus excavatus *Ameghino, 1889*	**Interatherium excavatum** *according to Sinclair (1909)*
Icochilus undulatus *Ameghino, 1889*	*Typotheria* incertae sedis *according to Sinclair (1909)*
Icochilus rotundatus *Ameghino, 1889*	*Typotheria* incertae sedis *according to Sinclair (1909)*
Patriarchus palmidens *Ameghino, 1889*	*Valid name, but the species has been proven to be collected in a western outcrop of the Santa Cruz Formation, and not from Río Santa Cruz (Fernández* et al., *2019a)*
Protypotherium claudum *Ameghino, 1889*	**P. australe** *according to Tauber (1996)*

Appendix 2. List of the notoungulates and astrapotheres specimens recorded in Barrancas Blancas (BB; Estancia Aguada Grande and Estancia Santa Lucia), Segundas Barrancas Blancas (SBB; Cordón Alto and Estancia El Tordillo) and Yaten Huageno (YH; Estancia El Refugio).

ASTRAPOTHERIA

Astrapotheriidae

Astrapotherium magnum

YH. MPM-PV 19927, left mandibular fragment with m1–2, talonid of right m2, and broken tusk, all from the same individual.

Astrapotherium **sp.**

BB. MPM-PV 19504, broken tusk; MPM-PV 19519, fragments of cheek teeth with enamel; and MPM-PV 19740, broken tusk.

SBB. MPM-PV 19719, fragments of broken teeth and enamel; MPM-PV 19759, isolated lower incisor; MPM-PV 19582, broken tusk; MPM-PV 19598, broken tusk; and MPM-PV 19918, axis.

NOTOUNGULATA

Toxodontia

Homalodotherium sp.

BB. MPM-PV 19546, broken upper cheek tooth; and MPM-PV 19563, right maxillary fragment with P4–M1?, fragment of left P2?, and tooth fragments, all from the same individual.

SBB. MPM-PV 19629, broken left M2?, and fragments of undetermined upper and lower teeth; MPM-PV 19641, fragments of upper right and left premolar; MPM-PV 19677, right C?; MPM-PV 19684, phalanx; MPM-PV 19725, two fragments of the same mandible, one with left p4–m1 and the other with right p4–m2, isolated right p3, p2, p1 and i1?, all from the same individual; MPM-PV 19750, left P2?; MPM-PV 19802, right maxillary fragment with P4–M1?; MPM-PV 19810, astragalus and two teeth fragments; MPM-PV 19842, fragments of upper and lower cheek teeth and broken postcranial fragments; and MPM-PV 19871, right C? and fragments of broken teeth.

Nesodon imbricatus

BB. MPM-PV 19560, almost complete mandible with its dentition.

Nesodon sp.

BB. MPM-PV 19515, two right mandibular fragments with p4–m1 and m2–3; MPM-PV 19568, maxillary fragment with broken M1–3; MPM-PV 19564, left maxillary fragment with dP3–4; MPM-PV 19530, left M1? (broken), M2 and p1; MPM-PV 19540, left M1, M2 and broken M3; MPM-PV 19543, right i2, p2, m1 or m2, and fragments of lower cheek teeth; and MPM-PV 19545, broken symphysis with broken i3 and alveoli of c–p3.

SBB. MPM-PV 19578, lingual portion of worn lower cheek tooth; MPM-PV 19615, right m1 or m2, and fragment of the premaxilla with I1(alveolus)–2; MPM-PV 19618, broken left M3; MPM-PV 19708, broken talonid of right m3; MPM-PV 19712, right mandibular fragment with dp4–m2, left mandibular fragment with erupting p3–4 and m1–3 (erupting), isolated left unworn m3 and right dp4, and postcranial fragments, all from the same individual; MPM-PV 19749, two mandibular fragments of the same individual with broken p2–p4 and m2–3; MPM-PV 19798, incomplete mandible with associated tooth fragments; MPM-PV 19801, isolated and broken p2, p3 and p4; MPM-PV 19829, broken right m2?; MPM-PV 19834, right P2 or P3; MPM-PV 19862, both p4, right m1, and left m2; and MPM-PV 19894, two mandibular fragments from the same individual, one with left m1 (broken)–3 and the other with right m2–3.

Adinotherium ovinum

SBB. MPM-PV 19717, almost complete skull with dentition.

Adinotherium sp.

BB. MPM-PV 19488, three fragments of lower cheek teeth; MPM-PV 19491, broken left M1 or M2; MPM-PV 19497, several fragments of a mandible, including a right mandibular fragment with broken m1–2; MPM-PV 19499, right p1, both p3, and fragments of lower cheek teeth; MPM-PV 19501, fragments of lower cheek teeth from the same individual; MPM-PV 19502, fragment of an upper cheek tooth; MPM-PV 19517, fragments of upper cheek teeth; MPM-PV 19520, right p2 and m2?, and left m1?; MPM-PV 19521, right mandibular fragment with p4–m1, isolated right I1 and m3 (unworn), all from the same individual; MPM-PV 19524, broken right m1? and m2?; MPM-PV 19528, fragments of lower cheek teeth; MPM-PV 19533, right p4?; MPM-PV 19535, left maxillary fragment with P3–M2 (broken); MPM-PV 19538, fragments of upper cheek teeth; MPM-PV 19542, broken left M3, and fragments of undetermined teeth; MPM-PV 19553, right maxillary fragment with broken P4–M1; MPM-PV 19561, badly preserved left maxillary fragment with broken P2–M1?; MPM-PV 19562, broken right i1 or i2, left mandibular fragment with broken alveoli of m1–3, right mandibular fragment with p3–m2, and broken right m3, all from the same individual; and MPM-PV 19567, incomplete mandible with its broken dentition.

SBB. MPM-PV 19662, trigonid of right cheek tooth; MPM-PV 19671, anterior portion of the skull with broken left I1–P3 and right I1–M1; MPM-PV 19692, anterior region of the skull with almost complete dentition poorly preserved; MPM-PV 19698, isolated p4?, m1?, and m2? (trigonid); MPM-PV 19672, left m3; MPM-PV 19718, labial portion of a lower right cheek tooth; MPM-PV 19724, left mandibular fragment with i3 and p2–3, left mandibular fragment with m3, and right mandibular fragment with broken m1–3 (trigonid); MPM-PV 19727, right mandibular fragment with m2–3; MPM-PV 19745, talonid of left p3 or p4; MPM-PV 19756, right dp3 or dp4; MPM-PV 19779, isolated right P4 and M1, and two fragments of upper cheek teeth; MPM-PV 19790, right p3?, and fragments of undetermined teeth; MPM-PV 19804, right m1 or m2; MPM-PV 19818, right mandibular fragment with m2–3; MPM-PV 19833, two right maxillary fragments from the same individual with P1 (alveolus)–2 and P3–M3 (erupting); and MPM-PV 19882, broken left P2 or P3.

YH. MPM-PV 19928, talonid of a right cheek tooth; and MPM-PV 19929, broken right m3; and MPM-PV 19930, isolated right i1; i2?, and m1 or m2; MPM-PV 20024, right ulna and fragments of postcranial elements.

Typotheria

Hegetotheriidae

Hegetotherium mirabile

BB. MPM-PV 19487, right mandibular fragment with p2–m2; MPM-PV 19489, right maxillary fragment with alveoli of P1–3, complete left P3–M1, and isolated left M3; MPM-PV 19498, left maxillary fragment with M2 (broken)–2, left mandibular fragment with m1–2, and postcranial fragments; MPM-PV 19507, left upper cheek tooth; MPM-PV 19508, left M1 or M2; MPM-PV 19511, fragments of lower and upper cheek teeth; MPM-PV 19513, right maxillary fragment with P3 (erupting)–M3; MPM-PV 19527, right mandibular fragment with p4–m2; MPM-PV 19547, left mandibular fragment with p3–4, and isolated left m1; and MPM-PV 19555, incomplete skull with C (alveolus)–M2 (broken), left mandibular fragment with m1–2, and fragments of postcranial elements.

SBB. MPM-PV 19570, right mandibular fragment with m1–2; MPM-PV 19577, right lower cheek tooth; MPM-PV 19626, right maxillary fragment with broken P2 (alveolus)–4 and complete M1; MPM-PV 19658, left mandibular fragment with p4–m3; MPM-PV 19695, right maxillary fragment with M2–3, and fragments of cranial elements; MPM-PV 19733, three partial lower cheek teeth; MPM-PV 19768, left maxillary fragment with alveoli of P1–3 and complete P4; MPM-PV 19786, left mandibular fragment with m1–3 (alveolus); MPM-PV 19808, a) right mandibular fragment with p4 (talonid)–m2, and b) isolated lower right and left molar; and MPM-PV 19890, right mandibular fragment with p2 (alveolus)–m1 (broken), and left m1, m2 and m3.

Pachyrukhos moyani

SBB. MPM-PV 19644, left mandibular fragment with p4–m1?; MPM-PV 19651, left mandibular fragment with p3–m2, and isolated fragments of right lower and upper cheek teeth; MPM-PV 19654, right I1; MPM-PV 19655, two partial right cheek; MPM-PV 19656, left mandibular fragment with p4–m3 and isolated undetermined broken teeth; MPM-PV 19571, left m3 and isolated left upper cheek tooth; MPM-PV 19572, broken isolated lower cheek teeth; MPM-PV 19574, right mandibular fragment with p2 (alveolus)–3; MPM-PV 19575, two isolated lower cheek teeth; MPM-PV 19580, two isolated lower cheek teeth, and one upper cheek tooth; MPM-PV 19581, broken isolated cheek tooth; MPM-PV 19583, a) upper cheek tooth, b) left mandibular fragment with p4–m2?, c) left mandibular fragment with p4–m3, and mandibular fragment with broken cheek teeth; MPM-PV 19584, left mandibular fragment with p4–m1?; MPM-PV 19585, left mandibular fragment with p3–4? and broken isolated cheek teeth; MPM-PV 19590, right lower cheek tooth; MPM-PV 19594, a) isolated left m3, b) left lower cheek tooth, c) left mandibular fragment with p3–m3, d) right mandibular fragment with p2 (alveolus)–m2; MPM-PV 19596, right upper cheek tooth; MPM-PV 19600, right mandibular fragment with p3–4?, and a right upper cheek tooth; MPM-PV 19605, left mandibular fragment with i1–m1; MPM-PV 19608, left mandibular fragment with p4–m3; MPM-PV 19610, isolated lower left cheek tooth, and upper right cheek tooth; MPM-PV 19613, isolated right cheek tooth and right mandibular fragment with m1–3; MPM-PV 19617, right mandibular fragment with p3–4? and m2–3; MPM-PV 19619, right mandibular fragment with p4–m3 (broken); MPM-PV 19621, right lower cheek tooth and right upper cheek tooth; MPM-PV 19624, broken isolated cheek teeth; MPM-PV 19634, a) right mandibular fragment with p2–4, b) left i1, left p2 and left mandibular fragment with p4–m1?; MPM-PV 19649, left mandibular fragment with p2–4; MPM-PV 19661, right upper cheek tooth; MPM-PV 19666, a) left mandibular fragment with p2–m2, b) right mandibular fragment with p2–4, c) three broken isolated lower cheek teeth; MPM-PV 19669, right maxillary fragment with M1–3; MPM-PV 19674, two broken cheek teeth; MPM-PV 19678, broken isolated cheek teeth; MPM-PV 19682, broken left P3 or P4; MPM-PV 19685, broken lower cheek teeth; MPM-PV 19690, left mandibular fragment with p3–m1; MPM-PV 19693, a) left mandibular fragment with broken p2–3 and complete p4–m1, b) left mandibular fragment with p2 (alveolus)–m1 (trigonid); MPM-PV 19697, broken isolated cheek teeth; MPM-PV 19699, almost complete articulated foot; MPM-PV 19700, right mandibular fragment with m2–m3; MPM-PV 19702, left mandibular fragment with m2–3, broken isolated cheek teeth, and fragments of postcranial elements; MPM-PV 19704, right mandibular fragment with p4–m2, and left mandibular fragment with p3–m3; MPM-PV 19706, two left mandibular fragments, one with p3–4 and the other with m1–3; MPM-PV 19711, right mandibular fragment with p4–m3; MPM-PV 19720, right mandibular fragment with p4–m2; MPM-PV 19721, broken upper and lower cheek teeth; MPM-PV 19744, right mandibular fragment with m1–3; MPM-PV 19755, left upper cheek tooth, and left mandibular fragment with p2–4; MPM-PV 19748, two mandibular fragments, each with one cheek tooth; MPM-PV 19757, left maxillary fragment with M1–3, left mandibular fragment with p3–m3, right mandibular fragment with p2–m1, and fragments of postcranial elements; MPM-PV 19769, a) left mandibular fragment with p4–m2, b) right mandibular fragment with p4–m1?, c) right mandibular fragment with p3–m2, d) left mandibular fragment with p3–m1?; MPM-PV 19778, a) left upper cheek tooth, b) left mandibular fragment with p2, c) left mandibular fragment with p3–m1, d) right mandibular fragment with two molariforms; MPM-PV 19787, upper right cheek tooth, right maxillary fragment with alveoli of P–4, left mandibular fragment with p2 (alveolus)–4, and left mandibular fragment with broken p4–m2; MPM-PV 19788, a) right mandibular fragment with right p3–m3, b) right mandibular fragment p3 (erupting)–m2; MPM-PV 19791, isolated cheek teeth; MPM-PV 19792, a) left mandibular fragment with p2–3, b) right mandibular fragment with p2 (alveolus)–m1, c) two lower cheek teeth; MPM-PV 19795, broken lower and upper cheek teeth; MPM-PV 19797, two broken lower cheek teeth; MPM-PV 19800, articulated skull and mandible; MPM-PV 19803, articulated skull and mandible; MPM-PV 19813, right maxillary fragment with P2–M3, right mandibular fragment with p2–m3; MPM-PV 19816, right mandibular fragment with p3–m3; MPM-PV 19817, right maxillary fragment with P2 (alveolus)–P4; MPM-PV 19819, articulated skull and mandible; MPM-PV 19828, right mandibular fragment with p3–m1?; MPM-PV 19835, right mandibular fragment with p2 (alveolus)–4; MPM-PV 19840, isolated lower cheek teeth; MPM-PV 19850, a) right mandibular fragment with p4–m2, b) right mandibular fragment with p3–2, c) isolated lower cheek teeth; MPM-PV 19854, left mandibular fragment with p3–m1; MPM-PV 19857, left broken lower cheek tooth; MPM-PV 19860, a) left mandibular fragment with p2–m2, b) right mandibular fragment with p2–m1; c) right mandibular fragment with p2 (broken)–p4; MPM-PV 19865, upper cheek teeth; MPM-PV 19866, left mandibular fragment with p3 (alveolus)–m2; MPM-PV 19867, right mandibular fragment with p2–p3 and m1–3, left mandibular fragment with p3–4, and two isolated lower left and right cheek teeth; MPM-PV 19874, right mandibular fragment with p2–4; MPM-PV 19880, a) lower left cheek tooth, b) left mandibular fragment with p2–3; MPM-PV 19884, broken cheek teeth; MPM-PV 19892, a) left mandibular fragment with p3–m2, b) left mandibular fragment with p4–m2, c) right mandibular fragment with p2 (broken)–3, d) left mandibular fragment with p2 (broken)–m2; e) right mandibular fragment with p4–m2?; MPM-PV 19895, maxillary fragment with the ectolophs of M1–M3; MPM-PV 19898, right lower cheek tooth; MPM-PV 19905, partial articulated skull and mandible, and fragments of postcranial elements; MPM-PV 19915, mandibular fragment with p4–m3, right mandibular fragment with p3–4?, left upper cheek tooth, left lower cheek tooth, and two isolated broken cheek teeth; MPM-PV 19917, palatal fragment with its dentition; MPM-PV 19919, right mandibular fragment with badly–preserved p2–m3; MPM-PV 19920, right mandibular fragment with p3–m2 (trigonid); and MPM-PV 19924, palatal fragment with left P2–M3 and right P2–M2.

Interatheriidae

Protypotherium australe

BB. MPM-PV 19539, right maxillary fragment with P3–M3.

SBB. MPM-PV 19824, left M1 or M2, and left m1 or m2; MPM-PV

19588, right maxillary fragment with P4 (broken)–M2; MPM-PV 19593, symphysis with broken anterior dentition, right mandibular fragment with alveoli p2–4, and complete m1–2; MPM-PV 19601, right mandibular fragment with m2–3; MPM-PV 19602, right premaxillary fragment with I1–3; MPM-PV 19609, left mandibular fragment with p4–m1; MPM-PV 19616, isolated right p2, p3 and p4, left m3, and mandibular fragment with left i2–3, right i3 and left c, left mandibular fragment with p3–m1, and right mandibular fragment with m1–2; MPM-PV 19620, incomplete mandible with right alveoli of i1–p4 and m1–3, left alveoli of i1–3 and p1–m2 (broken), and complete left c, right I2, and isolated broken undetermined teeth; MPM-PV 19630, left mandibular fragment with m1–3; MPM-PV 19631, left maxillary fragment with PM3–M3, right mandibular fragment with p4–m2, and fragments of postcranial elements; MPM-PV 19636, left mandibular fragment with m2–3; MPM-PV 19638, right mandibular fragment with m2–3; MPM-PV 19639, right mandibular fragment with p2 (alveolus)–4; MPM-PV 19642, left mandibular fragment with p2 (alveolus)–4; MPM-PV 19653, left maxillary fragment with M1–3 (broken); MPM-PV 19632, left mandibular fragment with broken m1 or m2; MPM-PV 19663, badly preserved skull included in sediment matrix; MPM-PV 19664, symphysis with alveoli of anterior teeth, isolated m1, m2 and m3, left M1 or M2 left; MPM-PV 19675, left mandibular fragment with alveoli of i1–c and complete p1 (broken)–p2 (alveolus)–p3–m2; MPM-PV 19676, right mandibular fragment with m1 (broken)–2; MPM-PV 19691, symphysis with alveoli of left i1–c and complete left series p1 (broken)–2, left mandibular fragment with p4–m1 (trigonid), and right mandibular fragment with p4–m2; MPM-PV 19714, left mandibular fragment with alveoli of p3–m1 (broken), and right mandibular fragment; MPM-PV 19715, right maxillary fragment with P3–4 (alveoli)–M1–3, and left maxillary fragment with P2–4 (broken), and right palatal fragment with alveoli of I2–P2; MPM-PV 19716, incomplete skull with both I1–2, and left I3–M1; MPM-PV 19723, right mandibular fragment with m1 (broken alveolus)–3; MPM-PV 19728, left mandibular fragment with m1–3; MPM-PV 19736, right mandibular fragment with alveoli of i3–m1 and complete m2; MPM-PV 19746, right mandibular fragment with alveoli of c–p3 and complete p4; MPM-PV 19758, left maxillary fragment with M2–3 (broken); MPM-PV 19761, right maxillary fragment with M1–2; MPM-PV 19763, left maxillary fragment with P4 (broken)–M2; MPM-PV 19767, right m1 or m2, and right p3 or p4; MPM-PV 19772, toothless symphysis, and left mandibular fragment with p3 (broken)–m2; MPM-PV 19774, right mandibular fragment with broken alveolus of m1, broken m2, and lingual portion of m2; MPM-PV 19776, right maxillary fragment with P4 (alveolus)–M1 (broken); MPM-PV 19781, left maxillary fragment with P2–M3, and right mandibular fragment with p2–m1; MPM-PV 19782, right m3; MPM-PV 19784, mandibular fragment with m1 (talonid)–3 (broken); MPM-PV 19785, left mandibular fragment with m1–3, and right mandibular fragment with p4–m1; MPM-PV 19794, both M3; MPM-PV 19799, left maxillary fragment with P4–M3, right maxillary fragment with C–P2, and premaxillary fragment with alveoli of I1–2 and complete I3; MPM-PV 19805, left mandibular fragment with broken alveoli of i2–p3 and complete p4, and isolated right m1; MPM-PV 19806, left mandibular fragment with p3–m3; MPM-PV 19815, right m1 and left m3 from the same individual; MPM-PV 19820, right maxillary fragment with PM4–M1; MPM-PV 19826, right mandibular fragment with alveoli of p2–3 and p4–m1 (broken); MPM-PV 19849, left mandibular fragment with broken alveoli of m1–2; MPM-PV 19856, left mandibular fragment with m1 (alveolus)–2; MPM-PV 19864, isolated broken cheek teeth, and postcranial elements; MPM-PV 19868, left mandibular fragment with m1–2; MPM-PV 19870, left mandibular fragment with m2–3 (broken); MPM-PV 19876, badly preserved skull fragment, without teeth; MPM-PV 19877, left maxillary fragment with P4–M1; MPM-PV 19878, base of i1 or i2, left mandibular fragment with alveoli of p1–2 and complete p3–m1 (trigonid), and isolated right c; MPM-PV 19879, right I3, C?, P1, P2, P4, M1, M2, M3, and left P3 and P4; MPM-PV 19888, right mandibular fragment with p4–m1 and fragments of postcranial elements; MPM-PV 19893, right maxillary fragment with P4–M3, and left mandibular fragments with alveoli of i1–p3 and another with m1–3; MPM-PV 19914, left m1 or m2; MPM-PV 19921, left premaxillary fragment with alveoli of I1–3, left maxillary fragment with P3–M3, broken symphysis with both broken i1–2 and right i3–c, right mandibular fragment with m1 (broken)–2, left mandibular fragments with p3–4, another with m3 and another with m1, and fragments of postcranial elements; and MPM-PV 19925, left mandibular fragment with p4–m2.

Protypotherium praerutilum

BB. MPM-PV 19484, right mandibular fragment with m1–2; MPM-PV 19486, isolated left m1 and m2; MPM-PV 19492, right mandibular fragment m1–3; MPM-PV 19493, right m1 or m2; MPM-PV 19518, left mandibular fragment with m1–2; MPM-PV 19526, right mandibular fragment with p4–m2; and MPM-PV 19550, right mandibular fragment with m2, isolated m1, and two labial fragments of two molars.

SBB. MPM-PV 19586, right mandibular fragment with p4–m1; MPM-PV 19589, right M3, right m1, left I2?, and fragments of undetermined teeth; MPM-PV 19603, right maxillary fragment with M1–2; MPM-PV 19604, left maxillary fragment with alveoli of C–P1 and P2–M3; MPM-PV 19627, both m1 and m2, and right i3 or c; MPM-PV 19635, left mandibular fragment with p4 (alveolus)–m1; MPM-PV 19637, right mandibular fragment with p4 (alveolus)–m3 (broken); MPM-PV 19643, left mandibular fragment with p1–m1 (broken), right premaxillary fragment with I1 (alveolus)–3, and isolated left M3 and P2?; MPM-PV 19659, left maxillary fragment with P3–M2 ; MPM-PV 19673, left mandibular fragment with m1–3 (erupting); MPM-PV 19681, right premaxillary fragment with alveoli of I1–3, one left maxillary fragment with C–P3, and another with alveolus of M2, right maxillary fragment P3–4, isolated right I2?, lingual portion of right M1?, and fragments of cranial and postcranial elements ; MPM-PV 19688, right mandibular fragment with m2–3 (broken), broken left i3 or c, right I2 or I3, both P1, both P2, broken right M3, left P3, left P4, and broken undetermined teeth; MPM-PV 19689, two broken left m1 or m2; MPM-PV 19709, left mandibular fragment with p4 (erupting)–m2; MPM-PV 19710, right mandibular fragment with p4 (alveolus)–m2; MPM-PV 19734, right mandibular fragment with p3–p4 (alveolus)–m1–2; MPM-PV 19737, symphysis with alveoli of right i1–p3; MPM-PV 19743, left mandibular fragment with m1–3 and right mandibular fragment with p2 (alveolus)–m3; MPM-PV 19764, left maxillary fragment with P3–M3 (broken); MPM-PV 19841, left mandibular fragment with alveoli of p1–2 and complete p3–4; MPM-PV 19900, left mandibular fragment with broken m2–3; MPM-PV 19911, left mandibular fragment with m2–3; MPM-PV 19923, right mandibular fragment with m1–2 (trigonid).

Protypotherium attenuatum

BB. MPM-PV 19490, right mandibular fragment with m1–2; and isolated right p3 and p4; MPM-PV 19494, broken left m3, lingual portion of right m1 or m2, and right m1 or m2; MPM-PV 19516, right mandibular fragment with p4–m1; MPM-PV 19525, left mandibular fragment with p3–m1; MPM-PV 19534, right maxillary fragment with alveoli of P3–4 and complete M1–2, and isolated M3, left mandibular fragment with alveoli p1–3 and series p4–m1; and MPM-PV 19565, right m1 or m2.

SBB. MPM-PV 19667, right mandibular fragment with m2–3, MPM-PV 19614, right p3 or p4; MPM-PV 19640, right mandibular fragment with p4–m1; MPM-PV 19668, right maxillary fragment with P4–M2 (broken); MPM-PV 19679, left maxillary fragment with broken M1 or M2 and its posterior molar, and right I2 from the same individual; MPM-PV 19696, left m1 or m2 (almost unworn); MPM-PV 19751, right mandibular fragment with broken alveolus of m1, complete m2 and broken m3, and right mandibular fragment with p3 (broken)–m1 (trigonid); MPM-PV 19762, right maxillary fragment with alveoli of P3–4; MPM-PV 19773; right mandibular fragment with p4 (erupting)–m1; MPM-PV 19777, right maxillary fragment with P4–M1; MPM-PV 19793, left maxillary fragment with lingual portion of P4–M2 (alveolus), and left broken talonid of m3?; MPM-PV 19812, right mandibular fragment with p4–m2 (trigonid); MPM-PV 19821, skull fragment with alveoli I1–C and complete series P1 (broken)–M1 (broken); MPM-PV 19844, right mandibular fragment with m1–3; MPM-PV 19916, right m1 or m2; and MPM-PV 19922, isolated left m1 and m2.

Protypotherium sp.

BB. MPM-PV 19529, mandibular fragment of a juvenile individual with its symphysis and erupting c and p1; MPM-PV 19537, distal humerus; and MPM-PV 19551, left mandibular fragment with m3 (talonid), and calcaneus.

SBB. MPM-PV 19576, unworn left p4; MPM-PV 19607, left maxillary fragment with dP2–4, and fragments of postcranial elements; MPM-PV 19612, right mandibular fragment with m2–3; MPM-PV 19625, left m1 or m2; MPM-PV 19633, right dp4; MPM-PV 19657, left mandibular fragment with alveolus of m3; MPM-PV 19687, right mandibular fragment with dp2–p3–4 and isolated right i3 or c; MPM-PV 19731, left maxillary fragment with dP3–4; MPM-PV 19738, isolated left P3?, and worn left p2; PMPM-PV 19742, left p4; MPM-PV 19754, left dP3 or dP4; MPM-PV 19796, right dP3 or dP4 right, two right p2 barely worn; MPM-PV 19809, right p1; MPM-PV 19845, two right mandibular fragments with dp3–4 and m1–2 barely worn; MPM-PV 19853, both broken P3 or P4, and broken p3 or p4; MPM-PV 19858, broken undetermined teeth, right P3 or P4, labial portion of left M1 or M2; MPM-PV 19901, right mandibular fragment with alveoli of p2 and unworn p3; and MPM-PV 19913, mandibular fragment with both erupting dp4, and trigonid of m1.

Interatherium sp.

BB. MPM-PV 19483, left mandibular fragment with alveoli of p1–3 and broken p4–m1; MPM-PV 19485, left M3, and broken left M1 or M2; MPM-PV 19496, right P3?; MPM-PV 19503, right M1?, and left mandibular fragment with m1–2?; MPM-PV 19505, right mandibular fragment with alveoli of i2–p1 and complete series p2–m1; MPM-PV 19506, right P4 or M1; MPM-PV 19510, right I1; MPM-PV 19514, right P4 or M1; MPM-PV 19522, upper and lower isolated broken cheek teeth, and fragments of postcranial elements; MPM-PV 19523, right maxillary fragment with M1–2; MPM-PV 19531, left P4 o M1; MPM-PV 19536, distal humerus; MPM-PV 19554, right m2 and m3; MPM-PV 19556, right m1 or m2, and broken symphysis with alveoli of the anterior dentition; MPM-PV 19559, left lower cheek tooth; and MPM-PV 19566, left m3.

SBB. MPM-PV 19569, two broken lower cheek teeth; MPM-PV 19579, left m3; MPM-PV 19587, right M1; MPM-PV 19591, left M3; MPM-PV 19592, right mandibular fragment with p4–m3, left maxillary fragment with C–P3, isolated I1, and lingual and labial portions of two upper right and left cheek teeth; MPM-PV 19597, left M1; MPM-PV 19599, right mandibular fragment with m1–3 (erupting); MPM-PV 19606, lower broken cheek tooth; MPM-PV 19611, right m3; MPM-PV 19622, left M1 or M2 left; MPM-PV 19623, right mandibular fragment with p2–4; MPM-PV 19628, right dP3 or dP4; MPM-PV 19645, right maxillary fragment with P4–M2; MPM-PV 19646, left maxillary fragment with P2 (alveolus)–4; MPM-PV 19647, left mandibular fragment with p4–3, and right mandibular fragment with m1–2; MPM-PV 19648, isolated lower broken cheek teeth; MPM-PV 19652, right mandibular fragment with a cheek tooth; MPM-PV 19660, left cheek tooth; MPM-PV 19665, right P4?; MPM-PV 19680, lower cheek tooth; MPM-PV 19683, left mandibular fragment with p1(alveolus)–m1; MPM-PV 19686, right P2 or P3 right; MPM-PV 19694, left mandibular fragment with p3–m1; MPM-PV 19701, three broken upper cheek teeth; MPM-PV 19703, right maxillary fragment with P2–M3; MPM-PV 19705, two broken right upper cheek teeth; MPM-PV 19707, left mandibular fragment with p3–4; MPM-PV 19713, right mandibular fragment with p4–m3; MPM-PV 19722, left mandibular fragment with dp4–m2 (broken); MPM-PV 19726, left mandibular fragment with p3 (alveolus)–m2 (broken); MPM-PV 19729, right maxillary fragment with M1–2, isolated left P2, right P4, left M1, and left m3; MPM-PV 19732, right M3; MPM-PV 19739, left mandibular fragment with p3–m2; MPM-PV 19741, two broken lower cheek teeth; MPM-PV 19747, left lower premolar; MPM-PV 19752, right mandibular fragment with p3–m1; MPM-PV 19760, right mandibular fragment with m2–3; MPM-PV 19770, left maxillary fragment with M1, right maxillary fragment with M1–2, right mandibular fragment with dp4–m3, and fragments of postcranial elements; MPM-PV 19771, right mandibular fragment with p4–m1?; MPM-PV 19780, left maxillary fragment with dP3–P4–M2 (P3 below dP3), right mandibular fragment with p4–m1; and isolated left m3; MPM-PV 19789, right maxillary fragment with P4 (broken)–M2 (broken); MPM-PV 19811, two lower cheek teeth; MPM-PV 19822, right maxillary fragment with P2–3 (broken); MPM-PV 19825, right maxillary fragment with P3–M3; MPM-PV 19830, right mandibular fragment with p3–m2; MPM-PV 19831, right cheek tooth; MPM-PV 19839, right mandibular fragment with p4 (broken)–m3; MPM-PV 19838, left mandibular fragment with p2 (alveolus)-m3; MPM-PV 19843, right cheek tooth; MPM-PV 19846, right mandibular fragment with alveoli of p1–dp2 and complete series dp3–m1; MPM-PV 19847, left mandibular fragment with p3–m2; MPM-PV 19848, left mandibular fragment with p2–m2; MPM-PV 19851, left maxillary fragment with M1–3, and fragments of cranial and postcranial elements; MPM-PV 19861, right P4 or M1; MPM-PV 19873, right lower cheek tooth; MPM-PV 19875, right mandibular fragment with p3–m1; MPM-PV 19881, right cheek tooth; MPM-PV 19883, right dP3; MPM-PV 19885, left M1 or M2; MPM-PV 19886, right mandibular fragment with p1 (alveolus)–p4; MPM-PV 19887, left mandibular fragment with p4–m2; MPM-PV 19889, right mandibular fragment with m2–3, symphysis with alveoli of anterior teeth, and isolated broken teeth; MPM-PV 19891, right M3; MPM-PV 19896, lower cheek tooth; MPM-PV 19899, two mandibular fragments with p2 (broken)–p4 and m2–3; MPM-PV 19903, left mandibular fragment with p3–m2 (alveolus); MPM-PV 19904, lower right cheek tooth, and right mandibular fragment with alveoli of p2 and p4, and complete p3; MPM-PV 19906, left M3; MPM-PV 19907, right mandibular fragment with p4–m1; MPM-PV 19910, right P4 or M1; and MPM-PV 19912, left mandibular fragment with m1–2.

Appendix 3. Measurements (mm) of the dentition of the Santacrucian notoungulate specimens collected in the Río Santa Cruz.

Table 1 – Measurements of lower dentition of *Nesodon imbricatus*

	i1		*i2*		*i3*		*c*	
	MDL	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*
MPM-PV 19560	-	-	-	-	*27.9*	*14.9*	*14.9+*	*11.4+*

	p1		*p2*		*p3*		*p4*		*m1*		*m2*		*m3*	
	MDL	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*
MPM-PV 19560	*11.3*	*7.2*	*17.5*	*13.2*	*19.7*	*14.8*	*25.7*	*17.4*	*31.0*	*17.8*	*38.6*	*17.5*	*65.2*	*19.6*

+, measurement based on the alveolus.

Table 2 – Measurements of the upper dentition of *Adinotherium ovinum*

	I1		*I2*		*I3*		*C*	
	MDL	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*
MPM-PV 19717	-	-	*10.3*	*12.4*	*5.4*	*3.2*	*6.0*	*3.3*

	P1		*P2*		*P3*		*P4*		*M1*		*M2*		*M3*	
	MDL	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*
MPM-PV 19717	*6.0*	*5.7*	*8.3*	*8.6*	*9.0*	*9.9*	*10.8*	*11.8*	*16.0*	*15.2*	*19.3*	*15.3*	*26.2*	*13.8*

Table 3 – Cranial measurements of *Adinotherium ovinum*

	L	*Wc*	*Ow*	*Cw*	*Wpc*	*Lsc*	*Pl*	*PwP*	*PwM*
MPM-PV 19717	*230.0*	*32.0*	*>122.0*	*152.0**	*35.0*	*83.0*	*127.0*	*26.0*	*47.0*

*L, length of the skull; Wc, width at postorbital constriction; Ow, Occiput width at base; Cw, bicigomatic width; Wpc, width premaxillary constriction; Lsc, length sagittal crest; Pl, length of the palate in median line; PwP, Palatal width at P1; PwM, palatal width at M3. *, approximate measure.*

Table 4 – Measurements of the upper dentition of *Hegetotherium mirabile*

	P1		*P2*		*P3*		*P4*		*M1*		*M2*		*M3*	
	MDL	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*
MPM-PV 19489	-	-	-	-	*4.2*	*3.9*	*5.1*	*4.0*	*7.6*	*4.3*	-	-	*7.3*	*4.0*
MPM-PV 19555	*2.6*	*2.2*	*4.2*	*3.0*	*5.5*	*3.7*	*6.9*	*4.8*	*7.8*	*4.5*	-	-	-	-
MPM-PV 19695	-	-	-	-	-	-	-	-	-	-	*7.5+*	*5.0+*	*7.4**	*4.0**

*+, measurement based on the alveolus; *, approximate measurements.*

Table 5 – Measurements of the lower dentition of *Hegetotherium mirabile*

	p1		p2		p3		p4		m1		m2		m3	
	MDL	LLL	MDL	LLL	MDL	LLL	MDL	LLL	MDL	LLL	MDL	LLL	MDL	LLL
MPM-PV 19487	-	-	2.9	2.1	4.4	3.4	5.8	3.9	7.1	3.7	7.1	4.0	-	-
MPM-PV 19527	-	-	-	-	-	-	5.0	3.0	6.4	3.2	6.3	2.9	-	
MPM-PV 19555	-	-	-	-	-	-	-	-	6.5	3.3	6.6	3.6	-	-
MPM-PV 19570	-		-	-	-	-	-	-	6.0	3.2	6.8	3.5	-	-
MPM-PV 19658	-	-	-	-	-	-	5.8	-	6.1	3.0	6.1	2.9	8.6	2.7
MPM-PV 19786	-	-	-	-	-	-	5.9+	3.0+	6.1	2.8	7.0*	3.0*	10.0+	3.1+
MPM-PV 19808 a	-	-	-	-	-	-	-	-	6.6*	-	6.7	2.5	-	-

+, measurement based on the alveolus; *, approximate measurement.

Table 6 – Measurements of the upper dentition of *Pachyrukhos moyani*

	I1		I2	
	MDL	LLL	MDL	LLL
MPM-PV 19654	7.89	1.60	-	-
MPM-PV 19917	7.95	1.50*	-	-

	P2		P3		P4		M1		M2		M3	
	MDL	LLL	MDL	LLL	MDL	LLL	MDL	LLL	MDL	LLL	MDL	LLL
MPM-PV 19669	-	-	-	-	-	-	4.6	2.7	4.5	2.7	4.3	2.2
MPM-PV 19757	-	-	-	-	-	-	4.3	2.8	3.6	2.7	4.4	2.4
MPM-PV 19917	3.0	1.9	3.6	2.2	3.7*	2.7	4.4	3.2	4.1	2.8	4.3	2.3
MPM-PV 19813	3.6	1.4	3.6	2.2	3.9	2.5	4.1	2.7	4.0	2.6	3.9	2.1
MPM-PV 19924	3.3	1.8	3.3	2.2	3.9	2.5	4.2	2.7	4.0	2.8	4.0	2.6

*, approximate measurements.

Table 7 – Measurements of the lower dentition of *Pachyrukhos moyani*

	i1		i2	
	MDL	LLL	MDL	LLL
MPM-PV 19605	2.97	1.22	3.09	1.10

	p2		p3		p4		m1		m2		m3	
	MDL	LLL	MDL	LLL	MDL	LLL	MDL	LLL	MDL	LLL	MDL	LLL
MPM-PV 19583 a	-	-	-	-	3.3	2.2	3.6	2.2	3.9	2.3	-	-
MPM-PV 19583 b	-	-	-	-	3.2	2.3	3.6	2.2	3.8	2.2	5.1	2.2
MPM-PV 19594 a	-	-	-	-	-	-	-	-	-	-	4.5	2.1
MPM-PV 19594 c	-	-	3.2	2.0	3.2	2.2	3.3	2.0	3.2	2.1	5.1*	2.0*
MPM-PV 19594 d	3.4+	2.0+	3.0	2.1	3.4	2.3	3.8	2.3	3.9	2.3	-	-
MPM-PV 19605	2.3	1.3	2.6	1.9	2.9	2.2	3.9	2.2	-	-	-	-

TABLE 7 – Continued

	p2		*p3*		*p4*		*m1*		*m2*		*m3*	
	MDL	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*
MPM-PV 19608	-	-	-	-	3.2	2.1	3.9	2.3	3.6	2.5	5.6	2.3
MPM-PV 19613	-	-	-	-	-	-	3.7	2.2	4.0	2.3	5.5	2.2
MPM-PV 19619	-	-	-	-	2.8	1.9	3.5	2.2	3.4	2.2	-	-
MPM-PV 19651	-	-	2.9	1.6	2.8	1.9	3.1	2.1	3.1	2.0	-	-
MPM-PV 19656	-	-	-	-	3.5	1.5	3.8	2.0	3.8	2.3	4.5	1.8
MPM-PV 19666 a	2.3	1.4	2.5	2.0	2.5	2.1	3.2	2.2	3.2	2.3	-	-
MPM-PV 19666 b	2.1	1.4	3.0	2.0	3.6	2.3	-	-	-	-	-	-
MPM-PV 19693 a	2.6+	1.8+	3.1+	1.6+	3.2	2.2	3.5	2.3	-	-	-	-
MPM-PV 19693 b	2.2+	1.8+	3.1	2.0	2.8	2.2	-	-	-	-	-	-
MPM-PV 19700	-	-	-	-	-	-	-	-	3.4	2.0	4.7	2.0
MPM-PV 19704	-	-	3.4	2.0	3.4	2.3	3.7	2.3	3.7	2.2	5.0	2.5
MPM-PV 19706	-	-	3.1	2.0	3.2	2.1	3.7	2.0	4.1	2.0	4.7	2.1
MPM-PV 19711	-	-	-	-	3.3	2.2	3.8	2.2	3.8	2.2	5.4	2.1
MPM-PV 19720	-	-	-	-	3.0	2.3	3.3	2.2	3.8	2.5	-	-
MPM-PV 19744	-	-	-	-	-	-	4.1	2.5	3.8	2.2	5.2	2.2
MPM-PV 19757	-	-	3.2	1.9	3.2	2.3	3.6	2.5	3.6	2.5	5.7*	2.3
MPM-PV 19769 a	-	-	-	-	3.2	2.1	3.3	2.2	3.4	2.2	-	-
MPM-PV 19769 b	-	-	-	-	3.3	2.2	3.5	2.2	-	-	-	-
MPM-PV 19769 c	-	-	2.6	1.6	2.8	1.6	3.6	1.8	3.2	1.9	-	-
MPM-PV 19769 d	-	-	2.3	1.8	2.6	2.1	3.0	2.3	-	-	-	-
MPM-PV 19788 a	-	-	2.9	2.0	3.0	2.1	3.7	2.3	4.0	2.3	4.9	1.9
MPM-PV 19792 a	2.5	1.7	2.6	2.2	-	-	-	-	-	-	-	-
MPM-PV 19792 b	2.4+	2.0+	2.9	2.0	3.4	2.4	4.0	2.4	-	-	-	-
MPM-PV 19813	2.6	1.4*	2.6	1.9	2.7	2.1	3.1	2.2	3.6	2.1	5.1	1.8
MPM-PV 19816	-	-	2.8	2.1	3.2	2.1	4.0	2.2	3.9	2.2	5.6	2.3
MPM-PV 19828	-	-	2.6	1.6	3.0	1.7	3.5	2.0	-	-	-	-
MPM-PV 19835	2.4+	1.5+	2.8	2.0	3.2	2.1	-	-	-	-	-	-
MPM-PV 19850 a	-	-	-	-	3.4	2.0	3.7	2.4	4.4	2.3	-	-
MPM-PV 19850 b	-	-	2.9	1.8	2.6	2.1	3.2	2.2	3.7	2.3	-	-
MPM-PV 19854	-	-	2.8	1.9	3.4	2.2	3.3	2.2	-	-	-	-
MPM-PV 19860 a	2.8	1.7	2.8	2.0	3.1	2.2	3.4	2.2	3.5	2.3	-	-
MPM-PV 19860 b	2.3	1.4	2.8	1.9	3.2	2.2	3.9	2.3	-	-	-	-
MPM-PV 19860 c	-	-	2.4	1.7	2.9	1.8	-	-	-	-	-	-
MPM-PV 19866	-	-	2.4+	2.1+	2.7+	2.1	3.7+	2.4	4.0*	2.3	-	-
MPM-PV 19874	2.0	1.5	2.5	1.8	3.4	1.9	-	-	-	-	-	-
MPM-PV 19892 a	-	-	2.8	2.0	3.1	2.1	3.4	2.1	3.3	2.2		
MPM-PV 19892 b	-	-	-	-	3.0	1.9	3.0	2.0	3.2	2.0		
MPM-PV 19892 c	-	-	2.7	1.9	-	-	-	-	-	-	-	-
MPM-PV 19892 d	-	-	2.8	1.8	2.9	1.8	3.3	1.8	3.0	2.0	-	-
MPM-PV 19892 e	-	-	-	-	2.9	2.0	3.2	2.0	3.9	2.1	-	-
MPM-PV 19920	-	-	2.7	1.8	3.0	2.0	3.6	2.0	-	2.0*	-	

*+, measurement based on the alveolus; *, approximate measurement; deciduous teeth are indicate in parentheses.*

TABLE 8 – Measurements of the upper dentition of *Protypotherium australe*

	I1		*I2*		*I3*		*C*	
	MDL	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*
MPM-PV 19620	-	-	5.2	2.0	-	-	-	-
MPM-PV 19715	-	-	4.8+	3.0+	4.9+	3.0+	5.8+	3.1+
MPM-PV 19716	5.9	2.7	4.9	2.4	5.3	2.7	4.3	3.0
MPM-PV 19799	-	-	-	-	5.0	2.2	5.2	2.6
MPM-PV 19878	-	-	-	-	-	-	4.0	1.6
MPM-PV 19879	-	-	-	-	5.0	2.1	4.4	2.0

	P1		*P2*		*P3*		*P4*		*M1*		*M2*		*M3*	
	MDL	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*
MPM-PV 19603	-	-	-	-	-	-	-	-	7.0	5.1	6.4	3.7	-	-
MPM-PV 19631	-	-	-	-	6.0	5.0	6.9	6.0	9.5	6.3	7.9	6.0	7.3	4.3
MPM-PV 19715	4.5+	3.5+	4.2+	4.1+	5.4	5.0	6.5+	-	9.1	5.7	>7.0	5.1	8.4	4.1
MPM-PV 19716	3.2	2.0	5.2	3.8	6.2	4.9	7.1	5.6	8.3	5.2				
MPM-PV 19758	-	-	-	-	-	-	-	-	7.6*	5.5	-	4.8	-	-
MPM-PV 19799	4.5	2.3	5.3	3.3	-	-	5.7	5.1	8.4	5.3	7.6	4.9	7.0	4.0
MPM-PV 19878	-	-	-	-	5.2	3.1	5.0	3.3	8.1	4.0*	-	-	-	-
MPM-PV 19879	3.7	2.8	4.1	3.7	4.3	4.2	5.3	4.3	7.5	5.5	7.1	4.8	7.0	4.1
MPM-PV 19893	-	-	-	-	-	-	6.0	5.0	8.6	5.2	7.7	4.6	7.0	4.0

*+, measurement based on the alveolus; *, approximate measurements.*

TABLE 9 – Measurements of the lower dentition of *Protypotherium australe*

	i1		*i2*		*i3*		*c*	
	MDL	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*
MPM-PV 19620	-	-	-	-	-	-	4.7	1.9
MPM-PV 19631	-	-	-	-	-	-	4.7	2.1

	p1		*p2*		*p3*		*p4*		*m1*		*m2*		*m3*	
	MDL	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*
MPM-PV 19593	-	-	-	-	-	-	-	-	7.6	4.1	8.2	4.2	-	-
MPM-PV 19620	-	-	4.6+	2.5+	4.9+	2.7+	5.3+	5.3+	7.2	4.1	7.1	4.0	9.3	3.8
MPM-PV 19630	-	-	-	-	-	-	-	-	7.7	4.1	7.4	3.9	9.1	3.5
MPM-PV 19631	-	-	-	-	5.7	3.6	6.4	4.0	8.7	4.1	-	-	10.1	3.5
MPM-PV 19728	-	-	-	-	-	-	-	-	8.5	4.3	7.7	4.0	9.4	3.6
MPM-PV 19782	-	-	-	-	-	-	-	-	-	-	-	-	8.5	3.7
MPM-PV 19785	-	-	-	-	-	-	5.4	3.1	7.7	3.7	7.5	3.9	8.8	3.4
MPM-PV 19806	-	-	-	-	4.8+	3.0+	5.4	3.2	7.6	3.7	7.3	3.4	9.0	3.1
MPM-PV 19856	-	-	-	-	-	-	-	-	7.6+	5.1+	7.0	4.0	-	-
MPM-PV 19868	-	-	-	-	-	-	-	-	7.7	3.7	7.3	3.6	-	-
MPM-PV 19893	-	-	-	-	-	-	-	-	7.6	3.8	7.2	3.7	9.0	3.4
MPM-PV 19914	-	-	-	-	-	-	-	-	7.6	3.9	-	-	-	-
MPM-PV 19925	-	-	-	-	-	-	6.1	3.2	8.7	4.21	7.8	4.1	-	-

+, measurement based on the alveolus.

TABLE 10 – Measurements of the upper dentition of *Protypotherium praerutilum*

	I1		*I2*		*I3*		*C*	
	MDL	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*
MPM-PV 19681	*-*	*-*	*5.5*	*3.0*	*-*	*-*	*4.6*	*2.7*

	P1		*P2*		*P3*		*P4*		*M1*		*M2*		*M3*	
	MDL	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*
MPM-PV 19604	*2.4+*	*2.0+*	*3.5*	*3.4*	*3.9*	*3.6*	*4.2*	*3.9*	*6.3*	*4.1*	*5.7*	*3.6*	*5.5*	*3.1*
MPM-PV 19659	*-*	*-*	*-*	*-*	*3.5*	*4.1*	*4.9*	*4.3*	*6.7*	*4.5*	*6.7*	*4.4*	*-*	*-*
MPM-PV 19681	*3.3*	*2.5*	*3.7*	*3.8*	*4.5*	*4.5*	*4.9*	*4.5*	*-*	*-*	*-*	*-*	*-*	*-*
MPM-PV 19764	*-*	*-*	*-*	*-*	*4.2**	*4.2**	*5.5**	*4.6**	*-*	*4.7**	*6.5*	*4.2*	*-*	*-*

*+, measurement based on the alveolus; *, approximate measurements.*

TABLE 11 – Measurements of the lower dentition of *Protypotherium praerutilum*

	p1		*p2*		*p3*		*p4*		*m1*		*m2*		*m3*	
	MDL	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*
MPM-PV 19484	*-*	*-*	*-*	*-*	*-*	*-*	*-*	*-*	*6.0*	*3.1*	*5.8*	*3.1*	*-*	*-*
MPM-PV 19492	*-*	*-*	*-*	*-*	*-*	*-*	*-*	*-*	*6.3**	*3.4*	*6.6*	*3.3*	*8.3*	*3.4*
MPM-PV 19493	*-*	*-*	*-*	*-*	*-*	*-*	*-*	*-*	*6.2*	*3.5*	*-*	*-*	*-*	*-*
MPM-PV 19518	*-*	*-*	*-*	*-*	*-*	*-*	*-*	*-*	*6.5*	*3.6*	*6.2*	*3.6*	*-*	*-*
MPM-PV 19526	*-*	*-*	*-*	*-*	*-*	*-*	*4.4*	*2.9*	*6.1*	*3.5*	*5.9*	*3.5*	*-*	*-*
MPM-PV 19586	*-*	*-*	*-*	*-*	*-*	*-*	*4.3*	*2.9*	*6.5*	*3.1*	*-*	*-*	*-*	*-*
MPM-PV 19623	*-*	*-*	*-*	*-*	*4.2*	*2.1*	*4.3*	*2.6*	*6.4*	*2.9**	*-*	*-*	*-*	*-*
MPM-PV 19743	*-*	*-*	*-*	*-*	*4.0*	*2.4*	*4.0*	*2.8*	*6.0*	*2.8*	*5.4*	*2.7*	*6.8*	*2.9*
MPM-PV 19911	*-*	*-*	*-*	*-*	*-*	*-*	*-*	*-*	*-*	*-*	*6.2+*	*3.2*	*7.7*	*3.0*
MPM-PV 19923	*-*	*-*	*-*	*-*	*-*	*-*	*-*	*-*	*6.7*	*3.7*	*-*	*-*	*-*	*-*

**, approximate measurements.*

TABLE 12 - Measurements of the upper dentition of *Protypotherium attenuatum*

	P1		*P2*		*P3*		*P4*		*M1*		*M2*		*M3*	
	MDL	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*	*MDL*	*LLL*
MPM-PV 19534	*-*	*-*	*-*	*-*	*-*	*-*	*-*	*-*	*6.2*	*4.1**	*6.0*	*4.3*	*-*	*-*
MPM-PV 19668	*-*	*-*	*-*	*-*	*-*	*-*	*4.1*	*3.4*	*6.2*	*3.8*	*6.0**	*3.7**	*-*	*-*
MPM-PV 19777	*-*	*-*	*-*	*-*	*-*	*-*	*4.7*	*3.6*	*6.1*	*3.7*	*-*	*-*	*-*	*-*
MPM-PV 19821	*1.9*	*1.6*	*2.8*	*>2.5*	*3.7*	*>3.5*	*4.5*	*3.8*	*6.0**	*-*	*-*	*-*	*-*	*-*

*+, measurement based on the alveolus; *, approximate measurement; deciduous teeth are indicate in parentheses.*

TABLE 13 – **Measurements of the lower dentition of *Protypotherium attenuatum***

	p1		p2		p3		p4		m1		m2		m3	
	MDL	LLL	MDL	LLL	MDL	LLL	MDL	LLL	MDL	LLL	MDL	LLL	MDL	LLL
MPM-PV 19490	-	-	-	-	4.2	2.6	4.4	2.5	5.4	3.0	5.6	3.0	-	-
MPM-PV 19516	-	-	-	-	-	-	4.0	3.0	5.4	3.0	-	-	-	-
MPM-PV 19525	-	-	-	-	3.9	2.2	4.7	2.6	5.6	2.9	-	-	-	-
MPM-PV 19549	-	-	-	-	-	-	4.5	2.6	5.3	3.1	-	-	-	-
MPM-PV 19565	-	-	-	-	-	-	-	-	5.9	3.0	-	-	-	-
MPM-PV 19640	-	-	-	-	-	-	4.0	2.3	4.7	2.7	-	-	-	-
MPM-PV 19667											4.3	2.3	6.1*	2.2*
MPM-PV 19696	-	-	-	-	-	-	-	-	4.8	2.0	-	-	-	-
MPM-PV 19812	-	-	-	-	-	-	3.5	2.3	4.9	2.5	-	-	-	-
MPM-PV 19844	-	-	-	-	-	-	-	-	5.9	2.8	5.7	2.8	7.1	2.6
MPM-PV 19916	-	-	-	-	-	-	-	-	5.6	3.1	-	-	-	-
MPM-PV 19922	-	-	-	-	-	-	-	-	5.9	3.1	-	-	-	-

**, approximate measurements.*

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ARTÍCULO

LITOPTERNA (MAMMALIA) FROM THE SANTA CRUZ FORMATION (EARLY–MIDDLE MIOCENE) AT THE RÍO SANTA CRUZ, SOUTHERN ARGENTINA

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Abstract. Litopterna from fossiliferous exposures of the Santa Cruz Formation (Early–Middle Miocene) along the Río Santa Cruz, Patagonia Argentina, are analyzed and described. In the prospected localities, known as Barrancas Blancas (Estancia Aguada Grande and Estancia Santa Lucía) and Segundas Barrancas Blancas (Estancia Cordón Alto and Estancia El Tordillo), specimens belonging to the families Proterotheriidae and Macraucheniidae were recorded. Within Proterotheriidae, the species *Anisolophus australis*, *A. floweri*, *Tetramerorhinus lucarius*, *Te. cingulatum*, *Thoatherium minusculum* and *Diadiaphorus majusculus* have been identified. Macraucheniidae are scarcer and represented by *Theosodon* sp. Although the systematics of litopterns of the Santa Cruz Formation requires a review, the new remains from the Río Santa Cruz reported here, as well as others recently recovered from the same unit in the Atlantic coast, will be valuable to clarify the taxonomy of this peculiar group of South American extinct ungulates.

Key words. Systematics. Proterotheriidae. Macraucheniidae. Santacrucian. Patagonia.

Resumen. LITOPTERNA (MAMMALIA) PROCEDENTES DE LA FORMACIÓN SANTA CRUZ (MIOCENO TEMPRANO–MEDIO) EN EL RÍO SANTA CRUZ, SUR DE ARGENTINA. Se analizan y describen los Litopterna provenientes de los afloramientos de la Formación Santa Cruz (Mioceno Temprano–Medio) a lo largo del Río Santa Cruz, Patagonia Argentina. En las localidades prospectadas, conocidas como Barrancas Blancas (Estancias Aguada Grande y Santa Lucía) y Segundas Barrancas Blancas (Estancias Cordón Alto y El Tordillo), se hallaron especímenes asignables a las familias Proterotheriidae y Macraucheniidae. En el caso de los Proterotheriidae se han identificado *Anisolophus australis*, *A. floweri*, *Tetramerorhinus lucarius*, *Te. cingulatum*, *Thoatherium minusculum* y *Diadiaphorus majusculus.* Los Macraucheniidae son más escasos y se encuentran representados por *Theosodon* sp. Si bien la sistemática de los litopternos de la Formación Santa Cruz requiere una revisión, los nuevos restos reportados aquí del Río Santa Cruz, así como otros recientemente recuperados de la misma unidad en la costa atlántica, serán valiosos para aclarar la taxonomía de este particular grupo de ungulados extintos de América del Sur.

Palabras clave. Sistemática. Proterotheriidae. Macraucheniidae. Santacrucense. Patagonia.

DURING much of the Cenozoic, South America was geographically isolated from other landmasses. This isolation promoted the evolution of an endemic fauna: marsupials, edentates, primates, rodents, and numerous "ungulate" groups (Flynn and Wyss, 1998). The South American native ungulates include some endemic families of "Condylarthra" and the orders Litopterna, Notoungulata, Astrapotheria, Xenungulata, Pyrotheria, and Notopterna (Bond, 1986; Bond *et al.*, 1995; Schmidt and Ferrero, 2014). The order Litopterna is surpassed only by Notoungulata in terms of taxonomic richness (*e.g.*, Pascual *et al.*, 1996; Cifelli and Guerrero, 1997; Cassini *et al.*, 2012; Forasiepi *et al.*, 2016). The litoptern record spans from the Early Paleocene (Bonaparte and Morales, 1997) to the Early Holocene (Tonni, 1990; Bond, 1999; Schmidt and Ferrero, 2014), and the most abundant and diverse families of litopterns are Proterotheriidae and Macraucheniidae, the subjects of the present work.

Proterotheriids include small to medium-sized mammals traditionally compared with “tiny horses” due to the reduction of digits II and IV. This lead to a functional or even structural monodactyly, with the preservation of only the third digit in the case of *Thoatherium* Ameghino, 1887 (Kraglievich, 1930; Soria, 2001; Cassini *et al.*, 2012). In the geologic history of proterotheriids spanning Late Oligocene to Late Pleistocene/Early Holocene (Luna *et al.*, 2015; Corona *et al.*, 2018), there occurred two major peaks of taxonomic richness in the Early and Late Miocene (Santacrucian and Huayquerian South American Land Mammal Ages (SALMAs), respectively). By the Late Pleistocene/Early Holocene, the number of species had declined to two taxa: *Neolicaphrium recens* Frenguelli, 1921 and *Uruguayodon alius* Corona, Perea and Ubilla, 2019 (Villafañe *et al.*, 2006; Ubilla *et al.*, 2011; Luna *et al.*, 2015; Corona *et al.*, 2019).

Macraucheniids comprise medium to large-sized forms with long necks, three-toed feet, and a complete dentition (3.1.4.3/3.1.4.3). In basal forms, such as *Cramauchenia* Ameghino, 1902 (Late Oligocene–Early Miocene; Dozo and Vera, 2010) or *Theosodon* Ameghino, 1887 (Early Miocene–late Middle Miocene; McGrath *et al.*, 2018), the nasal aperture occupies an anterior position. In derived taxa such as *Huayqueriana* Kraglievich, 1934, *Macrauchenia* Owen, 1838 or *Xenorhinotherium* Cartelle and Lessa, 1988 (Late Miocene–Late Pleistocene/Early Holocene; Schmidt and Ferrero, 2014), the nasal aperture has retreated to a centrodorsal position in the skull, between the orbits (Forasiepi *et al.*, 2016). This posterior repositioning of the nasal aperture may indicate the presence of a proboscis or a similar structure, but there is no detailed anatomical study supporting this inference (Forasiepi *et al.*, 2016).

Litopterna are conspicuous representatives of Santa Cruz Formation (Early–Middle Miocene). During the Santacrucian, Proterotheriidae have been reported to include as many as seven genera and 13 species (Villafañe *et al.*, 2006; Ubilla *et al.*, 2011). In contrast, Macraucheniidae is represented by one genus with several species (Scott, 1910; Croft *et al.*, 2004; Cassini *et al.*, 2012; Schmidt and Ferrero, 2014; McGrath *et al.*, 2018, 2019).

Reports of Litopterna in the Santa Cruz Formation go back to the 19th century. The first specimen of Proterotheriidae was collected by Ramón Lista in the Río Chico (Province of Santa Cruz), and studied by Burmeister (1879), who named it *Anchitherium australe* Burmeister, 1879 (*Anchitherium* Meyer, 1844 is a perissodactyl from Northern Hemisphere; Soria, 2001). Later, several field trips carried out by Carlos Ameghino in Patagonia (since 1887 to 1902; see Vizcaíno, 2011) yielded important collections of litopterns and other mammals from the Santa Cruz Formation that were studied by his brother Florentino (*e.g.*, Ameghino, 1887, 1889, 1894, 1904a,b).

The number and variety of specimens collected in 1887 by C. Ameghino from the Santa Cruz Formation along the Río Santa Cruz allowed F. Ameghino to name and describe the Family Proterotheriidae (Ameghino, 1887; Soria, 2001). Ameghino (1887) named five species of proterotheriids: *Proterotherium cavum* Ameghino, 1887, *Thoatherium minusculum* Ameghino, 1887, *Diadiaphorus velox* Ameghino, 1887, *D. majusculus* Ameghino, 1887, and *Licaphrium parvulum* Ameghino, 1887. Some of these taxa are no longer recognized as distinct (see Soria, 2001). In the case of macraucheniids, Ameghino (1887) documented the presence of *Theosodon lydekkeri* Ameghino, 1887. The specimens used by Ameghino to name these species should be stored at the Museo de La Plata, the institution in charge of the field trip to the Río Santa Cruz. However, in the case of proterotheriids, only two holotypes are available in that museum (MLP 12-294, *P. cavum* and MLP 12-333, *D. majusculus*); the remaining three have not been located (Soria, 2001). Regarding *T. lydekkeri* in the collections of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” there is a specimen labeled as the type of the species (MACN-A 2487), but Mones (1986, p. 141) indicates that the type material of. *T. lydekkeri* is lost (-). This issue deserves clarification.

In this contribution, we undertake a detailed study of new Santacrucian litoptern remains (Proterotheriidae and Macraucheniidae) recovered during fieldwork (2013–2014) along the southern banks of the Río Santa Cruz (see Fernicola *et al.*, 2019). The prospected localities correspond to Barrancas Blancas (Estancia= Ea. Aguada Grande and Ea. Santa Lucía), Segundas Barrancas Blancas (Ea. Cordón Alto and Ea. El Tordillo), and Yaten Huageno (Ea. El Refugio)

(Fernicola *et al.*, 2014, 2019). The litopterns studied in this article come from the first two localities (Fig. 1); none was recovered at Yaten Huageno.

Along the Río Santa Cruz, the sediments of the Santa Cruz Formation (Burdigalian–early Langhian) are referred as a lateral continuous fluvial system across the three localities (Fernicola *et al.*, 2014). This system shows proximal trends to the West (towards Yaten Huageno) and distal trends to the East (towards Barrancas Blancas). Regarding the amount of sediments there is also a trend according to Fernicola *et al.* (2014), from thinner exposures to the West (80 m; Yaten Huageno) to thicker ones to the East (170 m; Barrancas Blancas) (see Cuitiño *et al.*, 2016, 2019 for an extensive geological description).

Background for the systematics of Santacrucian Litopterns

Ameghino (1889) described litoptern species based on specimens recovered on C. Ameghino's 1887 Río Santa Cruz expedition (Fernicola, 2011). Later, Ameghino (1891, 1894, 1902, 1904a,b, etc.) continued studying specimens of Santacrucian litopterns from other localities, recovered on succeeding trips by C. Ameghino to Patagonia until 1902 (Vizcaíno, 2011).

Mercerat (1891a), Lydekker (1894), Gaudry (1904, 1906), and Scott (1910) revised the Santacrucian proterotheriids. The anatomical and systematic study carried out by Scott (1910) deserves special attention. In his work, Scott fully described the Proterotheriidae *Proterotherium* Ameghino, 1883, *Licaphrium* Ameghino, 1887, *Thoatherium*, and *Diadiaphorus* Ameghino, 1887, although without studying the material directly and perpetuating some previous mistakes (Cassini *et al.*, 2012). On the one hand, some of these errors were directly associated with the personal differences between F. Ameghino and F. Moreno (Director of Museo de La Plata in 1887). As Moreno limited the access to revise the collections of the museum, Ameghino made some erroneous taxonomic assignations, because he could not examine the type specimens. One of the most common examples is the genus *Proterotherium*, which included a set of species belonging to different genera. On the other hand, Scott stayed only three months in La Plata in 1901 studying the Santacrucian fossils, what prevented him to compare directly the proterotheriid specimens stored at Museo de La Plata with those in the Ameghino's personal collection (Scott, 1910; Soria, 2001). Delupi de Bianchini and Bianchini (1971) studied in detail the holotype of *Proterotherium cervioides* Ameghino, 1883, from the lower levels of Ituzaingó Formation (Late Miocene–Pliocene), Province of Entre Ríos. They verified that some species from the Santa Cruz Formation included in this genus belonged to one or more genera, a taxonomic issue addressed by Soria (2001).

Tauber (1999) recorded some proterotheriids from the coastal deposits of the Santa Cruz Formation at the Estancia La Costa locality (see Fernicola *et al.*, 2019): "*Proterotherium*"

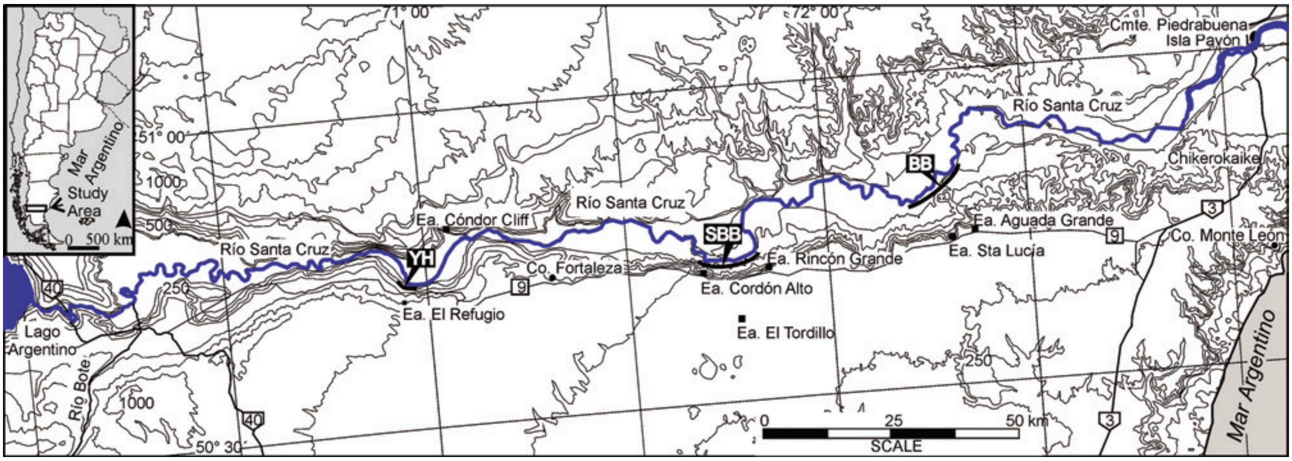


Figure 1. Map of the Río Santa Cruz with the prospected localities and estancias mentioned in the text. **BB,** Barrancas Blancas; **SBB,** Segundas Barrancas Blancas; **YH,** Yaten Huageno; **Ea.,** Estancia. Modified from Fernicola *et al.* (2014).

cavum; *Licaphrium floweri* Ameghino, 1887; *Diadiaphorus robustus* Ameghino, 1894; *Thoatherium minusculum*; *Licaphrium* sp.; and *Diadiaphorus* sp. At the Monte Tigre locality, he also recorded "*Proterotherium*" *intermedium* Ameghino, 1894 and a Proterotheriidae gen. indet. (see Fernicola *et al.*, 2019, figs. 1 and 5 for localities).

Soria (2001) reviewed the systematics of the Proterotheriidae. For the Santacrucian levels, he recognized *Tetramerorhinus lucarius* Ameghino, 1894; *Tetramerorhinus cingulatum* (Ameghino, 1891), with two subspecies: *Te. c. cingulatum* (Ameghino, 1891) and *Te. c. fleaglei* Soria, 2001 –but Kramarz and Bond (2005) considered them at species level, restricting *Te. fleaglei* to the Early Miocene Pinturas Formation–; *Tetramerorhinus mixtum* (Ameghino, 1894); *Thoatherium minusculum*; *Diadiaphorus majusculus*; *Anisolophus australis* (Burmeister, 1879); *Anisolophus floweri* (Ameghino, 1887), and *A. minusculus* (Roth, 1899). The last taxon has also been recognized in the Collón Curá Formation, Province of Río Negro (Kramarz and Bond, 2005; Cassini *et al.*, 2012).

Finally, Cassini *et al.* (2012) reported some of the taxa mentioned above (*i.e.*, *Anisolophus australis*, *Tetramerorhinus cingulatum*, *Thoatherium minusculum* and *Diadiaphorus majusculus*) from recent collections from the Santa Cruz Formation at the Atlantic coastal localities (see Fernicola *et al.*, 2019, fig. 5).

Following Scott (1910), the only macraucheniid recorded from the Santa Cruz Formation is *Theosodon*, which comprises several species: *T. lydekkeri*, *T. lallemanti* Mercerat, 1891b, *T. garrettorum* Scott, 1910, *T. fontanae* Ameghino, 1891, *T. gracilis* Ameghino, 1891, *T. karaikensis* Ameghino, 1904b (Scott, 1910), *T. pozzii* Kraglievich and Parodi, 1931, and *T.? frenguellii* Soria, 1981. Tauber (1999) recorded *Theosodon lallemanti* at the coastal levels of the Santa Cruz Formation, and Croft (2016) recognized the same species in the Early Miocene Chucal Formation, northern Chile, previously considered as *Theosodon* sp. (Croft *et al.*, 2004). McGrath *et al.* (2018) described "*Theosodon*" *arozquetai* McGrath, Anaya and Croft, 2018 in the late Middle Miocene (Laventan SALMA) of Quebrada Honda, Bolivia. Another species first ascribed to *Theosodon*, *T. hystatus* Cabrera and Kraglievich, 1931, from the Arroyo Chasicó Formation (Late Miocene), Province of Buenos Aires (Argentina), was reassigned to *Paranauchenia hystata* (Cabrera and Kraglievich, 1931) by Schmidt and Ferrero (2014). More recently, McGrath *et al.* (2019) recorded the presence of *Theosodon* sp. in Pampa Castillo Fauna (Early Miocene, Santacrucian), Chile.

MATERIALS AND METHODS

The 42 new specimens studied are housed at Museo Regional Provincial "Padre Manuel Jesús Molina" (**MPM-PV**), Río Gallegos, Province of Santa Cruz, Argentina. Most remains correspond to dental and cranial elements. Taxonomic assignments were carried out through morphological and metrical comparisons with other Santacrucian specimens housed in the following institutions (Appendix 1): **AMNH,** American Museum of Natural History, New York, USA; **FMNH,** Field Museum of Natural History, Chicago, USA; **MACN,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MLP,** Museo de la Plata, La Plata, Argentina; **PIMUZ,** Palaeontological Institute and Museum, University of Zurich, Zurich, Switzerland; **YPM-VPPU,** Yale Peabody Museum, Vertebrate Paleontology Princeton University Collection, New Haven, USA.

Metrical and anatomical abbreviations. **APDD**, anteroposterior diameter of diaphysis; **APDDA**, anteroposterior diameter of distal articulation; **APDO**, anteroposterior diameter of olecranon; **APDTu**, anteroposterior diameter of tuberosity; **D/d**, deciduous; **DC**, distance between crests; **DW**, distal width; **Fo**, frontal foramina; **HSC,** height of the sigmoid cavity; **HW**, head width; **L**, length; **LMd**, length of the middle portion (between crests); **M/m**, upper/lower molar; **NW**, neck width; **P/p**, upper/lower premolar; **SoF**, supraorbital foramen; **TDD**, transverse diameter of diaphysis; **TDDA**, transverse diameter of distal articulation; **TDDE**, transverse diameter of distal epiphysis; **TDO**, transverse diameter olecranon; **TDPA**, transverse diameter of proximal articulation; **TDPE,** transverse diameter of proximal epiphysis; **TDT**, transverse diameter of trochlea; **TDTu**, transverse diameter of tuberosity; **W**, width.

SYSTEMATIC PALEONTOLOGY

Order Litopterna Ameghino, 1889
Family Proterotheriidae Ameghino, 1887
Subfamily Proterotheriinae Ameghino, 1887

Genus ***Anisolophus*** Burmeister, 1885

Type species. *Anchitherium australe* Burmeister, 1879. Santa Cruz Formation (Early–Middle Miocene), Province of Santa Cruz, Argentina.

Referred species. *Anisolophus australis* (Burmeister, 1879); *A. floweri* (Ameghino, 1887); *A. minusculus* (Roth, 1899).

Anisolophus australis (Burmeister, 1879)

Figure 2.1; Table 1

List of synonymies. See Soria (2001, p. 72).

Referred material. MPM-PV 19444, left m2–m3.

Geographic distribution. Barrancas Blancas (Ea. Aguada Grande), Río Santa Cruz, Province of Santa Cruz, Argentina.

Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene, Santacrucian).

Description. In MPM-PV 19444 (Fig. 2.1; Tab. 1), the m2 has the paralophid longer than in m3, but its entoconid is smaller. The entoconid of m3 is separated from the hypoconulid by a small sulcus, and joined to the hypolophulid by a crest, and the hypoconulid does not form a third lobe.

Comments. The small size of MPM-PV 19444 resembles *Anisolophus australis*, *Tetramerorhinus lucarius* or *Thoatherium minusculum*. However, the m3 is different from *Te. lucarius* because the paralophid is short and the hypoconulid does not tend to form a third lobe. Assignment to *Th. minusculum* is unlikely due to the presence of entoconid in m2-m3. Moreover, MPM-PV 19444 is very similar in morphology and dimensions to MACN-A 8669, holotype of *Proterotherium intermedium*, a junior synonym of *A. australis*.

Anisolophus floweri (Ameghino, 1887)

Figures 2.2–4, 3.1–10; Tables 1–2

List of synonymies. See Soria (2001, p. 73).

Referred material. MPM-PV 19429, right maxillary fragment with M1 (partial), M2–M3; MPM-PV 19430, left maxillary fragment with M1 (partial), M2–M3 (without labial side); MPM-PV 19431, incomplete right upper molar (M3?); MPM-PV 19432, left mandibular fragment with p3–m3; MPM-PV 19433, right p4; MPM-PV 19434, left mandibular fragment with dp4; MPM-PV 19435, right mandibular fragment with p3–m2; MPM-PV 19436, right mandibular fragment with

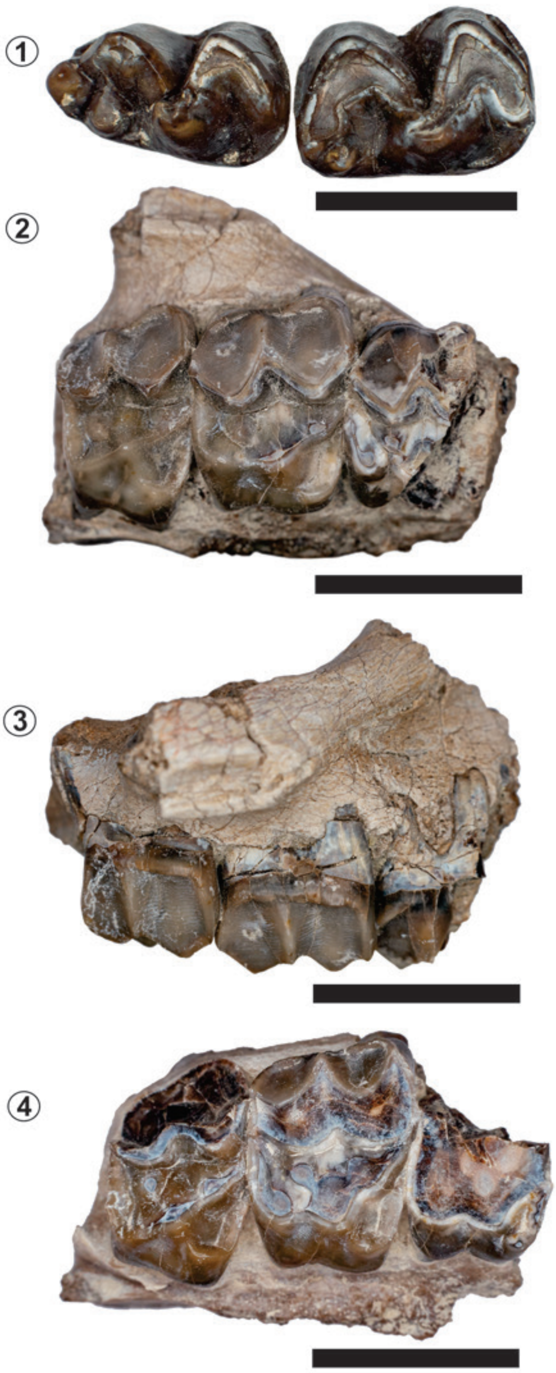


Figure 2. ***Anisolophus australis***; **1, MPM-PV 19444**, left m2–m3. ***Anisolophus floweri***; **2–3, MPM-PV 19429**, right maxillary fragment with M1 (partial), M2–M3; occlusal and labial views; **4, MPM-PV 19430**, left maxillary fragment (reversed) with M1 (partial), M2–M3. Scale bars: Fig. 1= 10 mm; Figs. 2–4= 20 mm.

Table 1 – **Lower tooth dimensions (mm) of the studied proterotheriid specimens**

Specimen	*Taxon*		*dp3*	*dp4*	*p2*	*p3*	*p4*	*m1*	*m2*	*m3*
MPM-PV	**Anisolophus**	*L*	-	-	-	-	-	-	*12.2*	*12.7*
19444	**australis**	*W*	-	-	-	-	-	-	*8.4*	*7.7*
MPM-PV	**Anisolophus**	*L*	-	-	-	*14.2*	*15.1*	*14.4*	*15.7*	*18.2*
19432	**floweri**	*W*	-	-	-	*9.9*	*12.7*	*13.3*	*13.5*	*12.1*
MPM-PV	**Anisolophus**	*L*	-	-	-	-	*15.2*	-	-	-
19433	**floweri**	*W*	-	-	-	-	*12.4*	-	-	-
MPM-PV	**Anisolophus**	*L*	-	*16.0*	-	-	-	-	-	-
19434	**floweri**	*W*	-	*11.5*	-	-	-	-	-	-
MPM-PV	**Anisolophus**	*L*	-	-	-	*15.24*	*13.8*	*13.61*	*16.5**	-
19435	**floweri**	*W*	-	-	-	*11.28*	*12.5*	*12.2*	*12.5*	-
MPM-PV	**Anisolophus**	*L*	-	-	-	-	-	*14.12*	-	-
19436	**floweri**	*W*	-	-	-	-	-	*11.03*	-	-
MPM-PV	**Anisolophus**	*L*	-	-	-	-	-	*14.05*	-	-
19437	**floweri**	*W*	-	-	-	-	-	*11.52*	-	-
MPM-PV	**Anisolophus**	*L*	-	-	-	-	*15.6*	-	-	-
19438	**floweri**	*W*	-	-	-	-	*10.2**	-	-	-
MPM-PV	**Anisolophus**	*L*	-	-	-	-	-	*15.0*	-	-
19439	**floweri**	*W*	-	-	-	-	-	*11.5*	-	-
MPM-PV	**Anisolophus**	*L*	-	-	-	-	*?*	-	-	-
19440	**floweri**	*W*	-	-	-	-	*11.4*	-	-	-
MPM-PV	**Anisolophus**	*L*	-	*14.8*	-	-	-	*14.9*	-	-
19441	**floweri**	*W*	-	*12.0*	-	-	-	*11.9*	-	-
MPM-PV	**Anisolophus**	*L*	-	-	-	-	-	-	-	*17.6*
19442	**floweri**	*W*	-	-	-	-	-	-	-	*9.9**
MPM-PV	**Anisolophus**	*L*	-	*16.1/16.2*	-	*15.2/15.2*	-	*15.3/15.2*	*16.3/16.4*	-
19443	**floweri**	*W*	-	*11.3/11.7*	-	*9.9/10.7*	-	*12.7/12.4*	*13.4/13.2*	-
MPM-PV	**Diadiaphorus**	*L*	-	-	-	-	-	-	-	*19. 6*
19461	**majusculus**	*W*	-	-	-	-	-	-	-	*11.6*
MPM-PV	**Diadiaphorus**	*L*	-	-	-	-	-	-	-	*20.3*
19462	**majusculus**	*W*	-	-	-	-	-	-	-	*11.1*
MPM-PV	**Tetramerorhinus**	*L*	-	*13.0**	-	-	-	-	*14.0**	-
19450	**cingulatum**	*W*	-	*11.1*	-	-	-	-	*11.3*	-
MPM-PV	**Tetramerorhinus**	*L*	-	-	-	*10.8*	*11.4*	*10.4*	*11.7/11.7*	*13.5*/14.1*
19446	**lucarius**	*W*	-	-	-	*7.7*	*9.6*	*10.3*	*10.4/10.1*	*9.4/9.0*
MPM-PV	**Tetramerorhinus**	*L*	-	-	-	-	-	-	*12.6/12.3*	*14.9/15.0*
19447	**lucarius**	*W*	-	-	-	-	-	-	*10.1/9.9*	*9.0/8.8*
MPM-PV	**Thoatherium**	*L*	-	-	*9.1*	-	-	-	-	*13.3*
19454	**minusculum**	*W*	-	-	*5.1*	-	-	-	-	*7.9*
MPM-PV	**Thoatherium**	*L*	-	-	-	-	-	*10.7*	-	-
19455	**minusculum**	*W*	-	-	-	-	-	*8.7*	-	-
MPM-PV	**Thoatherium**	*L*	-	-	-	-	*12.6*	-	*12.6*	-
19456	**minusculum**	*W*	-	-	-	-	*8.6*	-	*8.6*	-
MPM-PV	**Thoatherium**	*L*	-	-	-	-	-	*11.8**	*12.0*	*?*
19457	**minusculum**	*W*	-	-	-	-	-	*8.2*	*8.0*	*7.4*
MPM-PV	**Thoatherium**	*L*	*12.5*	-	-	-	-	-	-	-
19458	**minusculum**	*W*	*8.0*	-	-	-	-	-	-	-
MPM-PV	**Thoatherium**	*L*	*12.4*	*12.2*	-	-	-	*10.8*	-	-
19459	**minusculum**	*W*	*8.1*	*8.2*	-	-	-	*7.4*	-	-
MPM-PV	**Thoatherium**	*L*	*10.8**	*11.3*	-	-	-	*10.9*	*12.8*	*12.4*
19460	**minusculum**	*W*	*7.2*	*?*	-	-	-	*9.5*	*8.5*	*7.7*

**Approximate; right/left*

root of p4 and m1 complete; MPM-PV 19437, left mandibular fragment with m1; MPM-PV 19438, left mandibular fragment with alveolus of p2, roots of p3, and p4 almost complete; MPM-PV 19439, left fragment of m1; MPM-PV 19440, talonid of right p4; MPM-PV 19441, left mandibular fragment with talonid of dp3, dp4–m1; MPM-PV 19442, right and left m3; MPM-PV 19443, mandibular fragments with right and left p3, dp4, m1–m2.

Geographic distribution. Segundas Barrancas Blancas (Ea. Cordón Alto and Ea. El Tordillo). Río Santa Cruz, Province of Santa Cruz, Argentina.

Stratigraphic distribution of studied specimens. Santa Cruz Formation (Early-Middle Miocene, Santacrucian).

Description. The upper molars of MPM-PV 19429 (Fig. 2.2) are practically unworn (except the fragment of M1). They have shallow trigon basins, and rounded cusps. The M1–M2, metaconules are closer to the hypocone than to the protocone and the posterolingual groove is deeper in M1 than in M2. The M3 is unworn, lacks a hypocone and its posterior wall projects anteriorly and joins the apex of the protocone. The labial cingula are conspicuous, the styles have a moderate development, and the paracone fold is only visible labially (M2–M3, Fig. 2.3).

In MPM-PV 19430 (Fig. 2.4), the molars are more worn than in MPM-PV 19429. The fragment of M1 presents a shallow posterolingual groove, similar to that of M2. The M2 metaconule and the paraconule are rounded, and both are equidistant from the protocone, but in a more labial position. The hypocone is separated from the protocone by an enamel lagoon and a shallow posterolingual groove. The parastyle is the most developed style. In M1–M3, the anterolingual cingulum is developed and reaches the base of the protocone. The M3 lacks a hypocone.

The specimen MPM-PV 19431 is an incomplete upper molar, probably an M3 by comparison with MPM-PV 19429 and MPM-PV 19430. Its morphological and metrical similarities with the previous specimens are evident (Tab. 2), but its lingual wall is lower and not so inclined labially.

The specimens MPM-PV 19434 (Fig. 3.1), MPM-PV 19441 (Fig. 3.2) and MPM-PV 19443 (Fig. 3.3–6) preserve the dp4, more worn in MPM-PV 19441. These teeth are molariform, with well-developed paraconid and entoconid. The labial surface is rugose, the ectoflexid is pronounced, the talonid is longer than the trigonid, and the roots are thin. All of them show similar dimensions (Tab. 1).

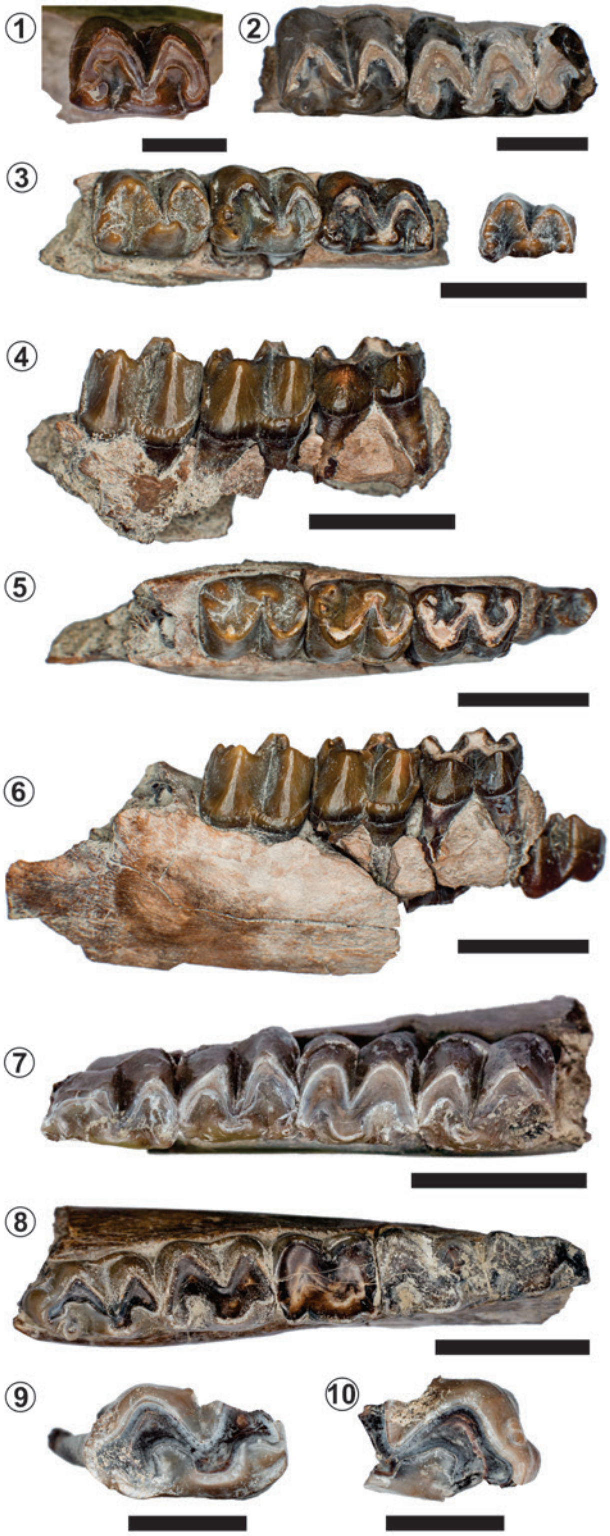
The specimen MPM-PV 19443 (Figs. 3.3–6) consists of two poorly preserved mandibular fragments, both with the p3 erupting and dp4 in place. The broken bone allows us to observe the right p4 below the dp4 (Fig. 3.6), while the left fragment only preserves a socket. The p3s have the border of the lophids with enamel crenulations (unworn). The trigonid is shorter and narrower than the talonid. The dp4s have paraconids, shallow flexids and entoconids.

The p3–p4 of MPM-PV 19432, MPM-PV 19433, MPM-PV 19435, MPM-PV 19438, and MPM-PV 19440 have entoconids. On MPM-PV 19435 (Fig. 3.7), the p3 has a well differentiated paraconid and parastylid, but on MPM-PV 19443 (Fig. 3.3) this anterior bifurcation is not so clear. The p4s show a long paralophid and the talonid longer and wider than the trigonid (Fig. 3.7–8).

The lower molars (m1–m2) are massive, with shallow flexids, without paraconids, and the well-developed entoconid more lingually placed than the hypoconulid. The m3 (MPM-PV 19432, MPM-PV 19442, Fig. 3.8–10) also lacks a paraconid, the paralophid is short, and the hypoconulid is very developed.

Comments. The described specimens possess low-crowned teeth; the upper molars show a wide trigon basin, low and rounded cusps, lingual cusps (protocone and hypocone) connected on M2 and M3 without hypocone. The p3–m3 have entoconids; the lower molars lack paraconids, and the m3 has a hypoconulid but without the tendency to form a third lobe. These features allow us to identify these specimens as *Anisolophus* as distinct from *Tetramerorhinus*, whose characteristics are the opposite (Soria, 2001).

As mentioned before, the parastyle of M2 in MPM-PV 19430 is more developed than in other specimens and the paraconule and the metaconule are nearer to the protocone than in MPM-PV 19429, which makes this specimen closer to *Tetramerorhinus* than to *Anisolophus*; however, MPM-PV 19430 is very different from the revised specimens of *Tetramerorhinus*: MACN-A 11626 *Te. prosistens* (Ameghino, 1899)], MACN-A 8667–68 (*Te. cingulatum*), MACN-A 1855 (*Te. lucarius*), MACN-A 8663 (*Te. mixtum*) and MACN-PV SC 129-30 (*Te. fleaglei*), in which protocone and hypocone are widely separated by a groove.



Other two taxa recognized for Santa Cruz Formation are *Thoatherium minusculum* and *Diadiaphorus majusculus* (Soria, 2001; Kramarz and Bond, 2005; Villafañe *et al*., 2006; Cassini *et al*., 2012). Our specimens are distinct from *Th. minusculum*, which has smaller M1 and M2 and a lophoid metaconule. *Diadiaphorus majusculus*, instead, is the largest Santacrucian proterotheriid, and presents a bunoid metaconule, as in *Anisolophus*, but this cusp is closer to the metacone than to the hypocone, and the M3 has a reduced hypocone, differing in these ways from *Anisolophus*.

Anisolophus includes three species mainly differentiated by size (Soria, 2001: p. 72). Based on Soria's measurements, the described specimens match *Anisolophus floweri* (Soria, 2001: tab. 15), which is larger than *A. australis* and *A. minusculus*. Nevertheless, we include some comments about these (see below).

The specimens MPM-PV 19429 and MPM-PV 19431 share with *Anisolophus floweri* (MACN-A 8999) the greater development of the mesostyle on M2. In MPM-PV 19430, instead, the parastyle is more developed, similar to MACN-A 9003–12 (*A. floweri*; Soria, 2001). In MPM-PV 19429, the posterolingual groove in M1 is deeper than in M2, and the protocone and the hypocone remain isolated. In M2, both cusps are connected by a low crest similar to YPM-VPPU 15711 and MACN-A 9003–12 of *A. floweri*. The M3 in MPM-PV 19429, MPM-PV 19431 and MPM-PV 19430 share with MACN-A 9003–12 the reduced metaconule and the posterior wall joining anteriorly the apex of the protocone.

We discard the assignment of our specimens with upper dentition to *Anisolophus australis*, because the M2 of MPM-PV 19429 and MPM-PV 19430 has the posterolingual groove less marked than in MACN-PV 2417 (holotype of *A. australis*; Burmeister, 1879). Moreover, the posterior wall of the M3 (in MPM-PV 19429 and MPM-PV 19431) joins the

Figure 3. ***Anisolophus floweri***; **1, MPM-PV 19434**, left mandibular fragment with dp4; **2, MPM-PV 19441**, left mandibular fragment with talonid of dp3, dp4–m1; **3–6, MPM-PV 19443,** right and left mandibular fragments with p3, dp4, m1–m2 (occlusal and labial views); **7, MPM-PV 19435**, right mandibular fragment with p3–m2; **8, MPM-PV 19432**, left mandibular fragment with p3–m3; **9–10, MPM-PV 19442**, fragments of right and left m3. Scale bars: Figs. 1, 2, 9, and 10= 10 mm; Figs. 3–8= 20 mm.

protocone at the apex, while in MACN-PV 2417 it joins the protocone at its base. MPM-PV 19429 and MPM-PV 19431 are similar to MACN-A 3107 of *A. australis* (G. Schmidt, pers. observation, 2015), but the cusps are less massive, and the teeth are larger.

Finally, although MPM-PV 19429 shows a significant morphological similarity with *Anisolophus minusculus* (MACN-A 9001b; Roth, 1899) concerning the position and development of the cusps and posterolingual groove more marked in M1 than M2, its size is clearly larger (Tab. 2). For this reason, MPM-PV 19429 is assigned to *A. floweri*, following the size criterion of Soria (2001) to separate these species.

Regarding lower teeth, the specimen MPM-PV 19433 is much worn and its talonid is wider than the trigonid. This tooth could be a p3, by a little anterior bifurcation, but it is similar in morphology and dimension to the p4 of MPM-PV 19435 and MPM-PV 19438 (Tab. 1), so we consider it a p4. Moreover, the entoconid morphology in all of them is similar to that observed in the p4 of MACN-A 9003–12 and MACN-A 3085 of *Anisolophus floweri*, where this cusp appears laterally compressed and anterolingually oriented.

The condition of having a better developed entoconid on m1–m2 and the entoconid more lingually placed than the hypoconulid is also observed in *Anisolophus floweri*: MACN-A 9003–12 (m1), YPM-VPPU 15309, MLP 12-289, and PIMUZ A/V 5293 (m1, see Zurita-Altamirano *et al.*, 2019). The m3s are also similar to MACN-A 9003–12, MLP 82-IV-3-3, MLP 82-IV-3-4, and YPM-VPPU 15309 of this species.

Genus **Tetramerorhinus** Ameghino, 1894

Type species. *Tetramerorhinus fortis* Ameghino, 1894. Santa Cruz Formation, Early–Middle Miocene, Province of Santa Cruz, Argentina.

Referred species. *Te. lucarius* Ameghino, 1894, *Te. cingulatum* (Ameghino, 1891), *Te. mixtum* (Ameghino, 1894), *Te. prosistens* (Ameghino, 1899), *Te. fleaglei* Soria, 2001.

Tetramerorhinus lucarius Ameghino, 1894

Figures 4.1–3; Tables 1–2

List of synonymies. See Soria (2001, p. 42).

Referred material. MPM-PV 19445, left M1; MPM-PV 19446, left mandible with partial symphysis and p3–m3, and right mandibular fragment with m2–m3; MPM-PV 19447, right mandibular fragment with alveoli of p3–m1, and complete m2–m3, and left mandibular fragment with m2–m3.

Geographic distribution. Barrancas Blancas (Ea. Aguada Grande, Ea. Santa Lucía) and Segundas Barrancas Blancas (Ea. Cordón Alto). Río Santa Cruz, Province of Santa Cruz, Argentina.

Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene, Santacrucian).

Description. MPM-PV 19445 (Fig. 4.1) is a small and much worn upper molar. It is wider than long (Tab. 2). The mesostyle is the most marked labial style and there are not labial folds. The anterolingual cingulum is developed, but does not reach the base of the protocone; the posterolingual groove is prominent, and separates protocone and hypocone.

The lower teeth of MPM-PV 19446 (Fig. 4.2) are more worn than in MPM-PV 19447 (Fig. 4.3), but they share the

Figure 4. ***Tetramerorhinus lucarius***; **1, MPM-PV 19445**, left M1; **2, MPM-PV 19446**, left mandible with partial symphysis and p3–m3, and right mandibular fragment with m2–m3; **3, MPM-PV 19447**, right mandibular fragment with alveoli of p3–m1 and complete m2–m3, and left mandibular fragment with m2–m3. Scale bars: Fig. 1= 10 mm; Figs. 2–3= 20 mm.

TABLE 2 - Upper tooth dimensions (mm) of the studied proterotheriid specimens

Specimen	*Taxon*		*DP1*	*DP2*	*DP3*	*DP4*	*P1*	*P2*	*P3*	*P4*	*M1*	*M2*	*M3*
MPM-PV 19429	**Anisolophus floweri**	*L*	-	-	-	-	-	-	-	-	*12.9**	*15.8*	*12.8*
		W	-	-	-	-	-	-	-	-	*18.5*	*20.7*	*21.1*
MPM-PV 19430	**Anisolophus floweri**	*L*	-	-	-	-	-	-	-	-	*14.1*	*15.6*	*13.3*
		W	-	-	-	-	-	-	-	-	*?*	*22.7*	*22.3*
MPM-PV 19431	**Anisolophus floweri**	*L*	-	-	-	-	-	-	-	-	-	-	*13.0*
		W	-	-	-	-	-	-	-	-	-	-	*?*
MPM-PV 19463	**Diadiaphorus majusculus**	*L*	-	-	-	-	-	-	-	-	-	-	*16.5*
		W	-	-	-	-	-	-	-	-	-	-	*23.2*
MPM-PV 19448	**Tetramerorhinus cingulatum**	*L*	-	-	-	-	-	-	-	-	*14.1*	-	-
		W	-	-	-	-	-	-	-	-	*?*	-	-
MPM-PV 19449	**Tetramerorhinus cingulatum**	*L*	*12.9*	*13.3*	*14.5*	*14.3*	-	-	-	-	*15.2*	-	-
		W	*8.3*	*12.5*	*14.6*	*16.6*	-	-	-	-	*19.7*	-	-
MPM-PV 19445	**Tetramerorhinus lucarius**	*L*	-	-	-	-	-	-	-	-	*11.2*	-	-
		W	-	-	-	-	-	-	-	-	*16.9*	-	-
MPM-PV 19452	**Thoatherium minusculum**	*L*	-	-	-	-	-	-	-	-	-	*12.7*	-
		W	-	-	-	-	-	-	-	-	-	*14.5*	-
MPM-PV 19453	**Thoatherium minusculum**	*L*	-	-	-	-	*8.2/8.2*	*8.8/8.8*	*9.4/9.8*	*9.9/10.3*	*11.4/11.5*	*12.1/12.0*	-
		W	-	-	-	-	*5.0/6.2*	*8.9/8.3*	*10.3/10.6*	*11.5/11.4*	*10.7*/12.3*	*13.5/13.2*	-
MPM-PV 19460	**Thoatherium minusculum**	*L*	-	-	-	-	*7.8*	-	-	-	*11.4*	*12.6*	-
		W	-	-	-	-	*5.9*	-	-	-	*14.8*	*?*	-
MPM-PV 19451	**Thoatherium minusculum**	*L*	-	-	-	-	*8.8*	-	-	-	-	-	-
		W	-	-	-	-	*6.6*	-	-	-	-	-	-

** Approximate; right/left*

presence of molar paraconids and the m3 entoconid is smaller than the hypoconulid, with the latter clearly tending to form a third lobe.

Comments. MPM-PV 19445 is morphologically and metrically similar to AMNH 9245 assigned to *Tetramerorhinus lucarius* (Scott, 1910: p. 75; Soria, 2001; Tab. 1). The deep posterolingual groove distinguishes MPM-PV 19445 from *Anisolophus*. Also, MPM-PV 19445 differs from *Thoatherium minusculum* because the protoloph area is square, not inclined antero-posteriorly, and its antero-posterior length is notably shorter than the bucco-labial breadth.

MPM-PV 19446 and MPM-PV 19447 are similar in size (Tab. 1) and morphology. The presence of a paraconid (particularly observable in m2–m3) and a third lobe in m3 are dissimilar to *Anisolophus australis*. A large paraconid is also present in lower molars of PIMUZ A/V 5434 assigned to *Tetramerorhinus lucarius* (Zurita-Altamirano *et al.*, 2019). Likewise, despite their small size, MPM-PV 19446 and MPM-PV 19447 do not correspond to *Thoatherium minusculum* because of the presence of entoconid and third lobe tendency in m3.

Tetramerorhinus cingulatum (Ameghino, 1891)

Figures 5.1–5; Tables 1–2

List of synonymies. See Soria (2001, p. 48).

Referred material. MPM-PV 19448, right incomplete upper molar; MPM-PV 19449, incomplete skull with left and right DP1–DP4 and M1 (right series poorly preserved); MPM-PV 19450, left mandibular fragment with dp4–m1? (poorly preserved).

Geographic distribution. Segundas Barrancas Blancas (Ea. Cordón Alto), Río Santa Cruz, Province of Santa Cruz, Argentina.

Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene, Santacrucian).

Description. MPM-PV 19448 (Fig. 5.1) lacks the labial side and roots. It is more worn than MPM-PV 19449 (Fig. 5.2–5), but the M1s are similar, as the metaconule is bunoid and a posterolingual groove is present.

In MPM-PV 19449 (Fig. 5.2), DP1–DP4 are antero-posteriorly elongated. DP1 and DP2 present only a labial cusp (paracone?) and DP2 is more labially concave. In occlusal view, both teeth are divided by a groove into two portions, the posterior being deeper and wider. The DP3 shows an intermediate morphology between premolars and molars, with all cusps present. The mesostyle is the most developed labial style (as it occurs in DP4 and M1), and the paracone and metacone folds are slightly marked. The lingual side is divided by a shallow groove and there is a weak cingulum. In DP3–DP4, protocone and hypocone are connected by a low crest. The DP4 is similar in morphology to the M1, but it is narrower.

The facial region of the skull is similar in length to the braincase. In dorsal view (Fig. 5.3), fragments of the left nasal bone and the frontals are preserved. Two frontal foramina with the respective grooves (oriented to the middle line) are preserved. On the cranial vault, a sagittal crest reaches the dorsal border of the occipital. In lateral view (Fig. 5.4), the dorsal profile is straight and horizontal. The left side is better preserved, and the infraorbital foramen opens at the level of DP3. The orbit lacks the posterior region (broken) and the supraorbital foramen is present. The zygomatic arch is not preserved. Posteriorly, the infratemporal crest is present. In ventral view (Fig. 5.5), the basicranium preserves the basisphenoid and the basioccipital. On the right side, the postglenoid and the paraoccipital processes are incomplete. The occipital condyles are compressed antero-posteriorly, and a bit deformed dorsoventrally by postmortem compression. The foramen magnum dimensions are 17.5 mm length by 19.8 mm width.

The dp4 of MPM-PV 19450 lacks the trigonid. The talonid presents an acute labial side and a small entoconid. This tooth is lower than m1.

Comments. The presence of a posterolingual groove on the M1 of MPM-PV 19448 and MPM-PV 19449 leads us to consider them as *Tetramerorhinus*. In contrast, *Anisolophus* has the protocone and hypocone connected by a low crest (*e.g.*, MPM-PV 19429, MPM-PV 19430, MACN-A 9003-12, see above). Regarding lower teeth, the dp4 with reduced entoconid and m1 with developed paraconid also agrees with *Tetramerorhinus* (*e.g.*, *Te. lucarius*: MLP 12-250, MLP 12-337, MACN-A 1859–60; *Te. cingulatum*: MACN-A 3106, MACN-A 8667–68; *Te. mixtum*: MACN-A 5987, MACN-A 3068–69). The dimensions of MPM-PV 19448, MPM-PV 19449 and MPM-PV 19450 fall within the size range of *Tetramerorhinus cingulatum* (data in Soria, 2001). According to the dental measurements, this species is the largest of the genus. This agrees with the mean body mass estimated by Cassini *et al.* (2012: tab. 14.7), for *Te. cingulatum*, *Te. lucarius* and *Te. mixtum*, with body masses of 41.71 kg, 29.50 kg, and 35.06 kg, respectively.

Genus ***Thoatherium*** Ameghino, 1887

Type species. *Thoatherium minusculum* Ameghino, 1887. Santa Cruz Formation, Early–Middle Miocene and Pampa Castillo Fauna (Early Miocene). Province of Santa Cruz (Argentina) and Pampa Castillo, Andes Mountains (southern Chile).

Referred species. *Thoatherium minusculum* Ameghino, 1887.

Thoatherium minusculum Ameghino, 1887

Figures 6.1–29, 7.1–12; Tables 1–4

List of synonymies. See Soria (2001, p. 57–58).

Referred material. MPM-PV 19451, right P1 and associated right astragalus; MPM-PV 19452, right upper molar (M2?); MPM-PV 19453, incomplete and distorted skull with right and left P1–M2 and M3 erupting; MPM-PV 19454, left fragmentary mandible with incisor alveolus, roots of p1, incomplete p2, and isolated m3; MPM-PV 19455, right mandibular fragment with talonid of p3, roots of p4 and m1; MPM-PV 19456, isolated left m2; MPM-PV 19457, left mandibular fragment with m1 (broken), m2–m3 (m3 erupting and broken); MPM-PV 19458, right dp3; MPM-PV 19459, right mandibular fragment with dp3–dp4, m1; MPM-PV 19460, right P1, left M1 and M2, left p3–m3 poorly preserved; and isolated right m3 (broken), associated to postcranial fragments (distal fragment of right humerus with proximal ulna and radius, two proximal fragments and distal epiphysis of Mt III with sesamoids, incomplete first phalanges and complete second phalanx).

Geographic distribution. Barrancas Blancas (Ea. Santa Lucía) and Segundas Barrancas Blancas (Ea. Cordón Alto), Río

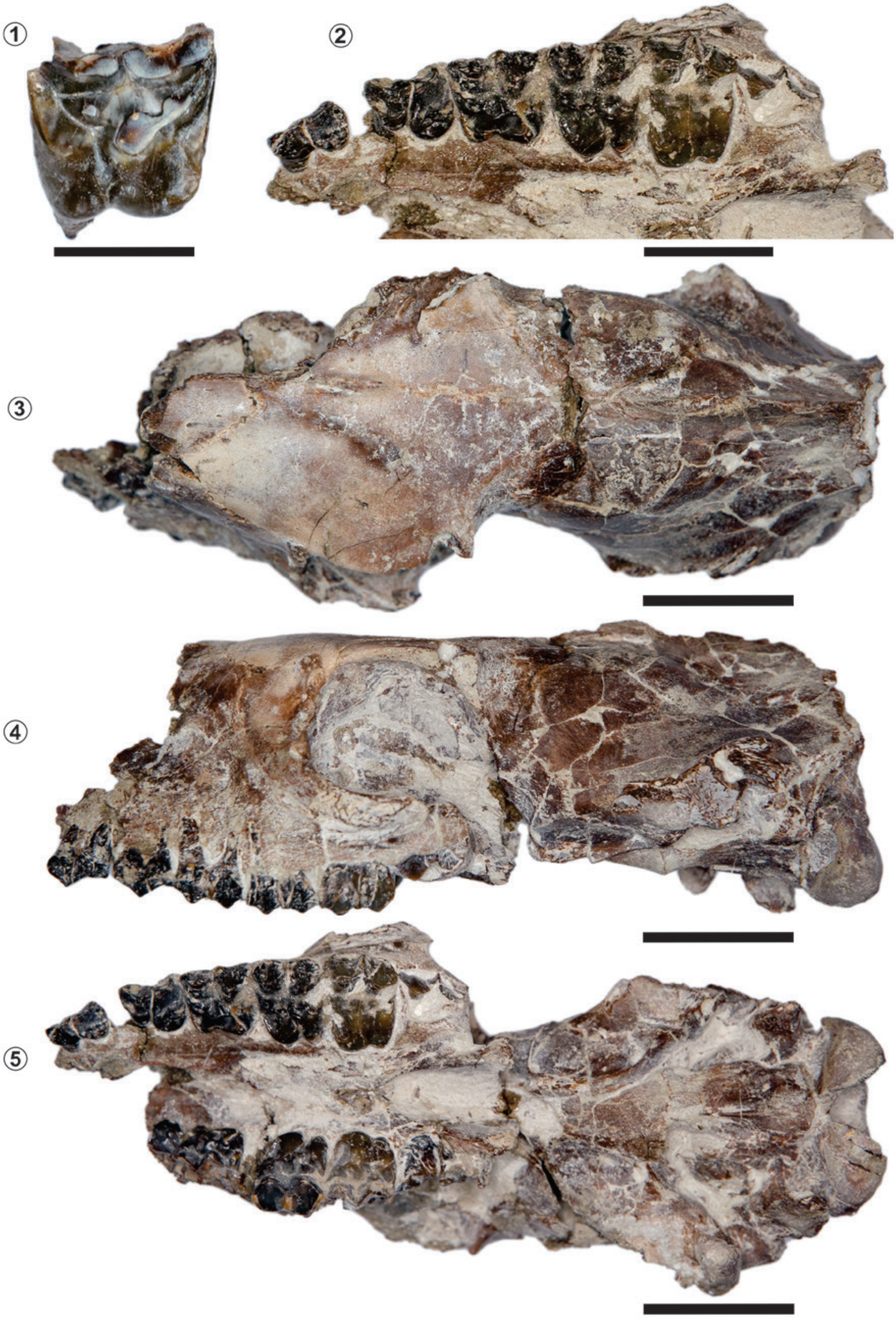


Figure 5. *Tetramerorhinus cingulatum*; **1, MPM-PV 19448**, right incomplete upper molar; **2–5, MPM-PV 19449**, incomplete skull with left and right DP1–DP4 and M1 (detail of left dental series; dorsal, lateral and ventral views). Scale bars: Fig. 1= 10 mm; Figs. 2–5= 30 mm.

Figure 6. ***Thoatherium minusculum***; **1–6, MPM-PV 19451**, right P1 (occlusal and labial views) and associated right astragalus (dorsal, ventral, lateral and medial views); **7, MPM-PV 19452**, right upper molar (M2?); **8–9, MPM-PV 19453**, incomplete and distorted skull with right and left P1–M2 and M3 erupting; **10–15, MPM-PV 19460**, right P1, left M1 and M2, left p3–m3 poorly preserved (occlusal and labial views; reversed); and isolated right m3 (broken); **16, MPM-PV 19458**, right dp3; **17–19, MPM-PV 19459**, right mandibular fragment with dp3–dp4–m1 (occlusal, labial and lingual views); **20–25, MPM-PV 19454**, left fragmentary mandible with incisor alveoli, roots of p1, incomplete p2, and isolated m3 (occlusal, labial and lingual views); **26, MPM-PV 19455**, right mandibular fragment with talonid of p3, roots of p4 and m1; **27–29, MPM-PV 19457**, left mandibular fragment with m1 (broken), m2–m3 (m3 erupting and broken; occlusal, labial and lingual views). Scale bars: Figs. 1–7; 10–13; 16; 20–25= 10 mm; Figs. 8–9; 14–15; 17–19; 26–29= 20 mm.

TABLE 3 – Astragalar dimensions (mm) of *Thoatherium minusculum* (MPM-PV 19451) and comparative set

Specimen	*L*	*DC*	*HW*	*NW*	*LMd*
MPM-PV 19451	*27.1*	*13.9*	*12.8*	*11.9*	*23.6*
MACN A-2974	*28.8*	*15.4*	*14.5*	*12.2*	-
MACN A-2983	*28.0*	*14.1*	*15.0*	*11.6*	-
MACN A-9048	*21.5*	*13.5*	*13.4*	-	-
MACN A-9049	*27.3*	*15.8*	*15.0*	*12.5*	-
FMNH P 13193	*27.3*	*14.8*	*14*	*11.5*	*21.6*

Santa Cruz, Province of Santa Cruz, Argentina.

Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene, Santacrucian).

Description. The P1 (MPM-PV 19451; Fig. 6.1–2) is labially straight and lingually rounded. The cingulum is restricted to the labial face. In occlusal view, the tooth is more worn in the posterior region. The astragalus (Fig. 6.3–6; Tab. 3) associated to P1 presents a nearly symmetrical trochlea. In dorsal view, there is a pit in the base of the neck (where the anterior tongue of the distal epiphysis of the tibia articulates). The distal articular surface is dorsoventrally convex and mediolaterally slightly convex. In ventral view, the sustentacular facet is smoothly convex and in lateral view, the ectal facet is markedly concave with a posterior convexity.

The upper molar (MPM-PV 19452; Fig. 6.7) lacks the anterolabial region. It is a worn tooth, probably an M2. In occlusal view, there are two fossettes. The antero-posteriorly elongated central one is separated from the small, rounded posterior one by a lophoid metaconule. Protocone, paraconule and hypocone are prominent. Also, there is an anterolingual cingulum that does not reach the base of the protocone.

The skull fragment MPM-PV 19453 (Fig. 6.8–9) partially preserves the maxilla and the orbits. In dorsal view, we observe fragments of the nasals, frontals and the frontal sulcus (Soria, 2001). Both dental series P1–M3 are unworn and almost complete; the M3 is not fully erupted. P1–P2 have the labial wall higher than the lingual, and a conspicuous cusp (paracone?). On the lingual side of P2, there is a well-developed anterior cusp (paraconule?), separated from a posteriorly displaced protocone by a concavity. P3–M2 are morphologically similar, increasing gradually in size; they show a reduced, lophoid metaconule that interrupts the anteroposterior groove, similar to MPM-PV 19460 (M1–M2) (Fig. 6.11–12).

The dp3s (MPM-PV 19458 and MPM-PV 19459) are very similar to MPM-PV 19459 but more worn. They show the trigonid longer and narrower than the talonid, the paralophid curved anteriorly, and lack the entoconid. In MPM-PV 19458 (Fig. 6.16), the hypoconulid is more pronounced than in MPM-PV 19459. The dp4 (MPM-PV 19459; Fig. 6.17–19) is very similar to dp3, with shorter paralophid.

The two-rooted p2 (MPM-PV 19454) lacks the antero-labial portion (Fig. 6.20–22). It is a simple tooth, with a median column on the lingual side that divides the premolar into an anterior and posterior part. It has smooth lingual and labial cingula.

The p3s of MPM-PV 19455 and MPM-PV 19460 (Fig. 6.26, 14–15 respectively), lack an entoconid. The m1 is heavily worn. It also lacks entoconid and has the trigonid shorter than the talonid. A smooth labial cingulum is evident at the base of trigonid. The m1–m2 (MPM-PV 19455, MPM-PV 19456, MPM-PV 19457, MPM-PV 19459, and MPM-PV 19460; Fig. 6.26, 27–29, 17–19, 13–14 respectively) are structurally similar but the m2 is slightly larger. The m1s of MPM-PV 19455 and MPM-PV 19456 have shorter and narrower trigonids compared with talonids. The m3 (MPM-PV 19460, MPM-PV 19454, MPM-PV 19457; Fig. 6.13–15, 23–25 respectively) lacks an entoconid (talonid incomplete in MPM-PV 19457). The paralophid is a bit longer than the hypolophulid in MPM-PV 19454, but the two are similar in length in MPM-PV 19460.

Incomplete forelimb and distal elements of a hind limb are preserved in MPM-PV 19460 (Fig. 7.1–12; Tab. 4). The fragment of the humerus preserves only the distal portion, with a broken distal articular surface and only the lateral epicondyle (Fig. 7.1–2). Ulna and radius are not fused (Fig. 7.3–5). The radius is anteroposteriorly flattened, with a smooth concavity on the posterior side where it contacts with the ulna. The proximal articular surface of the humerus has a sigmoidal mediolateral profile and is moderately concave anteroposteriorly. The proximal parts of the central metapodials (Mt III; Fig. 7.6–7) preserves part of the proximal articular surfaces for the ectocuneiform and cuboid. The distal part of the Mt III (Fig. 7.8) has a well-defined median keel, more pronounced on the posterior side. Two small sesamoids are joined to the posterior distal region of the Mt III; they are kidney-shaped with a slight difference in size (Fig. 7.12). Two fragments of first central phalanges are also present (Fig. 7.9–10). The best preserved is proximodistally elongated, its proximal articular surface is wider than the distal one, and has a medial concavity for the median metapodial keel. The second central phalanx presents a concave proximal surface and the distal trochlea is a bit narrower than the proximal articulation (Fig. 7.11).

Comments. The P1 of MPM-PV 19451 is very similar to that of MACN-A 2996a, MLP 3492, and FMNH P 13193 assigned to *T. minusculum*, and the associated astragalus coincides morphological and metrically with MACN-A 2974, MACN-A 2983, MACN-A 9048, MACN-A 9049, and FMNH P 13193 of this species (see Tab. 3).

The P1s of MPM-PV 19453 are similar to that of MPM-PV 19460 (Fig. 6.10) and a bit smaller than MPM-PV 19451 (Tab. 2). They show a proportional width anterior and posteriorly, similar to P1 of FMNH P 13193 or MPM-PV 3529 that (Cassini *et al.*, 2012) assigned to *Th. minusculum*. In *Tetramerorhinus lucarius* (MACN-A 1859–60 and AMNH 9245), instead, the posterior region is wider. In turn, the P1 of *Anisolophus australis* (YPM-VPPU 15368; Cassini *et al.*, 2012) is more quadrangular and with a smooth median lingual groove.

The presence of a lophoid metaconule in MPM-PV 19452, MPM-PV 19453 and MPM-PV 19460 is characteristic of *Thoatherium*, whereas this cusp is bunoid in *Tetramerorhinus lucarius* and *A. australis*.

Despite the different wear stage of MPM-PV 19452 and MPM-PV 19453, the general shape and size are very similar (Tab. 2). Moreover, MPM-PV 19452 presents great similarities with MACN-A 2996a, MACN-A 9043, and MLP 3682 assigned to *Thoatherium minusculum*.

The position of the mandibular foramen in MPM-PV 19454 and the presence of two roots allow us to determine this tooth as a p2. It is slightly worn and very similar in size and morphology to the p2 of FMNH P 13193, mentioned

Figure 7. ***Thoatherium minusculum***, **MPM-PV 19460**; **1–2,** distal fragment of right humerus (dorsal and ventral views); **3,** proximal portion of ulna; **4–5,** proximal fragment of radius (dorsal and ventral views); **6–8,** two proximal fragments and distal epiphysis of Mt III; **9–10,** incomplete first phalanges; **11,** complete second phalanx; **12,** sesamoids. Scale bars= 20 mm.

Table 4 – Postcranial dimensions (mm) of *Thoatherium minusculum* (MPM-PV 19460)

Humerus	*TDT*	*14.0*
Ulna	*HCS*	*16.2*
Radius	*TDPE*	*12.6*
	TDD	*13.0*
McIII	*TDPA*	*18.3*
	DW	*13.0*
	TDDA	*16.8*
PhI	*L*	*38.8*
	TDDA	*12.8*
PhII	*L*	*19.8*
	TDPA	*13.7*
	TDDA	*13.7*

above. The morphology and dimensions of the postcranial remains (MPM-PV 19460) are also very close to those of *Th. minusculum* FMNH P 13193 (G. Schmidt, pers. observation, 2015).

Genus ***Diadiaphorus*** Ameghino, 1887

Type species. *Diadiaphorus majusculus* Ameghino, 1887. Santa Cruz Formation, Early–Middle Miocene, Province of Santa Cruz, Argentina.

Referred species. *Diadiaphorus majusculus* Ameghino, 1887.

Diadiaphorus majusculus Ameghino, 1887

Figures 8.1–22; Tables 1, 2 and 5

List of synonymies. See Soria (2001, p. 65).

Referred material. MPM-PV 19461, left m3?; MPM-PV 19462, right m3?; MPM-PV 19463, right M3; MPM-PV 19464, fragment of skull and incomplete postcranial remains, including the articular heads of both humeri, distal fragment of humerus, proximal fragment of ulna, proximal and distal fragments of tibiae, incomplete right calcaneus, distal fragment of metapodial III.

Geographic distribution. Barrancas Blancas (Ea. Aguada Grande, Ea. Santa Lucía) and Segundas Barrancas Blancas (Ea. Cordón Alto), Río Santa Cruz, Province of Santa Cruz, Argentina.

Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene, Santacrucian).

Description. On both m3s (Fig. 8.1–2) the trigonid is a bit shorter than the talonid and the lophids are similar in length. The ectoflexid is very deep and the entoconid is absent. MPM-PV 19461 is more complete and preserves a basal cingulum that surrounds the entire tooth.

The upper M3 (MPM-PV 19463; Fig. 8.3; Tab. 2) is moderately worn. It is trapezoidal in occlusal view, with the anterior region wider than the posterior. The parastyle is well developed. The anteroposterior valley is interrupted posteriorly by a bunoid metaconule that becomes fused to the metacone with wear. The anterolingual cingulum is well developed, and reaches the base of the protocone. A hypocone is present.

MPM-PV 19464 preserves the upper right section of the frontal bone, with part of the orbit (Fig. 8.4); posterolaterally, there is a large supraorbital foramen accompanied by another smaller foramen. Two other foramina of different size, are placed medially in the frontal bone. The posterior border of the bone is sinuous.

The heads of the humeri of MPMP-PV 19464 (Tab. 5) are hemispherical and dorsally flattened (Fig. 8.5–6). The distal fragment has both epicondyles poorly preserved. The capitulum occupies a great proportion of the distal articular surface than the trochlea (Fig. 8.7–8).

The ulnar olecranon (Fig. 8.9–11) is well developed, proximally thickened and rugose, as described by Scott (1910) for *Diadiaphorus*.

The proximal portion of the tibia (Fig. 8.12–13) preserves the medial and lateral intercondyloid tubercles, which form the tibial spine. The distal epiphysis (Fig. 8.14–17) preserves the astragalar surface divided in two unequal well-excavated facets.

The fragment of calcaneum (Fig. 8.18–20) has a long and laterally compressed “neck”, with a dorsal border narrower than the ventral one. The proximal segment of the tuberosity projects anteriorly.

The distal portion of metapodial III (Fig. 8.21–22) presents a medial keel along the trochlea, on both sides of which

Figure 8. ***Diadiaphorus majusculus*****, 1, MPM-PV 19461**, left m3?; **2, MPM-PV 19462**, right m3?; **3, MPM-PV 19463**, right M3; **4–22, MPM-PV 19464**, **4,** fragment of skull; **5–6,** articular head of humeri; **7–8,** distal fragment of humerus (dorsal and ventral views); **9–11,** proximal fragment of ulna (dorsal, lateral and ventral views); **12–13,** proximal fragment of right tibia (posterior and proximal views); **14–17,** distal fragment of right tibia (lateral, anterior, posterior and medial views); **18–20,** incomplete right calcaneus (dorsal, ventral and medial views); **21–22,** distal fragment of metapodial III (dorsal and ventral views). Scale bars: Figs. 1–3= 10 mm; Figs. 4–13; 18–22= 20 mm; Figs. 14–17= 40 mm.

TABLE 5 – Postcranial dimensions (mm) of *Diadiaphorus majusculus* (MPM-PV 19464)

Humerus	*TDT*	*25.9*
Ulna	*APDO*	*25.5*
	TDO	*11.0*
Tibia	*APDD*	*17.9*
	TDD	*20.5*
	TDDE	*18.5*
	APDDA	*28.9*
	TDDA	*30.1*
Calcaneus	*TDTu*	*17.7*
	APDTu	*23.5*
Central metapodial	*TDDA*	*23.2*
	DW	*27.9*
	TDD	*18.2*

are depressions for ligament insertions.

Comments. The absence of entoconid and the lack of tendency to form a third lobe in m3 are characteristics shared with *Diadiaphorus*. Moreover, MPM-PV 19461 and MPM-PV 19462 are morphologically and metrically similar to MLP 12-320 and MLP 12-325 assigned to *Diadiaphorus majusculus* (Tab. 1; Soria, 2001: tab. 13). The M3 is also comparable to MACN-A 9198–99, MLP 12-305, MLP 12-306, and AMNH 9270 assigned to *D. majusculus* (Soria, 2001).

The fragment of skull presents important similarities with AMNH 9270 recognized as *D. majusculus* (Bergqvist, 2008; Scherer *et al*., 2009; Corona *et al*., 2018) and AMNH 14481 (plaster cast, Schmidt, pers. data, 2015) labelled as *D. majusculus*. The foramina in the frontal bone are comparable in morphology, position, and size. The postcranial remains associated to this fragment share size and morphology with *D. majusculus* (AMNH 9270).

Family MACRAUCHENIIDAE Gervais, 1855
Subfamily CRAMAUCHENIINAE Ameghino, 1902

Genus ***Theosodon*** Ameghino, 1887

Type species. *Theosodon lydekkeri* Ameghino, 1887. Santa Cruz Formation, Early–Middle Miocene, Province of Santa Cruz, Argentina.

Referred species. *Theosodon lydekkeri*, *T. lallemanti*, *T. garrettorum*, *T. fontanae*, *T. gracilis*, *T. karaikensis*, *T. pozzii*, *T.? frenguellii*, and "*Theosodon*" *arozquetai*.

Theosodon sp.
Figure 9.1–3; Table 6

Referred material. MPM-PV 19465, left and right maxillary fragments with M1 (broken), M2 and erupting M3; MPM-PV 19466, left p4; MPM-PV 19467, left mandibular fragment with m1–m2.

Geographic distribution. Barrancas Blancas (Ea. Santa Lucía) and Segundas Barrancas Blancas (Ea. Cordón Alto), Río Santa Cruz, Province of Santa Cruz, Argentina.

Stratigraphic distribution. Santa Cruz Formation (Early–Middle Miocene, Santacrucian).

Description. The M2 of MPM-PV 19465 (Fig. 9.1) is unworn and shows a well-developed metastyle. In occlusal view, the protocone is slightly more lingually placed than the hypocone, but they are relatively closer together than the buccal cusps; a small fossette intervenes between them. The hypocone is mesial to the metacone and the protocone is distal to the paracone. This arrangement gives a trapezoidal appearance to the tooth. The paraconule is smaller than the protocone and is placed opposite the paracone. The trigon basin is shallow. An acute crest extends posterolabially from the hypocone, forming a posterior basin, and a similar crest extends anterolabially from the paraconule, surrounding a little basin. The precingulum is not preserved. In the erupting M3, protocone and hypocone are more separated and the three basins are deeper.

The trigonid of p4 (MPM-PV 19466; Fig. 9.2) is taller than the talonid and its lophids are longer. The metaconid is prominent, with a wide base. Labially, the ectoflexid is deep and a weak cingulum runs at the base. Metaflexid and entoflexid are notably excavated.

The m1–m2 (MPM-PV 19467; Fig. 9.3) are heavily worn. The m1 is shorter than m2, and shows the entoconid, which also is present on m2. Labial cingula are continuous at the base of the teeth whereas lingual cingula are discontinuous, present only anteriorly and posteriorly (observable in m2).

Figure 9. ***Theosodon*** sp.; **1, MPM-PV 19465**, left maxillary fragment with M1 (broken), M2 and erupting M3; **2, MPM-PV 19466**, left p4; **3, MPM-PV 19467**, left mandibular fragment with m1–m2. Scale bars: Figs. 1 and 3= 20 mm; Fig. 2= 10 mm.

Table 6 - Dental dimensions (mm) of *Theosodon* sp.

		MPM-PV 19465	MPM-PV 19466	MPM-PV 19467
M2	*L*	*23.9*		
	W	*18.2*		
M3	*L*	*20.5**		
	W	*17.8**		
p4	*L*		*23.2*	-
	W		*12.7*	-
m1	*L*		-	*18.7*
	W		-	*12.0**
m2	*L*		-	*21.2*
	W		-	*13.1*

** Approximate*

Comments. The lack of metaconule in the M2 of MPM-PV 19465 coincides with *Theosodon* (Soria, 1981) and differs from *Cramauchenia* (Soria, 1981: fig. 2A). MPM-PV 19465 is morphologically similar to MACN-A 9269-88 (*T. lydekkeri*), FMNH P 13175 (*T. garrettorum*), and FMNH P 13187 (*T. lallemanti*). Concerning size, MPM-PV 19465 falls in the range of these species of *Theosodon*, being nearer to *T. lallemanti* after Scott's (1910) measurements.

Regarding lower teeth (m1–m2), *Cramauchenia* and *Theosodon* do not show significant morphological differences (Soria, 1981). However, the lingual position of the paraconid in m2 of MPM-PV 19467 is closer to *Theosodon* than to *Cramauchenia*, in which this cusp is more labially placed (Soria, 1981: plate 2A). Moreover, the morphological similarities of MPM-PV 19466 and MPM-PV 19467 with a specimen labelled as *Theosodon* sp. (MLP 12-381, G. Schmidt, pers. data, 2010) are evident. The measurements of p4, m1 and m2 (Tab. 6) exceed those assigned to *Cramauchenia* (Soria, 1981: 14) and are close to those of *T. gracilis* (MACN-A 2521, lectotype, MACN-A 9297, and AMNH 9230; Scott, 1910; Soria, 1981).

FINAL REMARKS

The new remains of Litopterna recorded from the Río Santa Cruz correspond to Proterotheriidae and Macraucheniidae. Within Proterotheriidae, six species were recognized: *Anisolophus australis*, *A. floweri*, *Tetramerorhinus lucarius*, *Te. cingulatum*, *Thoatherium minusculum*, and *Diadiaphorus majusculus*. The majority of these specimens come from Segundas Barrancas Blancas (Ea. Cordón Alto). *Thoatherium minusculum* and *D. majusculus* were originally included in the taxa nominated by Ameghino (1887) from the Río Santa Cruz.

Soria (2001) assigned some specimens from the Río Santa Cruz to *Anisolophus australis*, *Thoatherium minusculum* and *Tetramerorhinus mixtum*. The latter has not been identified within the recent new collection; instead, we recognized *Te. lucarius* and *Te. cingulatum.* It is worth to mention that different species within the same genus (*e.g.*, *Anisolophus*, *Tetramerorhinus*) are recognized based mainly on size, but some overlap exists, making it difficult to achieve an accurate assignment of individual specimen.

Macraucheniidae is represented by *Theosodon*, but assignment to a species was not possible due to the poorly preserved material. *Theosodon* remains were recovered from Barrancas Blancas and Segundas Barrancas Blancas (Ea. Santa Lucía and Ea. Cordón Alto, respectively). This genus should be revised in order to analyze its taxonomic richness during the Santacrucian. As it happens with some proterotheriids, several species of *Theosodon* are differentiated only by size.

The abundance of proterotheriid specimens (39) from the Río Santa Cruz localities exceeds by far that of macraucheniids (one specimen from Segundas Barrancas Blancas and two from Barrancas Blancas). This agrees with data published by Tauber (1999: tab. 1) where the presence of proterotheriids (eight records) surpasses those of macraucheniids (two records) in the Santacrucian localities prospected between the Río Coyle and Río Gallegos (Province of Santa Cruz). Kramarz and Bond (2005) pointed out the low relative abundance of Santacrucian representatives of both families in the MACN Ameghino collection, where they found that only 24 % of the litoptern remains in that collection belong to Macraucheniidae. In the same contribution, the authors highlighted that macraucheniids remains are also scarce for the levels of the Pinturas Formation (Early Miocene, Province of Santa Cruz).

In summary, the systematic of litopterns of the Santa Cruz Formation requires an update. The new remains from the Río Santa Cruz reported here, as well as others recently recovered from other Santacrucian localities, particularly from the Atlantic coast (Cassini *et al.*, 2012; Vizcaíno *et al.*, 2012), will be valuable to clarify the taxonomy of this peculiar group of South American extinct ungulates.

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REFERENCES

Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de Patagonia Austral y depositados en el Museo La Plata. *Boletín del Museo de La Plata* 1: 1–26.

Ameghino, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas de la Academia Nacional de Ciencias de Córdoba* 6: 1–1027.

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

Ameghino, F. 1894. Enumération synoptique des espèces de mammifères fossiles des formations éocènes de Patagonie. *Boletín de la Academia Nacional de Ciencias de Córdoba* 13: 259–455.

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

Ameghino, F. 1902. Première contribution à la connaissance de la faune mammalogique des couches à *Colpodon*. *Boletín de la Academia Nacional de Ciencias de Córdoba* 17: 71–138.

Ameghino, F. 1904a. Recherches de morphologie phylogénétique sur les molaires supérieures des ongulés. *Anales del Museo Nacional de Buenos Aires* 9: 1–541.

Ameghino, F. 1904b. Nuevas especies de mamíferos cretáceos y terciarios de la República Argentina. *Anales de la Sociedad Científica Argentina* 57: 162–175; 327–341.

Bergkvist, L.P. 2008. Postcranial skeleton of the upper Paleocene (Itaboraian) 'Condylarthra' (Mammalia) of Itaboraí Basin, Brazil. In: E.J. Sargis, and M. Dagosto (Eds.), *Mammalian evolutionary morphology: a tribute to Frederick S. Szalay*. Vertebrate Paleobiology and Paleoanthropology Series, Netherlands, p. 107–133.

Bonaparte, J.F., and Morales, J. 1997. Un primitivo Notonychopidae (Litopterna) del Paleoceno inferior de Punta Peligro, Chubut, Argentina. *Estudios geológicos* 53: 263–274.

Bond, M. 1986. Ungulados fósiles de Argentina: evolución y paleoambientes. *4° Congreso Argentino de Paleontología y Bioestratigrafía* (Mendoza), Actas 2: 173–185.

Bond, M. 1999. Quaternary native ungulates of Southern South America. A synthesis. In: J. Rabassa, and M. Salemme (Eds.), *Quaternary of South America and Antarctic Peninsula*. Rotterdam, Netherlands, p. 177–205.

Bond, M., Cerdeño, E., and López, G. 1995. Los ungulados nativos de América del Sur. In: M.T. Alberdi, G. Leone, and E.P. Tonni (Eds.), *Evolución biológica y climática de la región Pampeana durante los últimos cinco millones de años. Un ensayo de correlación con el Mediterráneo occidental.* Monografías del Museo Nacional de Ciencias Naturales, CSIC, Madrid, p. 259–275.

Burmeister, G. 1879. *Description physique de la République Argentine d'après des observations personnelles et étrangères. 3 (animaux vertébrés 1: Mammifères vivants et éteintes).* P.E. Coni, Buenos Aires, 555 p.

Burmeister, G. 1885. Examen crítico de los mamíferos y reptiles fósiles denominados por Don Augusto Bravard. *Anales Museo Nacional de Buenos Aires* 3: 95–173.

Cabrera, A., and Kraglievich, L. 1931. Diagnosis previas de los ungulados fósiles de la Formación Arroyo Chasicó. *Notas del Museo La Plata* 1: 107–113.

Cassini, G.H., Cerdeño, E., Villafañe, A.L., and Muñoz, N.A. 2012. Paleobiology of Santacrucian native ungulates (Meridiungulata: Astrapotheria, 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.

Cifelli, R.L., and Guerrero, J. 1997. Litopterns. In: R.F. Kay, R.H. Madden, R.L. Cifelli, and J.J. Flynn (Eds.), *Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington and London, p. 289–302.

Corona, A., Perea, D., and Ubilla, M. 2018. The humerus of Proterotheriidae (Mammalia, Litopterna) and its systematic usefulness: the case of "*Proterotherium berroi*" Kraglievich, 1930. *Ameghiniana* 55: 150–161.

Corona, A., Perea, D., and Ubilla, M. 2019. A new genus of Proterotheriinae (Mammalia, Litopterna) from the Pleistocene of Uruguay. *Journal of Vertebrate Paleontology* doi: 10.1080/02724634.2019.1567523

Croft, D.A. 2016. *Horned Armadillos and Rafting Monkeys: The Fascinating Fossil Mammals of South America*. Indiana University Press, Bloomington, 304 p.

Croft, D.A., Flynn, J.J., and Wyss, A.R. 2004. Notoungulata and Litopterna of the early Miocene Chucal Fauna, Northern Chile. *Fieldiana Geology* 50: 1–52.

Cuitiño, J.I., Fernicola, J.C., Kohn, M., Trayler, R., Naipauer, M., Bargo, M.S., Kay, R.F., and Vizcaíno, S.F. 2016. U-Pb geochronology of the Santa Cruz Formation (early Miocene) at the Río Bote and Río Santa Cruz (southernmost Patagonia, Argentina): implications for the correlation of fossil vertebrate localities. *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: 14–33.

Delupi de Bianchini, L.H., and Bianchini, J.J. 1971. Revisión de los Proterotheriinae (Mammalia, Litopterna) del "Mesopotamiense". *Ameghiniana* 8: 1–23.

Dozo, M.T., and Vera, B. 2010. First skull and associated postcranial bones of Macraucheniidae (Mammalia, Litopterna) from the Deseadan SALMA (late Oligocene) of Cabeza Blanca (Chubut, Argentina). *Journal of Vertebrate Paleontology* 30: 1818–1826.

Fernicola, J.C. 2011. Implicancias del conflicto Ameghino-Moreno sobre la colección de mamíferos fósiles realizada por Carlos Ameghino en su primera exploración al río Santa Cruz, Argentina. *Revista del Museo Argentino de Ciencias Naturales* 13: 41–57.

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.

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 Notohippidian. *Journal of South American Earth Sciences* 52: 91–107.

Flynn, J.J., and Wyss, A.R. 1998. Recent advances in South American mammalian paleontology. *Tree* 11: 449–454.

Forasiepi, A.M., MacPhee, R.D.E., Hernández Del Pino, S., Schmidt, G.I., Amson, E., and Grohé, C. 2016. Exceptional skull of *Huayqueriana* (Mammalia, Litopterna, Macraucheniidae) from the late Miocene of Argentina: anatomy, systematics, and paleobiological implications. *Bulletin of the American Museum of Natural History* 404: 1–76.

Gaudry, A. 1904. Fossiles de Patagonie. Dentition de quelques mammifères. *Mémoires de la Société Géologique de France. Paléontologie* 12: 1–27.

Gaudry, A. 1906. Fossiles de Patagonie: les attitudes de quelques animaux. *Annales de Paléontologie* 1: 1–42.

Gervais, P. 1855. Recherches sur les mammifères fossiles de l'Amérique méridionale. *Comptes Rendus de l'Académie des Sciences* 40: 1112–1114.

Kraglievich, L. 1930. La formación Friaseana del río Frías, río Fénix, Laguna Blanca, etc., y su fauna de Mamíferos. *Physis* 10: 127–161.

Kramarz, A.G., and Bond, M. 2005. Los Litopterna (Mammalia) de la Formación Pinturas, Mioceno Temprano-Medio de Patagonia. *Ameghiniana* 42: 611–625.

Luna, C.A., Schmidt, G.I., and Ochoa, J.G. 2015. Nuevos registros de *Neolicaphrium recens* Frenguelli (Litopterna, Proterotheriidae) procedentes de Corralito (Pleistoceno tardío-Holoceno temprano), Córdoba, Argentina. *Ameghiniana* 53 Abstracts Supplement: 20R.

Lydekker, R. 1894. Contributions to a knowledge of the fossil vertebrates of Argentina. 3. A study of extinct Argentine ungulates. *Anales del Museo de La Plata*, *Paleontología* 2: 1–91

McGrath, A.J., Anaya, F., and Croft, D.A, 2018. Two new macraucheniids (Mammalia: Litopterna) from the late middle Miocene (Laventan South American Land Mammal Age) of Quebrada Honda, Bolivia. *Journal of Vertebrate Paleontology* doi 10.1080/02724634.2018.1461632

McGrath, A., Flynn, J.J., and Wyss, A.R. 2019. Proterotheriids and macraucheniids (Litopterna: Mammalia) from the Pampa Castillo Fauna, Chile (early Miocene, Santacrucian SALMA) and a new phylogeny of Proterotheriidae. *Journal of Systematic Palaeontology* doi: 10.1080/14772019.2019.1662500

Mercerat, A. 1891. Sinopsis de la Familia Bunodontheriidae (Eoceno de Patagonia) conservada en el Museo de La Plata. *Revista del Museo de la Plata* 1: 447–471.

Mones, A. 1986. Paleovertebrata Sudamericana. Catálogo sistemático de los Vertebrados fósiles de América del Sur. Parte I. Lista preliminar y Bibliografía. *Courier Forschunginstitut Senckenberg* 82: 1–625.

Pascual, R., Ortiz-Jaureguizar, E., and Prado, J.L. 1996. Land mammals: paradigm for Cenozoic South American geobiotic evolution. In: G. Arratia (Ed.), *Contribution of Southern South America to Vertebrate Paleontology*. Munchner Geowissenshaftliche Abhandlungen, Munich, p. 265–319.

Roth, S. 1899. Aviso preliminar sobre mamíferos mesozoicos encontrados en Patagonia. *Revista del Museo de La Plata* 9: 381–388.

Scherer, C.S., Pitana, V.G., and. Ribeiro, A.M. 2009. Proterotheriidae and Macraucheniidae (Litopterna, Mammalia) from the Pleistocene of Rio Grande do Sul State, Brazil. *Revista Brasileira de Paleontologia* 12: 231–246.

Schmidt, G.I., and Ferrero, B.S. 2014. Taxonomic reinterpretation of *Theosodon hystatus* Cabrera and Kraglievich, 1931 (Litopterna, Macraucheniidae) and phylogenetic relationships of the family. *Journal of Vertebrate Paleontology* 34: 1231–1238.

Scott, W.B. 1910. Mammalia of the Santa Cruz beds. Part I: Litopterna. Reports of the Princeton University Expedition to

Patagonia. In: W.B. Scott (Ed.), *Reports of the Princeton University Expedition to Patagonia (1896–1899)*. Princeton University, E. Schweizerbart'sche Verlashandlung, Stuttgart, p. 1–156.

Soria, M.F. 1981. Los Litopterna del Colhuehuapense (Oligoceno Tardío) de la Argentina. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Serie Paleontología* 3: 1–54.

Soria, M.F. 2001. Los Proterotheriidae (Mammalia, Litopterna): sistemática, origen y filogenia. *Monografías del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* 1: 1–167.

Tauber, A.A. 1999. Los vertebrados de la Formación Santa Cruz (Mioceno inferior-medio) en el extremo sureste de la Patagonia y su significado paleoecológico. *Revista Española de Paleontología* 14: 173–182.

Tonni, E.P. 1990. Mamíferos del Holoceno de la Provincia de Buenos Aires. *Paulacoutiana* 4: 2–21.

Ubilla, M., Perea, D., Bond, M., and Rinderknecht, A. 2011. The first cranial remains of the Pleistocene proterotheriid *Neolicaphrium* Frenguelli, 1921 (Mammalia, Litopterna): a comparative approach. *Journal of Vertebrate Paleontology* 31: 193–201.

Villafañe, A.L., Ortiz-Jaureguizar, E., and Bond, M. 2006. Cambios en la riqueza taxonómica y en las tasas de primera y última aparición de los Proterotheriidae (Mammalia, Litopterna) durante el Cenozoico. *Estudios Geológicos* 62: 155–166.

Vizcaíno, S.F. 2011. Cartas para Florentino desde la Patagonia. Crónica de la correspondencia édita entre los hermanos Ameghino (1887-1902). In: J.C. Fernicola, A.R. Prieto, and D.G. Lazo (Eds.), *Vida y obra de Florentino Ameghino. Publicación Especial de la Asociación Paleontológica Argentina* 12: 51–67.

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.

Zittel, K.A. von. 1893. *Handbuch der Palaeontologie*. Abteilung I. Palaeozoologie. Bd. IV. Vertebrata (Mammalia), Munich, 799 p.

Zurita-Altamirano, D., Buffetaut, E., Forasiepi, A.M., Kramarz, A., Carrillo, J.D., Aguirre-Fernández, G., Carlini, A.A., Scheyer, T.M., and Sánchez-Villagra, M.R. 2019. The Allemann collection from the Santa Cruz Formation (late early Miocene), Argentina, in Zurich, Switzerland. *Swiss Journal of Palaeontology* doi: 10.1007/s13358-019-00185-5

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Appendix 1. List of the revised material of Litopterna.

Proterotheriidae

Anisolophus australis

MACN-PV 2417, holotype, incomplete palate with left P2–M3 without labial sides, and right P2–P4.

MACN-A 8669, holotype of *Proterotherium intermedium* (junior synonym of *A. australis*), right mandible with p3–m3.

MACN-A 3107, right M1–M3.

YPM-VPPU 15368, incomplete skull with left I, and P1–M3, and right P1–M3.

Anisolophus floweri

MACN-A 8999, incomplete skull with left D1–D4–M1–M2, and right M1–M2.

MACN-A 9003-12, holotype of *Licaphrium pyramidatum* (junior synonym of *A. floweri*), left P4–M3, right incomplete P4, M1 and M2 (isolated), right p4, m2–m3; and postcranial remains.

MACN-A 3085, right mandible with p2–m1 (m1 broken).

MLP 12-289, left mandibular fragment with m2–m3.

MLP 82-IV-3-3, right m3.

MLP 82-IV-3-4, left m3 (2).

PIMUZ A/V 5293, left m1.

YPM-VPPU 15711, holotype of *Licaphrium pyneanum* (junior synonym of *A. floweri*), skull almost complete with right P2–M3 and left P3–M3 (M3 erupting).

YPM-VPPU 15309, right mandibular fragment with p4–m3.

Anisolophus minusculus

MACN-A 9001b, right maxilla with D4–M1–2.

Tetramerorhinus lucarius

AMNH 9245, skull.

MACN-A 1855,left maxillary fragment with P3–M3.

MACN-A1859-60, incomplete skull with both series complete, and mandible with alveoli of internal incisives, external incisives, and p1–m3 of both sides.

MLP 12-250, incomplete mandible with left p1 and right p1–m2.

MLP 12-337, right p4–m1.

PIMUZ A/V 5434, isolated premolars and molars, including left dp3 or dp4, p3 or p4, left and right m1 or m2.

Tetramerorhinus cingulatum

MACN-A 8667–68, holotype of *Proterotherium divortium* (junior synonym of *Te. cingulatum*), left maxillary fragment with P4–M3, mandible with symphysis, and right and left p1–p3.

MACN-A 3106, left mandibular fragment with p4–m3.

Tetramerorhinus prosistens

MACN-A 11626, holotype, right maxillary fragment with P4–M3, left P3–P4, M2–M2; right mandible with p2, p4–m3, left mandible with p3–p4, incomplete m1?, and m3.

Tetramerorhinus mixtum

MACN-A 8663, holotype of *Proterotherium pyramidatum* (junior synonym of *Te. mixtum*), palate with incisives, right P3–M3, and left P1–M3.

MACN-A 5987, mandible with right c–m3 and left p1–m3.

MACN-A 3068–69, right mandible with p4–m3 and left m1–m3.

Tetramerorhinus fleaglei

MACN SC 129–30, holotype, right and left P4–M2.

Thoatherium minusculum

FMNH P 13193, skull, mandible and postcranial remains.

MACN-A 2996a, palate with right and left P1–M3.

MACN-A 2974, astragalus.
MACN-A 2983, astragalus.
MACN-A 9048, astragalus.
MACN-A 9049, astragalus.
MACN-A 9043, palate with left P2–M3, and right P4 (incomplete)–M3.
MPM-PV 3492, skull.
MPM-PV 3682, skull.
Diadiaphorus majusculus
AMNH 9270, skull and postcranial remains.
AMNH 14481, skull.
MACN-A 9198-99, right maxilla with P1–M3.
MLP 12-305, incomplete skull with right I and P1–M3, and left P1–P4.
MLP 12-306, palate with right and left P1–M3.
MLP 12-320, complete mandible.
MLP 12-325, right mandibular fragment with m2–m3.
Macraucheniidae
Theosodon lydekkeri
MACN-A 9269-88, skull and mandible.
Theosodon garrettorum
FMNH P 13175, skull.
Theosodon lallemanti
FMNH P 13187, skull poorly preserved with left P3–M3, and right P2–P3, M2–M3.
Theosodon gracilis
AMNH 9230, skull and incomplete mandible.
MACN-A 2521, lectotype, mandible with m1–m2? of both sides.
MACN-A 9297, right mandibular fragment with p1–m3.
Theosodon sp.
MLP 12-381, incomplete mandible with left i1–c, and right i1–p2, p4–m3.

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ARTÍCULO

REVISION OF THE MIOCENE CAVIOMORPH RODENTS FROM THE RÍO SANTA CRUZ (ARGENTINEAN PATAGONIA)

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Abstract. Fossil rodents from the Río Santa Cruz (RSC) classic localities (Santa Cruz Formation, Early–Middle Miocene) are known by the works of F. Ameghino and W.B. Scott since the end of the 19th and beginning of the 20th centuries. These caviomorph rodents have not been comprehensively reviewed since then. In this contribution, we studied new fossil specimens from the cliffs of the RSC (Province of Santa Cruz, Argentina) collected with accurate stratigraphic and geographic data during fieldtrips in 2013 and 2014. An increase in the caviomorph taxonomic richness is observed, based upon our taxonomic study of caviomorphs previously recorded in the RSC. Also, these fieldworks recovered for the first time several taxa previously found in other Santacrucian and even older Patagonian localities (Colhuehuapian, Early Miocene). As a general evolutionary pattern, we note an increase of derived euhypsodont taxa (*Prolagostomus*, *Pliolagostomus*, *Schistomys*, and *Eocardia*) in Segundas Barrancas Blancas (16.47–15.3 Ma). In addition, a taxonomic replacement of *Phanomys* by *Schistomys* is noted between Barrancas Blancas (17.21–16.3 Ma) and Segundas Barrancas Blancas, as well as a notably increase in the abundance of the large *Perimys onustus* in the latter locality. The present study provides a revision of the caviomorph systematics, and intends to be the starting point to understand the diversity (in all its aspects) and the evolution of this group during the Santacrucian, a major event in the South American mammalian history.

Key words. Santacrucian. Province of Santa Cruz. Hystricognathi. Taxonomy. Systematics. Biostratigraphy. Evolution.

Resumen. REVISIÓN DE LOS ROEDORES CAVIOMORFOS MIOCENOS DEL RÍO SANTA CRUZ (PATAGONIA ARGENTINA). Los roedores fósiles provenientes de localidades del Río Santa Cruz (RSC; Formación Santa Cruz, Mioceno Temprano–Medio) se conocen desde fines del siglo 19 y principios del 20, gracias a los trabajos de F. Ameghino y W.B. Scott. Sin embargo, no fueron estudiados a nivel integral desde ese momento. En este sentido, analizamos nuevos ejemplares recolectados en las barrancas del RSC (Santa Cruz, Argentina) durante los años 2013 y 2014 que cuentan con datos de procedencia estratigráfica y geográfica precisos. El estudio taxonómico permitió reconocer taxones previamente descriptos para el RSC, así como nuevos taxones conocidos en otras localidades santacrucenses o en localidades más antiguas de Patagonia (Colhuehuapense, Mioceno Temprano). Se corroboró un aumento en la riqueza taxonómica del conjunto de roedores del RSC. Como patrón evolutivo general, se observa un incremento de formas euhipsodontes derivadas (*Prolagostomus*, *Pliolagostomus*, *Schistomys*, *Eocardia*) en Segundas Barrancas Blancas (16,47–15,3 Ma). A su vez, observamos un reemplazo taxonómico de *Phanomys* por *Schistomys* desde la localidad de Barrancas Blancas (17,21–16,3 Ma) a Segundas Barrancas Blancas y un notable aumento en la abundancia de *Perimys onustus*, la especie más grande del género, en esta última localidad. El presente estudio es una puesta al día de la sistemática de los caviomorfos del RSC y pretende ser el punto de partida para entender la diversidad y la evolución de los caviomorfos durante el Santacrucense, un periodo crucial en la historia de los mamíferos sudamericanos.

Palabras clave. Santacrucense. Provincia de Santa Cruz. Hystricognathi. Taxonomía. Sistemática. Bioestratigrafía. Evolución.

CAVIOMORPHS are the endemic hystricognath rodents of Central and South America (Wood, 1955; Upham and Patterson, 2015). They constitute the most diverse group of rodents from a morphological and ecological point of view, and have a long evolutionary history during the Cenozoic (Vassallo and Antenucci, 2015; Vucetich *et al.*, 2015). The systematics and biology of extant taxa have been intensively studied and are relatively well-known (Álvarez *et al.*, 2011; Patton *et al.*, 2015; Vassallo and Antenucci, 2015). However, these aspects still require intensive study in fossils. In this regard, the Early Miocene represents a crucial moment in the evolutionary history of caviomorphs since the fossil record indicates that Santacrucian rodents were a critical part of an important caviomorph diversification (Pérez and Pol, 2012;

Arnal and Vucetich, 2015a; but see Verzi *et al.*, 2014). The Early–Middle Miocene of Patagonia (Colhuehuapian, "Pinturan", Santacrucian, and "Colloncuran" South American Land Mammal Ages, SALMA), has yielded an excellent record of mammals (*e.g.*, Ameghino, 1887a,b, 1889; Scott, 1905; Kramarz, 2001, 2002, 2004, 2006a,b; Kramarz *et al.*, 2010, 2013; Pérez, 2010a; Pérez *et al.*, 2010; Vucetich *et al.*, 2010; Pérez and Vucetich, 2012; Vizcaíno *et al.*, 2012a; Arnal and Pérez, 2013; González Ruiz *et al.*, 2013, 2017; Brandoni *et al.*, 2017, 2019; Vera *et al.*, 2017, 2018; Busker *et al.*, 2018; Rasia and Candela, 2019). In particular, the Santa Cruz Formation (Early–Middle Miocene; Santacrucian) is widely distributed in the Province of Santa Cruz, Argentina (Fig. 1; Cuitiño *et al.*, 2016, 2019). It is one of the richest Cenozoic vertebrate fossil units bearing abundant and well-preserved specimens. Caviomorphs recorded in the cliffs of the classic localities of the Río Santa Cruz (RSC; Fig. 1) were first studied by F. Ameghino (1887a,b, 1889, 1891a,b, 1894) who erected 23 caviomorph genera and 45 species (Tab. 1). These rodents were later revised by Scott (1905) who described new species from other Santacrucian localities of the Province of Santa Cruz (Fig. 1), but no new caviomorph genera were identified. In this regard, Scott (1905, p. 384) stated: "*It must not be supposed that the full number of Santa Cruz genera has been already discovered, though it is improbable that the list will be very greatly extended in the future*". Since that time, several other Santacrucian-age localities have been identified at high and middle latitudes of South America. However, caviomorphs have been listed or mentioned in only some of them: coastal localities in the Province of Santa Cruz (Tauber, 1997; Candela *et al.*, 2012), Las Hornillas, Province of San Juan, Argentina (López *et al.*, 2011), Alto Río Cisnes (Marshall and Salinas, 1990), Pampa Castillo (Flynn *et al.*, 2002), Laguna del Laja (Flynn *et al.*, 2008), and Sierra Baguales (Bostelmann *et al.*, 2013) of southern Chile, and Chucal of northern Chile (Croft *et al.*, 2004). In agreement with Scott's conclusion, almost no new taxa were formally recognized since Ameghino's work (but see Arnal and Vucetich, 2015b).

Santacrucian rodents are very abundant in number of specimens but relatively homogeneous in their morphological disparity (Scott, 1905; Vucetich *et al.*, 2015). When compared with rodents from the lower and middle sequences of the Pinturas and Sarmiento formations ("Pinturan" and Colhuehuapian SALMAS, Early Miocene), those from beds of the Santa Cruz Formation show some differences. Santacrucian octodontoids are characteristically more hypsodont and more lophate than their predecessors; euhypsodont cavioids predominate for the first time; erethizontoids are less abundant and less diverse, and chinchilloids reach their greatest diversity (Vucetich *et al.*, 2015, and literature therein). The dental changes toward increasing hypsodonty and trend towards more simplified occlusal surfaces were traditionally related to the environmental and climatic changes that occurred since the Late Eocene–Early Oligocene, which were more marked in Patagonia at that time (Pascual *et al.*, 1996; Zachos, 2001; Ortiz Jaureguizar and Cladera, 2006; Madden, 2015; Vizcaíno *et al.*, 2012a).

Despite the importance of this rodent fauna owing to their excellent fossil record and widespread geographical distribution, no comprehensive studies of the caviomorph assemblages either from the RSC or from other Santacrucian localities have been performed to date. Only partial revisions or isolated studies of specimens from different Santacrucian localities have been published (Pérez, 2010b; Arnal, 2012; Pérez and Vucetich, 2012; Arnal and Vucetich, 2015b; Arnal *et al.*, 2017).

A particular problem of this fauna is that the abundant fossil remains found by Carlos Ameghino in the RSC and other localities lack accurate geographic and stratigraphic data, which makes comparisons between localities and biostratigraphic correlations difficult (Fernicola *et al.*, 2019). Since those first collections, almost no new intensive field work had been made to remedy this deficiency. At the beginning of the 21th century a group of scientists headed by Drs. S.F. Vizcaíno, M.S. Bargo (Museo de La Plata, MLP), R.F. Kay (Duke University, USA), and J.C. Fernicola (Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"), launched a project focused on the Santa Cruz rocks (Santa Cruz Formation, Early–Middle Miocene) cropping out along the Atlantic coast of the Province of Santa Cruz, and along the cliffs on the southern bank of the RSC. Within this project, numerous new specimens with good stratigraphic provenance were collected (Vizcaíno *et al.*, 2012a; Fernicola *et al.*, 2014, 2019; Cuitiño *et al.*, 2016), which considerably

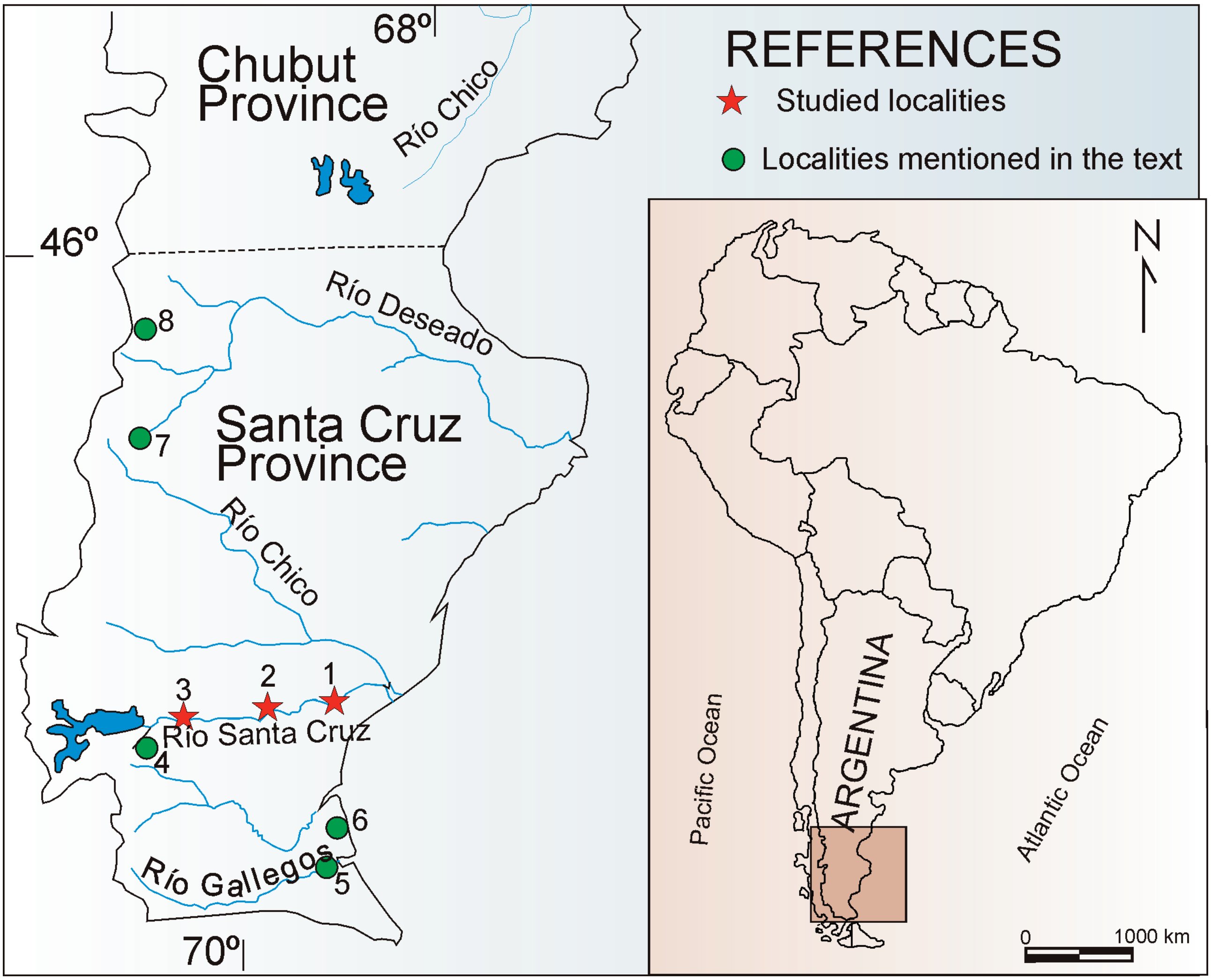


Figure 1. Location map showing the Santacrucian and other localities mentioned in the text. **1,** Barrancas Blancas **(BB)**; **2,** Segundas Barrancas Blancas **(SBB)**; **3,** Yaten Huageno **(YH)**; **4,** Río Bote; **5,** Killik Aike; **6,** Guer Aike; **7,** río Pinturas area; **8,** río Jeinemeni area.

enlarge the Santacrucian caviomorph collections and allow integral studies of the whole Santacrucian assemblage to be performed. Furthermore, on the basis of a systematic revision and owing to the precise provenance data, different Santacrucian localities bearing rodents can now be harnessed in the search for evolutionary trends related to climatic and environmental changes. In this contribution, a revision of the caviomorph rodents from the Santa Cruz Formation at the RSC is performed, including new specimens. Their taxonomic richness is compared with those from other Santacrucian localities of the Province of Santa Cruz (Scott, 1905; Candela *et al.*, 2012; Fernicola *et al.*, 2019). Additionally, general evolutionary trends of the group are also discussed.

MATERIALS AND METHODS

More than 750 fossil specimens (Appendix 1) housed at the Vertebrate Paleontology Collection of the Museo Regional Provincial "Padre Manuel Jesús Molina" (MPM-PV) were studied. Several Santacrucian caviomorphs specimens were used for comparison, mainly those housed at the American Museum of Natural History (AMNH), New York, USA; Field Museum of Natural History (FMNH), Chicago, USA; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ameghino National Collection (MACN-A), Buenos Aires, Argentina; Museo de La Plata, La Plata, Argentina (MLP); Museum National d'Histoire Naturelle (MNHN), Paris, France; Museo Paleontológico Egidio Feruglio (MPEF-PV),

TABLE 1 - Caviomorph rodents from the Río Santa Cruz described by Ameghino

Ameghino, 1887a	*Ameghino, 1887b*	*Ameghino, 1889*	*Ameghino,1891a,b*	*Ameghino, 1902*	*Current taxonomy*
Acaremys murinus					Acaremys murinus[1]
		Acaremys messor			Acaremys messor[1]
Acaremys minutus					Acarechimys minutus[2]
Acaremys minutissimus					Acarechimys minutissimus[2]
Sciamys principalis					Sciamys principalis
Sciamys varians					Sciamys varians
Adelphomys candidus					Adelphomys candidus
Stichomys regularis					Stichomys regularis
Stichomys constans					Acarechimys constans[2]
Spaniomys riparius					Spaniomys riparius
Spaniomys modestus					Spaniomys modestus
					Acarechimys gracilis[2]
					Pseudoacaremys kramarzii[1]
					Sciamys latidens[3]
					Dudumus *sp. nov.?*[3]
					Prospaniomys *sp. nov.?*[3]
Steiromys detentus					Steiromys detentus
Steiromys duplicatus					Steiromys duplicatus
Neoreomys australis					Neoreomys australis[4]
Neoreomys indivisus					
Neoreomys decisus					
		Neoreomys insulatus[4]			
	Eocardia montana				Eocardia montana[5]
Eocardia divisa					
Eocardia perforata					
			Dicardia excavata[b]		"Eocardia" excavata[5]
			Eocardia fissa[a]		"Eocardia" fissa[5]
Schistomys erro					Schistomys erro
Phanomys mixtus					Phanomys mixtus
			Phanomys vetulus[a]		Phanomys vetulus
Hedymys integrus					*Nomen nudum*[6]
Perimys erutus					Perimys erutus[7]
		Perimys procerus			
Sphodromys scalaris					
Perimys onustus					Perimys onustus
			Perimys planaris[a]		
				Perimys incavatus	Perimys incavatus[3]
Sphiggomys zonatus					Perimys zonatus[8]
		Olenopsis uncinus[9]			
Prolagostomus pusillus					Prolagostomus pusillus[10]
Prolagostomus divisus					
Prolagostomus profluens					
Prolagostomus imperialis					
		Lagostomus lateralis			
		Lagostomus primigenius			
Sphaeromys irruptus[11]					
Scotaeumys imminutus[12]					
Pliolagostomus notatus					Pliolagostomus notatus[13]
Scleromys angustus					Scleromys angustus
Calladontomys vastatus					*Nomen dubium*[14]

[1]*Arnal and Vucetich (2015b);* [2]*Arnal* et al. *(2017);* [3]*this work;* [4]*Kramarz (2006b);* [5]*Pérez (2010b);* [6]sensu *Wood and Patterson (1959);* [7]*Kramarz (2002);* [8]*Ameghino (1894) transferred this species to* **Perimys zonatus**; [9]*Candela and Nasif (2006) synonymized this species with* **Neoreomys**; [10]*Rasia (2016);* [11]*Scott (1905) synonymized this species with* **Prolagostomus pusillus**; [12]*Kramarz (2002) synonymized this species with* **Prolagostomus**; [13]*Rasia and Candela (2019);* [14]*Mones.*

Trelew, Argentina; and Princeton University Collection of the Yale Peabody Museum (YPM-PU), New Haven, USA.

Caviomorph systematics follow Pérez (2010a,b), Arnal (2012), Arnal and Vucetich (2015b), Rasia (2016), and references in Table 1.

The studied localities along the southern banks of the RSC are, from East to West (Fernicola *et al.*, 2014; Cuitiño *et al.*, 2016, 2019) (Fig. 1): Barrancas Blancas (BB; 17.21–16.3 Ma), with two sites, Estancia Aguada Grande (EAG) and Estancia Santa Lucía (ESL); Segundas Barrancas Blancas (SBB; 16.47–15.3 Ma), with three sites, Estancia Cordón Alto1 (ECA), Estancia Cordón Alto2 (ECA2), and Estancia el Tordillo (EET); Yaten Huageno (YH; 17.21–16.68 Ma) with one site, Estancia El Refugio (EER).

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Suborder HYSTRICOGNATHI Tullberg, 1899
Superfamily OCTODONTOIDEA Waterhouse, 1839

Genus ***Spaniomys*** Ameghino, 1887a

Type species. *Spaniomys riparius* Ameghino, 1887a. Pinturas Formation, Early Miocene and Santa Cruz Formation, Early–Middle Miocene, Province of Santa Cruz.

Spaniomys riparius Ameghino, 1887a

Referred materials. See Appendix 1.
Locality and Horizon. See Appendix 1.

Spaniomys sp.
Figure 2.1–4

Referred materials. See Appendix 1.
Locality and Horizon. See Appendix 1.
Comments. *Spaniomys* is characterized by being higher crowned than *Acaremys* Ameghino, 1887a and *Acarechimys* Patterson in Kraglievich, 1965. Cheek teeth have planar occlusal surfaces and undifferentiated cusps (Fig. 2.1–3), unlike *Acarechimys*, but resembling *Adelphomys* Ameghino, 1887a and *Stichomys* Ameghino, 1887a. This genus retains the deciduous premolar through life, unlike acaremyids (= *Acaremys*, *Sciamys* Ameghino, 1887a, *Pseudoacaremys* Arnal and Vucetich, 2015b, *Galileomys* Vucetich and Kramarz, 2003, and *Platypittamys* Wood, 1949; Arnal and Vucetich 2015b). Lophs and lophids are thin with pointed labial and lingual ends respectively, unlike *Adelphomys* and *Stichomys*. Lower cheek teeth have four lophids (MPM-PV 20178; Fig. 2.1–2) and upper cheek teeth have four (MPM-PV 20310; Fig. 2.3) or five lophs.

Ameghino recognized three species: *S. riparius*, *S. modestus* Ameghino, 1887a, and *S. biplicatus* Ameghino, 1894 that differ in size and in the number of flexi on lower cheek teeth. However, size differences are not great. In this work, several well-preserved specimens were recognized as *S. riparius* owing to their slightly larger size (MPM-PV 20115, MPM-PV 20524, MPM-PV 20557; Appendix 1; Tab. 2), but most of them (Fig. 2.1–4) were recognized as *Spaniomys* sp. (MPM-PV 20562; MPM-PV 20618; MPM-PV 20770; Appendix 1; Tab. 2) until a systematic revision is performed. Within the new rodents sample, *Spaniomys* is present and abundant in EAG and ESL (BB) and ECA, ECA2, and EET (SBB). In EER (YH) rodents are very scarce, but it is represented by one specimen (MPM-PV 20770; Tab. 2).

Genus ***Stichomys*** Ameghino, 1887a

Type species. *Stichomys regularis* Ameghino, 1887a. Pinturas Formation, Early Miocene, and Santa Cruz Formation, Early–Middle Miocene, Province of Santa Cruz; Río Frías Formation, Middle Miocene, Province of Chubut.

Stichomys regularis Ameghino, 1887a
Figure 2.5–6, 9–10

Referred materials. See Appendix 1.
Locality and Horizon. See Appendix 1.

Stichomys sp.
Figure 2.7–8

Referred materials. See Appendix 1.
Locality and Horizon. See Appendix 1.

Stichomys? sp.

Table 2 - Caviomorph rodents reported in this contribution with a comparison of the taxonomic richness between the Río Santa Cruz localities

Taxa		*n*	*BB*	*n*	*SBB*	*n*	*YH*
Octodontoidea	**Spaniomys riparius**	*X*	*1*	*X*	*6*		
	Spaniomys *sp.*	*X*	*18*	*X*	*38*	*X*	*1*
	Stichomys regularis			*X*	*14*	*X*	*1*
	Stichomys *sp.*	*X*	*7*	*X*	*28*		
	Acarechimys minutus			*X*	*5*		
	Acarechimys minutissimus	*X*	*1*	*X*	*14*		
	Acarechimys constans			*X*	*7*		
	Acarechimys gracilis			*X*	*6*		
	Dudumus *sp. nov.?*			*X*	*1*		
	Prospaniomys *sp. nov.?*	*X*	*1*	*X*	*2*		
	Acaremys murinus			*X*	*2*		
	Acaremys *sp.*	*X*	*2*	*X*	*1*		
	Sciamys principalis	*X*	*2*	*X*	*10*		
	Sciamys latidens			*X*	*1*		
	Sciamys *sp.*	*X*	*1*	*X*	*4*		
Erethizontoidea	**Steiromys detentus**	*X*	*1*	*X*	*5*		
	Steiromys duplicatus	*X*	*11*	*X*	*1*		
	Steiromys *sp.*	*X*	*2*				
Cavioidea	**Neoreomys australis**	*X*	*51*	*X*	*66*	*X*	*1*
	Phanomys mixtus	*X*	*13*				
	Phanomys *sp.*			*X*	*4*		
	Eocardia montana	*X*	*8*	*X*	*22*		
	"Eocardia" excavata	*X*	*5*	*X*	*4*		
	Eocardia *sp.*	*X*	*22*	*X*	*32*		
	Schistomys erro			*X*	*3*		
Chinchilloidea	**Prolagostomus pusillus**			*X*	*34*		
	Prolagostomus *sp.*	*X*	*2*	*X*	*80*		
	Pliolagostomus notatus			*X*	*37*		
	Perimys erutus	*X*	*11*	*X*	*3*		
	Perimys onustus	*X*	*1*	*X*	*23*		
	Perimys incavatus	*X*	*1*				
	Perimys *sp.*	*X*	*7*	*X*	*6*		
	Scleromys *sp.*	*X*	*8*	*X*	*4*		

*BB, barrancas Blancas; SBB, Segundas Barrancas Blancas; YH, Yaten Huageno; n, number of specimens (see Appendix 1). *Dubious taxa (?) are not included in the table.*

Referred materials. See Appendix 1.

Locality and Horizon. See Appendix 1.

Stichomys sp./***Adelphomys*** sp.

Referred materials. See Appendix 1.

Locality and Horizon. See Appendix 1.

Comments. *Stichomys* is characterized by being relatively high-crowned, resembling *Adelphomys* and *Spaniomys* in this respect. It has derived cheek teeth with planar occlusal surfaces, undifferentiated cusps, and retention of the deciduous premolars through life (Fig. 2.5–10), also as in *Adelphomys* and *Spaniomys*. Nevertheless, their cheek teeth have broader lophs/ids with rounded end tips (Fig. 2.5–7 and 2.9), as *Adelphomys* and unlike *Spaniomys*. Upper molars with four lophs and lowers with three main lophids, as in *Adelphomys* and *Spaniomys*. *Adelphomys* is very similar to *Stichomys*. The two genera differ in that the former has planar anterior face on the incisors and the latter convex ones (Ameghino, 1887a). In general terms, *Stichomys* is more abundant than *Adelphomys* (convex incisors are more abundant than planar incisors; see Appendix 1). Nevertheless, in the new rodent collection several specimens have no incisors preserved, and thus, they could not be recognized at generic level. These specimens were referred to as *Stichomys* sp./*Adelphomys* sp. (MPM-PV 20356, MPM-PV 20550; Appendix 1).

Seven species of *Stichomys* were described (Ameghino, 1887a, 1891a). Three of them were transferred to *Acarechimys* (Arnal *et al.*, 2017). The remaining species require taxonomic revision. At present, we recognize several large and well-preserved specimens as *S. regularis* (Fig. 2.5–6, 9–10), but the remaining specimens only as *Stichomys* sp. (MPM-PV 20415; Fig. 2.7–8).

Within the new rodent sample *Stichomys* is the most abundant octodontoid with more than 60 specimens (Appendix 1). We identified *Stichomys regularis*, *Stichomys* sp., *Stichomys* sp./*Adelphomys* sp., and *Stichomys*? sp. (Appendix 1). These taxa are more abundant in ECA, ECA2, and EET (SBB), while in BB (ESL and EAG) they are only represented by three specimens recognized as *Stichomys* sp. (Tab. 2). In EER (YH) there is one specimen recognized as *Stichomys regularis* (MPM-PV 20771). The phylogenetic relationships of *Stichomys* and *Adelphomys* are not clear. Based on the dental morphology they have been included in "Adelphomyinae", an echimyid fossil lineage (Wood and Patterson, 1959; Kramarz, 2001). Nevertheless, most phylogenetic analyses (Arnal *et al.*, 2014; Arnal and Vucetich, 2015a; Verzi *et al.*, 2014) do not recover this clade. In fact, both *Stichomys* and *Adelphomys*, together with *Spaniomys* and other fossil octodontoids (*i.e.*, *Eodelphomys* Frailey and Campbell, 2004 from the late Eocene? of Peru and *Xylechimys* Patterson and Pascual, 1968 from the late Oligocene of Patagonia), represent a basal radiation of crown-octodontoids (Arnal and Vucetich, 2015a).

Genus ***Acarechimys*** Patterson in Kraglievich, 1965

Type species. *Acaremys minutus* Ameghino, 1887a. Santa Cruz Formation, Early–Middle Miocene, Province of Santa Cruz; Collon Curá Formation, early Middle Miocene, Province of Neuquén; unnamed formation, late Middle Miocene, Quebrada Honda, Bolivia.

Acarechimys minutus (Ameghino, 1887a)

Figure 2.11–13

Referred materials. See Appendix 1.
Locality and Horizon. See Appendix 1.

Acarechimys minutissimus (Ameghino, 1887a)

Referred materials. See Appendix 1.
Locality and Horizon. See Appendix 1.

Acarechimys constans (Ameghino, 1887a)

Referred materials. See Appendix 1.
Locality and Horizon. See Appendix 1.

Acarechimys gracilis (Ameghino, 1891)

Figure 2.14–15

Referred materials. See Appendix 1.
Locality and Horizon. See Appendix 1.
Comments. *Acarechimys* was a successful evolutionary lineage of octodontoids with brachydont cheek teeth, thin loph/lophids, and identifiable cusps, unlike *Stichomys*, *Adelphomys*, and *Spaniomys*. It retained the deciduous premolars through life (Fig. 2.11, 14), unlike acaremyids. Upper cheek teeth have four lophs (Fig. 2.11) and lowers have three main lophids with another variably developed (Fig. 2.14; Arnal *et al.*, 2017). This genus represents the octodontoid with the widest temporal (Late Oligocene–Late Miocene) and geographic distribution (southern Argentinean Patagonia to Colombia), reaching its maximum recorded diversity in the Santacrucian (Arnal *et al.*, 2017). Five species are recognized: *A. leucotheae* Vucetich *et al.*, 2014 (Late Oligocene, Province of Chubut), *A. minutus*, *A. minutissimus* (Early–Middle Miocene of Argentinean Patagonia, Bolivia, and Colombia), *A. constans* and *A. gracilis* (Early–Middle Miocene, provinces of Chubut and Santa Cruz, Argentina). For detailed descriptions of the species see Arnal *et al.* (2017).

Acarechimys is represented in all the stratigraphic levels of SBB (Appendix 1). Four of the five known species are recorded: *A. minutus* (MPM-PV 15088, MPM-PV 15089; Fig. 2.11–13), *A. minutissimus* (MPM-PV 15100, MPM-PV 20069, MPM-PV 20346; see Appendix 1), *A. constans* (MPM-PV 15093, MPM-PV 15096, MPM-PV 20637; see Appendix 1), and *A. gracilis* (MPM-PV 17430; Fig. 2.14–15). On the other hand, only one specimen of *A. minutissimus* is recorded in BB (MPM-PV 20069; EAG-80 mts) and none in YH.

Genus ***Dudumus*** Arnal *et al.*, 2014

Type and only species. *Dudumus ruigomezi* Arnal *et al.*, 2014. Sarmiento Formation, Trelew Member, Early Miocene, Province of Chubut.

Dudumus sp. nov.?

Figure 2.16

Referred material. MPM-PV 20561, right M1-M2.

Locality and horizon. Segundas Barrancas Blancas (ECA2), Río Santa Cruz, Province of Santa Cruz, Early–Middle Miocene.

Comments. One small maxillary fragment with M1-M2 is here assigned to *Dudumus* sp. nov.? The molars are bunolophodont, brachydont, and slightly terraced (Fig. 2.16), as in *Dudumus ruigomezi* and *Caviocricetus* Vucetich and Verzi, 1996. As in *Dudumus ruigomezi* and *Caviocricetus*, the third loph, interpreted as a mesolophule, is shorter than the remaining lophs and does not reach the metacone. The length of this crest and the degree of terracing in the molars are more similar in these respects to *Dudumus ruigomezi* than to *Caviocricetus*. Nevertheless, the new specimen has different teeth proportions and therefore is here interpreted as a possible new species.

MPM-PV 20561 (Fig. 2.16) was found in ECA2 of SBB locality (Tab. 2). It represents the first record of *Dudumus* for the Santa Cruz Formation, since it was previously known for Colhuehuapian (Early Miocene) of the Province of Chubut.

Genus ***Prospaniomys*** Ameghino, 1902

Type species. *Prospaniomys priscus* Ameghino, 1902. Sarmiento Formation, Early Miocene, Province of Chubut.

Prospaniomys sp. nov.?

Figure 2.17–18

Referred materials. See Appendix 1.

Locality and horizon. Barrancas Blancas (ESL) and Segundas Barrancas Blancas (ECA2), Río Santa Cruz, Province of Santa Cruz, Early–Middle Miocene.

Comments. Three bunolophodont specimens are identified as *Prospaniomys* sp. nov.? MPM-PV 20294 (Fig. 2.17) is a right maxillary fragment with DP4-M1 and MPM-PV 20560 is an isolated upper molar. These cheek teeth have four lophs of which the anterior most (= anteroloph) does not contact the paracone and the third and fourth lophs are labially fused to the metacone, delimiting a posterior fossette (Fig. 2.17), unlike *Protacaremys* Ameghino, 1902. MPM-PV 20207 (Fig. 2.18) is an isolated lower molar that has four thin lophids and acuminated labial cuspids, as in *Prospaniomys priscus* and unlike *Protacaremys*. Nevertheless, these specimens seem to be a new species since they are smaller than the type species and have slightly higher crowns.

These new findings are remarkable since *Prospaniomys* was previously only recognized in Colhuehuapian sediments (Early Miocene) of the Province of Chubut. MPM-PV 20207 was recorded in ESL (BB); and MPM-PV 20294 and MPM-PV 20560 were found in ECA2 from SBB (Tab. 2; Appendix 1).

Family Acaremyidae Wood, 1949

Genus ***Acaremys*** Ameghino, 1887a

Type species. *Acaremys murinus* Ameghino, 1887a. Sarmiento Formation, Colhue Huapi Member, Early Miocene, Province of Chubut; Pinturas Formation, upper sequence, late Early Miocene, and Santa Cruz Formation, Early–Middle Miocene, Province of Santa Cruz.

Acaremys murinus Ameghino, 1887a

Referred materials. See Appendix 1.

Locality and Horizon. See Appendix 1.

Acaremys sp.

Referred material. See Appendix 1.

Locality and Horizon. See Appendix 1.

Comments. *Acaremys*, *Sciamys* and other octodontoids are grouped within Acaremyidae, the only extinct octodontoid family recognized (Arnal and Vucetich, 2015b). *Acaremys* is lower-crowned than *Sciamys* and higher-crowned than *Galileomys* and *Platypittamys*. Cheek teeth have discernible cusps, relatively thin lophs/ids, and replace the deciduous premolars with age, unlike most fossil octodontoids. Upper and lower molars have four main lophs/ids, unlike *Acarechimys*. *Acaremys* is recognized by three valid species: *A. murinus*, *A. messor* Ameghino, 1889 and *A. major* Scott, 1905 (Early–Middle Miocene, Province of Santa Cruz). For a detailed description of these species see Arnal and Vucetich (2015b).

Within the new rodent sample, *Acaremys* is represented in ESL from BB by *Acaremys* sp. (MPM-PV 20175, MPM-PV 20216; Tab. 2); in SBB by *A. murinus* in ECA (MPM-PV 20272) and ECA2 (MPM-PV 20538), and by *Acaremys* sp. in ECA2 (MPM-PV 20653) (Tab. 2).

Genus ***Sciamys*** Ameghino, 1887a

Type species. *Sciamys principalis* Ameghino, 1887a. Pinturas Formation, upper sequence, late Early Miocene and Santa Cruz Formation, Early–Middle Miocene, Province of Santa Cruz.

Sciamys principalis Ameghino, 1887a
Figure 2.19–20

Referred materials. See Appendix 1.

Locality and horizon. See Appendix 1.

Sciamys latidens Scott, 1905
Figure 2.21–22

Referred material. MPM-PV 20668, right mandible with p4-m2.

Locality and horizon. Segundas Barrancas Blancas (ECA2), Río Santa Cruz, Province of Santa Cruz. Early–Middle Miocene.

Sciamys sp.

Referred materials. See Appendix 1.

Locality and horizon. See Appendix 1.

Comments. *Sciamys* is similar to *Acaremys*, but differs in having higher crowns and less discernible cusps. As in *Acaremys*, it has upper and lower molars with four lophs/ids and replaces the deciduous premolar through life. *Sciamys* is more abundant than *Acaremys* (Appendix 1) and it is recognized by at least six species: *S. principalis*, *S. varians* Ameghino, 1887a, *S. robustus* Ameghino, 1894, *S. rostratus* Scott, 1905, *S. latidens* Scott, 1905 (Early–Middle Miocene, Province of Santa Cruz), and *S. petisensis* Arnal and Pérez, 2013 (Middle–Late Miocene, Province of Chubut).

Within the new rodent sample, the genus is present but scarce at EAG (*Sciamys principalis* and *Sciamys* sp.) of BB, but absent in ESL (Tab. 2). On the contrary, it is very abundant in SBB, especially in ECA2 where *S. principalis, S. latidens*, and *Sciamys* sp. have been identified (Tab. 2; Appendix 1). The genus is absent in YH. A notably new record for the RSC is the presence of *Sciamys latidens* in ECA2 (MPM-PV 20668; Fig. 2.19–20). This species is well-characterized by having a molarized posterior portion of the p4 (Fig. 2.19), as in *Sciamys petisensis* and unlike all the remaining Early Miocene species, and was previously known only for Killik Aike, coastal Santa Cruz Province, Argentina (Scott, 1905; Fig. 1).

Several specimens could not be recognized at generic level and are listed as Acaremyidae (Appendix 1).

Superfamily ERETHIZONTOIDEA Simpson, 1945
Family ERETHIZONTIDAE Thomas, 1897

Genus ***Steiromys*** Ameghino, 1887a

Type species. *Steiromys detentus* Ameghino, 1887a. Santa Cruz Formation, Early–Middle Miocene, Province of Santa Cruz.

Steiromys detentus Ameghino, 1887a
Figure 3.23–24

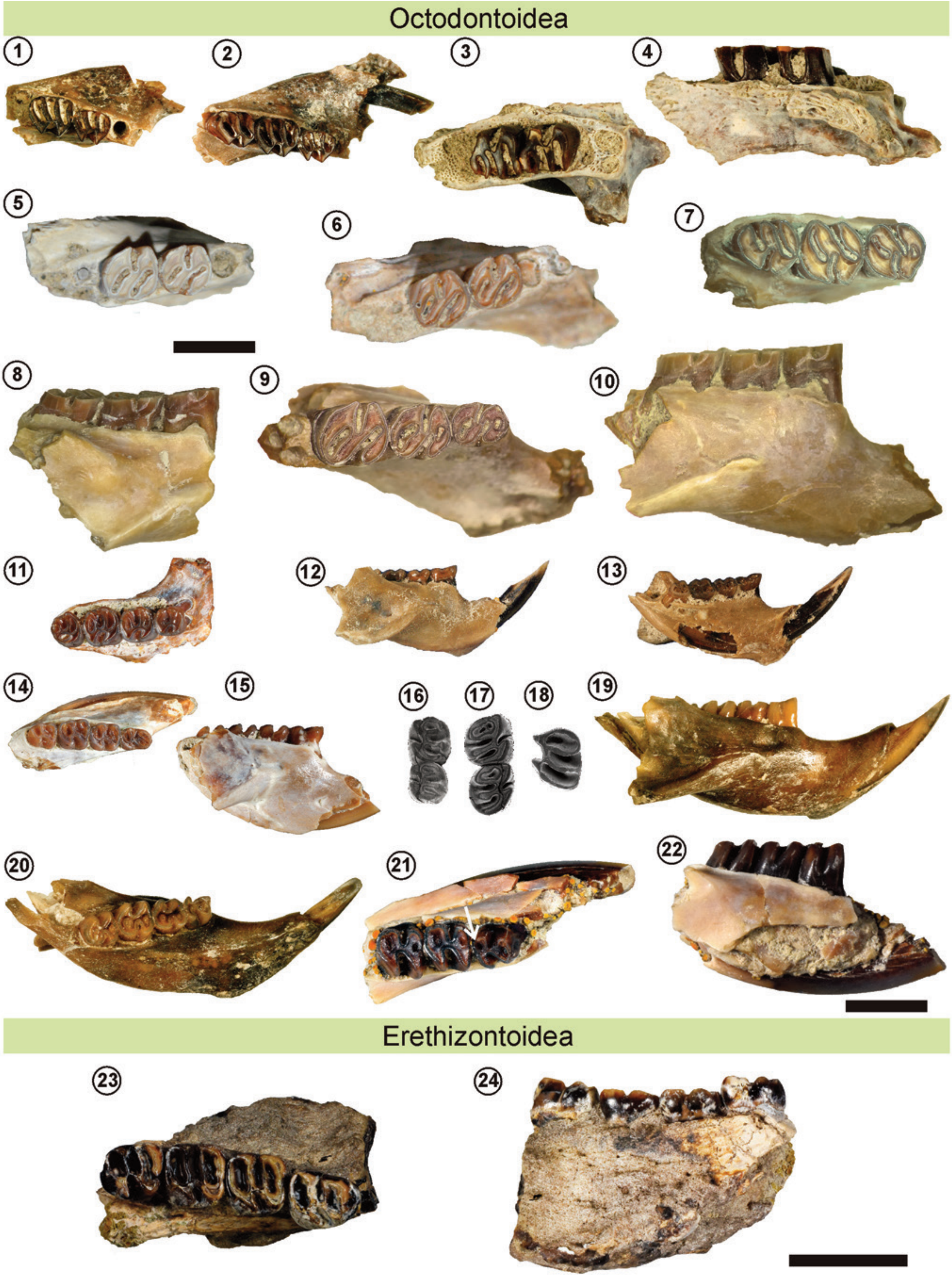
Referred materials. See Appendix 1.

Locality and horizon. See Appendix 1.

Steiromys duplicatus Ameghino, 1887a

Referred material. see Appendix 1.

Locality and horizon. See Appendix 1.


Octodontoidea
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Erethizontoidea
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***Steiromys duplicatus*?**

***Referred materials*. See Appendix 1.**
***Locality and horizon*.** See Appendix 1.

***Steiromys* sp.**

***Referred materials*.** See Appendix 1.
***Locality and horizon*.** See Appendix 1.
***Comments*.** Erethizontids are medium-size caviomorphs. Extant and fossil erethizontids have generally conservative skull and dental morphologies, with low-crowns and bunolophodont to lophodont cheek teeth (Patton *et al*., 2015). They replace the deciduous premolars, with the exception of the extant *Chaetomys* Gray, 1843 (Patterson and Wood, 1982). In occlusal view the dentine in erethizontids has very thin enamel (Fig. 2.23), unlike octodontoids. Laterally, the molar crowns are bulging (Fig. 2.24). *Steiromys* is slightly higher-crowned than *Eosteiromys* Ameghino, 1902.

Within the new rodent sample, *Steiromys detentus* was found in EAG (MPM-PV 20058) from BB, and ECA (MPM-PV 20384) and ECA2 (MPM-PV 20598; MPM-PV 20652) from SBB (Tab. 2; Appendix 1). Upper molars have four main lophs and relatively well-individualized cusps (MPM-PV 20058). Lower cheek teeth have four lophids that wear the two anterior and the two posterior ones delimiting an anterior and posterior fossettid (Fig. 2.23). Molars are rectangular. The p4 is relatively longer than the molars, the anterior portion is labio-lingually shorter, and can bear four (MPM-PV 20442; Fig. 2.23) or five lophids (MPM-PV 20384). The incisors are robust with a plane anterior face. *Steiromys duplicatus* is less abundant, but was also recorded in EAG (MPM-PV 20086–20095) from BB, and in ECA2 (MPM-PV 20630) from SBB (Appendix 1). This species differs from *S. detentus* in having five lophs in upper (MPM-PV 20087; MPM-PV 20630) and lower (MPM-PV 20094) molars.

Several broken teeth were recognized as *Steiromys* sp. in BB (MPM-PV 20096, MPM-PV 20097; Tab. 2; Appendix 1).

Superfamily CAVIOIDEA (Fischer de Waldheim, 1817)

Genus ***Neoreomys*** Ameghino, 1887a

***Type species*.** *Neoreomys australis* Ameghino, 1887a. Santa Cruz Formation, Early–Middle Miocene, Province of Santa Cruz.

Neoreomys australis Ameghino, 1887a

Figure 3.1–3

***Referred materials*.** See Appendix 1.
***Locality and horizon*.** See Appendix 1.
***Comments*.** *Neoreomys* is traditionally characterized by having hypsodont and rooted cheek teeth, more high crowned than in *Dasyprocta* Illiger, 1811, *Myoprocta* Thomas, 1903, *Asteromys* Ameghino, 1897, and *Luantus initialis* Ameghino, 1902. Cheek teeth have more penetrating flexus/id with persistent fossettes/ids: the hypoflexus is joined to the paraflexus and the hypoflexid joined to a posteroflexid (Fig. 3.1). The enamel is continuous around the entire crown and cementum is present in the hypoflexus/id.

Ameghino recognized nine species of *Neoreomys* from the Santa Cruz Formation (Ameghino, 1887a; 1891; 1894). Scott (1905) considered only three of those to be valid. Fi-

Figure 2. Octodontoidea (**1–22**) and Erethizontoidea (**23–24**). **1–4, *Spaniomys*** sp.; **1, MPM-PV 20182,** right mandibular fragment with m1-m2 in occlusal view; **2, MPM-PV 20178,** left mandible with m1-m3 and incisor in occlusal view (inverted); **3–4, MPM-PV 20310,** left maxillary fragment with M1-M2 (inverted) in occlusal (3) and lingual (4) views; **5–6, *Stichomys regularis***; **5, MPM-PV 20237,** left mandibular fragment with m1-m2; **6, MPM-PV 20276,** left mandibular fragment with m1-m2; **7–8, *Stichomys*** sp., **MPM-PV 20415,** left mandible with m1-m3 in occlusal (7) and labial (8) views; **9–10, *Stichomys regularis*, MPM-PV 20444,** left mandible (inverted) in occlusal and ventral views; **11–13, *Acarechimys minutus***; **11, MPM-PV 15088,** left maxilla with DP4-M3 in occlusal view (inverted); **12–13, MPM-PV 15089,** right mandible in labial (12) and lingual (13) views; **14–15, *Acarechimys gracilis*, MPM-PV 17430,** left mandible with dp4-m3 (inverted) in occlusal (14) and labial (15) views; **16, *Dudumus*** sp. nov.? **MPM-PV 20561,** right DP4-M1; **17–18, *Prospaniomys*** sp. nov.?; **17, MPM-PV 20294,** right DP4-M1; **18, MPM-PV 20207,** left lower molar; **19–20, *Sciamys principalis*, MPM-PV 20308,** right mandible with p4-m3; **21–22, *Sciamys latidens*, MPM-PV 20668,** right mandible with p4-m2; **23–24, *Steiromys detentus* MPM-PV 20442,** right mandible in occlusal (23) and lingual (24) views. Anterior to right. Scale bars= 5 mm (**1–15, 19–22**), 1 mm (**16–18**), and 10 mm (**23–24**).

nally, Fields (1957) and later authors (*e.g.*, Kramarz and Bellosi, 2005; Kramarz, 2006b; Pérez, 2010b; Vucetich *et al.*, 2015) recognized *Neoreomys australis* as the sole species present in the Santa Cruz Formation. Other two species of *Neoreomys* have been described elsewhere in South America: *Neoreomys huiliensis* Fields, 1957 from Villavieja Formation (La Venta, Colombia) and *N. pinturensis* Kramarz, 2006b from the Pinturas Formation (Province of Santa Cruz, Argentina). *Neoreomys australis* is the largest and most abundant caviomorph (more than 120 specimens; see Appendix 1). An exhaustive revision of this genus (currently under study by MEP) is necessary to corroborate the taxonomic status of the species of *Neoreomys*, and its specific richness in the Santa Cruz Formation. Within the new rodent sample, *Neoreomys* is the only cavioid present in YH, the oldest locality (Tab. 2). Moreover, this genus is well-represented in the other localities of the SCR: EAG and ESL from BB, and ECA, ECA2, and EET from SBB (Tab. 2; Appendix 1).

Genus **Phanomys** Ameghino, 1887a

Type species. *Phanomys mixtus* Ameghino, 1887a. Río Jeinemení Formation, Pinturas Formation and Santa Cruz Formation, Early–Middle Miocene, Province of Santa Cruz.

Phanomys mixtus Ameghino, 1887a

Figure 3.4–5

Referred materials**.** See Appendix 1.
Locality and horizon**.** See Appendix 1.

Phanomys sp.

Referred materials. See Appendix 1.
Locality and horizon**.** See Appendix 1.
Comments. *Phanomys* is known by two species *P. mixtus* and *P. vetulus* Ameghino, 1894*. Phanomys mixtus is* represented by fragmentary maxillae, mandibles, and isolated teeth (Appendix 1). *Phanomys* is characterized by having high-crowned and rooted cheek teeth (with a greater degree of hypsodonty compared with other basal cavioids such as species of *Luantus* Ameghino, 1902), the presence of cementum in earlier stages of wear, relatively ephemeral fossettes/ids, and enamel discontinuities along the entire labial wall of upper cheek teeth and the lingual wall of lower cheek teeth (Fig. 3.4–5; for a detail description of the genus see Pérez and Vucetich, 2012).

Interestingly, in RSC *Phanomys* is much more abundant in EAG from BB, but its richness decreases while that of the euhypsodont cavioids (*i.e.*, *Schistomys*) increases in ECA and ECA2 (SBB) (Tab. 2; Appendix 1).

Recent phylogenetic study suggests that *Phanomys* is the sister group of the euhypsodont cavioids. Additionally, *P. mixtus* was proposed as a useful biostratigraphic indicator because it was found in different Miocene localities of the Province of Santa Cruz (Pérez and Vucetich, 2012).

Genus **Eocardia** Ameghino, 1887b

Type species. *Eocardia montana* Ameghino, 1887b. Santa Cruz Formation, Early–Middle Miocene, Province of Santa Cruz.

Eocardia montana Ameghino, 1887b

Figure 3.6–9

Referred materials**.** See Appendix 1.
Locality and horizon**.** See Appendix 1.

"*Eocardia*" *excavata* Ameghino, 1891b

Figure 3.10

Referred materials**.** See Appendix 1.
Locality and horizon**.** See Appendix 1.

Eocardia sp.

Referred materials**.** See Appendix 1.
Locality and horizon**.** See Appendix 1.
Comments**.** *Eocardia* was originally defined by Ameghino (1887b) and traditionally several species were included in this genus or subgenus (*e.g.*, Ameghino, 1887a, 1891b, 1894, 1906; Scott, 1905). Pérez (2010b) reduced the nominal diversity of Santacrucian forms to three species: the type species *Eocardia montana*, "*E.*" *excavata* and the smaller "*E.*" *fissa* Ameghino, 1891a. *Eocardia* is characterized by having continuous growth of the cheek teeth without root formation, double and heart-shaped cheek teeth, ephemerous fossettes/ids, presence of cementum beginning at very

early ontogenetic stages, and a narrow and discontinuous enamel layer surrounding the crown (Fig. 3.6–10). *Eocardia* is the only euhypsodont cavioid whose upper premolar has only one lobe (Fig. 3.6). The new RSC remains are assigned to *E. montana*, "*E.*" *excavata*, and *Eocardia* sp. (Tab. 2). It is interesting to note that although "*E.*" *fissa* has not been recorded in the new collections, this species was mentioned as coming from the RSC by Ameghino (1891; Pérez, 2010).

Eocardia is present at EAG and ESL from BB, and ECA, ECA2, and EET from SBB.

Genus ***Schistomys*** Ameghino, 1887a

Type species. *Schistomys erro* Ameghino, 1887a. Santa Cruz Formation, Early–Middle Miocene, Province of Santa Cruz.

Schistomys erro Ameghino, 1887a
Figure 3.11

Referred materials. See Appendix 1.
Locality and horizon. See Appendix 1.
Comments. *Schistomys* was established by Ameghino (1887a); later, additional species were assigned to this genus (Ameghino, 1891; Scott, 1905). Currently, only two species are considered valid (Pérez, 2010): the type species *Schistomys erro* and *S. rollinsii* (Scott, 1905). *Schistomys* is characterized by the same morphological characters as *Eocardia*, however they differ in that the upper premolar (P4) has two well-developed lobes similar to those of molars (Fig. 3.11). The only species recorded at SCR is *S. erro* which is present at ECA2 and EET from SBB (Tab. 2; Appendix 1).

It should be noted that in ECA2 (SBB), where the abundance of *Phanomys* is lower, *Schistomys* appears for the first time at SCR (Tab. 2). Whereas in EET, where *Schistomys* abundance is greater, *Phanomys* is not recorded.

Superfamily CHINCHILLOIDEA Bennett, 1833
Family CHINCHILLIDAE Bennett, 1833

Genus ***Prolagostomus*** Ameghino, 1887a

Type species. *Prolagostomus pusillus* Ameghino, 1887a. Santa Cruz Formation, Early–Middle Miocene, Province of Santa Cruz.

Prolagostomus pusillus Ameghino, 1887a

Referred materials. See Appendix 1.
Locality and horizon. See Appendix 1.

Prolagostomus sp.
Figure 3.12

Referred materials. See Appendix 1.
Locality and horizon. See Appendix 1.
Comments. *Prolagostomus* is a small to medium sized caviomorph, similar to *Pliolagostomus* Ameghino, 1887a. The upper and lower cheek teeth are euhypsodont and bilophodont, with the exception of the M3, which has three lophs. The hypoflexus/id are narrower than in *Perimys* Ameghino, 1887a, but broader than in *Lagostomus* Brookes, 1828. Molar crown walls are more curved and hypoflexid is more sinuous (Fig. 3.12) than in *Pliolagostomus*. The anterior lophid of lower molars is more labially extended (Fig. 3.12), unlike *Perimys*. The p4 is more obliquely oriented than molars (Fig. 3.12), unlike *Pliolagostomus*.

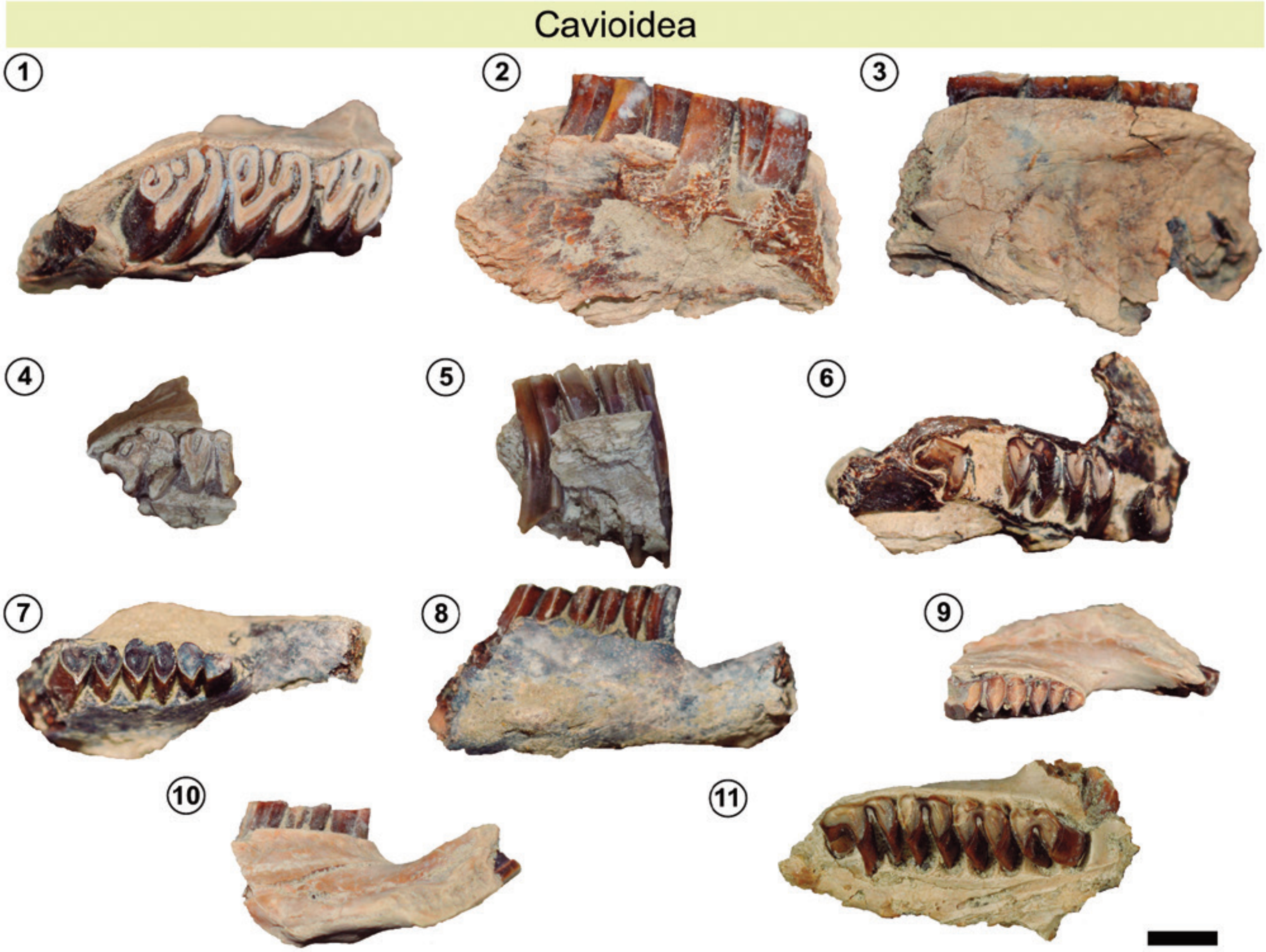
Prolagostomus is in general more abundant than *Pliolagostomus* (Appendix 1). Within the new rodent sample this genus is relatively well-represented in ECA, ECA2, and EET from SBB (Tab. 2; Appendix 1). It is only represented by two broken molars of *Prolagostomus* sp. (MPM-PV 20231, MPM-PV 20232; Tab. 2) in ESL from BB and is absent in YH.

Genus ***Pliolagostomus*** Ameghino, 1887a

Type species. *Pliolagostomus notatus* Ameghino, 1887a. Santa Cruz Formation, Early–Middle Miocene, Province of Santa Cruz.

Pliolagostomus notatus Ameghino, 1887a

Referred materials. See Appendix 1.
Locality and horizon. See Appendix 1.
Comments. *Pliolagostomus* is a small to medium sized caviomorph, similar to *Prolagostomus*. Upper and lower cheek teeth are euhypsodont and bilophodont, with the exception of the M3 which has three lophs. Cheek-tooth crown walls are straighter than *Prolagostomus*. Hypoflexus/


Cavioidea
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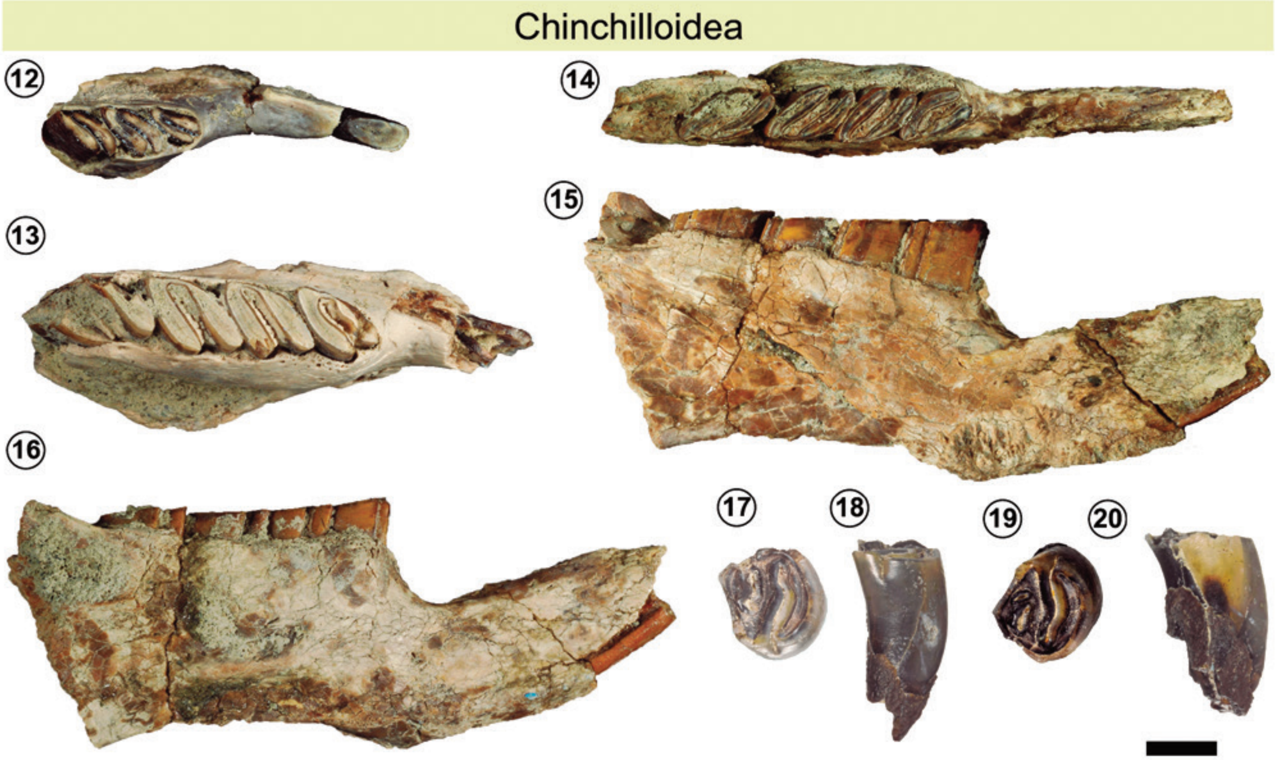
Chinchilloidea
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id is narrow, as in *Prolagostomus*. For a detailed description of this species see Rasia and Candela (2019).

As in *Prolagostomus*, this species is relatively well-represented in the three sites of SBB (ECA, ECA2, and EET; Tab. 2; Appendix 1). Notably, it is absent in BB and YH. Several specimens could not be identified at generic level and were assigned to *Prolagostomus* sp./*Pliolagostomus* sp. (MPM-PV 20259, MPM-PV 20349, MPM-PV 20381; Appendix 1).

Family Neoepiblemidae Kraglievich, 1926

Genus ***Perimys*** Ameghino, 1887a

Type species. *Perimys erutus* Ameghino, 1887a. Pinturas Formation, Early Miocene, and Santa Cruz Formation, Early–Middle Miocene, Province of Santa Cruz.

Perimys erutus Ameghino, 1887a

Figure 3.13

Referred materials**.** See Appendix 1.
Locality and horizon**.** See Appendix 1.

Perimys onustus Ameghino, 1887a

Figure 3.14–16

Referred materials. See Appendix 1.
Locality and horizon**.** See Appendix 1.

Perimys incavatus Ameghino, 1902

Referred materials. See Appendix 1.
Locality and horizon**.** See Appendix 1.

Perimys sp.

Referred materials. See Appendix 1.
Locality and horizon. See Appendix 1.
Comments. *Perimys* is a medium to large sized caviomorph. Cheek teeth are protohypsodont, unlike *Prolagostomus* and *Pliolagostomus*. Upper and lower cheek teeth are bilophodont, with the exception of the M3 which has three lophs, as in *Prolagostomus* and *Pliolagostomus*. Nevertheless, *Perimys* differs in that this third loph is parallel to the anterior two lophs, and in that the hypoflexus/id are conspicuously broader and filled with more cementum. Thus, these teeth have a U-shape occlusal surface (Fig. 3.13–16).

The genus was abundantly recovered in both in BB and SBB, but notably, the largest species, *P. onustus*, is very abundant in SBB, while in BB it is represented by a single specimen (MPM-PV 20160), and the small species, *P. incavatus*, is more abundant in BB (Tab. 2; Appendix 1).

Family Dinomyidae Alston, 1876

Genus ***Scleromys*** Ameghino, 1887a

Scleromys angustus. Ameghino, 1887a. Santa Cruz Formation, Early–Middle Miocene, Province of Santa Cruz.

Scleromys sp.

Figure 3.17–20

Referred materials. See Appendix 1.
Locality and horizon. See Appendix 1.
Comments. Among the species of *Scleromys* recognized in

Figure 3. Cavioidea (1-11) and Chinchilloidea (12-17). **1–3,** ***Neoreomys australis*** **MPM-PV 20292,** right maxillary fragment with M1-M3 in occlusal, lingual, and labial views; **4–5,** ***Phanomys mixtus*** **MPM-PV 20048,** right maxilla with M2-M3 in occlusal and lingual views; **6,** ***Schistomys erro*** **MPM-PV 20529,** right maxilla with P4-M3 in occlusal view; **7, "*Eocardia*" *excavata*** **MPM-PV 20241,** right maxilla with P4-M3 in occlusal view; **8–9,** ***Eocardia montana*** **MPM-PV 20401**, left mandible with p4-m2 in occlusal and labial views (inverted); **10–11,** ***Eocardia montana*** **MPM-PV 20053,** right mandible with p4-m2 in occlusal and lingual views; **12,** ***Prolagostomus*** **sp. MPM-PV 20314,** right mandible with p4-m2 in occlusal view; **13,** ***Perimys erutus*** **MPM-PV 20671,** right mandible with p4-m3 in occlusal view; **14–16,** ***Perimys onustus*** **MPM-PV 20670,** left mandible with p4-m3 in occlusal, lingual and labial views (inverted); **17–18,** ***Scleromys*** sp. **MPM-PV 20098,** left upper molar; **19–20,** ***Scleromys*** sp. **MPM-PV 20099,** left upper molar. Anterior to the right. Scale bars= 5 mm (**1–13**), 7.5 mm (**14–16**), and 3 mm (**17–20**).

the Santa Cruz Formation, S*. osbornianus* Ameghino, 1894 is the largest and the most abundant, whereas the type species, *S. angustus*, is less common. *Scleromys* is characterized by high-crowned molariforms with root formation and an occlusal pattern that consists in a long posterior labial flexid and an anterior lingual flexus. During the ontogeny, this genus displays a great amount of dental morphological change due to flexi/ids closure, fossette/ids disappearance, and changes in molar size and outline. For this reason, isolated teeth are difficult to assign to a species.

In the RSC the genus is not abundant, but *Scleromys* sp. was recorded both in BB and SBB (Tab. 2; Appendix 1).

DISCUSSION

Caviomorph assemblages of the Río Santa Cruz localities

In this contribution, a revision of the rodent fauna recorded in the localities of the RSC is presented (Tab. 1). The three fossil localities (BB, SBB, and YH; Appendix 1) represent different age ranges, and only the upper part of BB overlaps with the lowest part of SBB (Cuitiño *et al.* 2016, 2019). Not all the Santacrucian caviomorphs were found in all these localities (see above). SBB is the most fossiliferous locality with 557 specimens (72.5% of the fossil caviomorphs; ECA n= 179, ECA2 n= 272, and EET n= 106). In BB we found 208 specimens (27%; EAG n= 124, ESL n= 84) and in YH only three caviomorphs (0.4%) were recorded, making it the least fossiliferous locality (Appendix 1).

Octodontoidea. Octodontoids are the richest taxonomically and morphologically diverse group in the RSC with nine genera and 16 species (Appendix 1). This group is represented by low-crowned taxa. Some have low crowns with slightly terraced cheek teeth (*e.g.*, *Dudumus* sp. nov.? and *Acarechimys*). Others have slightly higher crowns (*e.g.*, *Prospaniomys* sp. nov.?, *Acaremys*). Still others have much higher crowns and planar occlusal surfaces (*e.g.*, *Sciamys*, *Stichomys*, *Spaniomys*). The most abundant taxa are *Spaniomys, Stichomys*, *Sciamys*, and *Acarechimys*, all of them broadly represented in all the localities of the RSC (see results above; Appendix 1). Within acaremyids we note the first record at RSC of *Sciamys latidens* from (ECA2, SBB; Appendix 1). It differs from the remaining Santacrucian *Sciamys* species in having a p4 with a molarized posterior portion (presence of hypolophid; Fig. 2.21). This species was previously known only by its holotype recorded at Killik Aike, near Río Gallegos, Province of Santa Cruz (Scott, 1905; Fig. 1). We also identify two new brachydont taxa (*Prospaniomys* sp. nov.? and *Dudumus* sp. nov.?). *Prospaniomys* sp. nov.? was recorded in ESL from BB and in ECA2 from SBB (Tab. 2; Appendix 1). In turn, *Dudumus* sp. nov.? was recorded in ECA2 (SBB). These records extend the biochron of both genera from the Colhuehuapian to the Santacrucian, as well as their geographic distributions (provinces of Chubut and Santa Cruz). Additionally, other brachydont specimens found in ESL (BB) could represent new taxa (*e.g.*, MPM-PV 20184, MPM-PV 20205; Appendix 1). These specimens are important because low-crowned octodontoids dominated older caviomorph assemblages of Patagonia (Vucetich *et al.*, 2010; Kramarz, 2004) and, until now, they were scarce in the Santa Cruz Formation –represented only by *Acarechimys*; Arnal *et al.* (2017)–. Thus, these new records expand the number of brachydont octodontoids for the Santacrucian.

Erethizontidae. Erethizontids have the least specific richness and abundance in the RSC. Within the new sample only 22 specimens are identified as *Steiromys detentus* (Fig. 3.23), *S. duplicatus*, and *Steiromys* sp. They have been found in BB (in EAG) and in SBB (in ECA, ECA2, and EET) (Appendix 1). This low abundance is in accordance with previous works (Ameghino, 1887a, 1889; Scott, 1905; Candela, 2000), in which *Steiromys* is the only recognized Santacrucian genus. Scott (1905) described *Steiromys intermedius*, another species from Guer Aike Department, Province of Santa Cruz (Fig. 1), that is not recorded in the RSC localities. As with octodontoids, the abundance of erethizontoids in the Santacrucian late Early–Middle Miocene greatly contrasts with that of the Colhuehuapian Early Miocene, where they are represented by four genera and several species (Vucetich *et al.*, 2015). Neither erethizontids nor octodontoids show any biostratigraphic zonation within the RSC localities.

Cavioidea. Unlike the above mentioned caviomorph clades, cavioids and chinchilloids have interestingly different distribution and taxonomic abundance in the different RSC localities. Within cavioids the derived euhypsodont *Schistomys* is present in SBB (ECA2 and EET) but absent in BB and YH. *Phanomys* and *Eocardia* are present in BB and in SBB

(Tab. 2; Appendix 1), but they differ in their generic distribution. On the one hand, the primitive protohypsodont *Phanomys* is more abundant in BB, in which it is represented by 17 specimens –EAG (n= 16) and ESL (n= 1)–, while in SBB only by 5 specimens –ECA (n= 1) and ECA2 (n= 4)–. On the other hand, the derived euhypsodont *Eocardia* is much more abundant in SBB (n= 65) than in BB (n= 36; Appendix 1). Although biostratigraphic information generally is based on presence/absence of taxa in each locality, we interpret that the differences in abundance of *Phanomys* and *Schistomys* observed in BB and SBB are related to a taxonomic replacement of both taxa. The euhypsodont *Eocardia* was present in both localities, but became much more abundant in SBB.

Neoreomys australis is the most abundant cavioid represented by 131 specimens found in the three localities of the RSC (BB, SBB, and YH; Appendix 1). Thus, this cavoid provides no biostratigraphic information.

Chinchilloidea. Within chinchilloids *Perimys* is present in BB (n= 21) and in SBB (n= 35). Nevertheless, between both localities the species distribution is different. In SBB the largest species, *Perimys onustus*, is clearly dominant with respect to the small and medium sized species of *Perimys* (*P. erutus*, *P. incavatus*, and *Perimys* sp.; Appendix 1), while in BB *P. onustus* is represented by a single specimen. In this regard, we note the first RSC record of the small species *Perimys incavatus* in BB (EAG). *P. incavatus* was previously recorded in the Colhuehuapian (Early Miocene) of the Province of Chubut (Vucetich *et al.*, 2010) and in the Santacrucian (Early–Middle Miocene) of southern Chile (Bostelmann *et al.*, 2013). A different generic and specific distribution is observed for the derived euhypsodont *Prolagostomus* and *Pliolagostomus*. They are the most abundant chinchilloids in SBB (n= 176), while they are represented by only two specimens of *Prolagostomus* sp. in BB (Appendix 1). *Scleromys* is represented in BB and SBB by 12 specimens assigned to *Scleromys* sp. (Appendix 1).

Caviomorphs of other Santacrucian localities are poorly known. Ameghino (1891a,b, 1894) described new species of those Santacrucian genera described in 1887a,b and 1889. But unfortunately, precise geographic and stratigraphic information is uncertain (Fernicola *et al.*, 2014). Scott (1905) studied several caviomorphs from the Santa Cruz Formation recovered from the cliffs of RSC and coastal localities of the east of the Province of Santa Cruz (Killik Aike, 10 miles south of Coy inlet; Marshall, 1976; Vizcaíno *et al.*, 2012b; Fig. 1). Except for a few species, all of them belong to the genera recovered previously in the RSC cliffs (*i.e.*, *Neoreomys*, *Phanomys*, *Schistomys*, *Eocardia, Stichomys*, *Spaniomys*, *Steiromys, Sciamys, Acaremys*, *Acarechimys*, and *Scleromys*).

In summary, we observed a reduction in the taxonomic diversity but an increased in the morphological disparity of the rodent assemblage from the RSC (Tab. 1 and discussion above) than previously known (Ameghino, 1887a,b, 1889, 1891; Scott, 1905; Tab. 1). This work is the first comprehensive attempt in revising the Santacrucian caviomorphs. Similar systematic revisions should be approached with the caviomorph materials collected in other Santacrucian localities, in order to better understand the Santacrucian caviomorph assemblage as a whole.

GENERAL EVOLUTIONARY ASPECTS

Santacrucian rodents show significant changes compared with those of older Colhuehuapian and "Pinturan" SALMAs (Kramarz, 2004, 2006a,b; Kramarz and Bellosi, 2005; Vucetich *et al.* 2010; Pérez and Pol, 2012; Arnal and Vucetich, 2015a). Several lineages experienced a progressive increase in hypsodonty (*e.g.*, octodontoids with *Sciamys*, *Stichomys*, *Spaniomys*) or even acquired euhypsodonty for the first time (*e.g.*, cavioids, chinchillids). Those rodents with more generalized dental patterns (*e.g.*, *Steiromys*) became less common. Within Cavioidea, the acquisition of hypsodonty is first seen during the Santacrucian SALMA (Pérez and Pol, 2012), but the increase in dental crown height is already recorded in previous ages (*e.g.*, *Luantus* in the Colhuehuapian and "Pinturan"; *Chubutomys* Wood and Patterson, 1959 in the Deseadan SALMA), unlike what is observed in octodontoids, which show increased crown height for the first time in the Santacrucian. In the RSC localities, meso-, proto, and euhypsodont taxa coexisted for some time during the Santacrucian (see previous section). Until now mesodont forms that would eventually give origin to the modern Dasyproctidae on the one hand and euhypsodont forms that would originate the Family Caviidae on the other hand, were recorded only in younger ages (*e.g.*, "Colloncuran", Laventan, Mayoan, early Late Miocene). Interestingly, a similar trend occurs within Chinchilloidea. During the Santacrucian, *Perimys* is the most abundant chinchilloid in BB and had the greatest specific richness. In SBB this taxonomic richness decreased (represented mostly by *P. onustus*); the record from SBB marks the last appearance of the genus. This taxonomic decrease is observed together with the rise in the abundance of specimens of the derived lagostomines *Pliolagostomus* and *Prolagostomus*. Noteworthy, one *Perimys* species in SBB coexisted, which is larger than the abovementioned lagostomines. This may be related to the biology of these taxa, probably *P. onustus* not competing for ecological requirements with the other chinchilloids.

Within octodontoids, the record of *Dudumus* sp. nov.? and *Prospaniomys* sp. nov.? expand the biochron and geographic distribution of these genera. Both taxa and *Acarechimys* are the only brachydont octodontoids in the RSC and are also recorded in older Colhuehuapian beds. Nevertheless, they differ in that *Dudumus* and *Prospaniomys* were abundant in older beds and are represented by only four specimens in the RSC, while *Acarechimys* is much more abundant in the Santacrucian. In addition, *Acarechimys* and *Sciamys* are the only octodontoids recorded in younger Middle Miocene beds (Arnal and Pérez, 2013; Arnal *et al.*, 2017). These younger *Acarechimys* maintained the brachydont cheek tooth structure, and are not recorded in Patagonia but in middle latitudes of the continent (Quebrada Honda, Bolivia; see Arnal *et al.*, 2017). This geographic distribution was proposed to be the result of a migration event (from Patagonia to lower latitudes regions) induced by the marked aridization and cooling of higher latitudes of South America after the Early Miocene (Arnal *et al.*, 2017). On the other hand, the last record of *Sciamys* is that of *Sciamys petisensis*, found in the locality of El Petiso, Province of Chubut (Arnal and Pérez, 2013). The fossil-bearing bed of El Petiso is estimated to be of Middle–Late Miocene Age. *Sciamys petisensis* is higher-crowned than its Santacrucian relatives. In fact, it is the highest-crowned and last recorded acaremyid (Arnal and Pérez, 2013). This survival would be the result not of a migration like *Acarechimys*, but of increasing hypsodonty in order to counteract the aridization of these latitudes. Erethizontids became scarce in Patagonia by the Santacrucian, being since then recorded only in lower latitudes (*e.g.*, Bolivia, Colombia).

In addition to this turnover in teeth morphology, Santacrucian rodents have different sizes: they were large (*Neoreomys*, *Perimys onustus*), medium-sized (*Scleromys*, *Steiromys*, *Eocardia*, and the remaining *Perimys* species) and small (octodontoids). This diversity reflects a wide range of habits, suggesting they had acquired broad paleobiologic adaptations by the Early–Middle Miocene (Candela *et al.*, 2012; Muñoz *et al.*, 2019). This, in turn, is related to the environment in which they lived. Recent works proposed more humid and forested paleoenvironments for the Santa Cruz Formation (Kay *et al.*, 2008, 2012; Brea *et al.*, 2012; Rasia, 2016) than historically proposed (Pascual *et al.*, 1996; Vucetich *et al.*, 2015). Evidently, these varied landscape scenarios (that resulted from considerable climatic changes) permitted the evolution and diversification of the Santacrucian caviomorphs. Paleobiological aspects deserve further detailed analyses which are beyond the scope of this systematic study.

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REFERENCES

Álvarez, A., Pérez, S.I., and Verzi, D.H. 2011. Ecological and phylogenetic influence on mandible shape variation of South American caviomorph rodents (Rodentia, Hystricomorpha). *Biological Journal of the Linnean Society* 102: 828–837.

Ameghino, F. 1887a. Enumeración sistemática de las especies de mamíferos fósiles coleccionadas por Carlos Ameghino en los terrenos eocenos de la Patagonia austral. *Boletín del Museo de La Plata* 1: 1–26.

Ameghino, F. 1887b. Observaciones generales sobre el orden de mamíferos extinguidos sudamericanos llamados toxodontes (Toxodontia) y sinopsis de los géneros y especies hasta ahora conocidos. *Anales del Museo de La Plata* (Entrega especial, 1936): 1–66.

Ameghino, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas de la Academia Nacional de Ciencias en Córdoba* 6: 1–1027.

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

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

Ameghino, F. 1894. Enumération synoptique des espéces des mammiferes fósiles des formations éocenes de Patagonie. *Boletín de la Academia Nacional de Ciencias de Córdoba* 13: 259–452.

Ameghino, F. 1897. Mammifères Crétacés de l'Argentine. Deuxième contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium*. *Boletín del Instituto Geográfico Argentino* 18: 460–521.

Ameghino, F. 1902. Première Contribution à la connaissance de la faune mammalogique des couches à *Colpodon*. *Boletín de la Academia Nacional de Ciencias en Córdoba* 17: 71–138.

Ameghino, F. 1906. Les Formations sedimentaires du Crétacé supérieur et du Tertiaire de Patagonie. *Anales del Museo Nacional de Buenos Aires* 8: 1–568.

Arnal, M. 2012. [*Sistemática, filogenia e historia evolutiva de roedores Octodontoidea (Caviomorpha, Hystricognathi) del Oligoceno tardío–Mioceno medio vinculados al origen de la familia Octodontidae*. Tesis doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, 317 p. Unpublished.].

Arnal, M., Kramarz, A.G., Vucetich, M.G., and Vieytes, C.E. 2014. A new Early Miocene octodontoid rodent (Hystricognathi, Caviomorpha) from Patagonia (Argentina) and a reassessment of the early evolution of Octodontoidea. *Journal of Vertebrate Paleontology* 34: 397–406.

Arnal, M., and Pérez, M.E. 2013. A new acaremyid rodent (Hystricognathi, Octodontoidea) from the Middle Miocene of Patagonia (South America) and considerations on the early evolution of Octodontoidea. *Zootaxa* 3616: 119–134.

Arnal, M., and Vucetich, M.G. 2015a. Main radiation events in Pan-Octodontoidea (Rodentia, Caviomorpha). *Zoological Journal of the Linnean Society* 175: 587–606.

Arnal, M., and Vucetich, M.G. 2015b. Revision of the fossil rodent *Acaremys* Ameghino, 1887 (Hystricognathi, Octodontoidea, Acaremyidae) from the Miocene of Patagonia (Argentina) and the description of a new acaremyid. *Historical Biology* 27: 42–59.

Arnal, M., Vucetich, M.G., Croft, D.A., Bargo, M.S., Fernicola, J.C., and Vizcaíno, S.F. 2017. Systematic revision and evolutionary history of *Acarechimys* Patterson in Kraglievich, 1965 (Rodentia, Caviomorpha, Octodontoidea). *Ameghiniana* 54: 307–330.

Bostelmann, J.E., Le Roux, J.P., Vásquez, A., Gutiérrez, N.M., Oyarzun, J.L., Carreño, C., Torres, T., Otero, R., Llanos, A., Fanning, C.M., and Herve, F. 2013. Burdigalian deposits of the Santa Cruz Formation in the Sierra Baguales, Austral (Magallanes) Basin: Age, depositional environment and vertebrate fossils. *Andean Geology* 40: 458–489.

Brandoni, D., González Ruiz, L., and Bucher, J. 2019. Evolutive implications of *Megathericulus patagonicus* (Xenarthra, Megatheriinae) from the Miocene of Patagonia Argentina. *Journal of Mammalian Evolution*. doi: 10.1007/s10914-019-09469-6

Brandoni, D., González Ruiz, L., Reato, A., and Martin, G. 2017. Chronological implications of the nothrotheriid '*Xyophorus*' (Mammalia, Xenarthra) from the Collón Curá Formation (Miocene of Patagonia, Argentina). *Historical Biology*. doi: https://doi.org/10.1080/08912963.2017.1398748

Brea, M., Zucol, A.F., Iglesias, A. 2012. Fossil plant studies from late Early Miocene of the Santa Cruz Formation: paleoecology and paleoclimatology at the passive margin of Patagonia, Argetina. In: S.F. Vizcaíno, R.F. Kay, and M.S. Bargo (Eds.), *Early Miocene Paleobiology in Patagonia*. Cambridge University Press, Cambridge, p. 104–128.

Busker, F., Pérez, M.E., Krause, J.M., and Vucetich, M.G. 2018. First record of *Banderomys leanzai* Kramarz, 2005 (Rodentia, Caviomorpha) in Chubut Province, Patagonia (Argentina). *Revista del Museo Argentino de Ciencias Naturales* 19: 121–129.

Candela, A.M. 2000. [*Los Erethizontidae (Rodentia, Hystricognathi) fósiles de Argentina. Sistemática e historia evolutiva y biogeografía*. Tesis doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, 352 p. Unpublished.].

Candela, A.M., and Nasif, N.L. 2006. Systematics and biogeographic significance of *Drytomomys typicus* (Scalabrini in Ameghino, 1889) nov. comb., a Miocene Dinomyidae (Rodentia, Hystricognathi) from northeast of Argentina. *Neues Jahrbuch für Geologie und Paläontologie* 3: 165–181.

Candela, A.M., Rasia, L.L., and Pérez, M.E. 2012. Paleobiology of Santacrucian caviomorph rodents: a morphofunctional approach. 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. 287–305.

Croft, D.A., Flynn, J.J., and Wyss, A.R. 2004. Notoungulata and Litopterna of the Early Miocene Chucal Fauna, northern Chile. *Fieldiana: Geology* (New Series) 50: 1–52.

Cuitiño, J.I., Fernicola, J.C., Kohn, M.J., Trayler, R., Naipauer, M., Bargo, M.S, Kay, R.F., and Vizcaíno, S.F. 2016. U-Pb geochronology of the Santa Cruz Formation (Early Miocene) at the Río Bote and Río Santa Cruz (southernmost Patagonia, Argentina): implications for the correlation of fossil vertebrate localities. *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: 14–33.

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.

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 Notohippidian. *Journal of South American Earth Sciences* 52: 94–107.

Fields, R.W. 1957. Hystricomorph rodents from the Late Miocene of Colombia, South America. *University of California Publications in Geological Sciences* 32: 273–404.

Flynn, J.J., Charrier, R., Croft, D.A., Gans, Ph.B., Herriott, T.M., Wertheim, J.A., and Wyss, A.R. 2008. Chronologic implications of new Miocene mammals from the Cura-Mallín and Trapa Trapa Formations, Laguna del Laja area, south central Chile. *Journal of South American Earth Sciences* 26: 412–423.

Flynn, J.J., Novacek, M.J., Dodson, H.E., Frassinetti, D., McKenna, M.C., Norell, M.A., Sears, K.E., Swisher III, C.C., and Wyss, A.R. 2002. A new fossil assemblage from the southern Chilean Andes: implications for geology, geochronology, and tectonics. *Journal of South American Earth Sciences* 15: 285–302.

Frailey, C.D., and Campbell, K.E. Jr. 2004. Paleogene Rodents from Amazonian Peru: The Santa Rosa Local Fauna. In: K.E.Campbell (Ed.), *The Paleogene Mammalian Fauna of Santa Rosa, Amazonian Peru*. Natural History Museum of Los Angeles County, Sciences Series 40, Los Angeles, p. 71–130.

González Ruiz, L., Góis Lima, F., Ciancio, M., and Scillato-Yané, G. 2013. Los Peltephilidae (Mammalia, Xenarthra) de la Formación Collón Curá (Colloncurense, Mioceno medio), Argentina. *Revista Brasileira de Paleontologia* 16: 319–330.

González Ruiz, L., Reato, A., Cano, M., and Martínez, O. 2017. Old and new specimens of a poorly known glyptodont from the Miocene of Patagonia and their biochronological implications. *Acta Palaeontologica Polonica* 62: 181–194.

Gray, J.E. 1843. *List of the specimens of Mammalia in the Collection of the British Museum*. British Museum, London, 216 p.

Illiger, J.K.W. 1811. *Prodomus systematics mammalium et avium additis terminis zoographicis utriusque classis, eorumque versione germanica*. Berolini, Berlin, 302 p.

Kay, R.F., Vizcaíno, S.F., Bargo, M.S., Perry, J.M.G., Prevosti, F., and Fernicola, J.C. 2008. Two new fossil vertebrate localities in the Santa Cruz Formation (late early–early Middle Miocene, Argentina), 51 South latitude. *Journal of South American Earth Sciences* 25: 87–195.

Kay, R.F., Vizcaíno, S.F., and Bargo, M.S. 2012. A review of the paleoenvironment and paleoecology of the Miocene Santa Cruz Formation. In: S.F. Vizcaíno, R.F. Kay, and M.S. Bargo (Eds.), *Early Miocene Paleobiology in Patagonia*. Cambridge University Press, Cambridge, p. 331–365.

Kraglievich, J.L. 1965. Speciation phyletique dans les rongeurs fossiles du genre *Eumysops* Ameghino (Echimyidae, Heteropsomyinae). *Extrait de Mammalia* 29: 258–267.

Kramarz, A.G. 2001. Un nuevo roedor Adelphomyinae (Hystricognathi, Echimyidae) del Mioceno medio–inferior de Patagonia, Argentina. *Ameghiniana* 38: 163–168.

Kramarz, A.G. 2002. Roedores chinchilloideos (Hystricognathi) de la Formación Pinturas, Mioceno temprano–medio de la provincia de Santa Cruz, Argentina. *Revista del Museo Argentino de Ciencias Naturales* 4: 167–180.

Kramarz, A.G. 2004. Octodontids and erethizontoids (Rodentia, Hystricognathi) from the Pinturas Formation, Early–Middle Miocene of Patagonia, Argentina. *Ameghiniana* 41: 199–216.

Kramarz, A.G. 2006a. Eocardiids (Rodentia, Hystricognathi) from the Pinturas Formation, late Early Miocene of Patagonia, Argentina. *Journal of Vertebrate Paleontology* 26: 770–778.

Kramarz A.G. 2006b. *Neoreomys* and *Scleromys* (Rodentia, Hystricognathi) from the Pinturas Formation, late Early Miocene of Patagonia, Argentina. *Revista del Museo Argentino de Ciencias Naturales* 8: 53–62.

Kramarz, A.G., and Bellosi, E.S. 2005. Hystricognath rodents from the Pinturas Formation, Early–Middle Miocene of Patagonia, biostratigraphic and paleoenviromental implications. *Journal of South American Earth Sciences* 18: 199–212.

Kramarz, A.G., Vucetich, M.G., and Arnal, M. 2013. A new Early Miocene chinchilloid hystricognath rodent. An approach to the understanding of the early chinchillid dental evolution. *Journal of Mammalian Evolution* 20: 249–261.

Kramarz, A.G., Vucetich, M.G., Carlini, A.A., Ciancio, M.R., Abello, M.A., Deschamps, C.M., and Gelfo, J.N. 2010. A new mammal fauna at the top of the Gran Barranca sequence and its biochronological significance. In: R.H. Madden, A.A. Carlini, M.G. Vucetich, and R.F. Kay (Eds.), *The Paleontology of Gran Barranca, evolution and environmental change through the middle Cenozoic of Patagonia*. Cambridge University, Cambridge, p. 264–277.

López, G.M., Vucetich, M.G., Carlini, A.A., Bond, M., Pérez, M.E., Ciancio, M.R., Pérez, D.J., Arnal, M., and Olivares, A.I. 2011. New Miocene mammal assemblage from Neogene Manantiales Basin, Cordillera Frontal, San Juan, Argentina. In: J.A. Salfity, and R.A. Marquillas (Eds.), *Cenozoic Geology of the Central Andes of Argentina*. SCS Publisher, Salta, p. 211–226.

Madden, R.H. 2015. *Hypsodonty in Mammals: evolution, geomorphology, and the role of earth surface processes*. Cambridge University Press, Cambridge, 423 p.

Marshall, L.G. 1976. Fossil localities for Santacrucian (Early Miocene) mammals, Santa Cruz Province, Southern Patagonia, Argentina. *Journal of Paleontology* 50: 1129–1142.

Marshall, L.G., and Salinas, P. 1990. Vertebrados continentales del Mioceno inferior de Magallanes, Chile. *Revista Geológica de Chile* 17: 57–87.

Muñoz, N.A., Toledo, N., Candela, A.M., and Vizcaíno, S.F. 2019. Functional morphology of the forelimb of Early Miocene caviomorph rodents from Patagonia. *Lethaia* 52: 91–106.

Ortiz-Jaureguizar, E., and Cladera, G.A. 2006. Paleoenvironmental evolution of southern South America during the Cenozoic. *Journal of Arid Environments* 66: 498–532.

Pascual, R., Ortiz-Jaureguizar, E., and Prado, J.L. 1996. Land mammals: paradigm of Cenozoic South American geobiotic evolution. In: G. Arratia (Ed.), *Contribution of Southern South America to Vertebrate Paleontology*. Müncher Geowissenschaftliche Abhandlungen, Munich, p. 265–319.

Patterson, B., and Pascual, R. 1968. New echimyids rodents from the Oligocene of Patagonia and a synopsis of the Family. *Breviora* 301: 1–14.

Patterson, B., and Wood, A.E. 1982. Rodents from the Deseadan Oligocene of Bolivia and the Relationships of the Caviomorpha. *Bulletin of the Museum of Comparative Zoology* 149: 371–543.

Patton, J.L., Pardiñas, U.F.J., and D'Elía, G. 2015. *Mammals of South America, vol. 2, Rodents*. University of Chicago Press, Chicago, 1336 p.

Pérez, M.E. 2010a. A new rodent (Cavioidea, Hystricognathi) from the Middle Miocene of Patagonia, mandibular homologies, and the origin of the crown group Cavioidea *sensu stricto. Journal of Vertebrate Paleontology* 30: 1848–1859.

Pérez, M.E. 2010b. [*Sistemática, ecología y bioestratigrafía de Eocardiidae (Rodentia, Hystricognathi, Cavioidea) del Mioceno temprano y medio de Patagonia*. Tesis Doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, 385 p. Unpublished.].

Pérez, M.E., and Pol, D. 2012. Major Radiations in the Evolution of Caviid Rodents: Reconciling Fossils, Ghost Lineages, and Relaxed Molecular Clocks. *PLoS ONE* doi: 10.1371/journal.pone.0048380

Pérez, M.E., and Vucetich, M.G. 2012. A revision of the fossil genus

Phanomys Ameghino, 1887 (Rodentia, Hystricognathi, Cavioidea) from the early Miocene of Patagonia (Argentina) and the acquisition of euhypsodonty in Cavioidea *sensu stricto*. *Paläontologische Zeitschrift* 86: 187–204.

Pérez, M.E., Vucetich, M.G., and Kramarz, A.G. 2010. The first Eocardiidae (Rodentia) in the Colhuehuapian (early Miocene) of Bryn Gwyn (Northern Chubut, Argentina) and the early evolution of the peculiar cavioid rodents. *Journal of Vertebrate Paleontology* 30: 528–534.

Rasia, L.L. 2016. [*Los Chinchillidae (Rodentia, Caviomorpha) fósiles de la República Argentina: sistemática, historia evolutiva y biogeográfica, significado bioestratigráfico y paleoambiental*. Tesis Doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, 246 p. Unpublished.].

Rasia, L.L., and Candela, A.M. 2019. *Prolagostomus amplus* Ameghino, 1894 is a junior synonym of the Patagonia rodent *Pliolagostomus notatus* Ameghino, 1887 (Chinchillidae; early Miocene, Santa Cruz Formation). *Ameghiniana* 56: 72–77.

Scott, W.B. 1905. Mammalia of the Santa Cruz beds. Part III, Glires. In: *Reports of the Princeton University Expeditions to Patagonia 1896-1899*. Princeton University Press, New Jersey, 348–487.

Tauber, A.A. 1997. Los vertebrados de la Formación Santa Cruz (Mioceno inferior–medio) en el extremo sureste de la Patagonia y su significado paleoecológico. *Ameghiniana* 34: 517–529.

Thomas, O. 1903. Notes in South American monkeys, bats, carnivores, and rodents, with descriptions of new species. *Annals and Magazine of Natural History* 12: 455–464.

Upham, N.S., and Patterson, B.D. 2015. Phylogeny and evolution of caviomorph rodents: a complete timetree for living genera. In: A.I. Vasallo, and D. Antenucci (Eds.), *Biology of Caviomorph Rodents: diversity and evolution*. SAREM Series A, Mammalogical Research (Investigaciones Mastozoológicas), Ciudad Autónoma de Buenos Aires, p. 63–120.

Vasallo, A.I., and Antenucci, D. 2015. *Biology of Caviomorph rodents: Diversity and Evolution*. SAREM Series A, Mammalogical Research (Investigaciones Mastozoológicas), Ciudad Autónoma de Buenos Aires, 329 p.

Vera, B., González Ruiz, L., Novo, N., Martin, G., Reato, A., and Tejedor, M.F. 2018. The Interatheriinae (Mammalia, Notoungulata) of the Friasian *sensu stricto* and Mayoan (middle to late Miocene), and the fossils from Cerro Zeballos, Patagonia, Argentina. *Journal of Systematic Palaeontology*. doi: 10.1080/14772019.2018.1511387

Vera, B., Reguero, M.A., and González Ruiz, L. 2017. The Interatheriinae (Notoungulata) from the Collón Curá Formation (middle Miocene), Argentina. *Acta Palaeontologica Polonica* 62: 845–863.

Verzi, D.H., Olivares, A.I., and Morgan, C.C. 2014. Phylogeny, evolutionary patterns and timescale of South American octodontoid rodents. The importance of recognizing morphological differentiation in the fossil record. *Acta Palaeontologica Polonica* 757–769.

Vizcaíno, S.F., Kay, R.F., and Bargo, M.S. 2012a. *Early Miocene Paleobiology in Patagonia: High-latitude Paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, 370 p.

Vizcaíno, S.F., Kay, R.F., and Bargo, M.S. 2012b. 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*. Cambridge University Press, Cambridge, p. 1–22.

Vucetich, M.G., Arnal, M., Deschamps, C.M., Pérez, M.E., and Vieytes, E.C. 2015. A brief history of caviomorph rodents as told by the fossil record. In: A.I. Vasallo, and D. Antenucci (Eds.), *Biology of Caviomorph Rodents: diversity and evolution*. SAREM Series A, Mammalogical Research (Investigaciones Mastozoológicas), Ciudad Autónoma de Buenos Aires, p. 11–62.

Vucetich, M.G., Dozo, M.T., Arnal, M., and Pérez, M.E. 2014. New rodents (Mammalia) from the Late Oligocene of Cabeza Blanca (Chubut) and the first rodent radiation in Patagonia. *Historical Biology: An International Journal of Paleobiology* 27: 236–257.

Vucetich, M.G., and Kramarz, A.G. 2003. New Miocene rodents of Patagonia (Argentina) and their bearing in the early radiation of the octodontiform octodontoids. *Journal of Vertebrate Paleontology* 23: 435–444.

Vucetich, M.G., Kramarz, A.G., and Candela, A.M. 2010. Colhuehuapian rodents from Gran Barranca and other Patagonian localities: the state of the art. In: R.H. Madden, A.A. Carlini, M.G. Vucetich, and R.F. Kay (Eds.), *The Paleontology of Gran Barranca: Evolution and Environmental Change through the Middle Cenozoic of Patagonia*. University of Cambridge Press, Cambridge, p. 206–219.

Vucetich, M.G., and Verzi, D.H. 1996. A peculiar octodontoid (Rodentia, Caviomorpha) with terraced molars from the Lower Miocene of Patagonia (Argentina). *Journal of Vertebrate Paleontology* 16: 297–302.

Wood, A.E. 1949. A new Oligocene rodent genus from Patagonia. *American Museum Novitates* 1435: 1–54.

Wood, A.E. 1955. A revised classification of the rodents. *Journal of Mammalogy* 36: 165–187.

Wood, A.E., and Patterson, B. 1959. The rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. *Bulletin of the Museum of Comparative Zoology* 120: 281–428.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., and Billups, K. 2001. Trends, rhytms, and aberrations in global climate 65 Ma to present. *Science* 292: 686–693.

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Appendix 1 - List of fossil caviomorph specimens from the Río Santa Cruz. In different shades of green: Barrancas Blancas (BB), Estancia Aguada Grande (EAG), and Estancia Santa Lucia (ESL); in different shades of blue: Segundas Barrancas Blancas (SBB), Estancia Cordón Alto (ECA), Estancia Cordón Alto2 (ECA2), and Estancia El Tordillo (EET); Orange: Yaten Huageno (YH) and Estancia El Refugio (EER)

Locality	*Estancia*	*Collection number*	*Systematic taxonomy*	*Material*
BB	*Estancia Aguada Grande (EAG)*	*MPM-PV 20773*	**Sciamys principalis**	*left mandible with p4-m3*
		MPM-PV 20036	**Phanomys mixtus**	*right P4*
		MPM-PV 20037	**Phanomys mixtus**	*right M1 or M2*
		MPM-PV 20038	**Neoreomys australis**	*right M1 or M2*
		MPM-PV 20039	**Perimys** *sp.*	*isolated upper tooth*
		MPM-PV 20040	**Spaniomys** *sp.*	*right upper molar*
		MPM-PV 20041	**Spaniomys** *sp.*	*right upper molar*
		MPM-PV 20042	**Spaniomys** *sp.*	*right upper molar*
		MPM-PV 20043	*Acaremyidae*	*left lower molar*
		MPM-PV 20044	**Sciamys***?*	*left p4*
		MPM-PV 20045	**Neoreomys australis**	*right maxilla with DP4-M3*
		MPM-PV 20046	**Neoreomys australis**	*left M1 or M2*
		MPM-PV 20047	**Neoreomys australis**	*right p4*
		MPM-PV 20048	**Phanomys mixtus**	*right M2-M3*
		MPM-PV 20049	**Perimys erutus**	*left M1 or M2*
		MPM-PV 20050	**"Eocardia" excavata***?*	*left upper molar*
		MPM-PV 20051	**"Eocardia" excavata***?*	*left m1*
		MPM-PV 20052	**"Eocardia" excavata***?*	*right m3*
		MPM-PV 20053	**Eocardia montana**	*right mandibular fragment with p4-m2*
		MPM-PV 20054	**Eocardia** *sp.*	*left m3*
		MPM-PV 20055	**Perimys/ Prolagostomus**	*right m3*
		MPM-PV 20056	**Neoreomys australis**	*right upper molar*
		MPM-PV 20057	*Octodontoidea*	*edentulous left zygomatic fragment*
		MPM-PV 20058	**Steiromys detentus**	*right upper molar*
		MPM-PV 20059	*Acaremyidae*	*broken P4*
		MPM-PV 20060	**Spaniomys**	*right lower tooth broken*
		MPM-PV 20061	**Neoreomys australis**	*right M1-M2*
		MPM-PV 20062	**Neoreomys australis**	*left m1 or m2*
		MPM-PV 20063	**Neoreomys australis**	*left M1 or M2*
		MPM-PV 20064	**Eocardia montana**	*left p4*
		MPM-PV 20065	**Eocardia montana**	*right m1*
		MPM-PV 20066	**Eocardia montana**	*right m2*
		MPM-PV 20067	**"Eocardia" excavata**	*left mandible with m1-m2*
		MPM-PV 20068	**Spaniomys** *sp.*	*right mandible with m1-m2*
		MPM-PV 20069	**Acarechimys minutissimus**	*right mandible with m1-m2*
		MPM-PV 20070	*Octodontoidea*	*lower incisor*
		MPM-PV 20071	*Caviomorpha*	*lower incisor*
		MPM-PV 20072	**Phanomys mixtus**	*left M3*
		MPM-PV 20073	**Phanomys mixtus**	*right M3*
		MPM-PV 20074	**Phanomys mixtus**	*right M1*
		MPM-PV 20075	**Phanomys mixtus**	*left M1*
		MPM-PV 20076	**Phanomys mixtus**	*right M2*
		MPM-PV 20077	**Phanomys mixtus**	*left M2*
		MPM-PV 20078	**Phanomys mixtus**	*right m1 or m2*
		MPM-PV 20079	**Phanomys mixtus**	*left m1*
		MPM-PV 20080	**Phanomys mixtus**	*left m1 or m2*

APPENDIX 1 - **Continued**

Locality	*Estancia*	*Collection number*	*Systematic taxonomy*	*Material*
🟩	🟩	MPM-PV 20081	**Spaniomys** *sp.*	upper cheek teeth
		MPM-PV 20082	**Neoreomys australis**	right M1 or M2
		MPM-PV 20083	**Scleromys** *sp.*	left M1 or M2
		MPM-PV 20084	**Scleromys** *sp.*	left M1 or M2
		MPM-PV 20085	**Scleromys** *sp.*	P4?
		MPM-PV 20086	**Steiromys duplicatus**	left DP4
		MPM-PV 20087	**Steiromys duplicatus**	right M1 or M2
		MPM-PV 20088	**Steiromys duplicatus**	right M1 or M2 (broken)
		MPM-PV 20089	**Steiromys duplicatus**	right M1 or M2 (broken)
		MPM-PV 20090	**Steiromys duplicatus**	left M1 or M2
		MPM-PV 20091	**Steiromys duplicatus**	left M1 or M2
		MPM-PV 20092	**Steiromys duplicatus**	left M3
		MPM-PV 20093	**Steiromys duplicatus**	left dp4
		MPM-PV 20094	**Steiromys duplicatus**	left mandibular fragment with m2
		MPM-PV 20095	**Steiromys duplicatus**	left lower incisor
		MPM-PV 20096	**Steiromys** *sp.*	2 incisor fragments
		MPM-PV 20097	**Steiromys** *sp.*	2 broken teeth
		MPM-PV 20098	**Scleromys** *sp.*	left upper molar
		MPM-PV 20099	**Scleromys** *sp.*	left upper molar
		MPM-PV 20100	*Rodentia?*	1 phalanx
		MPM-PV 20101	*Rodentia?*	distal left humerous
		MPM-PV 20102	*Rodentia?*	right astragalus
		MPM-PV 20103	**Stichomys** *sp.*	left maxillary fragment with DP4-M1
		MPM-PV 20104	**Stichomys** *sp.*	right m1 or m2
		MPM-PV 20105	*Octodontoidea*	left lower molar broken
		MPM-PV 20106	**Stichomys** *sp.*	right m3
		MPM-PV 20107	**Steiromys duplicatus***?*	right DP4?
		MPM-PV 20108	**Perimys erutus**	right M3
		MPM-PV 20109	**Eocardia montana**	right m1 or m2
		MPM-PV 20110	**Eocardia montana**	right m1 or m2
		MPM-PV 20111	*Caviomorpha*	2 incisors
		MPM-PV 20112	*cf.* **Scleromys**	right P4
		MPM-PV 20113	**Neoreomys***?*	mandibular fragment with incisor
		MPM-PV 20114	**Eocardia** *sp.*	right m1 or m2
		MPM-PV 20115	**Spaniomys riparius**	left mandibular fragment with dp4-m2
		MPM-PV 20116	**Perimys erutus**	left M1 or M2
		MPM-PV 20117	**Sciamys** *sp.*	left M1 or M2
		MPM-PV 20118	**Phanomys** *sp.*	left M1
		MPM-PV 20119	**Phanomys** *sp.*	left p4
		MPM-PV 20773	**Eocardia** *sp.*	broken tooth
		MPM-PV 20774	*Caviomorpha*	brachydont molar
		MPM-PV 20775	*Caviomorpha*	brachydont molar
		MPM-PV 20776	**Eocardia** *sp.*	left lower molar
		MPM-PV 20777	**Eocardia** *sp.*	left m2 or m3
		MPM-PV 20778	**Eocardia** *sp.*	left m3
		MPM-PV 20779	**Eocardia** *sp.*	right mandibular fragment with molar
		MPM-PV 20120	**Neoreomys australis**	right lower molar

Appendix 1 - Continued

Locality	*Estancia*	*Collection number*	*Systematic taxonomy*	*Material*
		MPM-PV 20121	**Neoreomys australis**	*left M1 or M2*
		MPM-PV 20122	**Eocardia** *sp.*	*left upper molar*
		MPM-PV 20123	*Octodontoidea*	*left lower incisor*
		MPM-PV 20124	**Neoreomys australis**	*left lower molar*
		MPM-PV 20125	**Neoreomys australis**	*right upper molar*
		MPM-PV 20126	**Neoreomys***?*	*lower incisor fragment*
		MPM-PV 20127	*Octodontoidea*	*incisor fragment*
		MPM-PV 20128	**Neoreomys australis**	*left p4*
		MPM-PV 20129	**Neoreomys australis**	*left m1 or m2*
		MPM-PV 20130	**Neoreomys australis**	*left m3 (broken)*
		MPM-PV 20131	**Neoreomys australis**	*lower tooth?*
		MPM-PV 20132	**Neoreomys australis**	*right P4*
		MPM-PV 20133	**Neoreomys australis**	*right M1 or M2*
		MPM-PV 20134	**Sciamys principalis**	*left lower molar*
		MPM-PV 20135	**Stichomys** *sp.*	*left DP4*
		MPM-PV 20136	**Stichomys** *sp.*	*right M1 or M2*
		MPM-PV 20137	**Stichomys** *sp.*	*left lower molar*
		MPM-PV 20138	**Perimys incavatus**	*right upper molar*
		MPM-PV 20139	**“Eocardia” excavata**	*left m1*
		MPM-PV 20140	**Eocardia** *sp.*	*right lower molar (broken)*
		MPM-PV 20141	**Phanomys/ Eocardia**	*left M1 or M3*
		MPM-PV 20142	*Caviomorpha?*	*long bone*
		MPM-PV 20143	**Spaniomys** *sp.*	*right mandible with m1-m2*
		MPM-PV 20144	**Phanomys mixtus**	*left M1 or M2*
		MPM-PV 20145	**Neoreomys australis**	*left mandible with p4-m1*
		MPM-PV 20146	**Neoreomys australis**	*right upper molar*
		MPM-PV 20147	**Neoreomys australis**	*left lower molar*
		MPM-PV 20148	**Neoreomys australis**	*left m1(broken)-m2 and left molar*
		MPM-PV 20149	**Spaniomys** *sp.*	*left mandible with m1(broken)-m2*
		MPM-PV 20150	**Neoreomys australis**	*right upper molar (broken)*
		MPM-PV 20151	**Perimys** *sp.*	*right P4*
		MPM-PV 20152	**Eocardia** *sp.*	*right lower molar*
	Estancia Santa Lucia (ESL)	*MPM-PV 20153*	**Neoreomys australis**	*mandibular symphysis with right m1, m2, and p4; and left ,1, m2, and p4*
		MPM-PV 20154	**Neoreomys australis**	*3 incisor fragments*
		MPM-PV 20155	**Perimys** *sp.*	*upper molar*
		MPM-PV 20156	**Eocardia** *sp.*	*right upper molar fragment*
		MPM-PV 20157	**Spaniomys** *sp.*	*right maxillary with DP4-M2*
		MPM-PV 20158	**Perimys** *sp.*	*right lower molar*
		MPM-PV 20159	**Neoreomys australis**	*right lower molar*
		MPM-PV 20160	**Perimys onustus**	*right mandible with p4-m1*
		MPM-PV 20161	**Perimys erutus**	*right mandibular fragment with p4*
		MPM-PV 20162	**Perimys erutus**	*right mandibular fragment with p4-m1*
		MPM-PV 20163	**Perimys erutus**	*left mandible with p4(broken)-m3*
		MPM-PV 20164	**Perimys erutus**	*left m3*
		MPM-PV 20165	**Eocardia montana**	*right mandible with m1-m2*
		MPM-PV 20166	**Neoreomys australis**	*right maxilla with DP4-M1*
		MPM-PV 20167	*Caviomorpha?*	*petrosal*

APPENDIX 1 - Continued

Locality	*Estancia*	*Collection number*	*Systematic taxonomy*	*Material*
		MPM-PV 20168	*Eocardidae*	*right mandible with cheek teeth*
		MPM-PV 20169	**Neoreomys***?*	*broken molar*
		MPM-PV 20170	**Scleromys** *sp.*	*right P4*
		MPM-PV 20171	**Perimys** *sp.*	*left upper tooth*
		MPM-PV 20172	**Neoreomys australis**	*left m1 or m2*
		MPM-PV 20173	**Neoreomys australis***?*	*incisor*
		MPM-PV 20174	**Eocardia** *sp.*	*tooth fragments and left DP4*
		MPM-PV 20175	**Acaremys** *sp.*	*p4, m1, and incisor*
		MPM-PV 20176	*Rodentia*	*edentulous right maxillary*
		MPM-PV 20177	**Perimys** *sp.*	*left lower tooth*
		MPM-PV 20178	**Spaniomys** *sp.*	*left mandible with m1-m3 and incisor*
		MPM-PV 20179	**Spaniomys** *sp.*	*right mandible with dp4-m2*
		MPM-PV 20180	**Spaniomys** *sp.*	*right maxillary fragment with DP4-M1*
		MPM-PV 20181	**Neoreomys australis**	*right mandibular fragment with m1*
		MPM-PV 20182	**Spaniomys** *sp.*	*right mandible with m1-m2*
		MPM-PV 20183	**Eocardia montana**	*right mandibular fragment with m2*
		MPM-PV 20184	*Octodontoidea*	*broken posterior portion of a lower tooth*
		MPM-PV 20185	*Acaremyidae*	*left upper molar*
		MPM-PV 20186	**Eocardia** *sp.*	*left M1*
		MPM-PV 20187	**Eocardia** *sp.*	*left M1*
		MPM-PV 20188	**Eocardia** *sp.*	*3 tooth fragments*
		MPM-PV 20189	**Perimys erutus**	*right mandibular fragment with p4*
		MPM-PV 20190	**Perimys erutus**	*left mandibular fragment with p4*
		MPM-PV 20191	**Perimys** *sp.*	*broken tooth*
		MPM-PV 20192	**Stichomys** *sp.*	*right M1 or M2*
		MPM-PV 20193	**Phanomys***?*	*broken lower tooth*
		MPM-PV 20194	**Neoreomys australis**	*left mandibular fragment with m1-m3*
		MPM-PV 20195	**Neoreomys australis**	*right upper molar*
		MPM-PV 20196	**Neoreomys australis**	*left m3*
		MPM-PV 20197	**Neoreomys australis**	*left m3*
		MPM-PV 20198	**Neoreomys australis**	*right p4*
		MPM-PV 20199	**Neoreomys australis**	*right mandibular fragment with m1 or m2*
		MPM-PV 20200	**Neoreomys australis**	*left m1 or m2*
		MPM-PV 20201	**Spaniomys** *sp.*	*left mandibular fragment with m1-m2*
		MPM-PV 20202	**Spaniomys** *sp.*	*left M3*
		MPM-PV 20203	**Spaniomys** *sp.*	*left upper molar*
		MPM-PV 20204	**Perimys erutus**	*right M3*
		MPM-PV 20205	*Octodontoidea*	*left mandibular fragment with dp4*
		MPM-PV 20206	**Eocardia** *sp.*	*left upper molar (broken)*
		MPM-PV 20207	**Prospaniomys** *sp. nov.?*	*left lower molar*
		MPM-PV 20208	**Perimys erutus**	*right P4*
		MPM-PV 20209	*Octodontoidea*	*right upper incisor*
		MPM-PV 20210	**Eocardia** *sp.*	*left lower molar*
		MPM-PV 20211	*Rodentia?*	*metapodial*
		MPM-PV 20212	**Scleromys** *sp.*	*left upper molar*
		MPM-PV 20213	**Neoreomys australis**	*right upper molar*
		MPM-PV 20214	**Neoreomys australis***?*	*incisor fragment*
		MPM-PV 20215	**Neoreomys australis***?*	*incisor fragment*
		MPM-PV 20216	**Acaremys** *sp.*	*left mandibular fragment with m2-m3(broken)*
		MPM-PV 20217	**Neoreomys australis**	*right lower molar*

Appendix 1 - Continued

Locality	*Estancia*	*Collection number*	*Systematic taxonomy*	*Material*
		MPM-PV 20218	*Caviomorpha*	*left auditory fragment*
		MPM-PV 20219	**Neoreomys australis**	*right P4*
		MPM-PV 20220	**Neoreomys australis**	*right upper molar*
		MPM-PV 20221	**Neoreomys australis**	*right upper molar*
		MPM-PV 20222	**Neoreomys australis**	*right M3*
		MPM-PV 20223	**Eocardia** *sp.*	*palatal fragment with broken left P4*
		MPM-PV 20224	**Eocardia** *sp.*	*right maxilla with M2-M3*
		MPM-PV 20225	**Eocardia** *sp.*	*2 broken upper tooth and 3 maxillary fragments*
		MPM-PV 20226	**Eocardia** *sp.*	*right m1 or m2*
		MPM-PV 20227	**Neoreomys australis**	*left M3?*
		MPM-PV 20228	**Neoreomys australis**	*right P4*
		MPM-PV 20229	**Eocardia** *sp.*	*right upper molar*
		MPM-PV 20230	**Spaniomys** *sp.*	*right upper molar*
		MPM-PV 20231	**Prolagostomus** *sp.*	*broken molar*
		MPM-PV 20232	**Prolagostomus** *sp.*	*broken molar*
		MPM-PV 20233	**Neoreomys australis***?*	*incisor fragment*
		MPM-PV 20234	**Neoreomys australis**	*left m3*
		MPM-PV 20235	**Neoreomys australis***?*	*incisor fragment*
		MPM-PV 20236	**Spaniomys** *sp.*	*left mandibular fragment with m1-m2*
SBB	*Estancia Cordón Alto (ECA)*	*MPM-PV 20237*	**Stichomys regularis**	*left mandibular fragment with m1-m2*
		MPM-PV 20238	**Prolagostomus** *sp.*	*isolated tooth*
		MPM-PV 20239	**Pliolagostomus notatus**	*left lower molar*
		MPM-PV 20240	**Pliolagostomus notatus**	*left lower molar*
		MPM-PV 20241	**"Eocardia" excavata**	*right maxilla with P4-M3*
		MPM-PV 20242	**Prolagostomus** *sp.*	*right lower molar*
		MPM-PV 20243	*Acaremyidae*	*right lower molar*
		MPM-PV 20244	**"Eocardia" excavata**	*right m1*
		MPM-PV 20245	**"Eocardia" excavata**	*right m2*
		MPM-PV 20246	*Octodontoidea*	*edentulous left mandible*
		MPM-PV 20247	*Acaremyidae*	*right upper molar*
		MPM-PV 20248	**Scleromys** *sp.*	*left p4*
		MPM-PV 20249	**Stichomys** *sp.*	*left DP4*
		MPM-PV 20250	**Phanomys** *sp.*	*left upper molar*
		MPM-PV 20251	**Pliolagostomus notatus**	*2 right low molars*
		MPM-PV 20252	**Pliolagostomus notatus**	*left lower molar*
		MPM-PV 20253	**Pliolagostomus notatus**	*2 left lower molars*
		MPM-PV 20254	**Pliolagostomus notatus**	*right p4*
		MPM-PV 20255	**Prolagostomus pusillus**	*2 left p4s*
		MPM-PV 20256	**Prolagostomus pusillus**	*right p4*
		MPM-PV 20257	**Prolagostomus pusillus**	*left upper molar*
		MPM-PV 20258	**Prolagostomus pusillus**	*right upper molar*
		MPM-PV 20259	**Pliolagostomus/Prolagostomus**	*2 broken tooth*
		MPM-PV 20260	**Prolagostomus pusillus**	*left lower molar*
		MPM-PV 20261	**Perimys onustus**	*right lower molar*
		MPM-PV 20262	**Prolagostomus pusillus**	*left lower tooth*
		MPM-PV 20263	**Neoreomys australis**	*right lower molar (broken)*
		MPM-PV 20264	**"Eocardia" excavata**	*right M3 (broken)*
		MPM-PV 20265	**Eocardia** *sp.*	*left lower molar*
		MPM-PV 20266	**Pliolagostomus notatus**	*right lower molar*
		MPM-PV 20267	**Prolagostomus** *sp.*	*right lower molar*

APPENDIX 1 - Continued

Locality	Estancia	Collection number	Systematic taxonomy	Material
		MPM-PV 20268	**Acarechimys***?*	right lower incisor
		MPM-PV 20269	**Neoreomys australis**	left upper molar
		MPM-PV 20270	**Neoreomys australis**	right upper molar (broken)
		MPM-PV 20271	**Perimys onustus**	broken molar
		MPM-PV 20272	**Acaremys murinus**	right mandibular fragment with m1-m3
		MPM-PV 20273	**Eocardia montana?**	right p4
		MPM-PV 20274	**Eocardia montana?**	right m1
		MPM-PV 20275	**Eocardia montana?**	left m1 or m2
		MPM-PV 20276	**Stichomys regularis**	left mandibular fragment with m1-m2
		MPM-PV 20277	**Stichomys regularis**	right mandibular fragment with m2-m3
		MPM-PV 20278	**Prolagostomus** *sp.*	lower cheek teeth
		MPM-PV 20279	**Eocardia montana**	left m1 or m2
		MPM-PV 20280	**Eocardia montana**	right p4
		MPM-PV 20281	**Eocardia montana**	right m1
		MPM-PV 20282	**Eocardia montana**	right m2
		MPM-PV 20283	**Neoreomys australis**	right maxillary fragment with M1-M2
		MPM-PV 20284	**Neoreomys australis**	left M1 or M2
		MPM-PV 20285	**Neoreomys australis**	right M3
		MPM-PV 20286	**Neoreomys australis**	left M3
		MPM-PV 20287	**Neoreomys australis**	left M1 or M2
		MPM-PV 20288	**Neoreomys australis**	right m1
		MPM-PV 20289	**Neoreomys australis**	right m2
		MPM-PV 20290	**Neoreomys australis**	right m3
		MPM-PV 20291	**Scleromys** *sp.*	left P4
		MPM-PV 20292	**Neoreomys australis**	right maxillary fragment with M1-M3
		MPM-PV 20295	**Eocardia** *sp.*	right maxillary fragment with DP4-M1
		MPM-PV 20296	**Eocardia** *sp.*	right upper molar
		MPM-PV 20297	**Pliolagostomus notatus**	left upper molar
		MPM-PV 20298	*Octodontoidea*	left upper incisor
		MPM-PV 20299	**Spaniomys** *sp.*	right mandible with dp4-m2
		MPM-PV 15098	**Acarechimys minutissimus**	left mandible with dp4 and broken incisor
		MPM-PV 20300	**Eocardia montana**	right mandible with m1-m2
		MPM-PV 20301	**Eocardia montana**	right m3
		MPM-PV 20302	**Prolagostomus** *sp.*	left m3
		MPM-PV 20303	*Caviomorpha*	mandibular fragment with broken incisor
		MPM-PV 20304	**Stichomys** *sp.*	left mandibular fragment with m2
		MPM-PV 20305	**Prolagostomus** *sp.*	right lower molar
		MPM-PV 20306	**Eocardia montana***?*	right mandibular fragment with p4-m2 and broken incisor
		MPM-PV 20307	**Eocardia montana***?*	left m1 or m2
		MPM-PV 20308	**Sciamys principalis**	right mandible with p4-m3
		MPM-PV 20309	*Octodontoidea*	left mandibular fragment with incisor
		MPM-PV 20310	**Spaniomys** *sp.*	left maxillary fragment with M1-M2
		MPM-PV 20311	*Octodontoidea*	right lower incisor fragment
		MPM-PV 20312	**Eocardia montana**	right mandible with p4-m3
		MPM-PV 20313	**Neoreomys australis**	right upper molar (broken)
		MPM-PV 20314	**Prolagostomus** *sp.*	left mandibular fragment with p4-m2 and incisor
		MPM-PV 20315	**Prolagostomus** *sp.*	left M3
		MPM-PV 20316	**Prolagostomus** *sp.*	isolated incisor

APPENDIX 1 - Continued

Locality	*Estancia*	*Collection number*	*Systematic taxonomy*	*Material*
		MPM-PV 20317	**Prolagostomus pusillus**	*right maxillary fragment with M1-M2*
		MPM-PV 20318	**Prolagostomus pusillus**	*right mandible with m1-m3*
		MPM-PV 20319	**Pliolagostomus***?*	*M3?*
		MPM-PV 20320	**Pliolagostomus***?*	*right mandibular fragment with p4*
		MPM-PV 15091	**Acarechimys constans**	*right mandible with dp4-m2*
		MPM-PV 20321	**Perimys erutus**	*right mandible with p4-m3*
		MPM-PV 20322	**Prolagostomus** *sp.*	*left lower molar*
		MPM-PV 20323	**Neoreomys australis**	*right lower molar*
		MPM-PV 20324	**Neoreomys australis**	*right lower molar*
		MPM-PV 20325	**Neoreomys australis**	*left P4*
		MPM-PV 20326	**Eocardia montana**	*left mandible with p4-m3*
		MPM-PV 20327	**Eocardia montana**	*left m2 or m3*
		MPM-PV 20328	**Eocardia***?*	*portion of a lower incisor*
		MPM-PV 20329	**Neoreomys australis**	*right M1 or M2*
		MPM-PV 20330	**Neoreomys australis**	*left M1 or M2*
		MPM-PV 20331	**Neoreomys australis**	*right M1 or M2*
		MPM-PV 20332	**Neoreomys australis**	*right upper premolar*
		MPM-PV 20333	**Neoreomys australis**	*left upper molar*
		MPM-PV 20334	**Neoreomys***?*	*2 incisor fragments*
		MPM-PV 20335	**Stichomys** *sp.*	*mandibular fragment with m2*
		MPM-PV 20336	**Prolagostomus** *sp.*	*right lower molar*
		MPM-PV 20337	**Spaniomys** *sp.*	*right lower molar*
		MPM-PV 20338	**Stichomys** *sp.*	*right lower molar*
		MPM-PV 20339	*cf.* **Scleromys**	*upper tooth fragment*
		MPM-PV 20340	*Octodontoidea*	*edentulous left mandibular fragment*
		MPM-PV 20341	**Stichomys** *sp.*	*right DP4-M1*
		MPM-PV 20342	**Stichomys** *sp.*	*left M1 or M2*
		MPM-PV 20343	**Prolagostomus pusillus**	*left p4-m2*
		MPM-PV 20344	**Neoreomys***?*	*right upper molar (broken)*
		MPM-PV 20345	**Stichomys***?*	*lower incisor*
		MPM-PV 20346	**Acarechimys minutissimus**	*left mandible with p4-m3*
		MPM-PV 20347	**Stichomys** *sp.*	*left DP4*
		MPM-PV 20348	**Prolagostomus** *sp.*	*right p4*
		MPM-PV 20349	**Prolagostomus/Pliolagostomus**	*upper molar*
		MPM-PV 20350	*Rodentia?*	*humerous distal portion*
		MPM-PV 20351	*Rodentia?*	*metatarsal?*
		MPM-PV 20352	**Sciamys** *sp.*	*left mandible with p4-m1 and incisor*
		MPM-PV 20353	**Pliolagostomus notatus**	*left lower tooth*
		MPM-PV 20354	**Eocardia** *sp.*	*lower molar fragment*
		MPM-PV 20355	**Perimys onustus**	*right mandible with m1-m3*
		MPM-PV 20356	**Stichomys/ Adelphomys**	*right mandible with dp4-m2*
		MPM-PV 20357	**Neoreomys australis**	*left upper molar*
		MPM-PV 20358	**Neoreomys australis**	*right lower molar*
		MPM-PV 20359	**Prolagostomus pusillus**	*left upper molar*
		MPM-PV 20360	**Pliolagostomus notatus**	*left lower molar*
		MPM-PV 20361	**Neoreomys australis**	*skull fragment and broken teeth*
		MPM-PV 20362	**Prolagostomus pusillus**	*right mandibular fragment with p4-m2(broken) and incisor*
		MPM-PV 20363	**Eocardia** *sp.*	*right p4*
		MPM-PV 20364	**Acarechimys minutissimus**	*right mandible with m1-m3*

APPENDIX 1 - Continued

Locality	*Estancia*	*Collection number*	*Systematic taxonomy*	*Material*
		MPM-PV 20365	**Eocardia** *sp.*	*right m3*
		MPM-PV 20366	**Neoreomys australis**	*right lower molar*
		MPM-PV 20367	**Prolagostomus pusillus**	*right mandible with m1-m3(broken)*
		MPM-PV 20368	**Prolagostomus pusillus**	*maxilla with right and left P4-M3*
		MPM-PV 15100	**Acarechimys minutissimus**	*right mandible with dp4(broken)-m2*
		MPM-PV 15101	**Acarechimys minutissimus**	*right mandible with dp4-m1*
		MPM-PV 20369	**Eocardia** *sp.*	*left upper cheek teeth*
		MPM-PV 20370	**Perimys** *sp.*	*right lower molar*
		MPM-PV 20371	**Prolagostomus pusillus**	*left maxillary fragment with P4-M3*
		MPM-PV 15092	**Acarechimys constans***?*	*right mandible with dp4-m2 and incisor*
		MPM-PV 20372	**Steiromys***?*	*left maxillary fragment with P4-M1*
		MPM-PV 20373	**Stichomys** *sp.*	*left M1 or M2*
		MPM-PV 20374	**Eocardia** *sp.*	*left mandible with m1 or m2*
		MPM-PV 20375	**Perimys onustus**	*left mandibular fragment with p4*
		MPM-PV 20376	**Prolagostomus pusillus**	*left mandibular fragment with p4-m3 and broken incisor*
		MPM-PV 20377	**Prolagostomus** *sp.*	*left maxillary fragment with P4-M2*
		MPM-PV 20378	**Eocardia** *sp.*	*left upper molar*
		MPM-PV 20379	**Prolagostomus pusillus**	*right p4*
		MPM-PV 20380	**Prolagostomus pusillus**	*right lower cheek teeth*
		MPM-PV 20381	**Prolagostomus/Pliolagostomus**	*broken cheek teeth*
		MPM-PV 20382	**Prolagostomus/Pliolagostomus**	*broken cheek teeth*
		MPM-PV 20383	**Acarechimys***?*	*right mandible with m1-m2*
		MPM-PV 20384	**Steiromys detentus**	*right mandible with dp4-m3(broken)*
		MPM-PV 20385	**Perimys onustus**	*left lower molar*
		MPM-PV 20386	**Neoreomys australis**	*right upper molar*
		MPM-PV 20387	**Pliolagostomus notatus**	*left M3*
		MPM-PV 20388	**Acarechimys minutissimus**	*right mandible with m1-m3*
		MPM-PV 20389	**Spaniomys** *sp.*	*right maxillary fragment with M1-M3*
		MPM-PV 20390	**Spaniomys** *sp.*	*left maxillary fragment with M1-M2*
		MPM-PV 20391	**Sciamys principalis**	*right mandibular fragment with p4-m2*
		MPM-PV 15099	**Acarechimys minutissimus**	*left mandible with m1-m2 and broken incisor*
		MPM-PV 20392	**Spaniomys** *sp.*	*M2-M3*
		MPM-PV 20393	**Eocardia** *sp.*	*right upper molar*
		MPM-PV 20394	**Eocardia montana**	*right upper molar*
		MPM-PV 20395	**Perimys** *sp.*	*left M1 or M2*
		MPM-PV 20396	**Prolagostomus** *sp.*	*left M3*
		MPM-PV 20397	**Prolagostomus** *sp.*	*left lower molar*
		MPM-PV 20398	**Prolagostomus/Pliolagostomus**	*broken tooth*
		MPM-PV 20399	*Cavioidea*	*broken tooth*
		MPM-PV 20400	**Eocardia** *sp.*	*isolated m1 or m2*
		MPM-PV 20401	**Eocardia montana**	*left mandible with p4-m2*
		MPM-PV 20402	**Eocardia** *sp.*	*left m3*
		MPM-PV 20403	**Prolagostomus pusillus**	*right M3*
		MPM-PV 20404	**Prolagostomus pusillus**	*left lower molar*
		MPM-PV 20405	**Pliolagostomus notatus**	*right maxillary fragment with P4-M3*
		MPM-PV 20406	**Pliolagostomus notatus**	*left lower molar*
		MPM-PV 20407	**Prolagostomus/Pliolagostomus**	*left p4*
		MPM-PV 20408	**Neoreomys australis**	*right lower molar*
		MPM-PV 20409	**Eocardia montana**	*left mandible with dp4-m1 and incisor*

APPENDIX 1 - Continued

Locality	*Estancia*	*Collection number*	*Systematic taxonomy*	*Material*
		MPM-PV 20410	**Eocardia** *sp.*	*right M3*
		MPM-PV 20411	**Eocardia** *sp.*	*right lower molar*
	Estancia Cordón Alto2 (ECA2)	*MPM-PV 20412*	*cf.* **Neoreomys**	*lower isolated molar*
		MPM-PV 20413	**Pliolagostomus notatus**	*right upper molar*
		MPM-PV 20414	**Prolagostomus** *sp.*	*left mandibular fragment with p4-m2*
		MPM-PV 20415	**Stichomys** *sp.*	*left mandibular fragment with m1-m3*
		MPM-PV 20416	**Spaniomys** *sp.*	*left lower molar*
		MPM-PV 20417	**Neoreomys australis**	*left dp4*
		MPM-PV 20418	*cf.* **Neoreomys**	*right dp4*
		MPM-PV 20419	**Phanomys***?*	*left upper molar*
		MPM-PV 20420	**Eocardia montana**	*left upper molar*
		MPM-PV 20421	**Perimys** *sp.*	*left p4?*
		MPM-PV 20422	**Pliolagostomus notatus**	*right lower molar*
		MPM-PV 20423	**Neoreomys australis**	*left m1 or m2*
		MPM-PV 20424	**Sciamys principalis**	*left mandibular fragment with p4(broken)-m1*
		MPM-PV 20425	**Spaniomys** *sp.*	*left mandibular fragment with m1-m2*
		MPM-PV 20426	**Stichomys** *sp.*	*left mandibular fragment with dp4-m2*
		MPM-PV 20427	**Prolagostomus** *sp.*	*left M3*
		MPM-PV 20428	**Prolagostomus** *sp.*	*left lower molar*
		MPM-PV 20429	**Stichomys** *sp.*	*right mandibular fragment with m1 and incisor*
		MPM-PV 20430	**Stichomys***?/***Adelphomys***?*	*left DP4*
		MPM-PV 20431	**Eocardia** *sp.*	*right mandibular fragment with p4-m2*
		MPM-PV 20432	**Eocardia***?*	*right M3*
		MPM-PV 20433	**Eocardia** *sp.*	*right upper molar*
		MPM-PV 20434	**Neoreomys australis**	*right lower molar*
		MPM-PV 20435	**Neoreomys australis**	*left M3*
		MPM-PV 20436	**Prolagostomus** *sp.*	*left mandible with p4 and incisor*
		MPM-PV 20437	**Neoreomys australis**	*left upper tooth*
		MPM-PV 20438	**Neoreomys australis**	*left p4*
		MPM-PV 20439	**Neoreomys australis**	*right lower molar (broken)*
		MPM-PV 20440	**Neoreomys australis**	*P4*
		MPM-PV 20441	**Eocardia** *sp.*	*left lower molar*
		MPM-PV 20442	**Steiromys detentus**	*right mandibular fragment with p4-m3*
		MPM-PV 20443	**Perimys erutus**	*right mandibular fragment with p4-m1*
		MPM-PV 20444	**Stichomys regularis**	*left mandibular fragment with dp4-m2*
		MPM-PV 20445	**Spaniomys** *sp.*	*right mandible with m1-m2*
		MPM-PV 20446	**Prolagostomus** *sp.*	*right maxillary fragment with M1-M2*
		MPM-PV 20447	**Stichomys** *sp.*	*right mandible with m1-m2*
		MPM-PV 20448	**Pliolagostomus notatus**	*right maxillary fragment with M1-M2*
		MPM-PV 20449	**Spaniomys** *sp.*	*left upper molar*
		MPM-PV 20450	**Eocardia** *sp.*	*right M1 or M2*
		MPM-PV 20451	**Eocardia** *sp.*	*broken upper molar*
		MPM-PV 20452	**Eocardia montana**	*lower molar*
		MPM-PV 20453	**Pliolagostomus notatus**	*right lower molar*
		MPM-PV 20454	**Pliolagostomus notatus**	*left lower molar*
		MPM-PV 20455	**Pliolagostomus notatus**	*left lower molar*
		MPM-PV 20456	**Prolagostomus** *sp.*	*isolated cheek teeth*
		MPM-PV 20457	**Prolagostomus** *sp.*	*isolated cheek teeth*
		MPM-PV 20293	**Neoreomys australis**	*right maxillary fragment with P4-M1*

APPENDIX 1 - Continued

Locality	*Estancia*	*Collection number*	*Systematic taxonomy*	*Material*
		MPM-PV 20294	**Prospaniomys** *sp. nov.?*	*right DP4-M1*
		MPM-PV 20458	**Neoreomys australis**	*right P4*
		MPM-PV 20459	**Neoreomys australis**	*right lower molar*
		MPM-PV 20460	**Prolagostomus** *sp.*	*right lower molar*
		MPM-PV 20461	**Sciamys principalis**	*right maxillary fragment with P4*
		MPM-PV 20462	**Sciamys principalis**	*left mandible with p4-m2*
		MPM-PV 20463	**Spaniomys** *sp.*	*left maxillary fragment with M1*
		MPM-PV 20464	**Spaniomys** *sp.*	*left upper molar*
		MPM-PV 20465	**Spaniomys** *sp.*	*right upper molar (broken)*
		MPM-PV 20466	**Stichomys** *sp.*	*right m3*
		MPM-PV 20467	*Acaremyidae*	*left lower molar*
		MPM-PV 20468	**Prolagostomus** *sp.*	*left lower molar*
		MPM-PV 20469	*Octodontoidea*	*right upper incisor*
		MPM-PV 20470	*Caviomorpha*	*right upper incisor*
		MPM-PV 20471	*Caviomorpha*	*left lower incisor*
		MPM-PV 20472	**Pliolagostomus/Prolagostomus**	*left p4*
		MPM-PV 20473	**Prolagostomus** *sp.*	*left mandibular fragment with p4-m2*
		MPM-PV 20474	**Pliolagostomus notatus**	*right mandibular fragment with p4*
		MPM-PV 20475	**Spaniomys** *sp.*	*left maxillary fragment with M1*
		MPM-PV 20476	**Spaniomys** *sp.*	*right maxillary fragment with DP4*
		MPM-PV 20477	*Chinchilloidea*	*broken teeth*
		MPM-PV 20478	**Acarechimys minutus**	*left mandibular fragment with dp4-m2*
		MPM-PV 20479	**Acarechimys minutissimus**	*left maxillary fragment with DP4-M1*
		MPM-PV 20480	**Acarechimys minutissimus**	*left maxillary fragment with M1-M2*
		MPM-PV 20481	*Octodontoidea*	*left mandibular fragment with incisor*
		MPM-PV 20482	*Caviomorpha*	*right mandibular fragment with incisor*
		MPM-PV 20483	**Spaniomys** *sp.*	*right upper cheek teeth*
		MPM-PV 20484	**Stichomys** *sp.*	*right DP4*
		MPM-PV 20485	**Stichomys** *sp.*	*left upper molar*
		MPM-PV 20486	**Stichomys** *sp.*	*right upper molar*
		MPM-PV 20487	*Acaremyidae*	*broken cheek teeth*
		MPM-PV 20488	**Prolagostomus** *sp.*	*right cheek teeth*
		MPM-PV 20489	**Prolagostomus** *sp.*	*left cheek teeth*
		MPM-PV 20490	**Prolagostomus** *sp.*	*left cheek teeth*
		MPM-PV 20491	**Prolagostomus** *sp.*	*left cheek teeth*
		MPM-PV 20492	**Pliolagostomus notatus**	*left upper cheek teeth*
		MPM-PV 20493	**Pliolagostomus notatus**	*right p4*
		MPM-PV 20494	**Pliolagostomus notatus**	*right upper cheek teeth*
		MPM-PV 20495	**Pliolagostomus notatus**	*right upper cheek teeth*
		MPM-PV 20496	**Pliolagostomus/Prolagostomus**	*isolated cheek teeth*
		MPM-PV 20497	**Pliolagostomus/Prolagostomus**	*isolated cheek teeth*
		MPM-PV 20498	**Eocardia** *sp.*	*left lower cheek teeth*
		MPM-PV 20499	**Eocardia** *sp.*	*upper cheek teeth*
		MPM-PV 20500	*Octodontoidea*	*left lower incisor*
		MPM-PV 20501	*Octodontoidea*	*edentulous left mandible*
		MPM-PV 20502	**Prolagostomus** *sp.*	*left M3*
		MPM-PV 20503	**Stichomys** *sp.*	*right m2*
		MPM-PV 20504	**Prolagostomus** *sp.*	*isolated cheek teeth*
		MPM-PV 20505	**Perimys onustus**	*left lower molar*
		MPM-PV 20506	**Prolagostomus** *sp.*	*right p4*

Appendix 1 - Continued

Locality	*Estancia*	*Collection number*	*Systematic taxonomy*	*Material*
		MPM-PV 20507	**Prolagostomus** *sp.*	*right lower molar*
		MPM-PV 20508	**Eocardia** *sp.*	*left lower molar*
		MPM-PV 20509	*Caviomorpha*	*left mandible with broken incisor*
		MPM-PV 20510	*Octodontoidea*	*left mandible with broken incisor*
		MPM-PV 20511	**Prolagostomus** *sp.*	*left mandibular fragment with p4-m3*
		MPM-PV 20512	**Pliolagostomus/Prolagostomus**	*isolated broken cheek teeth*
		MPM-PV 20513	**Pliolagostomus/Prolagostomus**	*isolated broken cheek teeth*
		MPM-PV 20514	**Stichomys** *sp.*	*right DP4*
		MPM-PV 20515	**Stichomys** *sp.*	*left dp4*
		MPM-PV 20516	**Stichomys** *sp.*	*upper molar (broken)*
		MPM-PV 20517	**Neoreomys australis**	*right lower cheek teeth*
		MPM-PV 20518	**Neoreomys australis**	*right lower cheek teeth*
		MPM-PV 20519	*Caviomorpha*	*incisor*
		MPM-PV 20520	*Octodontoidea*	*incisor*
		MPM-PV 20521	*Octodontoidea*	*left lower incisor*
		MPM-PV 20522	*Octodontoidea*	*left upper incisor*
		MPM-PV 20523	*Rodentia?*	*isolated phalanx*
		MPM-PV 20524	**Spaniomys riparius**	*right mandible with m1-m2*
		MPM-PV 20525	**Neoreomys australis**	*left lower tooth*
		MPM-PV 20526	**Neoreomys***?*	*upper tooth*
		MPM-PV 20527	**Neoreomys***?*	*broken tooth*
		MPM-PV 20528	**Prolagostomus** *sp.*	*right m1-m2*
		MPM-PV 20529	**Schistomys erro**	*right maxillary fragment with P4-M3*
		MPM-PV 20530	**Prolagostomus** *sp.*	*left lower molar*
		MPM-PV 20531	**Prolagostomus** *sp.*	*left lower molar*
		MPM-PV 20532	**Pliolagostomus/Prolagostomus**	*isolated tooth*
		MPM-PV 20533	**Stichomys** *sp.*	*DP4*
		MPM-PV 17430	**Acarechimys gracilis**	*left mandible with dp4-m3*
		MPM-PV 20534	**Perimys** *sp.*	*right lower molar*
		MPM-PV 20535	**Perimys** *sp.*	*right lower molar (broken)*
		MPM-PV 20536	*Chinchilloidea?*	*left mandibular fragment with incisor*
		MPM-PV 20537	**Prolagostomus** *sp.*	*right mandibular fragment with p4*
		MPM-PV 20538	**Acaremys murinus**	*right mandible with m2-m3 and isolated m1*
		MPM-PV 20539	**Neoreomys australis**	*left lower molar*
		MPM-PV 20540	**Neoreomys australis**	*broken lower molar*
		MPM-PV 20541	**Prolagostomus** *sp.*	*lower cheek teeth*
		MPM-PV 20542	**Eocardia/ Schistomys**	*left lower molar*
		MPM-PV 20543	**Eocardia montana**	*right mandibular fragment with m2*
		MPM-PV 20544	**Eocardia** *sp.*	*left mandibular fragment with m1-m2*
		MPM-PV 20545	**Eocardia** *sp.*	*left mandibular fragment with m3*
		MPM-PV 20546	*Caviomorpha*	*right maxilla with broken incisor*
		MPM-PV 20547	**Prolagostomus** *sp.*	*cheek teeth*
		MPM-PV 15093	**Acarechimys constans**	*right mandible with dp4-m2*
		MPM-PV 15102	**Acarechimys minutissimus**	*left mandible with m1*
		MPM-PV 17426	**Acarechimys minutissimus**	*right mandible with dp4-m1 and incisor*
		MPM-PV 20548	**Perimys***?*	*broken tooth*
		MPM-PV 20549	**Stichomys regularis**	*right mandible with m1-m2*
		MPM-PV 20550	**Stichomys/ Adelphomys**	*left mandibular fragment with m2*
		MPM-PV 20551	**Perimys onustus**	*right p4*
		MPM-PV 20552	**Prolagostomus** *sp.*	*broken tooth*

APPENDIX 1 - **Continued**

Locality	*Estancia*	*Collection number*	*Systematic taxonomy*	*Material*
		MPM-PV 20553	**Eocardia montana**	*right mandibular fragment with p4-m2*
		MPM-PV 20554	**Phanomys** *sp.*	*right mandible with p4-m1*
		MPM-PV 20555	**Steiromys detentus**	*right mandible with p4 and incisor*
		MPM-PV 20556	**Spaniomys riparius**	*right mandible with m1-m2*
		MPM-PV 20557	**Spaniomys riparius**	*left mandibular fragment with m1-m3*
		MPM-PV 20558	**Spaniomys riparius**	*left mandibular fragment with m1-m2*
		MPM-PV 20559	**Stichomys regularis**	*left mandibular fragment with m1-m2*
		MPM-PV 17433	**Acarechimys gracilis**	*left mandibular fragment with m1-m2*
		MPM-PV 17434	**Acarechimys gracilis**	*left mandibular fragment with dp4-m2*
		MPM-PV 20560	**Prospaniomys** *sp. nov.?*	*upper molar*
		MPM-PV 20561	**Dudumus** *sp. nov.?*	*right DP4-M1*
		MPM-PV 20562	**Spaniomys** *sp.*	*left lower molar*
		MPM-PV 20563	**Prolagostomus pusillus**	*right M3*
		MPM-PV 20564	**Prolagostomus pusillus**	*right mandibular fragment with p4-m2*
		MPM-PV 20565	**Prolagostomus pusillus**	*left maxillary fragment with P4*
		MPM-PV 20566	**Prolagostomus pusillus**	*left mandibular fragment with m2-m3*
		MPM-PV 20567	**Prolagostomus** *sp.*	*right lower molar*
		MPM-PV 20568	**Pliolagostomus notatus**	*right upper molar*
		MPM-PV 20569	**Prolagostomus** *sp.*	*right upper molar?*
		MPM-PV 20570	**Prolagostomus** *sp.*	*left lower molar*
		MPM-PV 20571	**Eocardia** *sp.*	*right upper molar*
		MPM-PV 20572	**Neoreomys australis**	*right upper molar*
		MPM-PV 20573	**Prolagostomus** *sp.*	*left maxillary fragment with M1-M2*
		MPM-PV 20574	**Prolagostomus pusillus**	*right mandibular fragment with p4*
		MPM-PV 20575	**Stichomys regularis**	*left dp4*
		MPM-PV 20576	**Pliolagostomus notatus**	*right maxillary fragment P4-M2*
		MPM-PV 20577	**Perimys onustus**	*right m3*
		MPM-PV 20578	**Eocardia** *sp.*	*left mandibular fragment with p4-m1*
		MPM-PV 20579	**Pliolagostomus/Prolagostomus**	*left maxilla with P4-M2 (broken)*
		MPM-PV 20580	**Pliolagostomus/Prolagostomus**	*left maxillary fragment with P4-M1*
		MPM-PV 20581	**Eocardia montana**	*right mandible with dp4-m1*
		MPM-PV 20582	**Eocardia** *sp.*	*left? broken molar*
		MPM-PV 20583	**Neoreomys australis**	*left lower molar*
		MPM-PV 20584	**Neoreomys australis**	*left lower molar (broken)*
		MPM-PV 20585	**Perimys onustus**	*left M1 or M2*
		MPM-PV 20586	**Prolagostomus pusillus**	*left maxillary fragment with P4*
		MPM-PV 20587	**Prolagostomus pusillus**	*left M1*
		MPM-PV 20588	**Eocardia montana**	*left p4*
		MPM-PV 20589	**Prolagostomus pusillus**	*left maxillary fragment with M1-M2*
		MPM-PV 20590	**Prolagostomus** *sp.*	*left upper molar*
		MPM-PV 20591	**Prolagostomus** *sp.*	*right upper molar*
		MPM-PV 20592	**Prolagostomus** *sp.*	*isolated tooth*
		MPM-PV 20593	**Prolagostomus** *sp.*	*isolated tooth*
		MPM-PV 20594	**Prolagostomus** *sp.*	*left maxillary fragment with P4*
		MPM-PV 20595	**Acarechimys** *sp.*	*left maxillary fragment with DP4-M1*
		MPM-PV 20596	*cf.* **Acarechimys minutissimus**	*left mandibular fragment with dp4-m3*
		MPM-PV 20597	**Prolagostomus** *sp.*	*isolated molar*
		MPM-PV 20598	**Steiromys detentus**	*left p4*
		MPM-PV 20599	**Pliolagostomus notatus**	*left M3*
		MPM-PV 20600	**Prolagostomus pusillus**	*right M3*

Appendix 1 - Continued

Locality	*Estancia*	*Collection number*	*Systematic taxonomy*	*Material*
		MPM-PV 20601	*Cavioidea*	*broken tooth*
		MPM-PV 20602	*Octodontoidea*	*maxillary fragment with tooth*
		MPM-PV 20603	**Prolagostomus** *sp.*	*isolated tooth*
		MPM-PV 20604	**Prolagostomus** *sp.*	*right lower molar*
		MPM-PV 20605	**Prolagostomus** *sp.*	*left upper molar*
		MPM-PV 20606	**Prolagostomus pusillus**	*right mandibular fragment with p4 and broken incisor*
		MPM-PV 20607	**Prolagostomus** *sp.*	*left mandibular fragment with p4*
		MPM-PV 20608	**Prolagostomus pusillus**	*left M3*
		MPM-PV 20609	**Prolagostomus pusillus**	*left M3*
		MPM-PV 20610	**Prolagostomus pusillus**	*left M3*
		MPM-PV 20611	**Prolagostomus** *sp.*	*isolated tooth*
		MPM-PV 20612	**Pliolagostomus/Prolagostomus**	*left p4*
		MPM-PV 20613	**Prolagostomus** *sp.*	*right upper molar*
		MPM-PV 20614	**Pliolagostomus notatus**	*left upper molar*
		MPM-PV 20615	**Prolagostomus** *sp.*	*isolated tooth*
		MPM-PV 20616	**Prolagostomus** *sp.*	*broken tooth*
		MPM-PV 20617	**Stichomys** *sp.*	*right M1 or M2*
		MPM-PV 20618	**Spaniomys** *sp.*	*left mandibular fragment with m2*
		MPM-PV 20619	**Stichomys** *sp.*	*left dp4*
		MPM-PV 20620	**Stichomys** *sp.*	*left m2*
		MPM-PV 20621	**Spaniomys** *sp.*	*upper molar (broken)*
		MPM-PV 20622	**Acarechimys***?*	*right DP4-M1*
		MPM-PV 20623	*Octodontoidea*	*broken upper tooth*
		MPM-PV 20624	**Neoreomys australis**	*left upper molar*
		MPM-PV 20625	**Neoreomys australis**	*left upper molar*
		MPM-PV 20626	**Neoreomys australis**	*left p4*
		MPM-PV 20627	**Prolagostomus pusillus**	*left p4*
		MPM-PV 20628	*Octodontoidea*	*left mandible with broken incisor*
		MPM-PV 15096	**Acarechimys constans**	*left mandible with dp4-m2 and incisor*
		MPM-PV 20629	**Prolagostomus** *sp.*	*right p4*
		MPM-PV 20630	**Steiromys duplicatus**	*left upper molar*
		MPM-PV 20631	**Stichomys** *sp.*	*left M1 or M2*
		MPM-PV 20632	**Spaniomys** *sp.*	*left upper molar*
		MPM-PV 20633	**Spaniomys** *sp.*	*left M3*
		MPM-PV 20634	**Stichomys regularis**	*left mandibular fragment with m2-m3*
		MPM-PV 20635	**Neoreomys australis**	*right upper molar*
		MPM-PV 20636	**Neoreomys australis**	*left lower molar*
		MPM-PV 20637	**Acarechimys constans**	*right mandible with dp4 and incisor*
		MPM-PV 20638	**Eocardia / Schistomys**	*broken tooth*
		MPM-PV 20639	**Prolagostomus pusillus**	*left M3*
		MPM-PV 20640	**Stichomys regularis**	*left mandible with m1-m2 and incisor*
		MPM-PV 17431	**Acarechimys gracilis**	*right mandible with m1-m3*
		MPM-PV 20641	**Acarechimys** *sp.*	*right mandible with m1-m2*
		MPM-PV 20642	**Stichomys regularis**	*left mandible with dp4-m1 and incisor*
		MPM-PV 20643	**Stichomys regularis**	*right maxillary fragment with DP4-M2*
		MPM-PV 20644	**Stichomys regularis**	*left maxillary fragment with DP4-M3*
		MPM-PV 20645	**Stichomys regularis**	*right mandibular fragment with m3*
		MPM-PV 20646	**Spaniomys riparius**	*right mandible with dp4-m3*
		MPM-PV 20647	**Spaniomys riparius**	*left maxillary fragment with DP4-M2*

Appendix 1 - Continued

Locality	*Estancia*	*Collection number*	*Systematic taxonomy*	*Material*
		MPM-PV 17432	**Acarechimys gracilis**	*right mandibular fragment with dp4 (broken)-m3*
		MPM-PV 20648	**Phanomys** *sp.*	*right mandible with m1-m2*
		MPM-PV 20649	*Octodontoidea*	*edentulous right mandibular fragment*
		MMP-PV 17427	**Acarechimys minutissimus**	*right mandible with dp4-m2 and incisor*
		MPM-PV 15094	**Acarechimys constans**	*left mandibular fragment with dp4-m1*
		MPM-PV 20650	**Sciamys** *sp.*	*left maxillary fragment with P4-M3*
		MPM-PV 20651	**Perimys onustus**	*right maxillary fragment with P4-M3*
		MPM-PV 20652	**Steiromys detentus**	*left mandibular fragment with p4*
		MPM-PV 20653	**Acaremys** *sp.*	*left mandibular fragment with p4-m2*
		MPM-PV 20654	*caviomorpha?*	*basicranium/left auditory bulla?*
		MPM-PV 20655	**Perimys onustus**	*left maxillary fragment with P4-M3*
		MPM-PV 15095	**Acarechimys constans**	*right mandibular fragment with m1-m3*
		MPM-PV 20656	**Stichomys/ Adelphomys**	*right m1*
		MPM-PV 20657	**Phanomys** *sp.*	*right upper molar?*
		MPM-PV 20658	**Perimys onustus**	*right p4*
		MPM-PV 20659	**Perimys onustus**	*right p4*
		MPM-PV 20660	**Perimys onustus**	*left M1 or right M3*
		MPM-PV 20661	**Perimys onustus**	*left lower molar?*
		MPM-PV 20662	**Perimys onustus**	*left lower molar?*
		MPM-PV 20663	**Perimys onustus**	*left lower molar?*
		MPM-PV 20664	**Perimys onustus**	*left lower molar?*
		MPM-PV 20665	**Perimys onustus**	*cheek tooth*
		MPM-PV 20666	**Perimys onustus**	*cheek tooth*
		MPM-PV 20667	**Sciamys principalis**	*right mandible with p4-m3*
		MPM-PV 20668	**Sciamys latidens**	*right mandibular fragment with p4-m2*
		MPM-PV 20669	**Neoreomys australis**	*right upper molar*
		MPM-PV 15097	**Acarechimys constans**	*right mandible with m2-m3*
	Estancia El Tordillo (EET)	*MPM-PV 20670*	**Perimys onustus**	*left mandible with p4-m3 and incisor*
		MPM-PV 20671	**Perimys erutus**	*right mandible with p4-m3*
		MPM-PV 20672	**Perimys***?*	*right mandible with broken incisor*
		MPM-PV 20673	**Perimys***?*	*incisor fragment*
		MPM-PV 20674	**Eocardia /Schistomys**	*right maxillary fragment with M1-M3*
		MPM-PV 20675	**Prolagostomus** *sp.*	*right lower molar*
		MPM-PV 20676	**Neoreomys australis**	*left p4*
		MPM-PV 20677	**Neoreomys australis**	*right p4*
		MPM-PV 20678	**Neoreomys australis**	*right M3*
		MPM-PV 20679	**Neoreomys australis**	*left lower molar*
		MPM-PV 20680	**Neoreomys australis**	*left lower molar*
		MPM-PV 20681	**Neoreomys australis**	*left P4*
		MPM-PV 20682	**Neoreomys australis**	*right p4*
		MPM-PV 20683	**Neoreomys australis**	*left upper molar*
		MPM-PV 20684	**Neoreomys australis**	*left upper molar*
		MPM-PV 20685	**Neoreomys australis**	*left lower molar*
		MPM-PV 20686	**Prolagostomus** *sp.*	*right mandibular fragment with p4-m2*
		MPM-PV 20687	**Stichomys regularis**	*palate with left and right DP4-M3*
		MPM-PV 20688	**Spaniomys** *sp.*	*right mandible with dp4-m2(broken)*
		MPM-PV 20689	**Spaniomys** *sp.*	*left mandibular fragment with dp4-m3*
		MPM-PV 20690	**Stichomys** *sp.*	*right mandible with dp4-m1*
		MPM-PV 20691	**Spaniomys** *sp.*	*left maxilla with 2 broken teeth*

APPENDIX 1 - Continued

Locality	*Estancia*	*Collection number*	*Systematic taxonomy*	*Material*
		MPM-PV 20692	**Prolagostomus** *sp.*	*2 right upper teeth*
		MPM-PV 20693	**Spaniomys** *sp.*	*left dp4*
		MPM-PV 20694	*Caviomorpha*	*left mandibular fragment with incisor*
		MPM-PV 20695	**Spaniomys** *sp.*	*right mandibular fragment with m1*
		MPM-PV 20696	**Prolagostomus** *sp.*	*right P4*
		MPM-PV 20697	**Stichomys/ Adelphomys**	*left m2*
		MPM-PV 20698	**Eocardia** *sp.*	*left upper molar*
		MPM-PV 20699	**Spaniomys** *sp.*	*left upper molar*
		MPM-PV 17438	**Acarechimys minutissimus**	*left mandibular fragment with dp4-m2*
		MPM-PV 15087	**Acarechimys minutus**	*right mandibular fragment with m2*
		MPM-PV 20700	**Neoreomys australis**	*right mandible with m2-m3*
		MPM-PV 20701	**Prolagostomus** *sp.*	*left maxillary fragment with P4-M2*
		MPM-PV 20702	**Stichomys** *sp.*	*right maxillary fragment with DP4-M1*
		MPM-PV 20703	**Stichomys** *sp.*	*left maxillary fragment with DP4*
		MPM-PV 20704	**Prolagostomus** *sp.*	*left upper molar*
		MPM-PV 20705	**Prolagostomus** *sp.*	*left M3*
		MPM-PV 20706	**Pliolagostomus notatus**	*right upper molar*
		MPM-PV 20707	**Pliolagostomus notatus**	*right upper molar*
		MPM-PV 20708	**Spaniomys** *sp.*	*right lower molar (broken)*
		MPM-PV 20709	**Prolagostomus** *sp.*	*left lower molar (broken)*
		MPM-PV 20710	**Neoreomys** *sp.*	*broken tooth*
		MPM-PV 20711	**Eocardia** *sp.*	*broken tooth*
		MPM-PV 20712	**Prolagostomus** *sp.*	*right lower molar*
		MPM-PV 20713	**Perimys** *sp.*	*upper molar*
		MPM-PV 20714	**Perimys onustus**	*P4 and small left maxillary with M1*
		MPM-PV 20715	**Prolagostomus** *sp.*	*left mandibular fragment with p4-m3*
		MPM-PV 20716	**Prolagostomus** *sp.*	*right mandibular fragment with p4*
		MPM-PV 20717	**Eocardia/ Schistomys**	*right maxillary fragment with M1-M2*
		MPM-PV 20718	**Prolagostomus** *sp.*	*right maxilla with M1-M3(broken)*
		MPM-PV 15088	**Acarechimys minutus**	*left maxillary fragment with DP4-M3*
		MPM-PV 20719	**Spaniomys** *sp.*	*left mandibular fragment with m1*
		MPM-PV 20720	**Spaniomys** *sp.*	*left lower molar*
		MPM-PV 20721	**Eocardia** *sp.*	*isolated tooth*
		MPM-PV 20722	**Prolagostomus** *sp.*	*right lower molar*
		MPM-PV 20723	**Sciamys principalis**	*left mandible with p4-m3*
		MPM-PV 20724	*cf.* **Scleromys**	*right p4*
		MPM-PV 20725	**Steiromys***?*	*left dp4*
		MPM-PV 20726	**Prolagostomus** *sp.*	*left mandibular fragment with m1-m3*
		MPM-PV 20727	**Stichomys/ Adelphomys**	*left DP4-M1*
		MPM-PV 20728	**Prolagostomus** *sp.*	*right upper molar*
		MPM-PV 20729	**Prolagostomus** *sp.*	*left p4*
		MPM-PV 20730	**Pliolagostomus notatus**	*left upper molar*
		MPM-PV 20731	**Pliolagostomus notatus**	*left M3*
		MPM-PV 20732	**Spaniomys** *sp.*	*left maxillary fragment with DP4*
		MPM-PV 20733	**Prolagostomus** *sp.*	*right lower molar*
		MPM-PV 20734	**Stichomys***?*	*left dp4*
		MPM-PV 20735	**Stichomys/ Adelphomys**	*right upper molar*
		MPM-PV 20736	**Prolagostomus** *sp.*	*2 broken teeth*
		MPM-PV 20737	**Prolagostomus/Pliolagostomus**	*right upper molar*

Appendix 1 - Continued

Locality	*Estancia*	*Collection number*	*Systematic taxonomy*	*Material*
		MPM-PV 20738	**Schistomys erro**	*right maxilla with P4-M1 and M2-M3 and left maxilla with M1-M2*
		MPM-PV 20739	**Spaniomys** *sp.*	*edentulous left mandible*
		MPM-PV 20740	**Sciamys principalis**	*left mandibular fragment with dp4-m1*
		MPM-PV 20741	**Sciamys principalis**	*right maxillary fragment with P4-M3*
		MPM-PV 20742	**Sciamys principalis**	*left mandibular fragment with p4-m3*
		MPM-PV 17436	**Acarechimys minutus**	*right mandibular fragment with dp4*
		MPM-PV 20743	**Sciamys** *sp.*	*right maxillary fragment with P4-M1*
		MPM-PV 20744	**Spaniomys** *sp.*	*right maxillary fragment with M2*
		MPM-PV 20745	**Spaniomys** *sp.*	*right M1 or M2 (broken)*
		MPM-PV 17439	**Acarechimys gracilis**	*left mandibular fragment with molar*
		MPM-PV 17437	**Acarechimys minutus**	*left dp4*
		MPM-PV 20746	**Spaniomys** *sp.*	*left DP4*
		MPM-PV 20747	*Octodontoidea?*	*left lower molar*
		MPM-PV 20748	**Schistomys erro***?*	*left M3*
		MPM-PV 20749	**Neoreomys australis**	*right m1 or m2*
		MPM-PV 20750	**Prolagostomus** *sp.*	*left mandibular fragment with m1-m2*
		MPM-PV 20751	**Perimys onustus**	*left upper molar*
		MPM-PV 20752	**Prolagostomus** *sp.*	*left p4*
		MPM-PV 20753	**Eocardia** *sp.*	*left lower molar*
		MPM-PV 20754	**Eocardia** *sp.*	*right lower molar (broken)*
		MPM-PV 20755	**Pliolagostomus notatus**	*isolated molar*
		MPM-PV 20756	**Pliolagostomus notatus**	*right lower molar*
		MPM-PV 20757	**Pliolagostomus notatus**	*right lower molar*
		MPM-PV 20758	**Pliolagostomus notatus**	*lower molar*
		MPM-PV 20759	**Pliolagostomus notatus**	*isolated molar*
		MPM-PV 20760	*Octodontoidea*	*right mandibular fragment with incisor*
		MPM-PV 20761	**Stichomys/ Adelphomys**	*right maxillary fragment with DP4(broken)-M2*
		MPM-PV 20762	**Sciamys** *sp.*	*right mandible with m1-m2*
		MPM-PV 20763	**Neoreomys** *sp.*	*right upper molar (broken)*
		MPM-PV 20764	*Caviomorpha?*	*proximal ulna fragment?*
		MPM-PV 20765	**Neoreomys australis**	*right lower molar*
		MPM-PV 20766	**Spaniomys** *sp.*	*left mandibular fragment with m1-m2*
		MPM-PV 20767	**Spaniomys** *sp.*	*right lower molar*
		MPM-PV 20768	**Prolagostomus** *sp.*	*left M3*
		MPM-PV 20769	**Spaniomys** *sp.*	*left maxillary fragment with DP4-M1*
Yaten Huageno (YH)	*Estancia El Refugio (EER)*	*MPM-PV 20770*	**Spaniomys** *sp.*	*left mandibular fragment with m1*
		MPM-PV 20771	**Stichomys regularis**	*right maxillary fragment with DP4-M1*
		MPM-PV 20772	**Neoreomys australis**	*left upper molar*

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ARTÍCULO

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 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

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 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

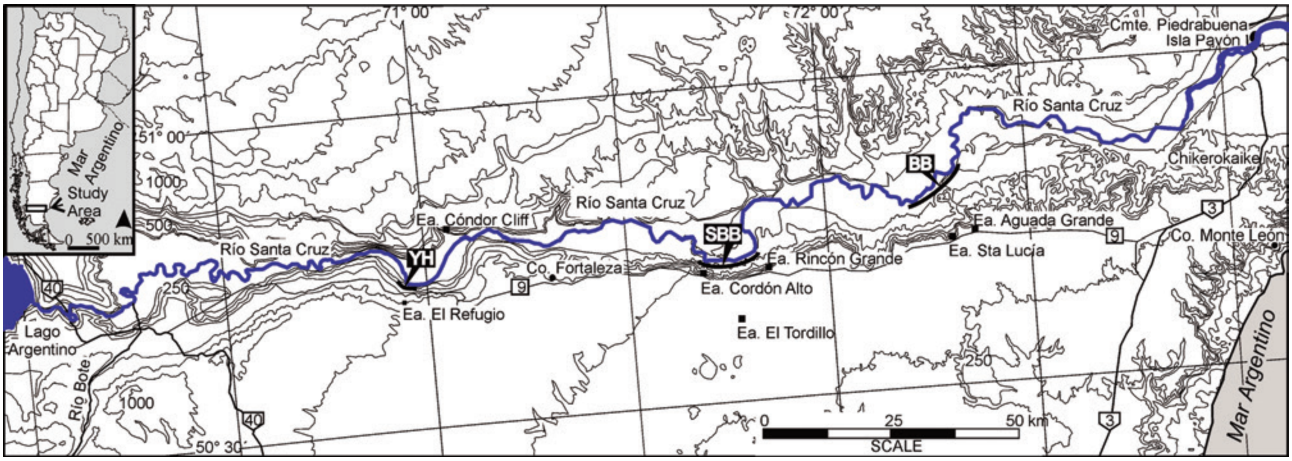

Figure 1. Map of the Río Santa Cruz with the prospected localities and estancias mentioned in the text. **BB,** Barrancas Blancas; **SBB,** Segundas Barrancas Blancas; **YH,** Yaten Huageno; **RB,** Río Bote; **Ea.,** Estancia. Modified from Fernicola *et al.* (2014).

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*	**Ecphantodon ceboides**	*right mandibular fragment with a damaged m1, per Mercerat, 1891*	*"Barrancas del Río Santa Cruz"*	—	—	—
2013	*N. Toledo*	*MPM-PV 19426 (Type)*	**Homunculus vizcainoi** *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*	**Homunculus vizcainoi** *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*	**Homunculus vizcainoi** *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*	**Homunculus** *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 trigonidand 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

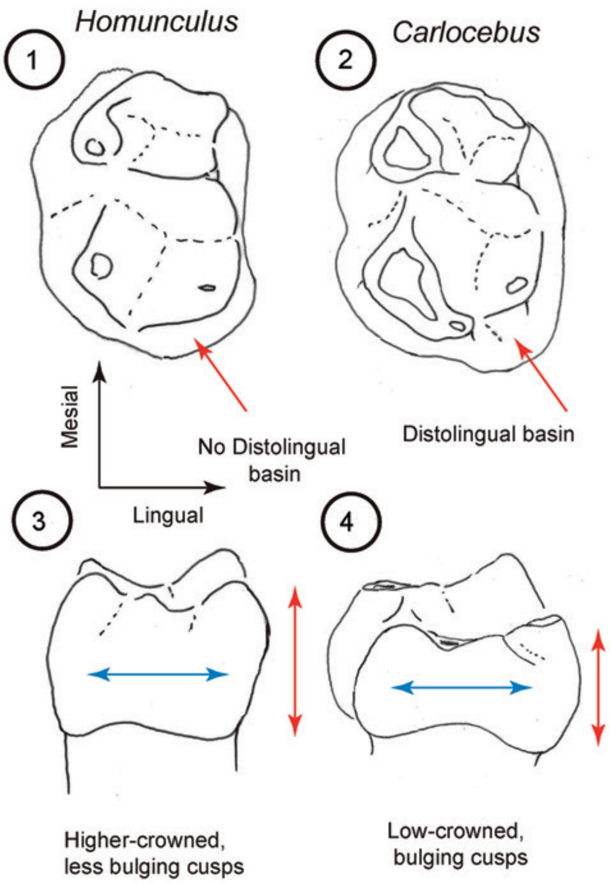

Figure 2. Line drawings illustrating the distinctive features of the lower molars of ***Homunculus patagonicus*** (**MPM-PV 4376**; left m2) and ***Carlocebus carmenensis*** (**MACN-PvSC 266**, right m2, image reversed). **1–2,** Occlusal views of m2; **3–4,** distal views of the m2.

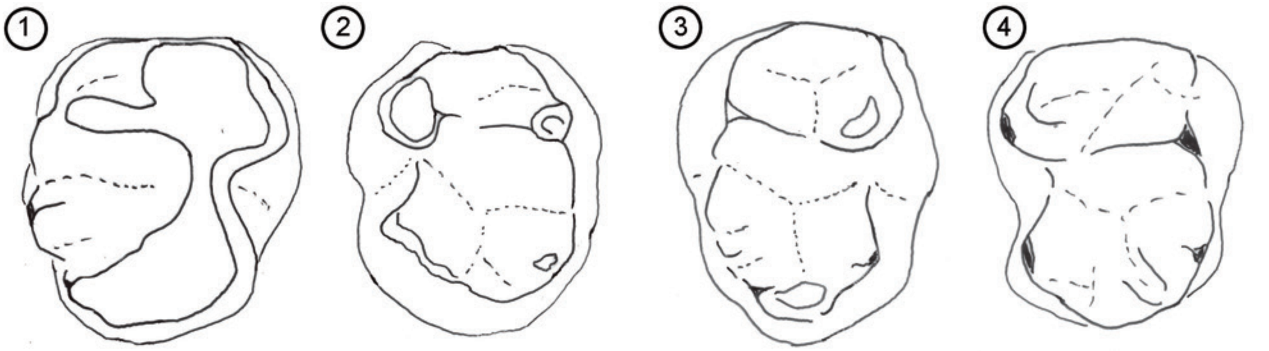

Figure 3. Line drawings of occlusal views of m3s of ***Homunculus*** and ***Carlocebus*** (drawings not to scale). **1, MACN-Pv SC 306**, ***Carlocebus***; **2, MACN-Pv SC 314**, ***Carlocebus***; **3, MPM-PV 3708**, ***Homunculus patagonicus***; **4, MPM-PV 17452**, ***Homunculus*** sp., m3 from Río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

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.

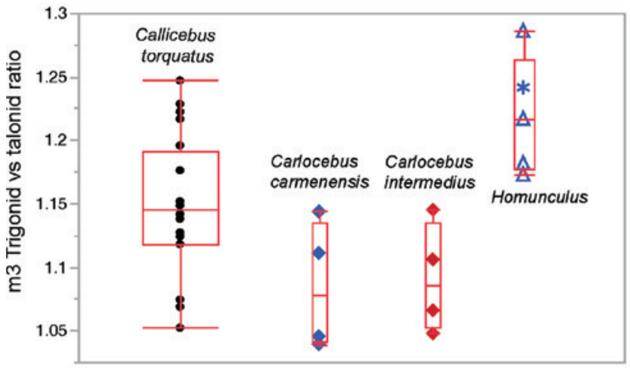

Figure 4. Box plot of the distribution of the ratio of m3 trigonid breadth versus m3 talonid breadth for the specimens listed in Table 2, with the addition of a sample of 20 specimens of the extant monkey ***Callicebus torquatus*** (Hoffmannsegg, 1807). The Río Bote m3 (**MPM-PV 17452** ***Homunculus***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

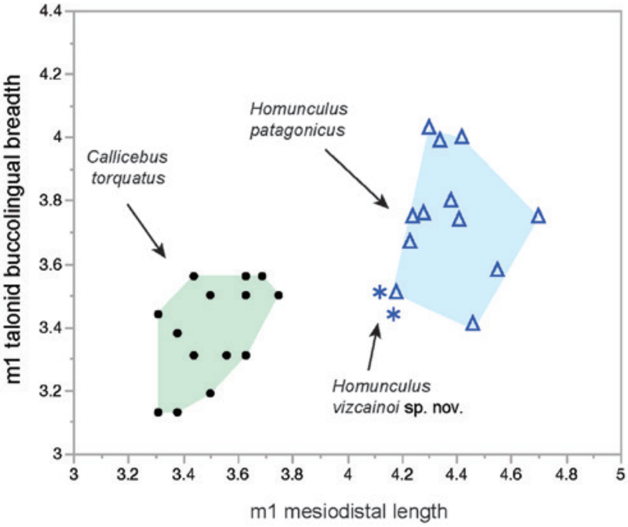

Figure 7. Bivariate plot of the mesiodistal versus buccolingual dimensions of the first lower molars of ***Homunculus*** species. Also included is a sample of 20 specimens of the extant platyrrhine ***Callicebus torquatus*** (black dots), which gives a sense of the amount of variation encountered in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

Homunculus vizcainoi sp. nov.

Figures 5–7

LSID. zoobank.org:pub: 97566577-28D5-41DE-B2BA-251ADFA0A661

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*

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

Taxon	*Catalog number*	*Formation*	*Locality*[1]	*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*	*4.45*	*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	*MSCN-PVSC 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*

[1] *Locality 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 *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, 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 *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 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.

ACKNOWLEDGEMENTS

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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. Enumération synoptique des espèces de mammifères 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 Societe Cientifica de Argentina* 54: 161–180, 220–240.

Ameghino, F. 1906. Les formations sédimentaires du Crétacé supérieur et du Tertiaire de Patagonie avec un parallele entre leurs faunes mammalogiques et celles de l'ancien continent. *Anales del Museo Nacional de Buenos Aires, Série 3* 15: 1–568.

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 ventanas 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., Villafañe, A.L., and Muñoz, N.A. 2012. Paleobiology of Santacrucian native ungulates (Meridiungulata: Astrapotheria, 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: 14–33.

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 Notohippidian. *Journal of South American Earth Sciences* 52: 94–107.

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.

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

Kay, R.F. 2010. A new primate from the Early Miocene of Gran Barranca, 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 fosil del Oligoceno superior (Colheuhuapiano) de Gaiman, Chubut. Comm. *Instituto Nacional Investigaciones Ciencias Naturales, II, Ciencias Zoologica* 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 Terciario 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.I., 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.

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

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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 permitt 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 Santacruceña* coming from the *Piso Santacruceño*. 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 Santacruceño* 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

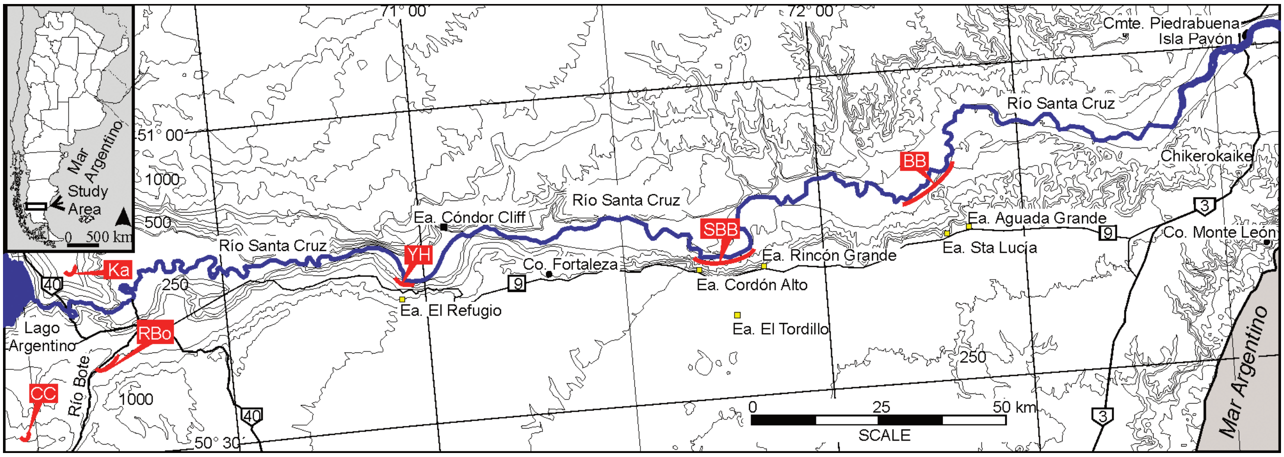

Figure 1. Map of the Río Santa Cruz with the prospected localities and estancias mentioned in the text. **BB,** Barrancas Blancas; **CC,** Cerro Centinela; **Ea.,** Estancia; **Ka,** Karaiken; **RBo,** Río Bote; **SBB,** Segundas Barrancas Blancas; **YH,** Yaten Huageno. Modified from Fernicola *et al.* (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 (Sacomani and Panza, 2011; Parras and Cuitiño, 2018); and (3) the terrestrial Early–Middle Miocene Santa Cruz Formation (Tauber *et al.*, 2008; Sacomani 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 Ar^{39}/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; Trayler *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° 09' 38.31" - W 69° 40' 23.40") to west (S 50° 12' 31.70" - W 69° 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

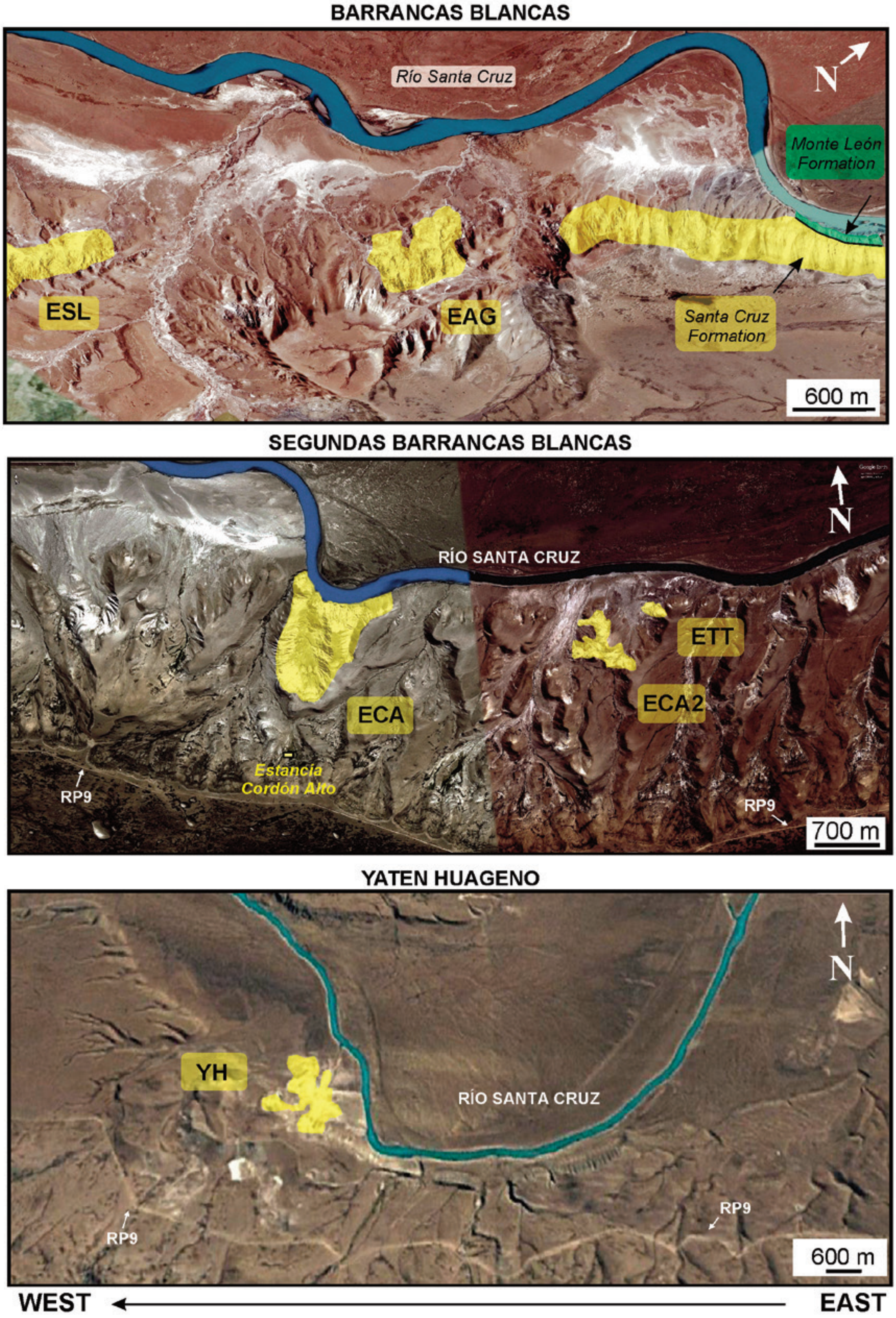

Figure 2. Satellite image (Google Earth TM; 2002) of the Barrancas Blancas, and Segundas Barrancas Blancas (Modified from Cuitiño *et al*., 2019b); and Yaten Huageno. Section of Monte Observación Member of the Monte León Formation and Santa Cruz Formation are highlighted in green and yellow, respectively. **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 cingulatum*****, 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 ovinum*****, 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 Macraucheniidae), 24 rodent species (11 Octodontoidea, two Erethizontoidea, five Cavioidea, 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 Macraucheniidae), and 25 Rodents (12 Octodontoidea, two Erethizontoidea, five Cavioidea, 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 (*Perathereutes 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).

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*	*–*

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, 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 Santacruceño* 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 (Fernicola *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 (Fernicola, 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 (Fernicola, 2011a,b; Fernicola *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 km^2) compared with BB (1.35 km^2) and SBB (1.5 km^2). 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 (Fernicola 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

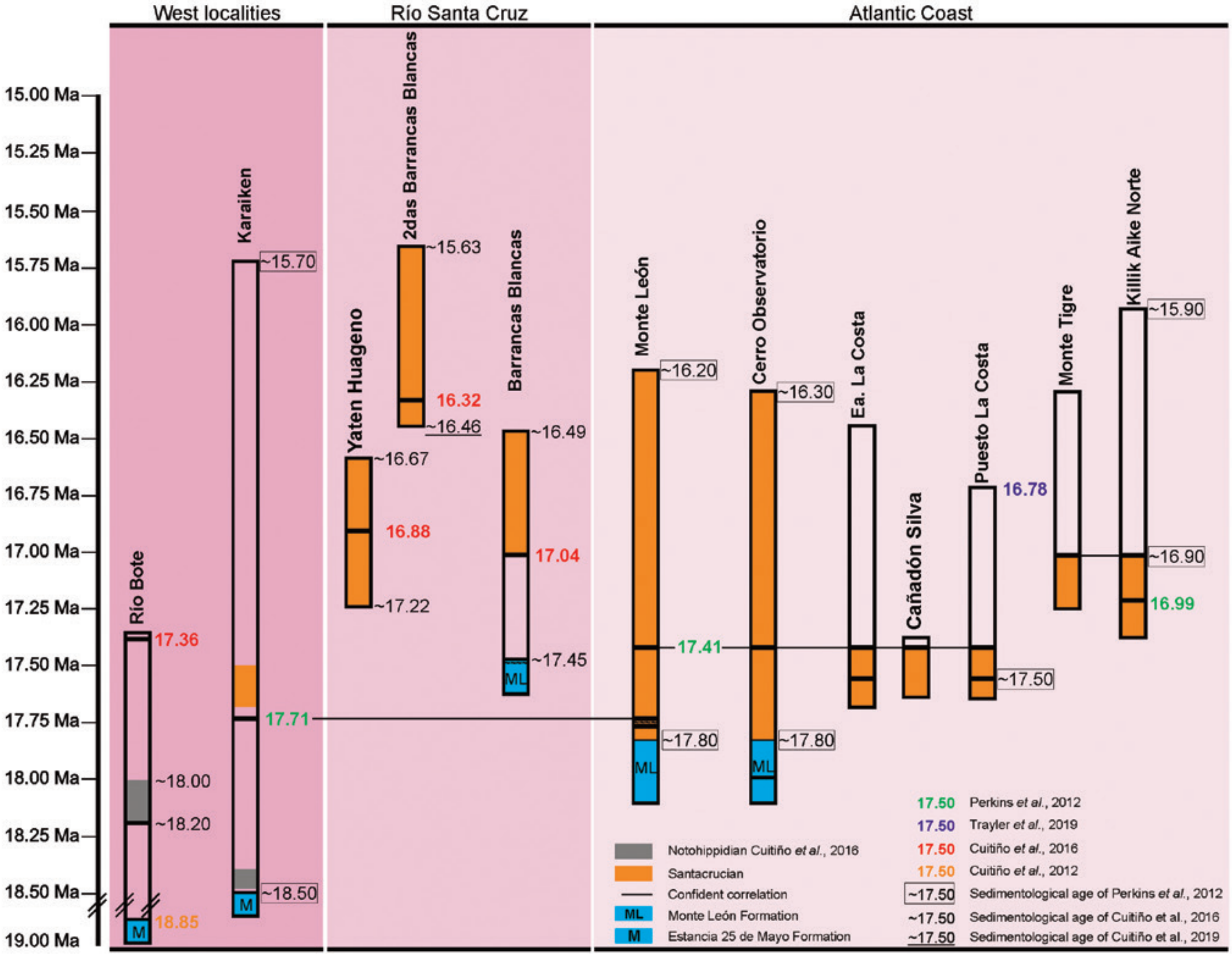

Figure 4. Chronostratigraphic correlation scheme for the Santacrucian sections of the Santa Cruz Formation at the Río Santa Cruz, Río Bote, and Atlantic Coast mentioned in this study The vertical extension of the columns is calculated assuming an average sedimentation rate of 150 m/Ma (Cuitiño *et al*., 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 phenomenon 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 sedimentological 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

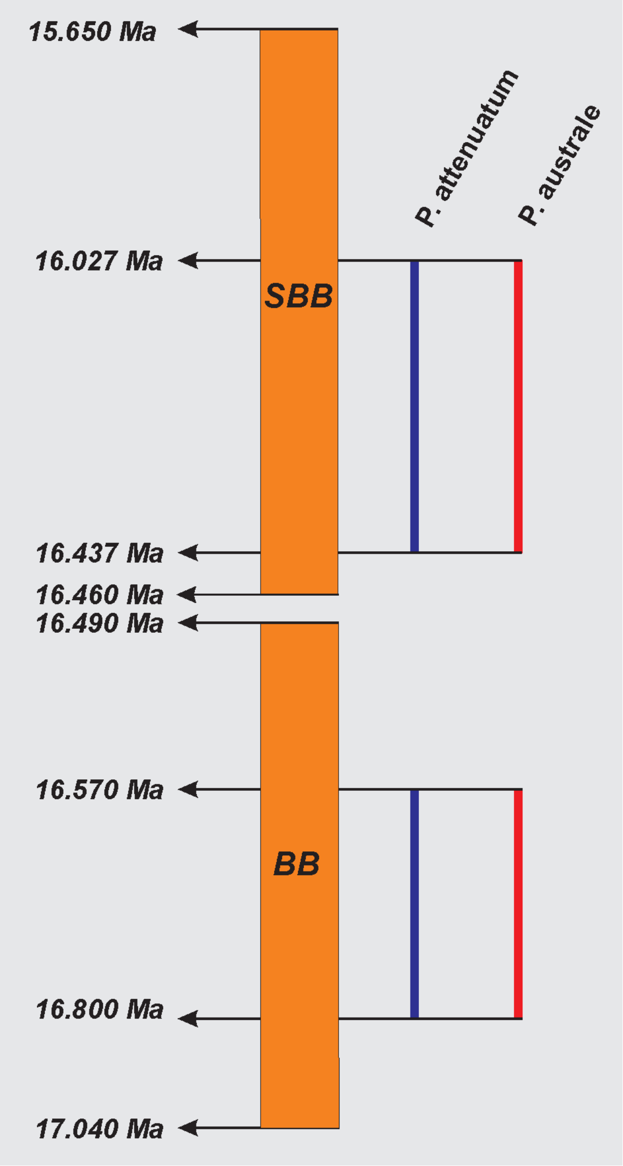

Figure 5. Temporal distribution of *Protypotherium attenuatum* (blue) and *P. australe* (red) at BB and SBB. The specimen of *P. australe* from BB was collected at Estancia Santa Lucía Section which estimated time span between ~16.8 to 16.57 Ma (Cuitiño *et al.*, 2019b).

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 reevaluation 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 understanding 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.

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REFERENCES

Ameghino, F. 1885. Nuevos restos de mamíferos fósiles oligocenos, recogidos por el profesor Pedro Scalabrini y pertenecientes al Museo Provincial de la Ciudad del Paraná. *Boletín de la Academia Nacional de Ciencias de Córdoba* 8: 5–207.

Ameghino, F. 1887a. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de Patagonia Austral y depositados en el Museo de La Plata. *Boletín del Museo de La Plata* 1–26.

Ameghino, F. 1887b. Observaciones generales sobre el orden de mamíferos extinguidos sub-americanos llamados Toxodontes (Toxodontia) y sinopsis de los géneros y especies hasta ahora conocidos. *Anales del Museo de La Plata* 1: 1–66.

Ameghino, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas de la Academia Nacional de Ciencias* 6: 1–1027.

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

Ameghino, F. 1900–1902. L'âge des formations sédimentaires de Patagonie. *Anales de la Sociedad Científica Argentina* 50: 109–130; 145–165; 209–229; 51: 20–39; 52: 65–91; 189–197; 244–250; 54: 161–180; 220–249; 283–342.

Ameghino, F. 1906. Les formations sédimentaires du Créetacé Superieur et du Tertaire de Patagonie avec un parallele entre leurs faunes mammalogiques et celles de l'ancien continent. *Anales del Museo Nacional de Buenos Aires* 15: 1–568.

Arnal, M. 2012. [*Sistemática, filogenia e historia evolutiva de roedores Octodontoidea (Caviomorpha, Hystricognathi) del Oligoceno tardío–Mioceno medio vinculados al origen de la familia Octodontidae*. Tesis doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, 317 p. Unpublished.].

Arnal, M., Kramarz, A.G., Vucetich, M.G., and Vieytes, C.E. 2014. A new Early Miocene octodontoid rodent (Hystricognathi, Caviomorpha) from Patagonia (Argentina) and a reassessment of the early evolution of Octodontoidea. *Journal of Vertebrate Paleontology* 34: 397–406.

Arnal, M., Pérez, M.E., and Deschamps, C.M. 2019. Revision of the

Miocene Caviomorph rodents from the Río Santa Cruz (Argentinean Patagonia). 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: 193–229.

Arnal, M., and Vucetich, M.G. 2015. Revision of the fossil rodent *Acaremys* Ameghino, 1887 (Hystricognathi, Octodontoidea, Acaremyidae) from the Miocene of Patagonia (Argentina) and the description of a new acaremyid. *Historical Biology* 27: 42–59.

Arnal, M., Vucetich, M.G., Croft, D.A., Bargo, M.S., Fernicola, J.C., and Vizcaíno, S.F. 2017. Systematic revision and evolutionary history of *Acarechimys* Patterson in Kraglievich, 1965 (Rodentia, Caviomorpha, Octodontoidea). *Ameghiniana* 54: 307–330.

Bargo, M.S., De Iuliis R., and Toledo, N. 2019. Early Miocene sloths (Xenarthra, Folivora) from the Río Santa Cruz valley (Southern Patagonia, Argentina). Ameghino, 1887 revisited. 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: 102–137.

Brinkman, P.D., and Vizcaíno, S.F. 2014. Clemente Onelli's sketch map and his first-hand, retrospective account of an early fossil-hunting expedition along the Río Santa Cruz, southern Patagonia, 1888–1889. *Society for the Bibliography of Natural History; Archives of natural history* 41: 326–337.

Cabrera, A. 1927. Datos para el conocimiento de los Dasiuroideos fósiles argentinos. *Revista del Museo de La Plata* 30: 271–315.

Cobos, J.C., Rodríguez, M.F., and Panza, J.L. 2014. Hoja Geológica 5172-II, Paso Río Bote, Provincia de Santa Cruz. *Boletín del Instituto de Geología y Recursos Minerales, Servicio Geológico Minero Argentino* 405: 1–99.

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

Cuitiño, J.I. Fernicola, J.C., Raigemborn, M.S., and Krapovickas, V. 2019b. 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: 14–33.

Cuitiño, J.I., and Scasso, R.A. 2010. Sedimentología y paleoambientes del Patagoniano y su transición a la Formación Santa Cruz al sur del Lago Argentino, Patagonia Austral. *Revista de la Asociación Geológica Argentina* 66: 406–417.

Cuitiño, J.I., Vizcaíno, S.F., Bargo, M.S., and Aramendía, I. 2019a. Sedimentology and fossil vertebrates of the Santa Cruz Formation (early Miocene) in Lago Posadas, southwestern Patagonia, Argentina. *Andean Geology* 46: 383–420.

Chornogubsky, L., Abello, M.A., and Barmak, G. 2019. The Metatheria from the Río Santa Cruz (Santa Cruz Formation, Early–Middle Miocene, Argentina): history and new findings. 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: 62–84.

Dalziel, I.W.D., De Wit, M.J., and Palmer, K.F. 1974. A fossil marginal basin in the southern Andes. *Nature* 250: 291–294.

Fernández, M., and Muñoz, N.A. 2019. Notoungulata and Astrapotheria (Mammalia, Meridiungulata) of the Santa Cruz Formation (Early–Middle Miocene) along the Río Santa Cruz, Argentine Patagonia. 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: 138–169.

Fernicola, J.C. 2011a. 1886–1888: Ascenso, auge y caída de la sociedad entre Florentino Ameghino y Francisco P. Moreno. *Publicación Especial de la Asociación Paleontológica Argentina* 12: 35–49.

Fernicola, J.C. 2011b. Implicancias del conflicto Ameghino-Moreno sobre la colección de mamíferos fósiles realizada por Carlos Ameghino en su primera exploración al río Santa Cruz, Argentina. *Revista del Museo Argentino de Ciencias Naturales, n.s.* 13: 41–57.

Fernicola, J.C., Bargo, M.S., Vizcaíno, S.F., and Kay, R.F. 2019a. 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.

Fernicola, J.C., Bargo, M.S., Vizcaíno, S.F., and Kay R.F. (Eds.) 2019b. *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:.

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 Notohippidian. *Journal of South America Earth Sciences* 52: 9–107.

Fernicola, J.C., and Vizcaíno, S.F. 2019. Cingulates (Mammalia, Xenarthra) of the Santa Cruz Formation (Early–Middle Miocene,) from the Río Santa Cruz, Argentine Patagonia. 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: 85–101.

Fleagle, J.G., Perkins, M.E., Heizler, M.T., Nash, B., Bown, T.M., Tauber, A.A., Dozo, M.T., Tejedor, M.F., 2012. Absolute and relative ages of fossil localities in the Santa Cruz and Pinturas formations. 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. 41–58.

Fosdick, J.C., Grove, M., Hourigan, J.K., and Calderón, M. 2013. Retroarc deformation and exhumation near the end of the Andes, southern Patagonia. *Earth and Planetary Science Letters* 361: 504–517.

Ghiglione, M.C., Ramos, V.A., Cuitiño, J.I., and Varberón, V. 2016. Growth of the Southern Patagonian Andes (46–53°S) and their Relation to Subduction Processes. In: A. Folguera, M. Naipauer, L. Sagripanti, M. Ghiglione, D. Orts, and L. Giambiagi (Eds.), *Growth of the Southern Andes*. Springer Earth System Sciences, Springer International Publishing, Switzerland, p. 201–240. Doi: 10.1007/978-3-319-23060-3.

Kay, R.F., and Perry, J.M.G. 2019. New primates from the valleys of the Río Santa Cruz and Río Bote (Early–Middle Miocene), Santa Cruz Province, 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: 230–238.

Kay, R.F., Vizcaíno, S.F., and Bargo, M.S. 2012. A review of the paleoenvironment and paleoecology of the Miocene Santa Cruz Formation. 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. 331–365.

Krapovickas, J., Tauber, A.A., and Rodríguez, P.E. 2008. Nuevo registro de *Protypotherium australe* Ameghino, 1887: implicancias bioestratigráficas en la Formación Santa Cruz. *17° Congreso Geológico Argentino* (San Salvador de Jujuy), *Actas*: 1020–1021.

Marshall, L.G., Drake, R.E., Curtis, G.H., Butler, R.F., Flanagan, K.M., Naeser, C.W. 1986. Geochronology of Type Santacrucian (Middle Tertiary) Land Mammal Age, Patagonia, Argentina. *The Journal of Geology* 94: 449–457.

Marshall, L.G., Hoffstetter, R., and Pascual, R. 1983. Mammals and stratigraphy: Geochronology of the continental mammal-bearing Tertiary of South America. *Paleovertebrata, Mémoire Extraordinaire* 1–93.

Marshall, L.G., and Pascual, R. 1977. Nuevos marsupiales Caenolestidae del "Piso Notohipidense" (SW de Santa Cruz, Patagonia) de Ameghino. Sus aportaciones a la cronología y evolución de las comunidades de mamíferos sudamericanos. *Publicación del Museo Municipal de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia"* 2: 91–22.

Mercerat, A. 1891. Notas sobre la paleontología de la República Argentina. II. Sinopsis de la familia de los Proxotodontidae conservados en el Museo de La Plata (Eoceno de Patagonia). *Revista del Museo de La Plata* 1: 381–444.

Moreno, F.P. 1879. *Viaje a la Patagonia Austral, emprendido bajo los auspicios del gobierno nacional, 1876-1877*. Imprenta de La Nación, Buenos Aires, 460 p.

Parras, A.M., and Cuitiño, J.I. 2018. The stratigraphic and paleoenvironmental significance of the regressive Monte Observación Member, early Miocene of the Austral Basin, Patagonia. *Latin American Journal of Sedimentology and Basin Analysis* 25: 25–47.

Pascual, R., Ortega Hinojosa, E.J., Gondar, D., and Tonni, E.P. 1965. Las edades del Cenozoico mamalífero de la Argentina, con especial atenci6n a aquellas del territorio Bonaerense. *Anales de la Comisión de Investigaciones Científicas* 6: 165–193.

Pérez, M.E. 2010. [*Sistemática, ecología y bioestratigrafía de Eocardiidae (Rodentia, Hystricognathi, Cavioidea) del Mioceno temprano y medio de Patagonia*. Tesis Doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, 385 p. Unpublished.].

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.

Racco, A., Fernicola, J.C., Bargo, M.S., Vizcaíno, S.F., and De Iuliis, G. 2018. On the type of *Schismotherium fractum* Ameghino, 1887 (Xenarthra, Folivora, Megatherioidea) from the Early Miocene Santa Cruz Formation (Santa Cruz province, Argentina). *Ameghiniana* 55: 117–125.

Raigemborn, M.S., Krapovickas, V., Zucol, A.F., Zapata, L., Beilinson, E., Toledo, N., Perry, J., Lizzoli, S., Martegani, L., Tineo, D., and Passeggi, E. 2018. Paleosols and related soil-biota of the early Miocene Santa Cruz Formation (Austral-Magallanes Basin, Argentina): a multidisciplinary approach to reconstructing ancient terrestrial landscapes. *Latin American Journal of Sedimentology and Basin Analysis* 25: 117–148.

Rasia, L.L. 2016. [*Los Chinchillidae (Rodentia, Caviomorpha) fósiles de la República Argentina: sistemática, historia evolutiva y biogeográfica, significado bioestratigráfico y paleoambiental*. Tesis Doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, 246 p. Unpublished.].

Rusconi, C. 1965. Carlos Ameghino. Rasgos de su vida y obra. *Revista del Museo de Historia Natural de Mendoza* 17: 1–160.

Sacomani, L.E., and Panza, J.L. 2011. Hojas Geológicas 5169-I y 5169-II, Puerto Coig y Puerto Santa Cruz, Provincia de Santa Cruz. *Boletín Instituto de Geología y Recursos Minerales, Servicio Geológico Minero Argentino* 392: 1–133.

Schmidt, G.I., Hernández del Pino, S., Muñoz, N.A., and Fernández, M. 2019. Litopterna (Mammalia) from the Santa Cruz Formation (Early–Middle Miocene) at Río Santa Cruz, Southern 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: 170–192.

Simpson, G.G. 1940. Review of the Mammal-Bearing Tertiary of South America. *Proceedings of the American Philosophical Society* 83: 649–709.

Sinclair, W.J. 1909. Mammalia of the Santa Cruz beds. Part I. Typotheria. In: W.B. Scott (Ed.), *Reports of the Princeton University Expeditions to Patagonia, 1896–1899*. Princeton, Princeton University, New Jersey, p. 1–110.

Scott, W.B. 1903. Mammalia of the Santa Cruz beds. Part I. Edentata. In: Scott W.B. (Ed.), *Reports of the Princeton University Expeditions to Patagonia 1896–1899*. Vol. 5, Paleontology 2, Princeton: Princeton University Press, New Jersey, p. 1–226.

Soria, M.F. 2001. Los Proterotheriidae (Mammalia, Litopterna): sistemática, origen y filogenia. *Monografías del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* 1: 1–167.

Tauber, A.A. 1996. Los representantes del género *Protypotherium* (Mammalia, Notoungulata, Interatheridae) del Mioceno Temprano del sudoeste de la Provincia de Santa Cruz, República Argentina. *Academia Nacional de Ciencias* 95: 1–29.

Tauber, A.A. 1997a. Biostratigraphy of the Santa Cruz Formation (Lower Miocene) in southeastern Patagonia. *Ameghiniana* 34: 413–426.

Tauber, A.A. 1997b. Palaeoecology of the Santa Cruz Formation (Lower Miocene) in the southeast border of Patagonia. *Ameghiniana* 34: 517–529.

Tauber, A.A. 1999. Los vertebrados de la Formación Santa cruz (Mioceno inferior–medio) en el extremo sureste de la Patagonia y su significado paleoecológico. *Revista Española de Paleontología* 14: 173–182.

Tauber, A.A., Palacios, M.E., Krapovickas, J., and Rodríguez, P. 2008. La Formación Santa Cruz (Mioceno temprano–medio) en la mitad occidental del Río Santa Cruz, Patagonia, Argentina. *17° Congreso Geológico Argentino* (San Salvador de Jujuy), *Actas*: 1500–1501.

Tejedor, M.F., Tauber, A.A., Rosenberger, A.L., Swisher, 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, D.M., Cuitiño, J.I., Kohn, M., Bargo, M.S., Kay, R.F., Strömberg, C.A.E., and Vizcaíno, S.F. 2019. An improved approach to age-modeling in deep time: Implications for the Santa Cruz Formation, Argentina. *GSA Bulletin* https://doi.org/10.1130/B35203.1

Vizcaíno, S.F. 2011. Cartas para Florentino desde la Patagonia. Crónica de la correspondencia édita entre los hermanos Ameghino (1887–1902). In: J.C. Fernicola , A. Prieto, and D. Lazo (Eds.), *Vida y obra de Florentino Ameghino*, *Publicación Especial de la Asociación Paleontológica Argentina* N° 12: 51–67.

Vizcaíno, S.F., Bargo, M.S., and Fernicola, J.C. 2013. Expediciones paleontológicas durante los siglos XIX y XX A la Formación Santa Cruz (Mioceno Inferior, Patagonia) y destino de los fósiles. *3° Congreso Argentino de Historia de la Geología* (Salta)*, Actas*: 231–246.

Vizcaíno, S.F., Kay, R.F., and Bargo, M.S. 2012a. 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.

Vizcaíno, S.F., Kay, R.F., and Bargo, M.S. 2012b. *Early Miocene Paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge, 370 p.

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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.
Mylodontoidea
Mylodontidae
    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)
Propalaehoplophoridae
    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
Pachyrukhos 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
Macraucheniidae
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
Neoepiblemidae
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*	
METATHERIA						
SPARASSODONTA						
Cladosictis patagonica	X^{1}	X^{11}	—	X^{11}	—	X^{13}
Sipalocyon gracilis	X^{1}	X^{11}	X^{11}	X^{11}	—	X^{13}
Perathereutes pungens	—	X^{11}	—	X^{11}	—	X^{13}
Acrocyon sectorius	X^{1}	—	—	—	—	—
Acyon tricuspidatus	X^{1}	—	—	—	—	—
Borhyaena tuberata	X^{1}	X^{11}	X^{11}	X^{11}	—	X^{13}
Lycopsis torresi	X^{2}	—	—	—	—	—
PAUCITUBERCULATA						
Stilotherium dissimile	X^{1}	—	—	—	—	—
Abderites meridionalis	X^{1}	X^{11}	X^{11}	X^{11}	—	X^{11}
Acdestis oweni	X^{1}	X^{11}	X^{11}	X^{11}	—	X^{13}
Palaeothentes lemoinei	X^{1}	X^{11}	X^{11}	X^{11}	—	X^{13}
P. intermedius	X^{1}	X^{11}	X^{11}	X^{11}	—	X^{11}
P. minutus	X^{1}	X^{11}	X^{11}	X^{11}	—	X^{13}
P. aratae	X^{1}	—	—	—	—	—
MICROBIOTHERIA						
Microbiotherium patagonicum	X^{1}	—	—	—	—	—
M. tehuelchum	X^{1}	X^{11}	—	X^{11}	—	X^{13}
XENARTHRA						
FOLIVORA						
Hapalops elongatus	—	X^{3}	X^{3}	X^{3}	—	X^{14}
H. rectangularis	X^{1}	—	—	—	—	—
H. indifferens	X^{1}	—	—	—	—	—
H. rostratus	X^{1}	—	—	—	—	—
H. infernalis	X^{1}	—	—	—	—	—
H. adteger	X^{1}	—	—	—	—	—
Schismotherium fractum	X^{1}	X^{3}	—	X^{3}	—	X^{19}
Xyophorus atlanticus	—	X^{3}	—	X^{3}	—	X^{3}
Planopinae indet.	—	X^{3}	—	X^{3}	—	—
Planops longirostratus	X^{1}	—	—	—	—	—
Eucholoeops ingens	X^{1}	—	—	—	—	—
Nematherium angulatum	X^{1}	—	—	—	—	—
N. longirostris	—	X^{3}	—	X^{3}	—	X^{3}
CINGULATA						
Peltephilus pumilus	X^{1}	X^{4}	X^{4}	X^{4}	—	X^{13}
P. strepens	X^{1}	—	—	—	—	—
Stegotherium tessellatum	X^{1}	X^{4}	X^{4}	—	—	—
Prozaedyus proximus	X^{1}	X^{4}	X^{4}	X^{4}	X^{4}	X^{13}
Stenotatus patagonicus	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*	
Proeutatus oenophorus	X[1]	X[4]	X[4]	X[4]	X[4]	X[13]
Propalaehoplophorus australis	X[1]	—	—	—	—	—
Cochlops muricatus	—	X[4]	X[4]	—	X[4]	X[13]
Eucinepeltus *sp.*	—	X[4]	X[4]	X[4]	—	—
ASTRAPOTHERIA						
Astrapotherium magnum	X[1]	X[5]	—	—	X[5]	X[13]
A. burmeisteri	X[6]	—	—	—	—	—
Astrapotherium *sp.*	—	—	X[5]	X[5]	—	—
NOTOUNGULATA						
TOXODONTIA						
Homalodotherium cunninghami	X[1]	—	—	—	—	—
Homalodotherium *sp.*	—	X[5]	X[5]	X[5]	—	—
Nesodon imbricatus	X[1]	X[5]	X[5]	—	—	X[13]
N. conspurcatus	X[1]	—	—	—	—	—
Nesodon *sp.*	—	—	—	X[5]	—	—
Adinotherium ovinum	X[1]	X[5]	—	X[5]	—	X[13]
A. splendidum	X[1]	—	—	—	—	—
A. nitidum	X[1]	—	—	—	—	—
Adinotherium *sp.*	—	—	X[5]	—	X[5]	—
Phobereotherium silvaticum	X[1]	—	—	—	—	—
Hyperoxotodon speciosus	X[1]	—	—	—	—	—
TYPOTHERIA						
Hegetotherium mirabile	X[1]	X[5]	X[5]	X[5]	—	X[13]
Pachyrukhos moyani	X[7]	X[5]	—	X[5]	—	X[5]
Protypotherium australe	X[1]	X[5]	X[5]	X[5]	—	X[13]
P. praerutilum	X[1]	X[5]	X[5]	X[5]	—	X[14]
P. attenuatum	X[1]	X[5]	X[5]	X[5]	—	X[14]
Interatherium rodens	X[1]	—	—	—	—	—
I. excavatum	X[1]	—	—	—	—	—
I. extensum	X[1]	—	—	—	—	—
Interatherium *sp.*	—	X[5]	X[5]	X[5]	—	—
LITOPTERNA						
Anisolophus australis	X[1]	X[8]	X[8]	—	—	X[16]
A. floweri	X[1]	X[8]	—	X[8]	—	X[16]
Tetramerorhinus lucarius	—	X[8]	X[8]	X[8]	—	X[16]
T. cingulatum	—	X[8]	—	X[8]	—	X[16]
Thoatherium minusculum	X[1]	X[8]	X[8]	X[8]	—	X[13]
Diadiaphorus majusculus	X[1]	X[8]	X[8]	X[8]	—	X[13]
Theosodon lydekkeri	X[1]	—	—	—	—	—
Theosodon *sp.*	—	X[8]	X[8]	X[8]	—	—
RODENTIA						
OCTODONTOIDEA						
Acarechimys minutus	X[1]	X[9]	—	X[9]	—	X[18]
Acarechimys minutissimus	X[1]	X[9]	X[9]	X[9]	—	X[18]
Acarechimys constans	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*	
Acarechimys gracilis	—	X^{9}	—	X^{9}	—	X^{18}
Dudumus *sp. nov.?*	—	X^{9}	—	X^{9}	—	—
Prospaniomys *sp. nov.?*	—	X^{9}	X^{9}	X^{9}	—	—
Stichomys regularis	X^{1}	X^{9}	—	X^{9}	X^{9}	X^{15}
Stichomys *sp.*	—	—	X^{9}	—	—	—
Spaniomys riparius	X^{1}	X^{9}	X^{9}	X^{9}	—	X^{14}
Spaniomys *sp.*	—	—	—	—	X^{9}	—
Spaniomys modestus	X^{1}	—	—	—	—	—
Adelphomys candidus	X^{1}	—	—	—	—	—
Acaremys murinus	X^{1}	X^{9}	—	X^{9}	—	X^{18}
Acaremys messor	X^{1}	—	—	—	—	—
Acaremys *sp.*	—	—	X^{9}	—	—	—
Pseudoacaremys kramarzii	X^{13}	—	—	—	—	—
Sciamys principalis	X^{1}	X^{9}	X^{9}	X^{9}	—	X^{17}
Sciamys latidens	—	X^{9}	—	X^{9}	—	X^{18}
Sciamys varians	X^{1}	—	—	—	—	—
ERETHIZONTOIDEA						
Steiromys detentus	X^{1}	X^{9}	X^{9}	X^{9}	—	X^{13}
Steiromys duplicatus	X^{1}	X^{9}	X^{9}	X^{9}	—	X^{13}
CAVIOIDEA						
Neoreomys australis	X^{1}	X^{9}	X^{9}	X^{9}	X^{9}	X^{13}
Eocardia montana	X^{1}	X^{9}	X^{9}	X^{9}	—	X^{13}
"Eocardia" excavata	—	X^{9}	X^{9}	X^{9}	—	X^{14}
"Eocardia" fissa	X^{20}	—	—	—	—	—
Schistomys erro	X^{1}	X^{9}	—	X^{9}	—	X^{20}
Phanomys mixtus	X^{1}	X^{9}	X^{9}	—	—	—
Phanomys *sp.*	—	—	—	X^{9}	—	—
CHINCHILLOIDEA						
Prolagostomus pusillus	X^{1}	X^{9}	—	X^{9}	—	X^{21}
Prolagostomus *sp.*	—	—	X^{9}	—	—	—
Pliolagostomus notatus	X^{1}	X^{9}	—	X^{9}	—	X^{21}
Perimys erutus	X^{1}	X^{9}	X^{9}	X^{9}	—	X^{14}
Perimys onustus	X^{1}	X^{9}	X^{9}	X^{9}	—	—
Perimys incavatus	—	X^{9}	X^{9}	—	—	—
Perimys zonatus	X^{1}	—	—	—	—	—
Scleromys angustus	X^{1}	—	—	—	—	—
Scleromys *sp.*	—	X^{9}	X^{9}	X^{9}	—	—
PRIMATES						
Homunculus vizcainoi *sp. nov.*	—	X^{10}	X^{10}	X^{10}	—	—
TOTAL N° OF SPECIES(*)	*79*	*64*	*47*	*60*	*9*	—

X^{1}: Ameghino, 1887a; X^{2}: Cabrera, 1927; X^{3}: Bargo et al., *2019; X^{4}: Fernicola and Vizcaíno, 2019; X^{5}: Fernández and Muñoz, 2019; X^{6}: Mercerat, 1891; X^{7}: Ameghino, 1885; X^{8}: Schmidt* et al., *2019; X^{9}: Arnal* et al., *2019; X^{10}: Kay and Perry, 2019; X^{11}: Chornogubsky* et al., *2019; X^{12}: Arnal and Vucetich, 2015; X^{13}: Kay* et al., *2012; X^{14}: Tauber, 1997a; X^{15} Tauber, 1996; X^{16}: Soria, 2001; X^{17}: Arnal, 2012; X^{18}: Arnal* et al., *2017; X^{19}: Racco* et al., *2018; X^{20}: Pérez, 2010; X^{21}: Rasia, 2016.*

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