

# The record of the tytothere *Pachyrukhos* (Mammalia, Notoungulata) and the Chinchillid *Prolagostomus* (Mammalia, Rodentia) in the Santa Cruz Formation (early–middle Miocene) south to the Río Coyle, Patagonia, Argentina

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# THE RECORD OF THE TYPOTHERE *PACHYRUKHOS* (MAMMALIA, NOTOUNGULATA) AND THE CHINCHILLID *PROLAGOSTOMUS* (MAMMALIA, RODENTIA) IN THE SANTA CRUZ FORMATION (EARLY–MIDDLE MIOCENE) SOUTH TO THE RÍO COYLE, PATAGONIA, ARGENTINA

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**Abstract.** The continental early–middle Miocene Santa Cruz Formation (SCF) from Patagonia is one of the most important stratigraphic units of southern South America in terms of the terrestrial Neogene record. Its fossil content was pivotal for establishing the succession of Cenozoic faunas from Patagonia and formed the basis of the Santacrucian South American Land Mammal Age. Despite the updated knowledge recently achieved, the stratigraphic distribution of many taxa within the SCF remains to be clarified. That is the case with the typotheriid notoungulate *Pachyrukhos* and the chinchillid rodent *Prolagostomus*. New information on the stratigraphy of the SCF along the north bank of the Río Gallegos and Cabo Buen Tiempo (Santa Cruz Province), together with a detailed analysis of the provenance information of the specimens in the principal old museum collections, sheds light on the record of these taxa south to Río Coyle. Our results show that the first recorded occurrence of both taxa in the area was between ~17 Ma and 17.41 Ma, restricted to the upper part of the SCF, including the upper part of the Estancia La Costa Member at Cañadón Las Totoras-Monte Tigre, and the superimposed Estancia La Angelina Member along the Río Gallegos and Cabo Buen Tiempo. Their presence suggests a trend to aridification in the upper part of the SCF south to the Río Coyle. These results are consistent with recent information obtained from other locations of the SCF north to the Río Coyle.

**Keywords.** Typotheria. Caviomorpha. Burdigalian–Langhian. Santacrucian. Patagonia.

**Resumen.** EL REGISTRO DEL TIPOTERIO *PACHYRUKHOS* (MAMMALIA, NOTOUNGULATA) Y EL CHINCHÍLLIDO *PROLAGOSTOMUS* (MAMMALIA, RODENTIA) EN LA FORMACIÓN SANTA CRUZ (MIOCENO TEMPRANO–MEDIO) AL SUR DEL RÍO COYLE, PATAGONIA, ARGENTINA. La Formación Santa Cruz (FSC; Mioceno temprano–medio de Patagonia) es una de las unidades estratigráficas más importantes de América del Sur austral por su registro del Neógeno terrestre. Su contenido fósil fue fundamental para el establecimiento de la sucesión de faunas del Cenozoico de Patagonia y constituyó la base de la Edad Mamífero Santacrucense de América del Sur. A pesar de la reciente actualización de su conocimiento, la distribución estratigráfica de muchos taxones dentro de la FSC aún no se ha esclarecido. Tal es el caso del notoungulado tipoterio *Pachyrukhos* y del roedor chinchíllido *Prolagostomus*. Nueva información sobre la estratigrafía de la FSC en la margen norte del Río Gallegos y en Cabo Buen Tiempo y el análisis de la procedencia de ejemplares en colecciones de museos permitieron esclarecer el registro de esos taxones al sur del Río Coyle. Nuestros resultados indican que el primer registro de ambos taxones en el área sería entre ~17 Ma y 17,41 Ma, restringidos a la parte superior de la FSC, incluyendo la sección más alta del Miembro Estancia La Costa, en Cañadón Las Totoras-Monte Tigre, y el suprayacente Miembro Estancia La Angelina a lo largo del Río Gallegos y en Cabo Buen Tiempo. Su presencia sugiere una tendencia a la aridificación en la parte superior de la FSC al sur del Río Coyle. Estos resultados son consistentes con información reciente de otras localidades de la FSC al norte del Río Coyle.

**Palabras clave.** Typotheria. Caviomorpha. Burdigaliano–Langhiano. Santacrucense. Patagonia.

THE CONTINENTAL early–middle Miocene (Burdigalian–early Langhian) Santa Cruz Formation (SCF) is one of the most important stratigraphic units of southern South America in terms of the terrestrial Neogene record. It extends through

much of southern Patagonian, Argentina, from the eastern area of the southern Patagonian Cordillera (Cordillera Patagónica Austral) southward from the Lago Buenos Aires to the Río Turbio region, and eastward from southern extra-Andean Patagonia to the Atlantic Ocean (Fig. 1.1; Cuitiño *et al.*, 2016, 2019a and references therein). Analysis of SCF tephra shows complex temporal relationships among different localities of the SCF, in some cases supporting previous suggestions based on stratigraphy and paleontology, but in others different or contradictory relationships (Fleagle *et al.*, 2012). Until recently, the stratigraphy, chronology, sedimentology and paleontology of the SCF have been better known from its exposures along the Atlantic coast of the

Santa Cruz Province (for a review, see Cuitiño *et al.*, 2019a). Lately, there have been advances in the knowledge of other important inland fossiliferous areas of the SCF along the Río Santa Cruz (Cuitiño *et al.*, 2019a; Fericola *et al.*, 2019; Kay *et al.*, 2021), south of Lago Posadas (Cuitiño *et al.*, 2019b), and in the valley of Río Chalia (Cuitiño *et al.*, 2021).

The fossil content of the SCF strongly impacts our understanding of the evolution of the Cenozoic biota when the continent was isolated. It was pivotal for establishing the succession of Cenozoic faunas from Patagonia (Ameghino, 1906) and its mammalian fauna is the basis of the Santacrucean South American Land Mammal Age (SALMA; Pascual *et al.*, 1965).

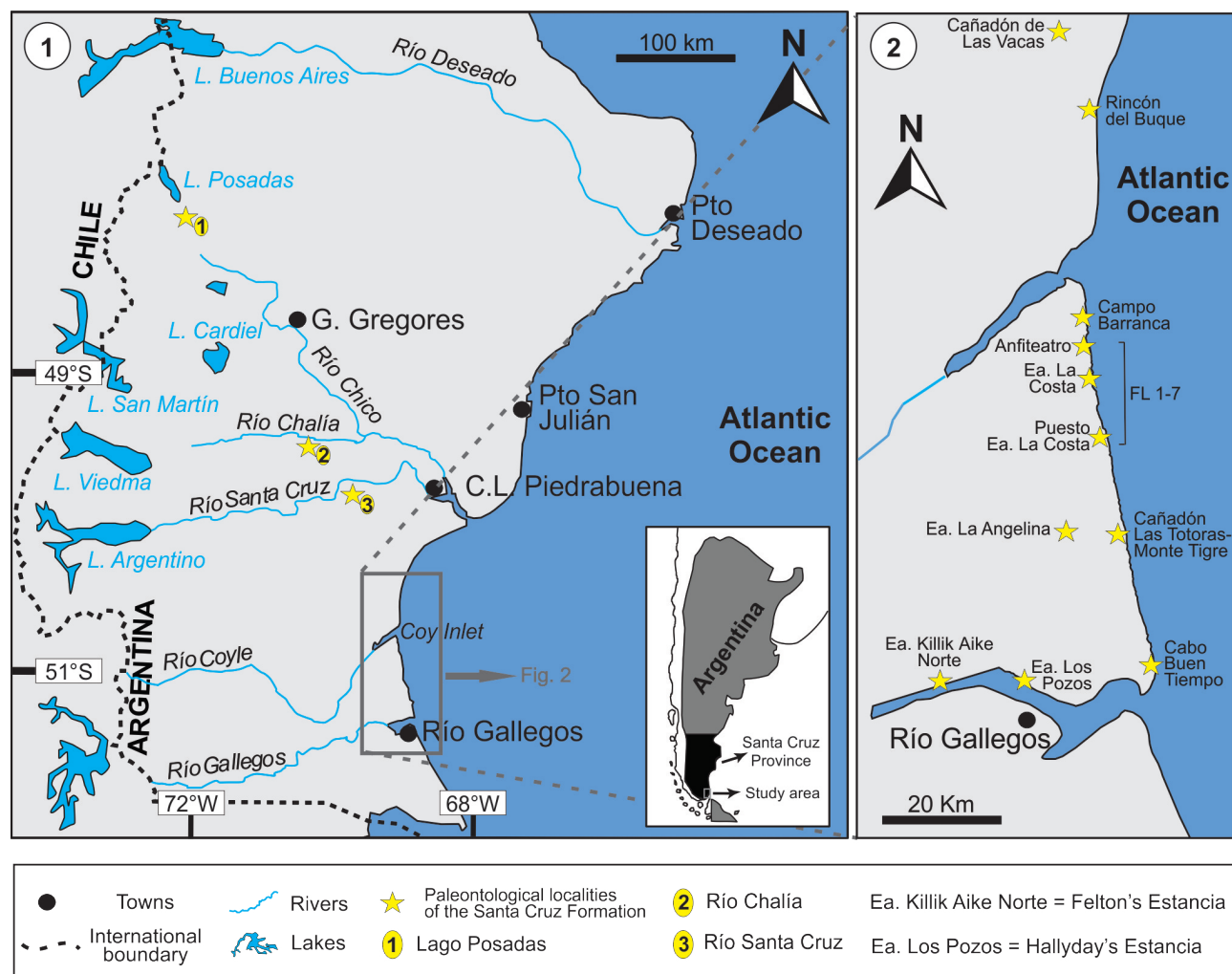


Figure 1. Geographic maps and Santa Cruz Formation fossil localities. 1, regional location map showing the position of the study area and non-coastal Santa Cruz Formation fossil localities. 2, location map of the study area and coastal Santa Cruz Formation fossil localities (modified from Vizcaíno *et al.*, 2012b). FL1-7: fossiliferous levels 1 to 7.

The coastal outcrops of the SCF south of the Río Coyle (which are limited to the Burdigalian) yield a rich assortment of skulls and articulated skeletons of vertebrates (mostly birds and mammals), probably in more abundance than anywhere else in South America (Vizcaíno *et al.*, 2012a). This allowed Vizcaíno *et al.* (2010) and Kay *et al.* (2012) to perform synthetic paleoecological studies based on a form-function approach, working with stratigraphically and geographically restricted samples obtained through extensive fieldwork.

Croft (2013) noted that the faunal lists of the Atlantic coastal localities Campo Barranca (CB) and Puesto Estancia La Costa (PLC; Fig. 1.2) reported by Vizcaíno *et al.* (2010) did not include several characteristic Santacrucian mammal taxa, such as the notoungulate *Pachyrukhos* Ameghino, 1885 (Typotheria, Hegetotheriidae), the litoptern *Theosodon* Ameghino, 1887 (Macraucheniidae), and the rodents *Prolagostomus* Ameghino, 1887 (Chinchillidae) and *Steiromys* Ameghino, 1887 (Erethizontidae). He investigated whether the absence of these genera could be explained, not by true absence, but by inadequate sampling.

As it turns out, *Steiromys* and *Theosodon* had already been reported for a series of coastal localities (including the above-mentioned PLC) by Kay *et al.* (2012), in a comprehensive volume edited by Vizcaíno *et al.* (2012a) and cited

by Croft (2013, p. 402). But the stratigraphic distribution of *Pachyrukhos* and *Prolagostomus* in the SCF along the Atlantic coastal localities south to the Río Coyle remains a matter of uncertainty and is the subject of this contribution.

New information on the stratigraphy of the SCF along the north bank of the Río Gallegos and “Cape Fairweather” (= Cabo Buen Tiempo, CBT; Raigemborn *et al.*, 2018; see Fig. 1.2), together with a detailed analysis of the provenance information of the specimens in the older collections made by Carlos Ameghino, John Bell Hatcher (Princeton University, USA), Barnum Brown (American Museum of Natural History, New York, USA), Handel T. Martin (University of Kansas, USA), and other collectors (Vizcaíno *et al.*, 2013, 2016, 2017) from the area south to the Río Coyle, sheds light on the record of *Pachyrukhos* and *Prolagostomus* in the Atlantic coastal localities studied by Vizcaíno *et al.* (2010, 2012a).

**LOCALITIES SOUTH TO THE RÍO COYLE AND STRATIGRAPHY**

Tauber (1994, 1997a, 1997b) and Vizcaíno *et al.* (2012b) mapped a series of relevant fossil localities of the SCF south of the Río Coyle along the Atlantic coast and on the north bank of the Río Gallegos (Fig. 1.2). Tauber (1994, 1997a, 1997b) established several fossil levels (FL) in this region. Based on a concept that the SCF beds dip gently to the southeast, he concluded that the outcropping levels were successively younger from north to south. However, based on the tephrostratigraphic correlations, Perkins *et al.* (2012) established that up to three of those levels crop out at all these localities and are very close to one another in age. Considering these observations, Kay *et al.* (2012) treated the localities from Anfiteatro to PLC (including Tauber’s FLs 1 to 7; Fig. 1.2) as a single area and paleofauna, which they called FL 1–7. Further interesting localities occur southward on the northern bank of the Río Gallegos, including Estancia Killik Aike Norte (KAN; = Felton’s Estancia in old collections) and Estancia Los Pozos (= Halliday’s Estancia in old collections) (Fig. 1.2).

Tauber (1994, 1997a, 1997b) divided the SCF on the coastal localities south to the Río Coyle into two members that from older to younger are: the Estancia La Costa Member (ELC Member) and the Estancia La Angelina Member (ELA Member) (Fig. 2). By the time of the publications of Vizcaíno

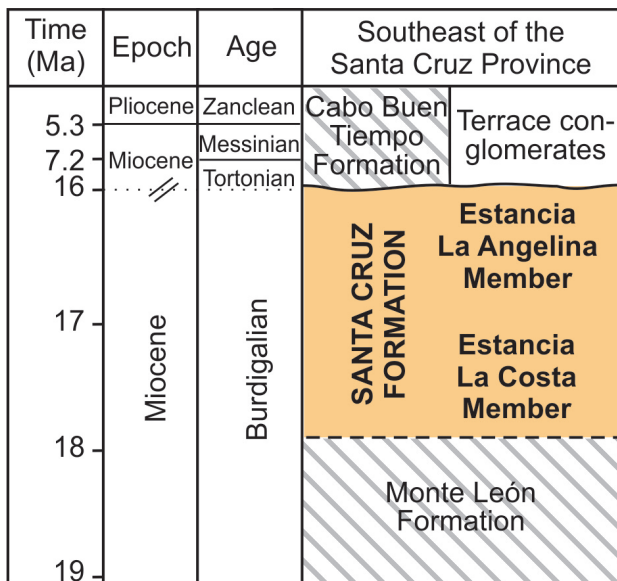


Figure 2. Stratigraphic chart of the southeast Santa Cruz Province. It extends through continental (light orange and white) and marine (striped) units (modified from Raigemborn *et al.*, 2018).



*et al.* (2010), Kay *et al.* (2012), and Croft (2013), Tauber *et al.* (2004) had proposed a provisional stratigraphic correlation between his FL 6 at PLC locality (ELC Member) and a productive tuff level at KAN, a proposal considered valid by Tejedor *et al.* (2006). The age of the FL 6 and 7 at PLC was estimated to be ~17.5 Ma (Perkins *et al.*, 2012) based on an average sedimentation rate and its stratigraphic position beneath a tuff called CO (= Cerro Observatorio) dated at ~17.41 Ma (Perkins *et al.*, 2012), more recently revised to 17.615±0.026 Ma (Trayler *et al.*, 2020).

Recently, Raigemborn *et al.* (2018) studied the stratigraphy and sedimentology of Cañadón Las Totoras-Monte Tigre (CT-MT), CBT and KAN. At CT-MT and KAN, the base of the SCF is not exposed, and the top is covered by the lower Pliocene terrace conglomerates (Panza & Sacomani, 2015) (Fig. 3). According to Raigemborn *et al.* (2018) the deposits of the SCF at CT-MT correspond to the uppermost part of the ELC Member and to the lower part of the ELA Member, while that at KAN corresponds to the lower part of the ELA Member (Fig. 3), and not to the ELC Member as proposed by Tauber *et al.* (2004). As in CT-MT and KAN, at CBT (approximately 25 km southward of CT-MT and 30 km eastward of KAN; Fig. 1.2) the base of the SCF is not exposed and its top is truncated by the upper Miocene–Pleistocene marine Cabo Buen Tiempo Formation. Also, at CBT the uppermost part of the ELC Member and the ELA Member are extensively exposed (Fig. 3), and near the base, lithological changes and geometric and architectural differences in the fluvial system are apparent, indicating that the CBT succession marks the transition between the two members of the SCF (Zapata, 2018).

A well-calibrated chronostratigraphic scheme indicates that at CT-MT and KAN-CBT areas the SCF spans the interval 16.99–15.9 Ma (Fleagle *et al.*, 2012; Perkins *et al.*, 2012; Trayler *et al.*, 2020). At CT-MT Perkins *et al.* (2012) dated a tuff at ~16.9 Ma. At CBT section, a tuff level at the lower part of the ELA Member was recently dated at ~16.95 Ma (Fig. 3; Trayler *et al.*, 2020). At KAN, a succession of tuff beds that crops out near to the base of the exposures has been dated by Tejedor *et al.* (2006) at 16.45–16.5 Ma, and recalibrated by Perkins *et al.* (2012) at ~16.7 Ma. These tuff levels, which are 5 m below the correlated position of the CBT tuff (Fig. 3), were dated at 16.99±0.025 Ma (Trayler *et al.*, 2020).

Thus, given 1) that KAN and CBT localities are only separated by ~30 km, 2) that the available correlative ages are very similar, 3) that south of the Río Coyle the SCF strata are subhorizontal with regional dips no higher than 3° to the southeast (Tauber, 1994), and 4) the absence of any tectonic structure in the area such as faults or folds, it is highly probable that much of the exposures along the northern bank of the Río Gallegos represent the upper part of the SCF (*i.e.*, the ELA Member), as occur in the well exposed CBT locality (see figure 3 in Trayler *et al.*, 2020). In summary of the above, the SCF at KAN and CBT localities are younger than the FL 1–7 recognized at Anfiteatro-PLC area (~17.5 Ma following Perkins *et al.*, 2012), from 500 Ka up to ~1.5 Ma. For a detailed description of the sedimentology and stratigraphy of the Anfiteatro-PLC area see Matheos and Raigemborn (2012).

Finally, the distinction between members equivalent to ELC and ELA has not been recognized in outcrops of the SCF in other areas north to the Río Coyle, such as Rincón del Buque (Raigemborn *et al.*, 2015) and Cañadón de las Vacas (Trayler *et al.* 2020), or westward as in the Río Santa Cruz (Cuitiño *et al.*, 2019a), Lago Posadas (Cuitiño *et al.*, 2019b), and Río Chaliá (Cuitiño *et al.*, 2021).

## MATERIALS AND METHODS

All the specimens collected since 2003 by us south to the Río Coyle (about 1220 vertebrate specimens; ~260 of which are typotheres and ~410 are caviomorph rodents) are housed in the Museo Regional Provincial Padre M. J. Molina (MPM-PV) of Río Gallegos, Argentina. Virtually all of them were recovered from the coastal localities, from Río Coyle to CT-MT (Fig. 1.2); only 10 of our specimens come from KAN and 17 from CBT.

The most important collections with specimens of the coastal and the Río Gallegos localities were evaluated by us. They are those of the MACN-A, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Colección Ameghino, Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; YPM-VPPU, Yale Peabody Museum, Princeton University Collection, New Haven, USA; FMNH, The Field Museum, Chicago, USA; AMNH, American Museum of Natural History, New York, USA; KUNHM, Kansas University Natural History Museum, Lawrence, USA.

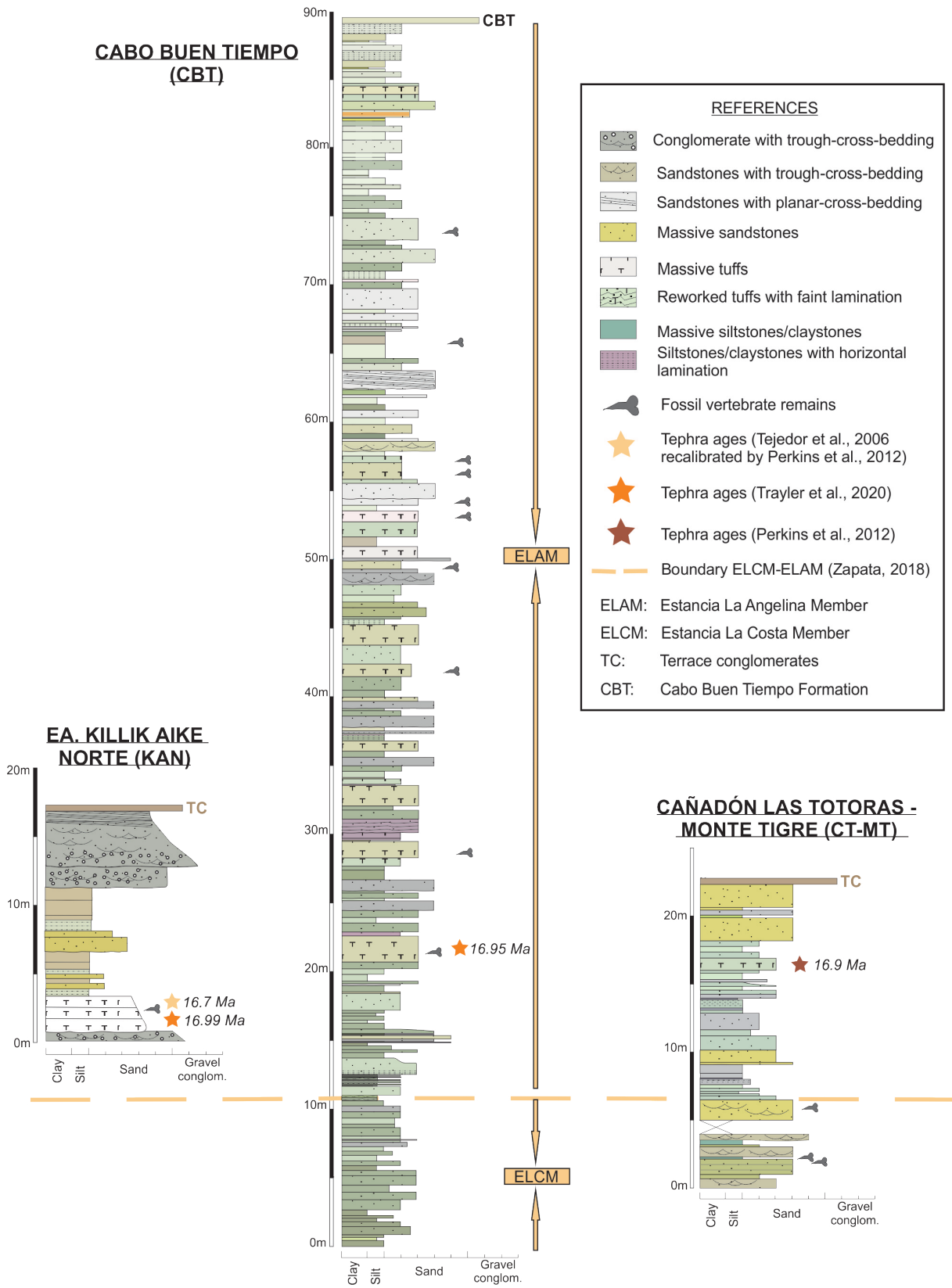


Figure 3. Sedimentary sections of the Cañadón las Totoras–Monte Tigre, Cabo Buen Tiempo and Killik Aike Norte localities including the internal stratigraphy of the Santa Cruz Formation (modified from Raigemborn *et al.*, 2018).

It is worth remembering that the Santacrucian collection currently at YPM-VPPU, was originally obtained by Princeton University (PU) expeditions at the end of the 19<sup>th</sup> century. The collection remained in PU until the 1980s when the research program ceased and almost the complete collection (960 pieces; Vizcaíno *et al.*, 2013) was moved to YPM together with the accompanying photographic records (Vizcaíno *et al.*, 2017).

The records of *Pachyrukhos* and *Prolagostomus* in the museum collections are listed in Appendix 1.

## RESULTS

### The record of *Pachyrukhos*

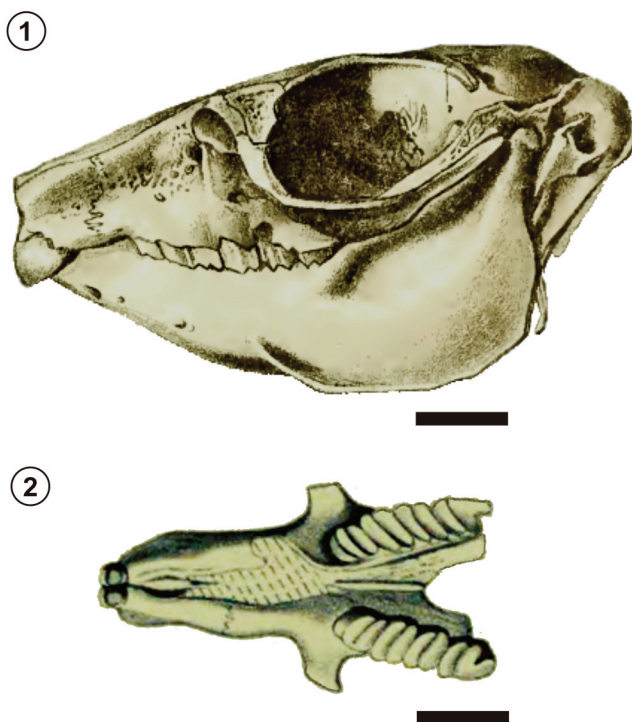
A recent systematic review of *Pachyrukhos* (Fig. 4.1) by Seoane & Cerdeño (2019) indicates that the genus is recorded during Colhuehuapian (early Miocene), Santacrucian, and Colloncuran (middle Miocene) SALMAs. Seoane & Cerdeño (2019) recognize two valid species, *Pachyrukhos politus* Ameghino, 1902 (Colhué Huapi Member of the Sarmiento Formation, Colhuehuapian) and *P. moyani* Ameghino, 1885 (SCF, Santacrucian, and Collón Curá Formation, Colloncuran).

The collections of MLP and MACN-A hold numerous specimens of *Pachyrukhos* from the SCF (Appendix 1). The majority of the specimens come from Santa Cruz Province without further locality information. Several come from the Río Santa Cruz—west and north of the deposits south to the Río Coyle—and one comes from Monte Observación (= Cerro Observatorio), a locality north of Río Coyle prospected by C. Ameghino in 1890–1891 on lands now part of Estancia Cañadón de las Vacas (Fig. 1.2). Only one specimen (MLP 68-I-16-2) comes from the Atlantic coast south to the Río Coyle. The specimen is labelled as coming from Estancia La Angelina, from where we recognize two adjacent localities (CT-MT; Fig. 1.2).

Sinclair (1909, p. 96) listed 20 specimens of *Pachyrukhos* in the collections of the Princeton and AMNH expeditions that were collected along the north bank of the Río Gallegos. The numbers in the collections today are somewhat at variance with Sinclair's count (Appendix 1). In the YPM-VPPU collection there are 13 specimens, 10 from Felton's Estancia), two from Halliday's Estancia, and one from Cape Fairweather. In the AMNH collections there are 13 specimens, eight from Felton's Estancia, one from Halliday's Estancia,

three from the region of Río Gallegos and one of unknown origin. In the collections of FMNH (not studied by Sinclair), there are five specimens from "Felton's Ranch" and one from the area of Río Gallegos. In the KUNHM collections (also not examined by Sinclair) there are seven specimens of uncertain provenance along the Río Gallegos, although Martin's catalog identifies two specimens of *Pachyrukhos* as coming from Felton's Estancia (see below), and one of unknown origin. The precise stratigraphic levels are unknown for all these specimens from Felton's Estancia, Halliday's Estancia, and CBT.

In the YPM-VPPU collection there are two specimens of *Pachyrukhos* collected in 1896 by J. B. Hatcher for Princeton University: YPM-VPPU 15197 and YPM-VPPU 15060 (Appendix 1), cataloged as coming from "17 miles north of Cape Fairweather". Assuming the calculation of the distance is correct, that would represent the localities CT-MT on the Atlantic coast (Fig. 1.2; Tauber, 1997a; Vizcaíno *et al.* 2012b), and some 16 km south of PLC. YPM-VPPU 15197 is



**Figure 4.** Specimens of *Pachyrukhos* and *Prolagostomus* from Felton's Estancia (Killik Aike Norte) on the North bank of the Río Gallegos, Santa Cruz Province (see Appendix 1). **1**, *Pachyrukhos moyani*, AMNH 9283; modified from Sinclair (1909, Plate 10, Fig. 1); **2**, *Prolagostomus divisus*, YPM-VPPU 15570; modified from Scott (1905, Plate 68, Fig. 16). Scale bar= 10 mm.

an incomplete left pelvis, difficult to assign with certainty at the genus level. In the tray of the specimen YPM-VPUP 15060 there are three other specimens, two skulls assigned to *Pachyrukhos* and a third to another tyotherid, *Protyotherium* Ameghino, 1885, and postcranial elements of both genera.

In addition to the above mentioned *Pachyrukhos* specimens in the FMNH collection from Felton's Estancia and other localities along the Río Gallegos (Appendix 1), there are two specimens supposedly collected at PLC. Croft (2013) mentions these two specimens but he does not provide catalog numbers. Our catalog revisions lead us to consider these records extremely dubious. The first, FMNH P 13055, was recovered from "Estancia La Costa: 4 mi S of Caleta Coig ('Coy' or 'Coyle' Inlet)". The specimen was originally identified as *Pachyrukhos*, but is more likely a specimen of *Interatherium* Ameghino, 1887, as indicated in a note attached to the specimen cards by R. Cifelli in 1982 and by R. Madden in 1990. The second, FMNH P 13054, is cataloged with the same provenance information, but the card accompanying the material indicates that it came from Felton's Ranch on the Río Gallegos, a more probable provenance for *Pachyrukhos* according with all the evidence presented here, and not to Estancia La Costa (ELC), 60 km north on the Atlantic coast. Furthermore, P 13054 consisted of a collection of different specimens from which three partial skulls have been assigned to the rodents *Stichomys* Ameghino, 1887 (PM 62485 and 62486) and *Perimys* Ameghino, 1887 (PM 62502) by María Encarnación Pérez in 2015 (as recorded in the FMNH catalog and confirmed by MEP, pers. comm., 2020), and other fragments remain unrevised.

There is considerable uncertainty about the localities of most of the specimens collected by H. T. Martin. At least seven of Martin's *Pachyrukhos* specimens remain in the KUNHM collections, and several others collected by him are preserved in the Field Museum (Appendix 1). Of these, only one specimen is associated with a locality—the FMNH specimen label says it was collected by Martin in the vicinity of Río Gallegos, which could be at Felton's or Halliday's Estancias. In Martin's field catalog he identifies only two specimens of *Pachyrukhos*, both from Felton's Estancia: "No. 10, skull and lower jaws, very fine probably *Pachyrukhos* (Ameg) teeth very like his figures. In talus of cliffs ½ mile above Mr. Felton's house, Río Gallegos river, St. Cruz beds."

and "No. 126, Parts of two under [*i.e.*, mandible] and one upper jaw. One under jaw probably *Pachyrukhos*; others not figured by Ameghino. 4 miles above [presumably up-river] F's [Felton's] house."

Neither of these two specimens in Martin's catalog is definitely associated with any currently preserved specimen. Many other specimens were identified by Martin as being "*Tyotherium*". *Tyotherium* Bravard, 1856 is a Pleistocene genus within which Martin may have clumped any specimens of hegetotheres or even any interatheres. The best we can say is that Martin did not certainly identify any *Pachyrukhos* specimens as coming from other than Felton's Estancia.

In the collections made in the last part of the 20<sup>th</sup> and this century, Tauber (1997a, 1997b, 1999), Vizcaíno *et al.* (2010) and Kay *et al.* (2012) did not report *Pachyrukhos* from any coastal locality between Río Coyle and CBT of the SCF, including from Campo Barranca and PLC as mentioned before. Fernández & Muñoz (2019) listed one specimen of *Pachyrukhos* from PLC, based on an unprepared fragmentary mandible, but its large size renders the allocation to this genus dubious. Tauber *et al.* (2004) did not mention any *Pachyrukhos* from KAN, and we did not record the genus there or at CBT.

In summary, the record of *Pachyrukhos* south to the Río Coyle for which we have precise information is restricted to the upper part of the ELC Member in the coastal area (Cañadón Las Totoras-Monte Tigre area) and the superimposed ELA Member of the SCF where it crops out at the north bank of Río Gallegos, from KAN to CBT. The oldest recorded occurrence of *Pachyrukhos* in this area is at Cañadón Las Totoras-Monte Tigre, would be somewhat older than ~17 Ma, but certainly younger than 17.41 Ma, the age of FL 1–7, according to the dates in Perkins *et al.* (2012) and Trayler *et al.* (2020).

### The record of *Prolagostomus*

In a review of the fossil chinchillids from Argentina, Rasia (2016) indicated that the genus *Prolagostomus* (Fig. 4.2) is recorded in the "Pinturan" (early Miocene), Santacrucian and Colloncuran SALMAs. Rasia (2016) recognized three valid species: *Prolagostomus pusillus* Ameghino, 1887, *Pr. obliquidens* Scott, 1905, and *Pr. rosendoi* Vucetich, 1984. *Prolagostomus*



*pusillus* is recorded in the Santa Cruz, Collon Curá, and Río Frías ("Friasian") formations; *Pr. obliquidens* is exclusive to the SCF, and known only for the type and one other specimen mentioned by Tauber (1997a, 1999; see below), and *Pr. rosendoi* occurs in the Collon Curá Formation.

*Prolagostomus* specimens housed at MLP collection come from the "Barrancas del Río Santa Cruz", recovered by Carlos Ameghino's expeditions in 1887. The Ameghino Collection at MACN contains 38 records (remains, not individuals) of *Prolagostomus*, 20 from Monte Observación (= Cerro Observatorio; see above); five from Sehuén (= Río Chalfía), and others (~10) without locality information (Appendix 1).

At YPM-VPPU there are seven specimens of *Prolagostomus* from the north bank of the Río Gallegos; six from Felton's Estancia, one from Halliday's Estancia, and one from an uncertain locality. At FMNH there is only one specimen from Felton's Estancia. There are no records of *Prolagostomus* in the KUNHM collection.

Tauber (1997a, 1997b, 1999) reported one record (CORD-PZ 1335; Museo de Paleontología, Universidad Nacional de Córdoba) from Monte Tigre locality (Fig. 1.2) and Tauber *et al.* (2004) one from KAN. As mentioned above *Prolagostomus* was not reported for Atlantic coast localities south to the Río Coyle by Kay *et al.* (2012), nor has field work in the area turned up any new specimens. We did not record the taxon at KAN or CBT.

Thus, *Prolagostomus* is certainly recorded in the ELA Member along the north bank of Río Gallegos and CBT, and probably the upper part of the ELC Member at Cañadón Las Totoras-Monte Tigre. The oldest record of *Prolagostomus* in the area would be synchronous with the first appearance of *Pachyrukhos*, somewhat older than ~17 Ma, but certainly younger than 17.41 Ma according to the dates in Perkins *et al.* (2012) and Trayler *et al.* (2020).

## DISCUSSION

The absence of *Pachyrukhos* and the rarity of *Prolagostomus* in the collection from the KAN-CBT area along the Río Gallegos made by us and the one reported by Tauber *et al.* (2004) may be explained as due to low sampling, as we visited the area briefly and collected only 27 mammal specimens. In contrast, the large collections made by Hatcher (at YPM-VPPU), Martin (at KUHNM), and E. S. Riggs (at FMNH)

at the end of the 19<sup>th</sup> and the beginning of the 20<sup>th</sup> centuries along the Río Gallegos resulted from long seasons (Vizcaíno *et al.*, 2013, 2016).

After a rarefaction analysis of the SCF fossil mammals in the YPM-VPPU collection, Croft (2013) suggested that the absence of *Pachyrukhos* and *Prolagostomus*, as well as the lioptern *Theosodon* and the erethizontid rodent *Steiromys* in the FL 1–7 area in Vizcaíno *et al.* (2010) could be explained by inadequate sampling. On one hand, as explained above, Kay *et al.* (2012) reported *Theosodon* and *Steiromys* for that area. On the other hand, the information reported and analyzed here shows that the undisputed first stratigraphic occurrence of *Pachyrukhos* along the Atlantic coast south to the Río Coyle is in the uppermost part of the ELC Member. Conversely, *Pachyrukhos* is quite common in the ELA Member along the north bank of the Río Gallegos. Likewise, the chinchillid rodent *Prolagostomus* also is restricted to the upper part of the coastal SCF, certainly in the ELA Member, and probably the upper part of the underlying ELC Member (from Monte Tigre locality, according to Tauber, 1997a, 1999).

Interestingly, the record of both taxa in recent reports from the Río Santa Cruz (Arnal *et al.*, 2019; Fernández & Muñoz, 2019), northwest of the area considered here, shows a similar distributional pattern between the lower and upper parts of the SCF (not the ELC and ELA members as mentioned above) in two separate localities (Barrancas Blancas and Segundas Barrancas Blancas) with only a brief interval of stratigraphic overlap between them (Cuitiño *et al.*, 2019; Kay *et al.*, 2021). The eastern Barrancas Blancas locality encompasses the lower section (between ~17.2 and ~16.3 Ma); the western Segundas Barrancas Blancas represents the upper section (between ~16.5 and ~15.6 Ma). *Pachyrukhos* is limited to the upper section (Segundas Barrancas Blancas; Fernández & Muñoz, 2019). *Prolagostomus* is very rare at the lower Barrancas Blancas, where it is represented by only two loose isolated molar fragments (Arnal *et al.*, 2019; Fericola *et al.*, 2019), from Estancia Santa Lucía, where the upper part of the lower section crops out (between ~16.8 and 16.57, Cuitiño *et al.*, 2019). Conversely, it represents 26% of all rodent records in the geologically younger Segundas Barrancas Blancas locality (Arnal *et al.*, 2019; Kay *et al.*, 2021).

From a paleoecological point of view, our studies of the SCF along the Río Santa Cruz (Kay *et al.*, 2021) refocus attention on these two taxa, as they are absent (*Pachyrukhos*) or rare (*Prolagostomus*) in large samples from the lower stratigraphic levels, but common in the upper levels. Notably, Kramarz & Bellosi (2005) reported a more primitive species of *Prolagostomus* for the middle and upper sequence of the earlier Pinturas Formation (early Miocene) in north-western Santa Cruz Province. The genus then disappears in the lower parts of SCF at Río Santa Cruz, only to again appear in the upper beds in that region. This pattern of occurrence in the Pinturas Formation has been interpreted as an environmental indicator by Kramarz & Bellosi (2005, p. 210), who suggest its presence in the middle and upper sequence of the Pinturas Formation “probably correspond[s] to more xeric environments”. Following this suggestion, we propose that the absence of *Pachyrukhos* in the lower part of the SCF south of Río Coyle may indicate more mesic conditions than occurred in the Pinturas Formation. More xeric conditions like that of the upper Pinturas Formation then returned in the upper SCF after ~17.4–17.0 Ma.

Kay *et al.* (2021) reconstructed the paleoenvironmental and community structure of the Río Santa Cruz faunas, compared with numerous extant lowland mammalian localities across South America, ranging from tropical rainforest to semi-arid savanna. Using this niche-base model they obtained a general Mean Annual Precipitation between 1450 mm and 1635 mm and a Mean Annual Temperature between ~16° C and ~22° C, and concluded the SCF paleoenvironment consisted largely of semi-deciduous forests ranging into savannas with gallery-forest components. In this context, the presence of *Pachyrukhos* and *Prolagostomus*, together with an increased overall abundance and richness of caviomorph rodents with ever-growing cheek teeth, suggest a trend to aridification in the upper part of the SCF at Segundas Barrancas Blancas locality, compared with FL 1–7 and Barrancas Blancas. It appears that a similar trend also occurred in the upper part of the ELC Member and throughout the ELA Member south to the Río Coyle.

Croft (2013) argued that single-locality samples are not necessarily more appropriate than multi-locality samples for paleoecological analyses of the SCF mammalian fauna given the large regional extent of this formation and the

large geographic area encompassed by most modern communities used for comparison. Croft (2013) also highlighted the need for more precise stratigraphic correlations among Santa Cruz localities and integration of important historical collections into a modern stratigraphic framework. Certainly, we agree with Croft’s (2013) last claim and this contribution, and many others cited here, are examples of our efforts in that direction. However, detailed paleoecological analyses of the fauna of the SCF comparing the community structure with that of numerous communities of extant mammals across South America shows that fossil collections from restricted areas with good stratigraphic control are comparable to restricted extant faunas (Kay *et al.*, 2012, 2021).

## CONCLUSIONS

In this contribution, we have established that in the coastal SCF south of Río Coyle *Pachyrukhos* and *Prolagostomus* show the same distribution patterns recorded along the Río Santa Cruz: they are absent or rare in the lower stratigraphic levels and present, or even common, in the upper levels. Studies in progress based on new material collected by the authors indicates that both taxa also appear only at the higher levels of the unit in other areas north to the Río Coyle, such as at Cañadón de las Vacas and Rincón del Buque in the east, and Río Chalfía in central Santa Cruz Province.

As mentioned above the first occurrence of both taxa south of Río Coyle is between ~17 and 17.41 Ma, whereas at Río Santa Cruz it is at ~16.5 Ma, so it would be up to ~500 Kyr younger along the former than in the latter. Whether the timing of the first appearance of these two taxa is similar in the two regions (*i.e.*, the Río Santa Cruz and south of Río Coyle) is uncertain and depends on improving the stratigraphic and chronologic resolution of the fossil-bearing levels at the upper part of the ELC Member. The timing for the last appearance of both taxa south to the Río Coyle would depend on further collection work along KAN-CBT area, where the SCF has been dated at ~15.9 Ma (Fleagle *et al.*, 2012; Perkins *et al.*, 2012; Trayler *et al.*, 2020) still during the Burdigalian. Instead, the youngest levels of the SCF should be searched at Río Chalfía where the uppermost exposures have been estimated as young as 15.2 Ma (*i.e.*, early Langhian; Cuitiño *et al.*, 2021).

The presence of *Pachyrukhos* and *Prolagostomus* in the upper part of the ELC Member and in the ELA Member suggests a trend to aridification in the upper part of the SCF south to the Río Coyle. Finally, we highlight the value of focusing paleoenvironmental and paleoecological studies of the SFC on stratigraphically and geographically controlled fossil samples instead of on the entire temporal and geographic distribution of the formation based on historical collections with limited provenance information.

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**APPENDIX 1.** Records of *Pachyrukhos* and *Prolagostomus* from the Santa Cruz Formation from the catalogs of the museum collections mentioned in the text (see Material and methods). Names of localities are indicated as in the original catalogs; between brackets the names in Spanish as they are known today. Ea., Estancia.

SPECIES	COLLECTION NUMBER	LOCALITY (Santa Cruz Province, Argentina)	COLLECTOR	COMMENTS
<i>Pachyrukhos</i> sp.	YPM-VPPU 15060	17 miles north of Cape Fairweather (Cabo Buen Tiempo)	J.B. Hatcher	See text
<i>Pachyrukhos</i> sp.	YPM-VPPU 15197	17 miles north of Cape Fairweather (Cabo Buen Tiempo)	J.B. Hatcher	See text
<i>Pachyrukhos</i> sp.	YPM-VPPU 15961	Cape Fairweather (Cabo Buen Tiempo)	J.B. Hatcher	
<i>Pachyrukhos moyani</i>	YPM-VPPU 15369	Felton's Estancia (Ea. Killik Aike Norte), north bank of Río Gallegos	J.B. Hatcher	
<i>Pachyrukhos moyani</i>	YPM-VPPU 15438	Felton's Estancia (Ea. Killik Aike Norte), north bank of Río Gallegos	J.B. Hatcher	
<i>Pachyrukhos moyani</i>	YPM-VPPU 15671	Felton's Estancia (Ea. Killik Aike Norte), north bank of Río Gallegos	J.B. Hatcher	
<i>Pachyrukhos moyani</i>	YPM-VPPU 15744	Felton's Estancia (Ea. Killik Aike Norte), north bank of Río Gallegos	J.B. Hatcher, O.A. Peterson	
<i>Pachyrukhos moyani</i>	YPM-VPPU 15888	Felton's Estancia (Ea. Killik Aike Norte), north bank of Río Gallegos	J.B. Hatcher	
<i>Pachyrukhos</i> sp.	YPM-VPPU 15360	Felton's Estancia (Ea. Killik Aike Norte), north bank of Río Gallegos	J.B. Hatcher	
<i>Pachyrukhos</i> sp.	YPM-VPPU 15426	Felton's Estancia (Ea. Killik Aike Norte), north bank of Río Gallegos	J.B. Hatcher	
<i>Pachyrukhos</i> sp.	YPM-VPPU 15662	Felton's Estancia (Ea. Killik Aike Norte), north bank of Río Gallegos	J.B. Hatcher	
<i>Pachyrukhos</i> sp.	YPM-VPPU 15940	Felton's Estancia (Ea. Killik Aike Norte), north bank of Río Gallegos	O.A. Peterson	
<i>Pachyrukhos moyani</i>	YPM-VPPU 15743	Felton's Estancia, 4 miles east of Ea. Killik Aike Norte	O.A. Peterson	
<i>Pachyrukhos moyani</i>	YPM-VPPU 15939	Halliday's Estancia (?) (Ea. Los Pozos), north bank of Río Gallegos	Princeton Expeditions	
<i>Pachyrukhos moyani</i>	YPM-VPPU 15603	Halliday's Estancia (Ea. Los Pozos), north bank of Río Gallegos	O.A. Peterson	
<i>Pachyrukhos</i> cf. <i>moyani</i>	YPM-VPPU 15703	Lago Pueyrredón	J.B. Hatcher	
<i>Pachyrukhos</i> cf. <i>moyani</i>	YPM-VPPU 15735	Lago Pueyrredón	J.B. Hatcher	
<i>Pachyrukhos</i> cf. <i>moyani</i>	YPM-VPPU 15850	Lago Pueyrredón	J.B. Hatcher	
<i>Pachyrukhos</i> cf. <i>moyani</i>	YPM-VPPU 16038	Lago Pueyrredón	J.B. Hatcher	
<i>Pachyrukhos</i> sp.	YPM-VPPU 15922	Monte Observación, Atlantic coast, at the mouth of Cañadón de las Vacas, on its northern bank	J.B. Hatcher	
<i>Pachyrukhos</i> sp.	YPM-VPPU 15920	Río Chico	J.B. Hatcher	
<i>Pachyrukhos</i> sp.	YPM-VPPU 15088	South side of Río Santa Cruz, 60 miles east of Lago Argentino.	J.B. Hatcher	
<i>Pachyrukhos</i> sp.	AMNH 9242	Felton's Estancia (Ea. Killik Aike Norte)	B. Brown	
<i>Pachyrukhos moyani</i>	AMNH 9282	Felton's Estancia (Ea. Killik Aike Norte)		
<i>Pachyrukhos moyani</i>	AMNH 9283	Felton's Estancia (Ea. Killik Aike Norte)		Fig. 4.1 this work
<i>Pachyrukhos moyani</i>	AMNH 9285	Felton's Estancia (Ea. Killik Aike Norte)	B. Brown 1899	
<i>Pachyrukhos moyani</i>	AMNH 9481	Felton's Estancia (Ea. Killik Aike Norte)	B. Brown 1899	
<i>Pachyrukhos</i> sp.	AMNH 9506	Felton's Estancia (Ea. Killik Aike Norte)	B. Brown	
<i>Pachyrukhos</i> sp.	AMNH 9528	Felton's Estancia (Ea. Killik Aike Norte)	B. Brown	
<i>Pachyrukhos</i> sp.	AMNH 9551	Felton's Estancia (Ea. Killik Aike Norte)		
<i>Pachyrukhos moyani</i>	AMNH 9219	Halliday's Estancia		
<i>Pachyrukhos</i> sp.	AMNH 9508	Río Gallegos	B. Brown	
<i>Pachyrukhos</i> sp.	AMNH 9525	Río Gallegos		
<i>Pachyrukhos</i> sp.	AMNH 9558	Río Gallegos		



## APPENDIX 1. Continuation.

SPECIES	COLLECTION NUMBER	LOCALITY (Santa Cruz Province, Argentina)	COLLECTOR	COMMENTS
<i>Pachyrukhos</i> sp.	AMNH 9535	unknown		
<i>Pachyrukhos</i> sp.	FMNH P12051	Río Gallegos vicinity	H.T. Martin	
<i>Pachyrukhos</i> sp.	FMNH P12994	Felton's Ranch (Ea. Killik Aike Norte)	J.B. Abbott	
<i>Pachyrukhos moyani</i>	FMNH P13049	Felton's Ranch (Ea. Killik Aike Norte)	G.F. Sternberg, E.S. Riggs	
<i>Pachyrukhos</i> sp.	FMNH P13051	Felton's Ranch (Ea. Killik Aike Norte), near Halliday's Ranch (Ea. Los Pozos)		
<i>Pachyrukhos</i> sp.	FMNH P13052	Felton's Ranch (Ea. Killik Aike Norte): 2 miles above ranch house	G.F. Sternberg	
<i>Pachyrukhos</i> sp.	FMNH P13053	Felton's Ranch (Ea. Killik Aike Norte)	# 504 Abbot	
<i>Pachyrukhos</i> sp.	FMNH P13054	Estancia La Costa: 4 mi S of Caleta Coig ('Coy' or 'Coyle' Inlet)		Include three rodent skulls. See text
<i>Pachyrukhos</i> sp.	FMNH P13055	Estancia La Costa: 4 mi S of Caleta Coig ('Coy' or 'Coyle' Inlet)		Identified as <i>Interatherium</i> sp. See text
<i>Pachyrukhos moyani</i>	KUNHM 69254	Río Gallegos, Patagonia*	H.T. Martin 1903-04	*The locality is provided in the KUNHM catalog as ARGENTINA: KU-ZSA-002
<i>Pachyrukhos moyani</i>	KUNHM 650	Río Gallegos, Patagonia	H.T. Martin 1903-05	
<i>Pachyrukhos</i> sp.	KUNHM 11653	Río Gallegos, Patagonia	H.T. Martin 1903-06	
<i>Pachyrukhos</i> sp.	KUNHM 69251	Río Gallegos, Patagonia	H.T. Martin 1903-07	
<i>Pachyrukhos</i> sp.	KUNHM 69255	Río Gallegos, Patagonia	H.T. Martin 1903-08	
<i>Pachyrukhos</i> sp.	KUNHM 69256	Río Gallegos, Patagonia	H.T. Martin 1903-09	
<i>Pachyrukhos</i> sp.	KUNHM 69257	Río Gallegos, Patagonia	H.T. Martin 1903-10	
<i>Pachyrukhos</i> sp.	KUNHM 5060			
<i>Pachyrukhos moyani</i>	MACN-A 259-261	Santa Cruz	C. Ameghino	MACN catalog
<i>Pachyrukhos moyani</i>	MACN-A 262	Santa Cruz	C. Ameghino	Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MACN-A 272-276	Río Santa Cruz	C. Ameghino	Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MACN-A 277	Santa Cruz	C. Ameghino	Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MACN-A 279-296	Santa Cruz	C. Ameghino	Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MACN-A 297	Santa Cruz	C. Ameghino	Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MACN-A 298-318	Santa Cruz	C. Ameghino	MACN-A catalog
<i>Pachyrukhos moyani</i>	MACN-A 319-321	Santa Cruz	C. Ameghino	Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MACN-A 322-324	Santa Cruz	C. Ameghino	Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MACN-A 326-327	Santa Cruz	C. Ameghino	MACN-A catalog
<i>Pachyrukhos moyani</i>	MACN-A 328-329	Santa Cruz	C. Ameghino	MACN-A catalog
<i>Pachyrukhos moyani</i>	MACN-A 330-335	Santa Cruz	C. Ameghino	Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MACN-A 3304-3312	Santa Cruz	C. Ameghino 1890-91	Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MACN-A 3314-3317	Santa Cruz	C. Ameghino 1890-91	Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MACN-A 3318-3320	Santa Cruz	C. Ameghino 1890-91	Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MACN-A 9957-9958	Monte Observación (=Cañadón de las Vacas)	C. Ameghino 1891-92	MACN-A catalog
<i>Pachyrukhos moyani</i>	MLP 12-2002	Barrancas del Río Santa Cruz	C. Ameghino 1887	MLP catalog
<i>Pachyrukhos moyani</i>	MLP 12-1922	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-1924	Santa Cruz		Seoane & Cerdeño (2019)

## APPENDIX 1. Continuation.

SPECIES	COLLECTION NUMBER	LOCALITY (Santa Cruz Province, Argentina)	COLLECTOR	COMMENTS
<i>Pachyrukhos moyani</i>	MLP 12-1930	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-1932	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-1934	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-1959	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-1964	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-1966	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-1968	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-1971	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-1985	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-1987	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-1989	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-1991	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-1996	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2007	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2017	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2018	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2036	Barrancas del Río Santa Cruz	C. Ameghino 1887	Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2042	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2044	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2075	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2077	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2078	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2086	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2087	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2103	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2108	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2110	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2113	Barrancas del Río Santa Cruz		MLP catalog
<i>Pachyrukhos moyani</i>	MLP 12-2115	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2117	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2118	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2120	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2121	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2123	Barrancas del Río Santa Cruz	C. Ameghino 1887	Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2125	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2136	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2138	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2141	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2142	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2145	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2146	Santa Cruz		Seoane & Cerdeño (2019)

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SPECIES	COLLECTION NUMBER	LOCALITY (Santa Cruz Province, Argentina)	COLLECTOR	COMMENTS
<i>Pachyrukhos moyani</i>	MLP 12-2148	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2149	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2151	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2156	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2158	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12- 2163	Barrancas del Río Santa Cruz	C. Ameghino 1887	Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12- 2166	Barrancas del Río Santa Cruz	C. Ameghino 1887	Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12- 2735	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12- 2738	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12- 2749	Santa Cruz		Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2830	Barrancas del Río Santa Cruz	C. Ameghino 1887	Seoane & Cerdeño (2019)
<i>Pachyrukhos moyani</i>	MLP 12-2852	Santa Cruz	C. Ameghino	Seoane & Cerdeño
<i>Pachyrukhos</i> sp.	MLP 68-I-16-2 y 3	Estancia La Angelina (=Monte Tigre)	R. Pascual & O. Odreman	MLP catalog; see text
<i>Protagostomus obliquidens</i>	YPM-VPPU 15655	Felton's Estancia (Ea. Killik Aike Norte), north bank of Río Gallegos	J.B. Hatcher	Holotype. Scott (1905, fig. 42)
<i>Protagostomus divisus</i>	YPM-VPPU 15570	Felton's Estancia (Ea. Killik Aike Norte), north bank of Río Gallegos	J.B. Hatcher	Fig. 4.2 this work
<i>Protagostomus divisus</i>	YPM-VPPU 15882	Felton's Estancia (Ea. Killik Aike Norte), north bank of Río Gallegos	J.B. Hatcher	
<i>Protagostomus imperialis</i>	YPM-VPPU 15602	Halliday's Estancia, north bank of Río Gallegos	O.A. Peterson	
<i>Protagostomus imperialis?</i>	YPM-VPPU 15429	Felton's Estancia (Ea. Killik Aike Norte), north bank of Río Gallegos	J.B. Hatcher	
<i>Protagostomus profluens</i>	YPM-VPPU 15622	Felton's Estancia (Ea. Killik Aike Norte), north bank of Río Gallegos	J.B. Hatcher	
<i>Protagostomus</i> sp.	YPM-VPPU 15938	Felton's Estancia (Ea. Killik Aike Norte), north bank of Río Gallegos	J.B. Hatcher	
<i>Protagostomus</i> sp.	YPM-VPPU 16809	Santa Cruz Province, Patagonia	J.B. Hatcher	
<i>Protagostomus profluens</i>	FMNH P13265	Felton's Ranch (Ea. Killik Aike Norte)	E.S. Riggs	
<i>Protagostomus pusillus</i>	MACN-A 392	Santa Cruz	C. Ameghino	Syntype of <i>Lagostomus lateralis</i> . Rasia (2016)
<i>Protagostomus pusillus</i>	MACN-A 394	Santa Cruz	C. Ameghino	Syntype of <i>Lagostomus primigenius</i> . Rasia (2016)
<i>Protagostomus</i> sp.	MACN-A *	Monte Observación, Sehuén and Santa Cruz	C. Ameghino	* MACN-A catalog 38 entries; see text
<i>Protagostomus pusillus</i>	MLP 15-136	Barrancas del Río Santa Cruz	C. Ameghino 1887	Holotype. Rasia (2016)
<i>Protagostomus pusillus</i>	MLP 15-385	Barrancas del Río Santa Cruz	C. Ameghino 1887	Rasia (2016)
<i>Protagostomus pusillus</i>	MLP 15-152	Barrancas del Río Santa Cruz		Rasia (2016)
<i>Protagostomus pusillus</i>	MLP 15-110	Santa Cruz		Rasia (2016)
<i>Protagostomus pusillus</i>	MLP 15-88	Santa Cruz	C. Ameghino	Rasia (2016)
<i>Protagostomus pusillus</i>	MLP 15-65	Barrancas del Río Santa Cruz		Rasia (2016)
<i>Protagostomus pusillus</i>	MLP 15-115	Barrancas del Río Santa Cruz		Rasia (2016)
<i>Protagostomus pusillus</i>	MLP 15-294	Barrancas del Río Santa Cruz	C. Ameghino 1887	Rasia (2016)
<i>Protagostomus pusillus</i>	MLP 15-304	Barrancas del Río Santa Cruz	C. Ameghino 1887	Rasia (2016)
<i>Protagostomus pusillus</i>	MLP 15-354	Barrancas del Río Santa Cruz	C. Ameghino 1887	Rasia (2016)
<i>Protagostomus pusillus</i>	MLP 26-IV-15-6	Río Santa Cruz	E.S. Riggs	Donation of the FMNH
<i>Protagostomus pusillus</i>	MLP 68-IX-2-1	Santa Cruz	A. Borello	Rasia (2016)