

Fossil vertebrates of the early-middle Miocene Cerro Boleadoras Formation, northwestern Santa Cruz Province, Patagonia, Argentina

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ABSTRACT. The early-middle Miocene continental Cerro Boleadoras Formation (CBF) crops out in the area of Cerro Boleadoras and Cerro Plomo on the western slope of the Meseta del Lago Buenos Aires, northwestern Santa Cruz Province, Argentina. The lower levels of the CBF consist of laterally extensive medium to pebbly sandstone beds with trough cross-bedding, interpreted as fluvial channel deposits, interbedded with tabular fine-grained floodplain deposits. Recent fieldwork provided fossil vertebrates from these levels with an estimated age between ~16.5 Ma and 15.1 Ma (late Burdigalian-early Langhian). The studied section temporally overlaps with the middle or upper sections of the Santa Cruz Formation (SCF) in the Austral-Magallanes Basin of southern Patagonia, the Río Frías Formation in Chile, and the lower Collón Curá Formation of northern Patagonia. We compile an integrated faunal list for this locality, including specimens from previous collections, and discuss its chronological and paleoenvironmental implications. The taxa list includes most of the groups recorded in the SCF: one anuran, three birds, and at least 33 mammals (metatherians, xenarthrans, litopterns, notoungulate typotheres and caviomorph rodents), indicating a Santacrucian age *sensu lato*. We also recorded a testudine, which constitutes the southernmost record of tortoises in South America and worldwide. Faunal dissimilarities between the vertebrate fossil content of the CBF and the mentioned sections of the Santa Cruz, Río Frías and Collón Curá formations may reflect ecologic, climatic and geographic differences rather than temporal ones. The

co-occurrence of arboreal or semiarboreal, browsing, frugivorous, and grazing mammals suggests the presence of both forested and open environments for the area occupied by the CBF rocks. However, it is not possible to discern whether these two environments coexisted or alternated, and whether one environment predominated over the other. Marker taxa, such as the chinchillid rodents *Prolagostomus* and *Pliolagostomus*, and the typothere *Pachyrukhos* indicate a trend to aridification during the Miocene in southern Patagonia, as previously reported for the upper part of the SCF along the Río Santa Cruz and south to the Río Coyle, along the Atlantic coast and the Río Gallegos.

Keywords: South America, Andes, Burdigalian-Langhian, Vertebrate paleontology, Paleoenvironment.

RESUMEN. Vertebrados fósiles de la Formación Cerro Boleadoras (Mioceno temprano-medio), noroeste de la provincia de Santa Cruz, Patagonia, Argentina. Sedimentos continentales del Mioceno temprano-medio de la Formación Cerro Boleadoras (FCB) afloran en el área de los cerros Boleadoras y Plomo, en la vertiente occidental de la meseta del lago Buenos Aires, noroeste de la provincia de Santa Cruz, Argentina. Los niveles inferiores de la FCB consisten en estratos de areniscas medianas a gruesas con estratificación entrecruzada, lateralmente extensos, interpretados como depósitos de canales fluviales, que se intercalan con depósitos finos de planicie de inundación. Trabajo de campo reciente permitió recuperar vertebrados fósiles de estos niveles, con una edad estimada entre ~16,5 y 15,1 Ma (Burdigaliano tardío-Langhiano temprano). Estos niveles se solapan temporalmente con las secciones media y superior de la Formación Santa Cruz (FSC) en la cuenca Austral-Magallanes de la Patagonia Austral, la Formación Río Frías en Chile y la parte inferior de la Formación Collón Curá en el norte de la Patagonia. En este trabajo se recopila una lista faunística actualizada para esta localidad, que incluye especímenes de colecciones previas, y se discuten sus implicaciones cronológicas y paleoambientales. La lista incluye la mayoría de los grupos registrados en la FSC: un anuro, tres aves y al menos 33 mamíferos (metaterios, xenartros, litopternos, notoungulados tipoterios y roedores caviomorfos), indicando una edad del Santacrucense *sensu lato*. También registramos un testudínido, que constituye el registro más austral de tortugas terrestres en América del Sur y en el mundo. La disimilitud faunística registrada con las secciones mencionadas de las formaciones Santa Cruz, Río Frías y Collón Curá reflejarían diferencias ecológicas, climáticas y geográficas más que temporales. La coocurrencia de mamíferos arbóreos o semiarbóreos, ramoneadores, frugívoros y pastadores sugiere la presencia de árboles y ambientes abiertos para el área ocupada por las rocas de la FCB. Sin embargo, no es posible discernir si estos 2 ambientes coexistieron o alternaron y si un ambiente predominó sobre el otro. Taxones claves, como los roedores chinchilidos *Prolagostomus* y *Pliolagostomus* y el tipoterio *Pachyrukhos*, indican una tendencia a la aridificación para el Mioceno de Patagonia Austral, como se reportó anteriormente para la parte superior de la FSC a lo largo del río Santa Cruz y al sur del río Coyle, a lo largo de la costa atlántica y el río Gallegos.

Palabras clave: América del Sur, Andes, Burdigaliano-Langhiano, Paleontología de vertebrados, Paleoambiente.

1. Introduction

The early-middle Miocene (Burdigalian-early Langhian) fossil record from Austral Patagonia provides insights on the evolution of continental environments, climates, and biota of the Southern part of South America when it was essentially isolated from other continental landmasses (Kay *et al.*, 2012, 2021). In a volume published a decade ago (Vizcaino *et al.*, 2012a), we launched a research program to evaluate the ecological changes that occurred during this time interval, integrating the information from well-studied outcrops and biota of the Santa Cruz Formation (SCF) along the Atlantic coast of the Santa Cruz Province (Argentina) with other much less studied and more distant inland localities. As part of that endeavour, in recent years we have produced a valuable body of knowledge,

particularly for the SCF along Río Santa Cruz (Fornicola *et al.*, 2019a; Kay *et al.*, 2021) and Río Chaliá (Cuitiño *et al.*, 2021) in the central region of the province, and in the northwestern part of the province at Lago Posadas, on the eastern slope of the Patagonian Andes (Cuitiño *et al.*, 2019a). In the northwestern Santa Cruz, the early-middle Miocene record still is much less known than that from east of the Andes in the widely distributed SCF (Cuitiño *et al.*, 2019b, 2021).

The Cerro Boleadoras and Cerro Plomo region, very close to the border with Chile, ~50 km south to the Lago Buenos Aires-General Carrera (Fig. 1), is promising for understanding the evolution of the Miocene continental biota in northwestern Santa Cruz Province (~47° S, 71° W). In this area the most fossiliferous levels of the early-middle Miocene continental Cerro Boleadoras Formation (CBF) crop out.

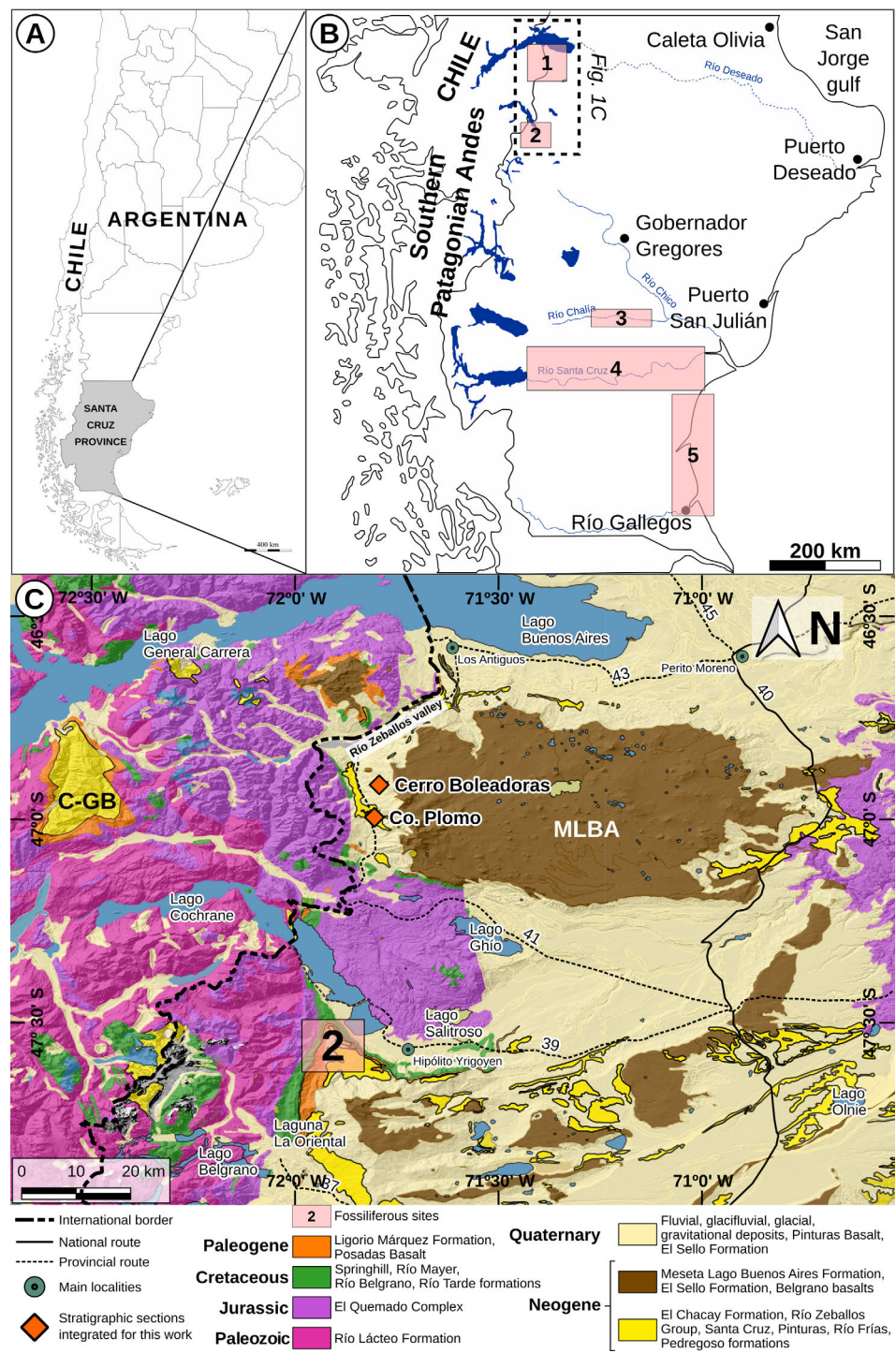


FIG. 1. Maps of the study area. **A.** Regional geographic location of the Santa Cruz Province. **B.** Fossiliferous localities mentioned in the text. 1. Cerro Boleadoras and Cerro Plomo area this work; 2. Lago Posadas (Cuitiño *et al.*, 2019a); 3. Río Chalia (Cuitiño *et al.*, 2021); 4. Río Santa Cruz (Fericola *et al.*, 2019a); 5. Atlantic coastal localities (Vizcaino *et al.*, 2012a). **C.** Geological map of the study area; location of the Cerro Boleadoras and Cerro Plomo sections integrated for the stratigraphic section of figure 2. C-GB: Cosmelli-Guadal Basin; MLBA: Meseta Lago Buenos Aires.

So far there are few reports of the vertebrate fossils from CBF, consisting exclusively of mammals. Ugarte (1956) recorded the presence of South American native ungulates *Nesodon?* and *Astrapotherium magnum?*, the glyptodont *Propalaeohoplophorus* and the megatheriid ground sloth *Prepootherium*. The present repository of these specimens is unknown. In 1990 and 1991 Austral summers, joint expeditions of the Museo de La Plata (Argentina) and Duke University (NC, USA) collected some 220 specimens from CBF now housed in the collection of the División Paleontología Vertebrados of that museum. Of this collection, only some xenarthrans (Carlini et al., 1993; Scillato-Yané and Carlini, 1998; Carlini et al., 2013) caviomorph rodents (Vucetich, 1994), and typotheres (Vera et al., 2021), have been examined. Although none of the taxa is exclusive of middle Miocene faunas, some authors have considered a Friasian s.l. South American Land Mammal Age (SALMA; middle Miocene) for the fauna from CBF (Ugarte, 1956; Scillato-Yané et al., 1993; Scillato-Yané and Carlini, 1998). Instead, based on the rodents, Vucetich (1994) referred the CBF to the early Miocene and established correlations with the Santacrucian age. Recently, a radiometric date near the base of the CBF provided a maximum U-Pb age from detrital zircons of ca. 16.5, i.e., Burdigalian (early Miocene; Folguera et al., 2018; see below), suggesting a most probable Santacrucian age for the fauna.

During recent fieldwork (February 2020), we made a new collection of fossil vertebrates from the CBF, particularly from the lower levels of Cerro Boleadoras and Cerro Plomo (Fig. 1). The aim of this contribution is to report this new collection of fossil vertebrates, to compile an integrated faunal list for this locality including other specimens from previous collections when possible, and to discuss its affinities and chronological and paleoenvironmental implications.

2. Geological Setting

The Cerro Boleadoras and Cerro Plomo area is located in the headwaters of the Río Zeballos valley, on the western slope of the Meseta del Lago Buenos Aires, northwestern Santa Cruz Province (Figs. 1, 2). This region is part of the northwestern end of the Austral-Magallanes Basin, within the foothills of the Southern Patagonian Andes (Ugarte, 1956; Escosteguy et al., 2003; Lagabrielle et al., 2004; Folguera et al.,

2018; Aramendía et al., 2019; Ghiglione et al., 2019). The area is characterized by outcrops of Paleozoic rocks, grouped in the Río Lácteo Formation, overlain by the Jurassic volcanic and volcanoclastic deposits of the El Quemado Complex (Escosteguy et al., 2003). In nearby localities, the Lower Cretaceous marine Springhill and Río Mayer formations (Escosteguy et al., 2003; Ghiglione et al., 2015, 2016) and the Upper Cretaceous volcanoclastic Río Tarde Formation (Giacosa and Franchi, 2001; Escosteguy et al., 2003) crop out.

The Paleogene system is represented by the Eocene fluvial deposits of the Ligorio Márquez Formation and the Eocene basic lava beds of the Posadas Basalt (Escosteguy et al., 2003; Suárez et al., 2000; De La Cruz et al., 2003; Aramendía et al., 2019). The Miocene sedimentary succession in this region is widely represented and begins with shallow marine deposits of the El Chacay Formation (Guadal Formation in Chile), representing an Atlantic marine transgression that occurred in a wide area of Patagonia during the early Miocene (Ugarte, 1956; Malumíán and Nández, 2011; Encinas et al., 2019; Cuitiño et al., 2019a; Parras and Cuitiño, 2021). South of the study area in Lago Posadas, these marine beds were dated between 20.3 and 18.1 Ma by $^{87}\text{Sr}/^{86}\text{Sr}$ ratios from oyster shells (Cuitiño et al., 2015), whereas to the northwest in Meseta Guadal (Chile) they were dated by U-Pb in detrital zircons at 19.8 Ma (Encinas et al., 2019), constraining the age of marine sedimentation between ~21 and 18 Ma. Transitionally overlying the El Chacay Formation is the Río Zeballos Group (Ugarte, 1956), composed of a ~1,000 m thick continental, coarsening-upward succession including from base to top the Río Jeinemeni, Cerro Boleadoras and Río Correntoso formations (Ugarte, 1956; Escosteguy et al., 2003; Dal Molin and Colombo, 2003; Aramendía et al., 2019; Aramendía et al., 2022). These units represent the transition from mixed-load fluvial deposits (Río Jeinemeni and Cerro Boleadoras formations) to alluvial fan deposits (Río Correntoso Formation) (Aramendía et al., 2019, Aramendía, 2021; Pujana et al., 2020).

The stratigraphic section studied in this work results from the integration of Cerro Boleadoras and Cerro Plomo successions of the CBF at the Río Zeballos valley (Figs. 2, 3). The basal sector of the CBF consists of laterally extensive medium to pebbly sandstone beds with trough cross-bedding interpreted

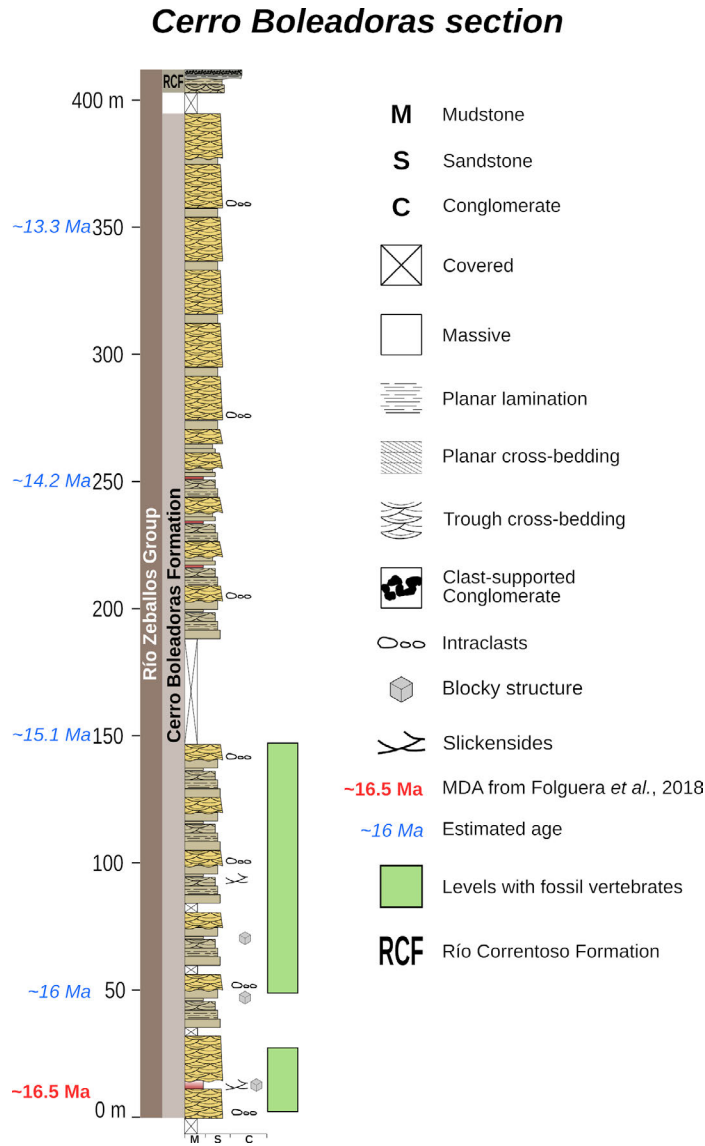


FIG. 2. Integrated stratigraphic section of Cerro Boleadoras Formation (Río Zeballos Group) in the study area. Maximum Depositional Age (MDA) from Folguera *et al.* (2018) and ages estimated from the sedimentary rate are indicated (see text for detail).

as fluvial channel deposits. Interspersed are fluvial floodplain mudstone deposits showing incipient soil-horizonation, slickensides and cuneiform blocky structures (Fig. 3). The thickness of the fluvial channel deposits increases upwards from 10 m to nearly 25 m, whereas the floodplain deposits decrease their thickness upwards from 3 to 1 m. Both sedimentary facies show increased grain-size up section, from mudstones and fine to medium sandstones to fine sandstones and fine conglomerates. In most of its

exposures, the Río Zeballos Group is covered by late Miocene to Quaternary basalts of the Meseta del Lago Buenos Aires Formation (Gorring *et al.*, 1997; Kay *et al.*, 2002).

2.1. Age of the fossil-bearing succession

Based on a U-Pb detrital zircon maximum age, the lower part of the CBF in the Río Jeinemani area is estimated at *ca.* 16.5 Ma, *i.e.*, Burdigalian

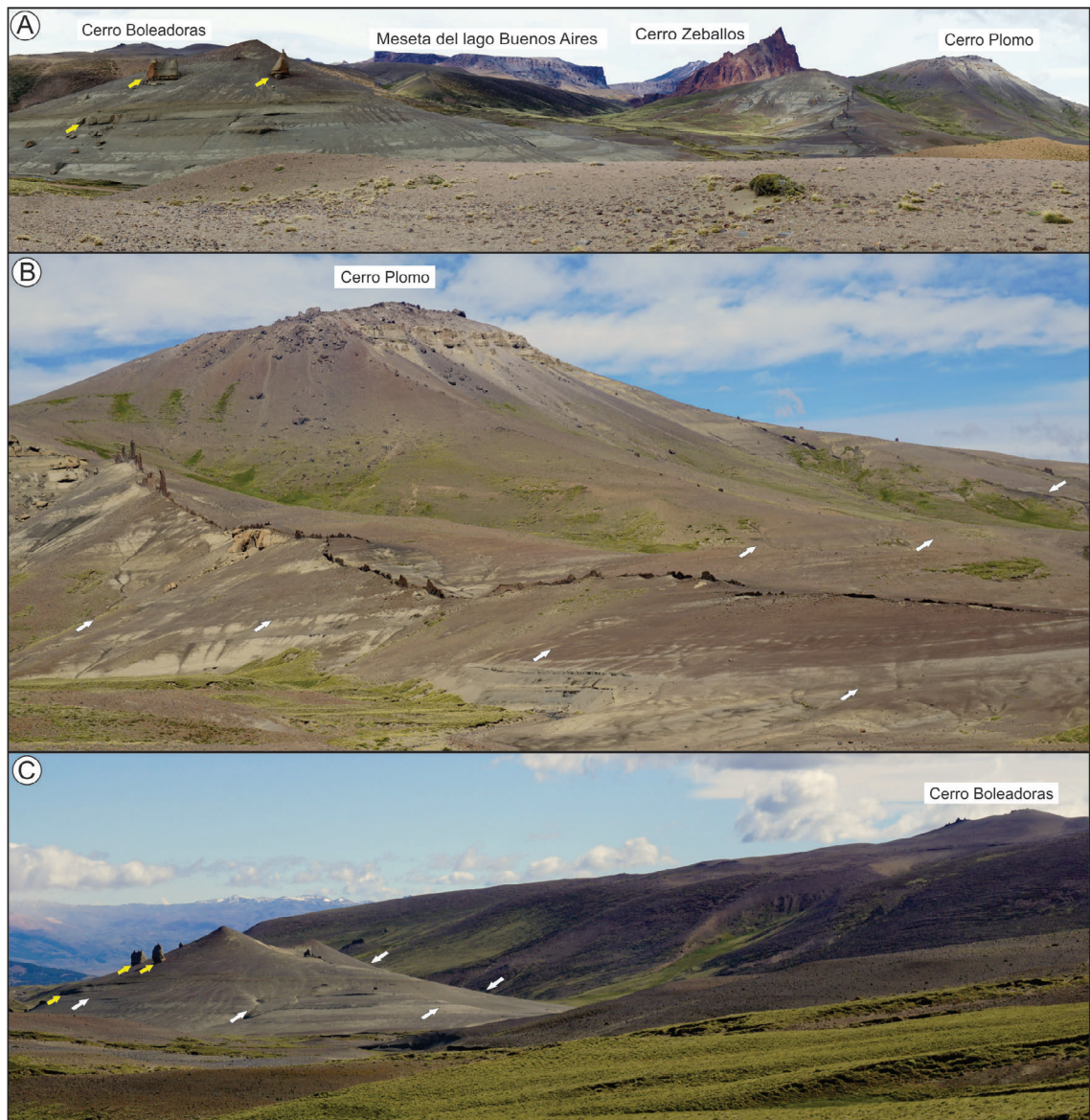


FIG. 3. Exposures of the Cerro Boleadoras Formation at the Cerro Boleadoras and Cerro Plomo area. **A.** Panoramic view, from the west, of the collecting area. In the background the Cerro Zeballos and Meseta del Lago Buenos Aires volcanic rocks are visible. **B.** Views of the Cerro Plomo from the north, and **C.** The Cerro Boleadoras from the south. White arrows indicate the exposures where fossils were collected; yellow arrows in A and C indicate the same channelized sandstone deposits.

(Folguera *et al.*, 2018; Fig. 2). This is consistent with the recently obtained early Miocene detrital U-Pb ages for the underlying Río Jeinemeni Formation as well as middle-late Miocene for the overlying Río Correntoso Formation (Aramendía *et al.*, 2022). The fossil-bearing fluvial deposits of the SCF exposed near Lago Posadas (Fig. 1B, C) are

temporally equivalent to the Río Jeinemeni and Cerro Boleadoras formations, with an age constrained between 18 and 14 Ma based on $^{40}\text{Ar}/^{39}\text{Ar}$ tuff ages (Blisniuk *et al.*, 2005), tephrochronology (Perkins *et al.*, 2012) and $^{87}\text{Sr}/^{86}\text{Sr}$ ages for the underlying marine deposits (Cuitiño *et al.*, 2015, 2019a). Although no radiometric ages are available for the

Cerro Boleadoras and Cerro Plomo area, based on facies similarity, the studied stratigraphic interval is assigned to the lower part of the CBF, whose ~16.5 Ma age is extrapolated from that of the Río Jeinemeni area. Facies similarity is also evident with the nearby SCF in Lago Posadas, allowing us to hypothesize that the average sedimentation rate value of 114 m/Myr calculated for that area (Blisniuk *et al.*, 2005) could be extrapolated to the 150 m-thick surveyed succession of the lower part of the CBF, which would range between *ca.* 16.5–15.1 Ma (Fig. 3).

3. Materials and methods

The new fossil collection consists of approximately 100 specimens of vertebrates, including frogs, turtles, birds and mammals that are housed in the Museo Regional Provincial Padre M.J. Molina (MPM-PV) of Río Gallegos, Argentina. The collection comes from the CBF at Cerro Boleadoras and Cerro Plomo between 1,290 and 1,450 m a.s.l., representing a ~150 m-thick section, integrated on the basis of lateral correlation between both hills (Figs. 2, 3). Most of the specimens were found loose on the surface, so they were collected in lots, except for one specimen found *in situ*.

Unfortunately, due to the restrictions related to the COVID-19, the MLP and Duke University (MLP-DU) collections from CBF housed at MLP have been virtually unreachable since April 2020. However, we had access to the tortoises (two specimens) and rodents (44 specimens) that were studied herein and information from colleagues that possess other taxa specimens on loan from MLP.

For taxonomic identifications, comparisons were made with Santacrucian specimens in the collections of the MPM-PV, MACN-A (Museo Argentino de Ciencias Naturales “B. Rivadavia”, Colección Ameghino, Buenos Aires, Argentina), MLP (Museo de La Plata, La Plata, Argentina), MPEF-PV (Museo Paleontológico Egidio Feruglio, Trelew, Argentina), LIEB (Laboratorio de Investigaciones en Evolución y Biodiversidad, Universidad Nacional de la Patagonia “San Juan Bosco”, Esquel, Argentina), AMNH (American Museum of Natural History, New York, USA), FMNH (The Field Museum, Chicago, USA), and YPM-VPPU (Yale Peabody Museum, Princeton University Collection, New Haven, USA).

4. Paleontology

In this section we provide a systematic list and general descriptions of the specimens from CBF collected by us (MPM-PV collection) and those from the MLP-DU collection that we had access to (see Material and methods; Table 1). The geographic and stratigraphic occurrence of all the specimens listed here is Cerro Boleadoras and Cerro Plomo area, RP 41, 60 km South of Lago Buenos Aires, Santa Cruz Province, Argentina. Cerro Boleadoras Formation, Río Zeballos Group, early-middle Miocene.

**Anura/Neobatrachia/Australobatrachia/
Calyptocephalellidae
Calyptocephalella Strand, 1928
cf. Calyptocephalella (Fig. 4)**

Referred material. See Appendix 1.

Description. The material includes many bone fragments of the roof of the skull and some fragmentary maxillae (MPM-PV 19140; Fig. 4A). The roofing bones are ornamented with discrete ridges and low conical tubercles that are distributed over the outer surface of each bone. A distal part of a left humerus of MPM-PV 19140 preserves the distal ball and the two epicondyles (Fig. 4B). There are several vertebrae, all disarticulated; most lack neural arches (Fig. 4C–D). The vertebral bodies are procoelic and range from 8.8 to 27.5 mm in length, 7 to 34.2 mm in transverse diameter, and 5.3 to 14.8 mm in vertical diameter. The largest is a sacral vertebra with a flattened, procoelous centrum and the characteristic posterior two condyles for the articulation with the cotyles of the urostyle (MPM-PV 19143).

Comments. The remains belong to several individuals. As a whole, they show the ornamentation, size range, and degree of ossification resembling *Calyptocephalella*, the most common among fossil anuran from Patagonia (Muzzopappa, 2019). For those reasons, we tentatively assign them to *Calyptocephalella* (late Cretaceous–Miocene, Patagonia Argentina; present, Chile). *Calyptocephalella* sp. had been recorded in the Santa Cruz Formation (SCF) from the outcrops along the Atlantic coast (Tauber, 1999; Fernicola and Albino, 2012), while *Calyptocephalella cf. C. canqueli* Schaeffer, 1949 was reported for the Barrancas Blancas locality along the Río Santa Cruz (Muzzopappa, 2019).

TABLE 1. LIST OF TAXA FROM CERRO BOLEADORAS FORMATION (SANTA CRUZ PROVINCE).

TAXA			MPM-PV*	MLP*
ANURA	Calyptocephalellidae	cf. <i>Calyptocephalella</i>	5	-
TESTUDINES	Testudinidae	<i>Chelonoidis</i> cf. <i>Ch. gringorum</i>	5	2
AVES	Phorusrhacidae	<i>Phorusrhacos longissimus</i>	1	-
		<i>Patagornis marshi</i>	1	-
		cf. <i>Psilopterus lemoinei</i>	1	-
MAMMALIA				
Metatheria	Sparassodonta		-	10**
	Paucituberculata		-	11**
Xenarthra-Cingulata	Dasypodidae	<i>Proeutatus</i> cf. <i>Pr. oenophorus</i>	4	-
		<i>Stenotatus</i> cf. <i>S. planus</i>	7	-
		<i>Vetelia puncta</i>	4	-
		<i>Prozaedyus proximus</i>	3	-
	Peltephilidae	<i>Peltephilus</i> sp.	2	-
	Propalaeohoplophoridae	Propalaeohoplophoridae indet.	9	-
Xenarthra-Folivora	Megatherioidea	Megatherioidea indet.	6	-
	Megatheriidae	<i>Prepoplanops</i> cf. <i>P. boleadorensis</i>	1	-
Litopterna	Proterotheriidae	<i>Thoatherium minusculum</i>	1	-
		<i>Anisolophus</i> sp.	1	-
Notoungulata-Typotheria	Hegetotheriidae	<i>Hegetotherium mirabile</i>	3	-
		<i>Pachyrukhos</i> cf. <i>P. moyani</i>	3	-
	Interatheriidae	<i>Protypotherium</i> sp.	8	-
		<i>Interatherium</i> sp.	2	-
Rodentia-Cavioidea		<i>Neoreomys australis</i>	7	12
		<i>Eocardia montana</i>	-	3
		<i>Luanus propheticus</i>	-	1
Chinchilloidea	Neopiblemidae	<i>Perimys</i> sp.	3	-
	Chinchillidae	<i>Prolagostomus pusillus</i>	-	8
		<i>Pliolagostomus notatus</i>	-	4
		<i>Pliolagostomus?</i>	1	-
Octodontoidea		<i>Acarechimys minutus</i>	-	1
		<i>Acarechimys minutissimus</i>	-	1
		<i>Acarechimys?</i>	-	1
		<i>Stichomys</i> sp.	-	4
		Adelphominae indet.	1	-
Octodontoidea	Octodontoidea	3 sp. nov.	-	6
Erethizontoidea	Erethizontidae	<i>Steiromys</i> sp.	-	1
Caviomorpha	Caviomorpha	Caviomorpha indet.	1	2

* Number of specimens collected by us housed at MPM-PV collection; specimens housed at MLP collection.

** Not revised in this contribution.

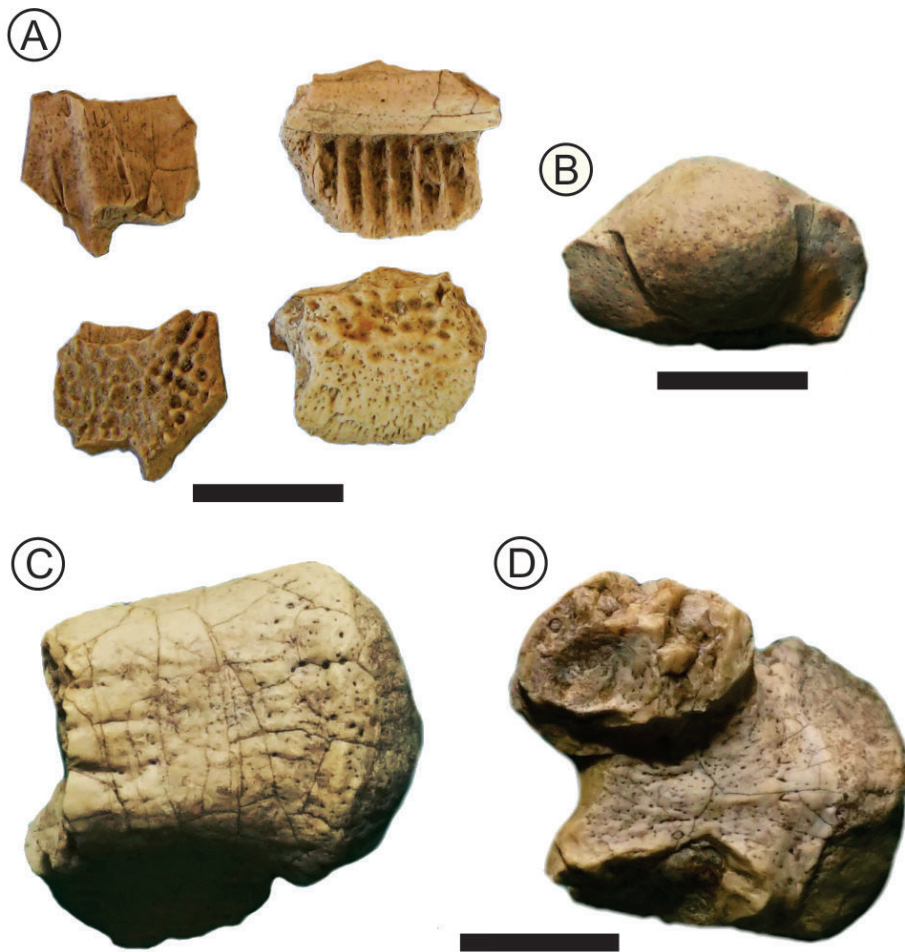


FIG. 4. Anurans (Calyptocephalellidae) from the Cerro Boleadoras Formation (Santa Cruz Province, Argentina). cf. *Calyptocephalella* A-B. MPM-PV 19140, skull fragments (A) and distal humerus (B). C-D. MPM-PV 19142, vertebra in ventral (C) and dorsal (D) views. Scale bars=10 mm..

Testudines/Cryptodira/Testudinidae

Chelonoidis Fitzinger, 1835

Chelonoidis cf. *Ch. gringorum* (Simpson, 1942) (Fig. 5)

Referred material. See Appendix 1.

Description. Although most of the recovered specimens are small and unidentifiable fragments of the carapace, some provide valuable anatomical information. A partial costal plate (MLP 90-III-5-161; Fig. 5A-C) preserves three medial sutural contacts with its three adjacent neurals, indicating the presence of an alternating pattern of octagonal and rectangular neurals. Dorsally, the presence of relatively narrow

vertebral scutes can be recognized. The costals of the new collection (MPM-PV 19149; Fig. 5D-F) confirm the alternating pattern and the typical ornamentation of the testudinids. The peripheral plates of the border of the carapace (MLP 90-III-5-161; Fig. 5G-I) are short, narrow, and gently curved, whereas peripheral 11 (MLP 90-III-5-161; Fig. 5J-L) is trapezoidal and without curvature. Both peripheral plates are only crossed by the marginal sulci, suggesting a good coincidence between the pleuro-marginal sulci and the costo-peripheral sutures. The partial anterior lobe, consisting of an almost complete left and a partial right epiplastron (MPM-PV 19149; Fig. 5M-O) is perhaps one of the most informative

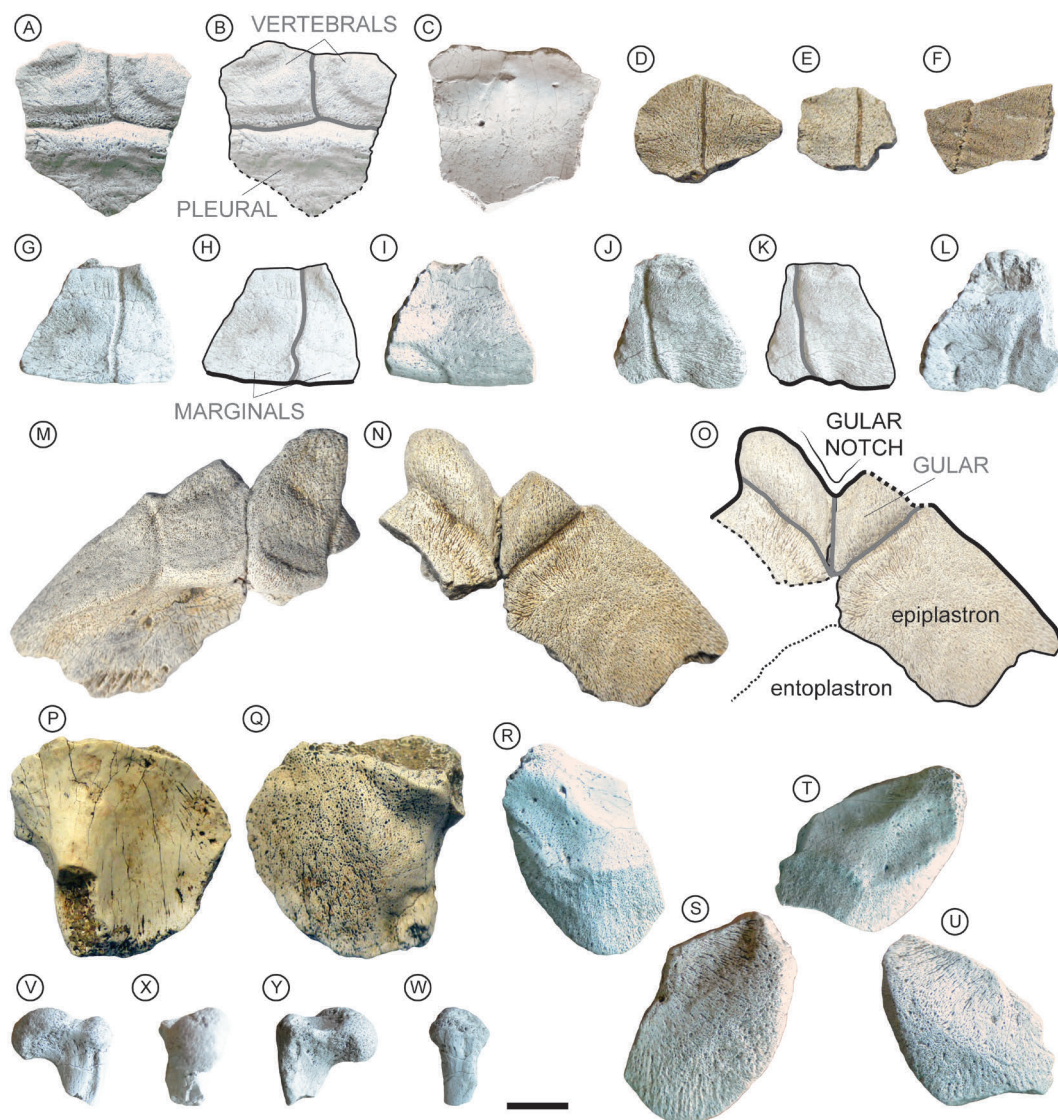


FIG. 5. Shell and skeletal elements of the testudinid *Chelonoidis* cf. *gringorum* from the Cerro Boleadoras Formation (Santa Cruz Province, Argentina). **A-C**. MLP 90-III-5-161, a partial costal plate in (A) dorsal, (B) drawing of dorsal, and (C) visceral views. **D-F**. MPM-PV 19148, three partial costal plates in dorsal views. **G-L**. MLP 90-III-5-161, two complete peripheral plates in (G-J) dorsal, (H-K) drawing of dorsal, and (K-L) visceral views. **M-O**. MPM-PV 19149, associated left and right epiplastra in (M) visceral, (N) ventral, and (O) drawing of ventral visceral views. **P-Q**. MPM-PV 19149, plastron fragment, probably a hyo/hyoplastron in (P) visceral and (Q) ventral views. **R-U**. MLP 90-III-5-161, two partial xiphiplastral fragments in (R, T) visceral, and (S, U) ventral views. **V-Y**. MLP 90-III-5-161, a partial left femur in (V) posterior, (X) dorsal, (Y) anterior, and (W) ventral views. Bony plates are indicated with black lines and small letters, scutes with grey lines and capital letters, natural borders with thicker black lines, broken borders with dashed lines. Scale bars=10 mm.

specimens of the collection. The left epiplastron is missing its anterior tip, whereas the right lacks its entire posterior part; there is a tight suture between the two. There is a clearly developed epiplastral lip, with a straight-to-slightly concave dorsal surface,

well-developed ventral pads on the gular part, with rounded and flattened epiplastral tips. The lateral sides of the epiplastral extremities are parallel to each other, and there is a deep and narrow gular notch developed up to the point where the gularo-humeral

contacts the border. Based on the morphology of the anterior-most part of the anterior lobe, we can infer that this specimen belonged to a male individual. On the visceral side, the epiplastral lip is tall, but with a straight vertical border not overhanging the entoplastron (that is, there is no gular pocket). Ventrally, the two gular scutes are narrow and the gularo-humeral sulcus creates a near-right angle, terminating on the epiplastra and at a considerable distance anteriorly to the entoplastron. Based on the part that can be reconstructed, the entoplastron was wide and placed towards the posterior part of the anterior lobe. A partial hyo/hypoplastron fragment from the near-bridge area also is preserved (MPM-PV 19149; Fig. 5P-Q). On its ventral side there is only a small part of a sulcus preserved, and there is no evidence of the presence of axillary/inguinal scutes, something that does not allow species-level identification. The posterior lobes of the left and right partial xiphiplastron are preserved as well (MLP 90-III-5-161; Fig. 5R-U). These parts exhibit rounded and flattened xiphiplastral extremities with narrow (Fig. 5R, S) or wide (Fig. 5T-U) anal notches. A partial left femur (MLP 90-III-5-161; Fig. 5V-W) preserves the rounded femoral head, which is as tall as wide, expanded perpendicularly to the diaphysis of the bone. The head has a similar width to the width of the trochanters. Ventrally, the two trochanters are fused, and do not project above the height of the femoral head. A deep and rounded intertrochanteric fossa is developed between the head and the trochanters.

Comments. The preserved specimens allow a clear allocation to Testudinidae, based on the presence of an alternating pattern of neural/costal associations, the good coincidence between the pleuro-marginal sulci and the costo-peripheral sutures on the peripherals, the presence of a well-developed epiplastral lip, and the presence of fused femoral trochanters. Moreover, the observed morphology of the most diagnostic elements of the new collection (*e.g.*, the associated epiplastra in Fig. 5M-O) is consistent with several of the referred specimens to *Chelonoidis gringorum*, like those from the early Miocene of the Bryn Gwyn Geopark, Chubut Province (MPEF-PV collection; Sterli *et al.*, 2021), and some of the specimens from the middle Miocene Río Chubut area in NW Chubut (LIEB collection; Oriozabala *et al.*, 2018). Given the disarticulated nature of the Cerro Boleadoras remains and the considerable range of the morphological variability on the specimens

referred to *Chelonoidis gringorum*, it is more prudent to refer the Cerro Boleadoras material to *Chelonoidis* cf. *Ch. gringorum*. *Chelonoidis* has been recorded from the late Oligocene of Argentina and Bolivia, Miocene of Argentina, Bolivia, Brazil, Colombia, to the Pleistocene of Argentina, Brazil, Ecuador, Paraguay, Uruguay-present (extant).

The occurrence of *Chelonoidis* cf. *Ch. gringorum* in Cerro Boleadoras is the southernmost occurrence of the entire family in South America and the world. Previously its most southerly Miocene record is from Bajo de la Oriental in the Santa Cruz Province (erroneously listed as Pampa del Castillo in de la Fuente *et al.*, 2018). It is worth mentioning that there are no other turtle or testudinid remains recorded farther south in the abundant fossil records of the penecontemporaneous SCF.

Aves/Cariamiformes/Phorusrhacidae/

Phorusrhacinae

Phorusrhacos Ameghino, 1887

Phorusrhacos longissimus Ameghino, 1887 (Fig. 6A-B)

Referred material. See Appendix 1.

Description. MPM-PV 19162 is an ungual phalanx of the left digit II, preserving approximately two thirds of its assumed total length and lacking the *apex phalangis* (partial length=41 mm; height at the base=35 mm; maximum width=21 mm; Fig. 6A-B). Ungual phalanges of digit II are more strongly curved in dorsal and lateral aspects, higher dorsoventrally and more laterally compressed (*i.e.*, subelliptic in section) than other ungual phalanges. The tuberculum flexoriosis is well developed and ends in a rounded plantar surface. The *corpus phalangis* exhibits well marked *sulci neurovascularis* on both sides (Jones, 2010).

Comments. The genus has been recorded in the early-middle Miocene of Patagonia, Argentina. *Phorusrhacos longissimus* is known by very abundant and well-preserved remains from outcrops of the SCF along the Atlantic coast (Degrange *et al.*, 2012), from the Cerro de los fósiles locality at Lago Belgrano (Degrange *et al.*, 2019) and from Río Chalfía (=Sehuén) (Alvarenga and Höfling, 2003; Noriega *et al.*, 2021). Although the type specimen comes from the Río Santa Cruz (Ameghino, 1887); however, the species is not recorded in more recent collections from the Río Santa Cruz (Diederle and Noriega, 2019).

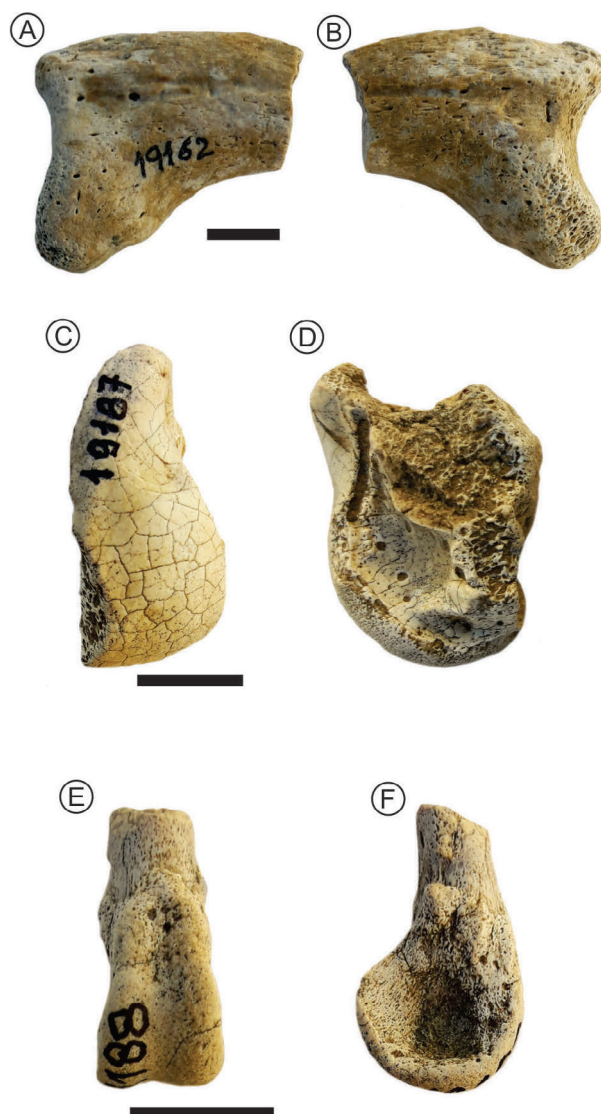


FIG. 6. Phorusrhacid birds from the Cerro Boleadoras Formation (Santa Cruz Province, Argentina). **A-B.** MPM-PV 19162, *Phorusrhacos longissimus*, ungual phalanx of the left digit II, medial (A) and lateral (B) views. **C-D.** MPM-PV 19187, *Patagornis marshi*, right trochlea metatarsi II, anterior (C) and medial (D) views. **E-F.** MPM-PV 19188, cf. *Psilopterus lemoinei*, right trochlea metatarsi III, anterior (E) and lateral (F) views. Scale bars=10 mm.

**Aves/Cariamiformes/Phorusrhacidae/
Patagornithinae**

***Patagornis* Moreno and Mercerat, 1891**

***Patagornis marshi* Moreno and Mercerat, 1891
(Fig. 6C-D)**

Referred material. See Appendix 1.

Description. MPM-PV 19187 is a damaged trochlea metatarsi II, lacking the posteromedial process, comparable in size to that of *Patagornis marshi*

(partial measurements: length=32 mm; depth 26 mm; width 15 mm; Fig. 6C-D).

Comments. *Patagornis* has been recorded in the early-middle Miocene of Patagonia, Argentina. Abundant and well-preserved remains of *Patagornis marshi* are known in the SCF along the Atlantic coast (Alvarenga and Höfling, 2003; Degrange et al., 2012) and at Río Chaliá (=Sehuén) (Noriega et al., 2021). It is not recorded in SCF outcrops along the Río Santa Cruz (Diederle and Noriega, 2019).

**Aves/Cariamiformes/Phorusrhacidae/
Psilopterinae**

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

**cf. *Psilopterus lemoinei* (Moreno and Mercerat, 1891)
(Fig. 6E-F)**

Referred material. See Appendix 1.

Description. MPM-PV 19188 consists of an isolated trochlea metatarsi III (length=12.25 mm; transverse width=9.4 mm; Fig. 6E-F). It is larger than that of *P. bachmanni* (Moreno and Mercerat, 1891), but somewhat smaller than that of *P. lemoinei*, with flanges proximally convergent, more similar to that of *P. lemoinei* than to *P. affinis* (Ameghino, 1899). The dimensions of the specimen together with the porous texture of its bony cortex suggest that it probably belongs to a subadult individual.

Comments. *Psilopterus* has been recorded in the early-middle Miocene of Patagonia, Argentina. Recently, it was recorded from the SCF along the Atlantic coast (Degrange *et al.*, 2012), from the Barrancas Blancas locality along the Río Santa Cruz (Diederle and Noriega, 2019), and along the Río Chalia (Noriega *et al.*, 2021). *Psilopterus lemoinei* is one of the best-known phorusrhacid species.

**Xenarthra/Folivora/Megatherioidea/
Megatheriidae/Planopinae**

***Prepoplanops* Carlini, Brandoni and Dal Molin, 2013**

**cf. *Prepoplanops boleadorensis* Carlini, Brandoni
and Dal Molin, 2013
(Fig. 7A-C)**

Referred material. See Appendix 1.

Description. The calcaneum MPM-PV 19138 is very large and robust, with a well-developed, broad, plate-like tuber (Fig. 7A-B). The sustentaculum is prominent compared to that of basal megatherioids (*e.g.*, *Hapalops*, *Peleciodon*, *Schismotherium*) and megalonychids (*e.g.*, *Eucholoeops*). The sustentacular facet for the astragalus is dorsally positioned, at a right angle to the plane of the cuboid facet, but forming a continuous articular area with it. The sustentacular and cuboid facets are separated from the ectal facet by a broad sulcus (Fig. 7C). The total length of the bone (from the distal border of the tuber to the most anterior border of the cuboid facet) is 102.0 mm, and the maximum width of the tuber is 64.5 mm.

Comments. The Planopinae megatheriids *Planops*, *Prepootherium*, and *Prepoplanops* are recorded in early-middle Miocene deposits of Patagonia: in

the SCF (*Planops* and *Prepootherium*) and CBF (*Prepoplanops*) of Santa Cruz Province and in Collón Curá Formation (*Planops grandis*) of Neuquén Province (Scillato-Yané and Carlini, 1998; Carlini *et al.*, 2013; Brandoni *et al.*, 2016). Calcanei of planopines are very rare in the collections. They were described only for *Prepootherium potens* (Scott, 1904), *Planops martini* (Hoffstetter, 1961), and for *Prepoplanops boleadorensis* (Carlini *et al.*, 2013). This new specimen is clearly referable to a Planopinae because of its large size and the morphology of its proximal articular surface. The morphology of the astragalar (ectal and sustentacular) and cuboid facets resembles the holotype of *Prepoplanops boleadorensis* (MLP 97-XI-3-1), so we refer our specimen provisionally to this species.

**Xenarthra/Folivora/Megatherioidea
Megatherioidea indet.**

Referred material. See Appendix 1.

Comments. Sloths are common elements of the early-middle Miocene deposits of Patagonia. Skulls and mandibles are rare, and isolated postcranial elements are particularly abundant. However, associations between the two are rare, making the taxonomic allocation of isolated postcranial elements difficult. We refer the postcranial elements (*e.g.*, pes and manus elements, fragments of long bones, vertebrae, etc.) reported here to Megatherioidea indet., a clade that includes the most common Santacrucian genera (see Bargo *et al.*, 2019 and references therein).

**Xenarthra/Cingulata/Peltephilidae
Peltephilus Ameghino, 1887**

***Peltephilus* sp**

(Fig. 7D)

Referred material. See Appendix 1.

Description. MPM-PV 19125 consists of four isolated osteoderms: two with irregularly polygonal shape and a very rugose surface, characteristic of the cephalic shield (Fig. 7D), and two of the caparace. The carapace osteoderms of *Peltephilus* have different sizes and shapes, with coarsely pitted surfaces and marginal pits. One of the new osteoderms belonging to the fixed part of the carapace is large, pentagonal, and thick (16.0 mm anteroposterior length; 9.0 mm transverse width; 5.25 mm thickness). It has an inverted u-shaped groove anteriorly. The other is a quadrangular movable osteoderm, small and thin



FIG. 7. Xenarthrans (Folivora and Cingulata) from Cerro Boleadoras Formation (Santa Cruz Province, Argentina). A-C. MPM-PV 19138, right calcaneum of the megatheriid *Planopinae* cf. *Preoplanops boleadorensis* (A, dorsal, B, ventral and C, proximal (articular) views). D. MPM-PV 19125, *Peltephilus* sp., two osteoderms from the cephalic shield (above) and two from the carapace (below). E. MPM-PV 17526, *Vetelia* sp. three movable (above) and three fixed (below) osteoderms. F. MPM-PV 17520, *Prozaedyus proximus*, six articulated osteoderms of the pelvic shield. G. MPM-PV 19120, *Stenotatus* cf. *S. planus*, movable osteoderm. H. MPM-PV 19128, *S. cf. S. planus*, five fixed osteoderms. I. MPM-PV 19121, *Proeutatus* cf. *Pr. oenophorus*, five fixed osteoderms. J. MPM-PV 17515, Propalaehoplophoridae indet., five isolated osteoderms. Scale bars=10 mm.

(9.15 mm anteroposterior length; 8.15 mm transverse width; 3.3 mm thickness); it has two conspicuous anterior pits and a bisel shaped anterior border. MPM-PV 17524 is similar to MPM-PV 19125, but its anterior border is missing.

Comments. The genus *Peltephilus* was recorded in the late Oligocene-middle Miocene of Patagonia Argentina, and early Miocene of San Juan Province, Argentina; early Miocene of Chile, and late Oligocene and middle Miocene of Bolivia. In the SCF it has been reported at Karaiken (Notohippidian?), at Río Santa Cruz localities, at Río Chalia (=Sehuén), Monte Leon, and the Atlantic coastal localities south to Río Coyle (González-Ruiz, 2010; Cuitiño *et al.*, 2021; Vizcaíno *et al.*, 2012b; Fernicola and Vizcaíno, 2019). Vizcaíno *et al.* (2012b) and Fernicola and Vizcaíno (2019) considered five species of *Peltephilus* to be valid for the SCF: *Pe. strepens*, *Pe. pumilus*, *Pe. giganteus*, *Pe. nanus*, and *Pe. ferox*. The limited number of osteoderms in our collections and the fact that they are all isolated does not permit a precise analysis of morphological variability, preventing us from assigning a specific identification.

**Xenarthra/Cingulata/Chlamyphoridae/
Tolypeutinae
Vetelia Ameghino, 1891b
Vetelia puncta Ameghino, 1891b
(Fig. 7E)**

Referred material. See Appendix 1.

Description. MPM-PV 17526 shows the moveable osteoderms with a wide longitudinal central figure separated by two shallow grooves from two similarly wide lateral figures (Fig. 7E). The grooves and the figures reach the posterior margin of the osteoderm. The grooves enclose four large foramina and other smaller ones. There are also small foramina on both lateral osteoderm margins, and on the posterior margin there are four large foramina with two or three alternate smaller ones. Fixed osteoderms of the referred specimens (MPM-PV 17517, 17522, 17526 and 19127) are variable in size (anteroposterior length from 14 to 17 mm, transverse width 9 mm and thickness from 4-8.5 mm). They have three to eight conspicuous foramina on the posterior margin. The lateral and anterior margins have continuous and well-defined rows of foramina. Four or five peripheral figures surround the central figure; most of the grooves that delimit these figures have foramina.

Comments. The genus *Vetelia* is currently considered to be phylogenetically related to the extant Tolypeutinae *Priodontes*, *Cabassous*, and *Tolypeutes* (Barasoain *et al.*, 2021). It was recorded from the early-middle Miocene of Patagonia Argentina and Chile, and late Miocene of Buenos Aires, La Pampa, San Juan, La Rioja y Catamarca. According to González-Ruiz (2010) *Vetelia* is recorded in the “Nothippidian” fauna of the SCF at Karaiken, the enigmatic “la Cueva” locality (see Marshall, 1976), the SCF of Río Chalia, and the middle Miocene of Río Frías (at Río Cisnes) and Collón Curá formations. Cuitiño *et al.*, (2021) confirmed the presence of *Vetelia* sp. at Río Chalia, but Fernicola and Vizcaíno (2019) did not report it for the SCF along the Río Santa Cruz. According to González-Ruiz (2010) and Vizcaíno *et al.* (2012b), *Vetelia puncta* was first reported from the north bank of the Río Santa Cruz, in outcrops referred by Ameghino (1902) to the “Nothippidian” (the oldest Santacrucian faunal assemblage according to Marshall *et al.*, 1983). Fernicola *et al.* (2009) reported a single osteoderm of the species from the coast of Santa Cruz Province, south of the mouth of the Río Coyle. The species has previously been reported from the Cerro Boleadoras and the Río Frías Formations (González-Ruiz, 2010; Barasoain *et al.*, 2021).

**Xenarthra/Cingulata/Chlamyphoridae/
“Euphractinae”/“Euphractini”
Prozaedyus Ameghino, 1891a
Prozaedyus proximus (Ameghino, 1887)
(Fig. 7F)**

Referred material. See Appendix 1.

Description. Osteoderms of the movable bands (MPM-PV 17525 and 19126) are long and narrow, with three longitudinal ridges, the laterals slightly divided transversely into tubercles. The fixed osteoderms (MPM-PV 17520; Fig. 7F) are shorter and relatively wider posteriorly (anteroposterior length, 7 mm; transverse width, 5 mm); the median ridge is reduced anteriorly; the lateral ridges constitute rows of tubercles, which extend across the anterior border of the osteoderm.

Comments. The genus *Prozaedyus* has been recorded in the late Oligocene-middle Miocene of Patagonia, and early Miocene of San Juan Province, Argentina; also from the early Miocene of Chile and the early-middle Miocene of Bolivia. In the Santacrucian fauna

Prozaedyus is reported from the upper part of the Pinturas Formation, the “Nothippidian” fauna of the SCF at Karaiken, and the SCF along the Río Santa Cruz, at Río Chaliá, Monte León, the Atlantic coast South to Río Coyle and Río Gallegos; it also occurs in the Collón Curá Formation (González-Ruiz, 2010; Cuitiño et al., 2021; Vizcaíno et al., 2012b; Fernicola and Vizcaíno, 2019). González-Ruiz (2010) considered two valid Santacrucian species, *Prozaedyus proximus* and *P. exilis*. Fernicola and Vizcaíno (2019) observing that metric and morphological differences provided by Scott (1903) for the two species are slight and within the range of variation of different species of extant cingulates such as *Chaetophractus vellerosus* and *Zaedyus pichiy*, concluded that there is just one valid species, *Prozaedyus proximus*.

Xenarthra/Cingulata/Chlamyphoridae/

“Euphractinae”/“Eutatini”

***Stenotatus* Ameghino, 1891a**

***Stenotatus* cf. *S. planus* Scillato-Yané and Carlini, 1998**

(Fig. 7G-H)

Referred material. See Appendix 1.

Description. Movable osteoderms of MPM-PV 19120 (Fig. 7G) have three longitudinal ridges of nearly equal width and prominence. The median ridge vanishes before reaching the distal margin. The lateral ridges are complete, showing hardly any tendency to break up into rows of figures. The foramina on the posterior margin are conspicuous. Marginal movable osteoderms are smooth and coarsely pitted. Fixed osteoderms of MPM-PV 19128 (Fig. 7H) have a median ridge that does not reach the posterior border, but become confluent with the raised posterior margin, thus forming an inverted ‘T’. There are four or five anterior figures. Further descriptions are pending of the complete preparation of the specimen MPM-PV 19120. According to Scillato-Yané and Carlini (1998) and González-Ruiz (2010) *Stenotatus planus* differs from *S. patagonicus* mainly in having wider, flatter primary figures, and from *S. hesternus* in having smaller pits along the longitudinal sulcus. As we could not compare our specimen with the type specimen of *S. planus* (MLP 91-I-10-54), we refer the new specimens provisionally to *S. cf. S. planus*.

Comments. The genus *Stenotatus* was recorded from the early Oligocene to middle Miocene of Patagonia Argentina, early Miocene of San Juan Province, Argentina, early Miocene of Chile, and early- middle Miocene of Bolivia. It has been

reported for the Pinturan and Santacrucian faunas of the Pinturas Formation (lower-middle and upper section of the formation respectively), the Pinturan of the Upper Fossil Zone of the Sarmiento Formation at Gran Barranca, the “Notohippidian” fauna of the SCF, the SCF of the Río Santa Cruz, Río Chaliá, the Atlantic coast, and Río Gallegos, and the Collón Curá Formation (González-Ruiz, 2010; Kramarz et al., 2010; Vizcaíno et al., 2012b; Fernicola and Vizcaíno, 2019; Cuitiño et al., 2019b, 2021). González-Ruiz (2010) and Fernicola and Vizcaíno (2019) considered two valid Santacrucian species, *Stenotatus patagonicus* and *S. hesternus*. Scillato-Yané and Carlini (1998) claimed *S. planus* was exclusively found in the CBF and, consequently, temporally restricted to an interval encompassing the latest Santacrucian or the earliest Friasian ages. González-Ruiz (2010) agreed that *S. planus* as the only species found in the CBF, but also reported *S. planus* in the localities La Olguita y La Porteña (Scillato-Yané y Carlini, 1998; González-Ruiz et al., 2005; González-Ruiz, 2010) which would also belong to the Río Zeballos Group based exclusively on faunal correlations. Croft et al. (2009) reported *Stenotatus planus* from early-middle Miocene outcrops from Bolivia.

Xenarthra/Cingulata/Chlamyphoridae/

“Euphractinae”/“Eutatini”

***Proeutatus* Ameghino, 1891a**

***Proeutatus* cf. *Pr. oenophorus* (Ameghino, 1887)**

(Fig. 7I)

Referred material. See Appendix 1.

Description. The movable osteoderms are long and narrow (23.0 mm anteroposterior length; 11.35 mm transverse width; 4.5 mm thickness; MPM-PV 17513), more than one third of each is overlapped by the adjacent cranial plate. The exposed area bears a lageniform central figure, i.e., having an enlarged base tapering to a narrower neck, with a prominent keel along its midline. A lateral figure lies on either side of the neck of the main figure. The posterior margin has three or four large foramina, separated from one another by a thin bony septum. The fixed osteoderms are rectangular, thick, shorter and broader compared with the movable osteoderms (18.0 mm anteroposterior length; 8.00 mm transverse width; 6.0 mm thickness; MPM-PV 19121; Fig. 7I), with a sculptural pattern which is a modification of that seen in the movable osteoderms.

Comments. The genus *Proeutatus* has been recorded in the early-middle Miocene of Patagonia Argentina. It was reported for the Pinturan and Santacrucian faunas of the Pinturas Formation (lower-middle and upper section of the formation respectively), the Upper Fossil Zone (UFZ) of the Sarmiento Formation at Gran Barranca, the “Notohippidian” fauna of the SCF, the SCF of Río Santa Cruz, Río Chalia, along the Atlantic coast, and at Río Gallegos. It is also recorded in the Río Frías and Collón Curá formations (González-Ruiz, 2010; Kramarz *et al.*, 2010; Vizcaíno *et al.*, 2012b; Fernicola and Vizcaíno, 2019). González-Ruiz (2010) considered *Proeutatus oenophorum*, *Pr. lagena*, *Pr. deleo*, and *Pr. carinatus* as valid species. Fernicola and Vizcaíno (2019) recognized the species *Pr. oenophorus*, *Pr. deleo*, and *Pr. carinatus* for the SCF, but could not distinguish the three species based only on osteoderms. Considering the general morphology and size of the new material reported here, we assigned the material from CBF to *Proeutatus* cf. *Pr. oenophorus*.

Xenarthra/Cingulata/Propalaeohoplophoridae
Propalaeohoplophoridae indet.
(Fig. 7J)

Referred material. See Appendix 1.

Description. The osteoderms vary greatly in size and thickness. They all show the pattern of a large central subcircular figure in a slightly eccentric position, somewhat nearer to the posterior margin (Fig. 7J). In most osteoderms the figure is flat, but it may be distinctly convex and in some instances have a small, rough tubercle in the center. The central figure is bounded by a polygonal groove, from which radiate other short grooves, delineating smaller peripheral figures. The anterior peripherals are somewhat larger than the posterior ones. Some osteoderms have a more or less complete second row of anterior peripherals. Small foramina are placed at the junctions of the main groove with the radiating grooves and at the intersections of the two.

Comments. Propalaeohoplophorids has been reported from virtually all the Miocene fossiliferous outcrops of Patagonia (González-Ruiz, 2010; Vizcaíno *et al.*, 2012b; Cuitiño *et al.*, 2019a, 2021; Fernicola and Vizcaíno, 2019). González-Ruiz (2010) considered valid the species *Propalaeohoplophorus australis*, *Pro. minus*, *Cochlops muricatus*, “*Cochlops*”*debilis*, *Eucinepeltus petesatus*, “*Metopotoxus*”*anceps*

and *Eonaucum informis*, and named a new species (*Paraeucinepeltus raposeirasi*; González-Ruiz *et al.*, 2011). González-Ruiz (2010) reported *Eucinepeltus petesatus* for the localities La Olguita y La Porteña, that could correlate stratigraphically with the CBF. Instead, Fernicola and Vizcaíno (2019) recognized for the SCF only the species *Cochlops muricatus*, *Eucinepeltus petesatus*, *Eu. crassus*, and *Eu. complicatus*. But due to the lack of homologous elements with the ones that distinguish the species, they only reported *Cochlops muricatus*, *Eucinepeltus* sp., and Propalaeohoplophoridae indet. for the SCF along the Río Santa Cruz. Considering the difficulties in identifying the species of glyptodonts with isolated osteoderms we assigned the material from CBF to the family level only.

Notoungulata/Typotheria/Hegetotheriidae
***Hegetotherium* Ameghino, 1887**
***Hegetotherium mirabile* Ameghino, 1887**
(Fig. 8A)

Referred material. See Appendix 1.

Description. The three specimens reported here do not preserve incisors and canines. The cheek teeth show some features characteristic of the genus. The upper molars have slightly convex lingual faces; M1-M2 have distinct parastyles and parastylar grooves, but lack lingual grooves; the lower molars lack lingual inflection, and m1-m2 have lingually projecting posterolingual corners (Seoane and Cerdeño, 2019). In MPM-PV 19184, the P3-P4 are sub-rectangular, the M1 has an ectoloph at a right angle to the posterior surface and the M3 has a distal notch and a conspicuous metastyle (Fig. 8A). The m3 of MPM-PV 19158 shows a conspicuous labial groove in the talonid. These features allowed us to refer the new specimens to *Hegetotherium mirabile*.

Comments. The genus *Hegetotherium* has been recorded in the early-middle Miocene of Patagonia Argentina and Bolivia, and late Miocene of Chile. Seoane and Cerdeño (2019) performed a systematic review and a phylogenetic analysis of Hegetotheriidae, and concluded that *Hegetotherium* includes three valid species. *Hegetotherium novum* occurs in the early Miocene (Sarmiento Formation), Chubut Province; *H. mirabile*, occurs in the early-middle Miocene (SCF) in Santa Cruz Province, and in the middle Miocene (Collón Curá Formation) in Río Negro and Neuquén provinces, and *H. cerdasensis*

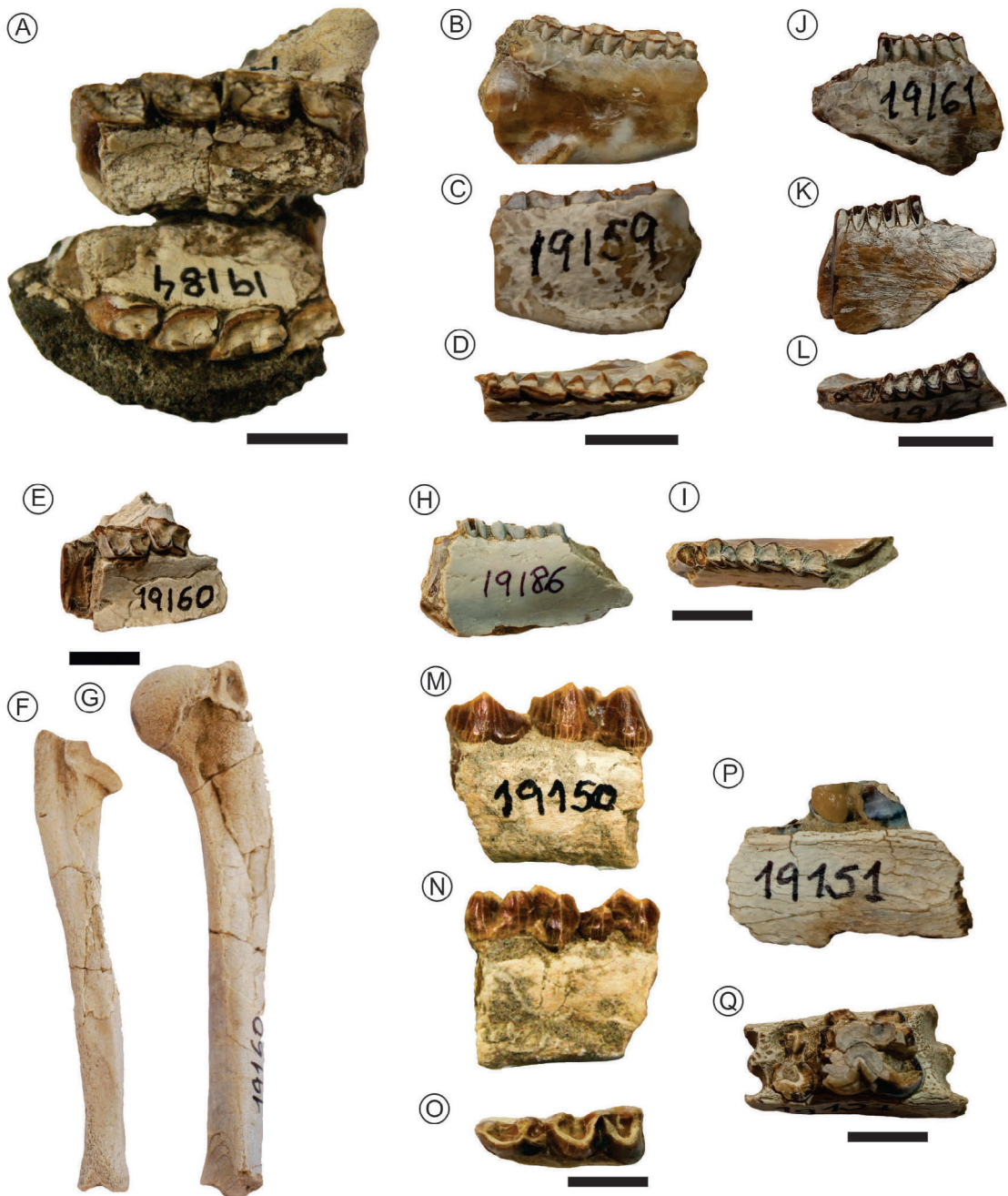


FIG. 8. Typothere notoungulates and proterotheriid litopterns from Cerro Boleadoras Formation (Santa Cruz Province, Argentina). **A.** MPM-PV 19184, *Hegetotherium mirabile*, associated fragments of left maxilla with P4-M3 and right maxilla with P3-M2. **B-D.** MPM-PV 19159, *Pachyrukhos* cf. *P. moyani*, fragment of right dentary with p4-m3 in labial (B), lingual (C), and occlusal (D) views. **E-G.** MPM-PV 19160, *Protypotherium* sp., fragment of left maxilla with fragment of P4 and M2 (E), ulna (F), humerus (G). **H-I.** MPM-PV 19186, *Protypotherium* sp., fragment of right dentary with p3-m2 in labial (H) and occlusal (I) views. **J-L.** MPM-PV 19161, *Interatherium* sp., left dentary fragment with p2-p4 in labial (J), lingual (K), and occlusal (L) views. **M-O.** MPM-PV 19150, *Thoatherium minusculum*, left mandibular fragment with dp2-dp3 in labial (M) lingual (N) and occlusal (O) views. **P-Q.** MPM-PV 19151, *Anisolophus* sp., left mandibular fragment with p4 (broken) and m1 in labial (P) and occlusal (Q) views. Scale bars=10 mm.

occurs in the middle Miocene, "Cerdas beds" and the Nazareno Formation, Bolivia, as well as in the late Miocene, Huaylas Formation, Chile. Recently, *Hegetotherium mirabile* was reported from the SCF at Lago Posadas (Cuitiño *et al.*, 2019a), along the Río Santa Cruz (Fernández and Muñoz, 2019), and the Río Chalia (Cuitiño *et al.*, 2021).

Notoungulata/Typotheria/Hegetotheriidae
***Pachyrukhos* Ameghino, 1885**
***Pachyrukhos* cf. *P. moyani* Ameghino, 1885**
(Fig. 8B-D)

Referred material. See Appendix 1.

Description. The specimens reported here are fragmentary dentaries with premolars and/or molars. The available material does not allow us to observe whether there is a conspicuous diastema between the cheek teeth and the anterior teeth, a distinctive feature of *Pachyrukhos*. However, the lower cheek teeth of the referred specimens have the straight lingual faces, conspicuous labial sulci and the very small size diagnostic of *Pachyrukhos* (e.g., MPM-PV 19159; Fig. 8B-D) compared with other typotheres, features that let us to refer these specimens provisionally to *P. cf. P. moyani*.

Comments. The genus has been recorded in the early-middle Miocene of Patagonia, Argentina and the early Miocene of Chile. Seoane and Cerdeño (2019) recognized two valid species within *Pachyrukhos*: *P. politus*, early Miocene (Sarmiento Formation) Chubut Province, and *P. moyani*, early-middle Miocene (SCF) Santa Cruz Province, and middle Miocene (Collón Curá Formation) Río Negro and Neuquén provinces. *Pachyrukhos moyani* was also reported from the SCF at Lago Posadas (Cuitiño *et al.*, 2019a), along the Río Santa Cruz (Fernández and Muñoz, 2019), and at Río Chalia (Cuitiño *et al.*, 2021). In the Atlantic coastal localities south to the Río Coyle, *P. moyani* was reported only for the upper levels of the SCF (Vizcaino *et al.*, 2021).

Notoungulata/Typotheria/Interatheriidae
***Protypotherium* Ameghino, 1885**
***Protypotherium* sp.**
(Fig. 8E-I)

Referred material. See Appendix 1.

Description. The genus *Protypotherium* has euhypsodont premolars and molars, and premolariform premolars. The upper molars have a lingual sulcus that

separates the protoloph from the metalophs (MPM-PV 19160; Fig. 8E). The P3-P4s have a sub-triangular shape, with the mesio-distal length shorter than the labio-lingual breadth and a smaller size than M1-M2. The i1-i3s are compact (lacking spaces between the teeth) and are imbricated another mesiodistally. The p2 has a shorter talonid than the trigonid; the p3-p4 are relatively smaller than the m1-m2 (e.g., MPM-PV 19186; Fig. 8H-I). The m1-m3 have sub-triangular trigonids; the m1-m2 have longer talonids than the trigonids. Together, these features of our specimens allow their allocation at the genus level; they remain under study for specific identifications.

Comments. *Protypotherium* is widely distributed both temporally and geographically: late Oligocene-middle Miocene of Patagonia Argentina, late Miocene of Buenos Aires, Entre Ríos and La Rioja provinces, late Oligocene of Uruguay, early-middle Miocene of Chile, and late Miocene of Bolivia and Venezuela. Fernández and Muñoz (2019) recognized *Protypotherium australe*, *Protypotherium praerutilum*, and *Protypotherium attenuatum* for the penecontemporaneous SCF at the localities of the Río Santa Cruz. After the manuscript of this article was accepted, Vera *et al.* (2021) described intheratheres from CBF, including a new genus and species.

Notoungulata/Typotheria/Interatheriidae
***Interatherium* Ameghino, 1887**
***Interatherium* sp.**
(Fig. 8J-L)

Referred material. See Appendix 1.

Description. The molariforms of *Interatherium* are euhypsodont. The p1 is incisiform, p2 has the trigonid and talonid less differentiated than p3-p4, which are fully molarized, and p2-p4 are longer mesio-distally than labio-lingually (MPM-PV 19161; Fig. 8J-L). The p3-m1 differ only in their gradual increase in size; the trigonid and talonid are well defined, forming a bilobed crown. The features observed and described in our specimens allow their allocation at the genus level; they remain under study for specific identifications.

Comments. The genus has been recorded in early-middle Miocene of Patagonia Argentina. The species are distinguished mainly by cranial and upper dental elements (Sinclair, 1909). However, the genus is also characterized by molarized lower premolars, with the trigonid and talonid of p3-p4 exhibiting a similar development (Fernández and Muñoz, 2019),

features present in our specimens. Thus, we are confident about the generic allocation but refrain from proposing a specific identification. *Interatherium* has been reported for the “Pinturan” levels of the Sarmiento Formation (Chubut Province), the SCF along the Río Santa Cruz, the Río Chalia, and South to the Río Coyle, and Lago Posadas, and the Collón Curá Formation (Río Negro Province) (Fernández and Muñoz, 2019; Cuitiño et al., 2019a, 2021; Kay et al., 2021).

Litopterna/Lopholipterna/Proterotheriidae
***Thoatherium* Ameghino, 1887**
***Thoatherium minusculum* Ameghino, 1887**
(Fig. 8M-O)

Referred material. See Appendix 1.

Description. MPM-PV 19150, a juvenile, has virtually unworn dp2-dp3 although the enamel is cracked (Fig. 8M-O). The dp2-dp3 paralophids bifurcate into a paraconid and a parastylid. The dp2 (9 mm in length, 4.5 mm in width) is smaller than the dp3 (11.2 mm in length, 7 mm in width). In labial view, the dp2 has a single cusp surrounded by a low cingulid and there is an incipient ectoflexid (Fig. 8M). On dp2, a short crest runs posterolabially to the base of the paralophid. Also on dp3, the paraconid and metaconid are well developed, the latter dividing the tooth into two lingual valleys, an anterior metaflexid, which is larger and deeper than a posterior entoflexid. Finally, a low cristid extends between the paraconid and the metaconid. On the dp3 the protoconid and the hypoconid are separated by a deep ectoflexid. The labial cingulid is better developed than the lingual one and is more marked than in dp2. In the occlusal view, the trigonid is longer and narrower than the talonid, but the metaflexid and the entoflexid have the same width (Fig. 8O). Paraconid, metaconid, and hypoconulid are placed at the same lingual level.

Comments. The genus *Thoatherium* has been recorded in the SCF (early-middle Miocene) of Santa Cruz Province at Río Santa Cruz (Schmidt et al., 2019), Río Chalia (Cuitiño et al., 2021; Monsalvo et al., 2021), and the Atlantic coastal localities (Cassini et al., 2012), and in the Galera Formation (early Miocene), Pampa Castillo, Aisén Region of

Chile (McGrath et al., 2020). MPM-PV 19150 is comparable in size to *Thoatherium minusculum* and *Tetramerorhinus lucarius*, but smaller than *Anisolophus floweri*. The dp2 of MPM-PV 19150 shares with *Th. minusculum* (Scott, 1910; Soria, 2001) the anterior bifurcation of the paralophid, a strong metaconid, a weak external groove, and a short and posteriorly directed hypolophid. The dp3 of MPM-PV 19150 is similar to *Th. minusculum*, with the trigonid longer and narrower than the talonid (Scott, 1910; Soria, 2001). MPM-PV 19150 also is similar in morphology and size to *Th. minusculum* recorded from the Río Santa Cruz (Schmidt et al., 2019) and from Pampa Castillo (Chile; McGrath et al., 2020). MPM-PV 19150 differs from *A. floweri* because the latter has deciduous teeth with thicker enamel, shallower flexids, and a larger dp3 with an entoconid (Soria, 2001).

Litopterna/Lopholipterna/Proterotheriidae
***Anisolophus* Burmeister, 1885**
***Anisolophus* sp.**
(Fig. 8P-Q)

Referred material. See Appendix 1.

Description. MPM-PV 19151 preserves the posterior roots of the p4 and an m1 (Fig. 8P-Q). The m1 (10.9 mm in length and 9.7 mm in width) is poorly preserved and heavily worn. It is square in occlusal view, with the talonid longer than the trigonid, and has thick enamel. Labially, there is a well-developed cingulid and a wide ectoflexid.

Comments. The thick enamel, the well-developed labial cingulid, and the shallow ectoflexid are features shared by MPM-PV 19151 with *Anisolophus* (Soria, 2001), a genus previously recorded in the SCF (early-middle Miocene) of Santa Cruz Province at Lago Posadas (Cuitiño et al., 2019a), Río Santa Cruz (Schmidt et al., 2019) and Río Chalia (Cuitiño et al., 2021; Monsalvo et al., 2021). The m1 trigonid of MPM-PV 19151 is shorter than the talonid, as in *Anisolophus australis*, *A. minusculus* (Soria, 2001) and *A. floweri* (Corona et al., 2019). Although its measurements fall in the range of size of *A. australis* (Soria, 2001), the poor preservation and degree of wear of MPM-PV 19151 led us to consider it as *Anisolophus* sp.



FIG. 9. Caviomorph rodents from Cerro Boleadoras Formation (Santa Cruz Province, Argentina). **A.** MPM-PV 19179, *Neoreomys australis*, right mandibular fragment with dp4-m2: A, occlusal, A', labial. **B.** MLP 91-I-10-2b, *Neoreomys australis*, isolated left m1 or m2: B, occlusal (reversed), B', labial. **C.** MLP 91-I-10-1, *Eocardia montana*, right dentary fragment with m1-m2: C, occlusal, C', labial (reversed), C'', lingual. **D.** MLP 90-III-5-12, *E. montana*, left dentary fragment with dp4-m1: D, occlusal (reversed), D', labial. **E.** MLP 91-I-10-8c, *Luantus propheticus*, right m1 or m2: E, occlusal, E', lingual, E'', labial. **F.** MLP 91-I-10-8d, *L. propheticus*, right m1 or m2: F, occlusal, F', lingual, F'', labial. **G.** MLP 91-I-10-8e, *L. propheticus*, small right dentary fragment with m3: G, occlusal, G', lingual, G'', labial. **H.** MLP 90-III-5-11, *Prolagostomus pusillus*, left dentary fragment with i, m1-m3: H, occlusal (reversed). **I.** MLP 90-III-5-16, *P. pusillus*, right maxillary fragment with M1-M2 in occlusal view. **J.** MLP 90-III-5-34, *Pliolagostomus notatus*, left dentary fragment with p4-m2: J, occlusal (reversed), J', labial. **K.** MLP 90-III-5-13, *Pl. notatus*, left maxillary fragment with M1-M2 in occlusal view. **L.** MPM-PV 19169, *Pliolagostomus*?, left mandibular fragment with p4: L, labial, L' occlusal (reversed). **M.** MPM-PV 19170, *Perimys* sp., left upper M1 in occlusal view. **N.** MPM-PV 19172, *Perimys* sp., right m1 or m2 in occlusal view. **O.** MLP 91-I-10-5, *Acarechimys minutus*, right mandibular fragment with m1-m2 in occlusal view. **P.** MLP 90-III-5-4, *Acarechimys minutissimus*, right mandibular fragment with m1-m2: P, labial (reversed); P', occlusal. **Q.** MLP 91-I-10-18, *Stichomys* sp., left mandibular fragment with m1-m3 in occlusal (reversed) view. **R.** MLP 91-I-10-10, *Stichomys* sp., right dentary fragment with p4-m2 in occlusal view. **S.** MLP 91-I-10-9, *Stichomys* sp., left mandibular fragment with p4-m1, S, occlusal (reversed); S', labial. Scale bars=1 mm.

**Rodentia/Hystricognathi/Caviomorpha/
Cavioidea
Neoreomys Ameghino, 1887
Neoreomys australis Ameghino, 1887
(Fig. 9A-B)**

Referred material. See Appendix 1.

Description. The assignment of the new specimens from CBF to *Neoreomys australis* is based on the high-crowned but rooted cheek teeth (the protohypsodont condition); this species has the highest crowns of the genus (Kramarz, 2006a). The hypoflexus/id has cementum in moderate stages of wear, and the flexus/ids-fossetes/ids are more elongated and narrower than in *Luantus*, *Chubutomys*, or *Phanomys*. The teeth are larger than in the cavioids mentioned above, and the enamel is thicker (similar to *Alloiomys* and *Australoprocta*) and continuous around the perimeter of the crown (Fig. 9A-B). The dental series resembles the condition of *Luantus* in being more convergent towards the midline than in *Dasyprocta* but less so than the euhypsodont cavioids, such as *Eocardia*, *Guimys*, or crown Caviidae. The mandible is robust and the notch for the tendon insertion of the *masseter medialis pars infraorbitalis* muscle (nMpi) is confluent with the masseteric crest (Fig. 9A').

Among the new specimens reported here, MPM-PV 19168 is a mandible of a juvenile individual with dp4, m1, and erupting m2 (Fig. 9A). The dp4 is similar in size and morphology to that of *N. australis*, and different from those of *N. huilensis* (La Victoria and Villavieja formations, La Venta, Colombia, middle Miocene) in that the type species is larger and with less persistent flexids and fossetids. Deciduous premolars of *N. pinturensis* (Pinturas Formation, early Miocene) are not known so far. Labially, the dentary has a delicate nMpi below of dp4-m1. Lingually, the incisor extends distally to m2. The specimens grouped in the lot MPM-PV 19175 are probably associated and, although they are in poor condition, can be easily assignable to *N. australis*.

Comments. Several specimens (mainly isolated teeth and one mandibular fragment) from Cerro Boleadoras housed at MLP were assigned to *Neoreomys* sp. by Vucetich (1994: 368-369). The genus has a wide geographic distribution, including the early-middle Miocene of Patagonia, and early Miocene of San Juan Province, Argentina, the early-middle Miocene of Chile, and middle Miocene of Colombia. *Neoreomys australis* has been recorded in the Pinturas Formation

(Kramarz, 2006a), and Santa Cruz Formation at the Atlantic coast (Candela et al., 2012), Río Santa Cruz (Arnal et al., 2019), and Río Chalia (Cuitiño et al., 2021), Santa Cruz Province, Argentina.

**Rodentia/Hystricognathi/Caviomorpha/
Cavioidea
Eocardia Ameghino, 1887
Eocardia montana Ameghino, 1887
(Fig. 9C-D)**

Referred material. See Appendix 1.

Description. These specimens (see Appendix 1) of *Eocardia montana* are characterized by euhypsodont molars, with double-heart shaped occlusal profile and a constriction in the labial apex of each lobe, a funnel-shaped hypoflexid with cementum, enamel interrupted on the lingual wall, and absence of lingual flexids/fossetids in moderate stages of wear. In the mandibular fragment MLP 91-I-10-1 (Fig. 9C), the m2 has a small lingual flexid (metaflexid) that remains open throughout the entire crown height (Fig. 9C, C"). The persistence of a flexid in euhypsodont taxa, although uncommon, is a variable condition in *E. montana* (e.g., MACN-A 4455). On MLP 91-I-10-1, the notch for the tendon insertion of nMpi is located near the ventral margin of the dentary, between m1-m2, and connected to a poorly developed masseteric crest (Fig. 9C').

MLP 90-III-5-12 (Fig. 9D) is a left dentary fragment of a juvenile, with a slightly worn dp4 and m1. The nMpi (Fig. 9D') is located on the labial wall of the dentary between dp4-m1. Both teeth are high-crowned, with open flexids, and continuous enamel around the entire crown, without cementum. The dp4 is pentalophodont and mesiodistally elongated, with a convex posterolophid. The mesial margin of the tooth is concave with a slight anterior extension. In this stage of wear, the metaconid is well-developed. The hypoflexid has concave margins and it extends transversely about halfway across the occlusal surface. The lingual flexids are open. The second crest (metalophulid II?) is long; the mesolophid and hypolophid are short. The mesial and distal mesoflexids (*sensu* Boivin and Marivaux, 2018) are short. The m1 has a convex metalophulid I and posterolophid. The m1 hypoflexid is wide and slightly posteriorly concave in its anterior margin. MLP 90-III-5-12 is very similar to MACN-A 10205, a right mandibular fragment with dp4-m1, collected by C. Ameghino

in the SCF (without provenance), and assigned to *Eocardia montana* by Pérez (2010). The CBF specimen MACN-A 10205 is a little larger and is slightly more worn than MLP 90-III-5-12, which is evident in the dp4 because the antero- and mesial mesoflexid are closed and the metaconid is indistinct.

Comments. Vucetich (1994) assigned to *Eocardia*? five specimens from Cerro Boleadoras, indicating that all probably correspond to a single species. The genus *Eocardia* has been reported for the early-middle Miocene of Patagonia Argentina and early Miocene of San Juan Province, Argentina. The revision performed here allows us to assign two of them (MLP 90-III-5-12 and MLP 91-I-10-1) to *Eocardia montana*, following Scott (1905) and Pérez (2010), being the first record of this species in CBF. This species is a very common element of the SCF in Patagonia (Pérez, 2010; Arnal *et al.*, 2019). López *et al.* (2011) reported this species for the Chinchas Formation (early Miocene, San Juan Province). Other CBF specimens not examined here—MLP 90-III-5-37 (90-390), MLP 90-III-5-15 (90-347), and MLP 90-III-5-10 (90-289)—were assigned as ?*Eocardia* by Vucetich (1994).

**Rodentia/Hystricognathi/Caviomorpha/
Cavioidea
Luantus Ameghino, 1899
Luantus propheticus Ameghino, 1899
(Fig. 9E-G)**

Referred material. See Appendix 1.

Description. Two isolated teeth MLP 91-I-10-8c-d (Fig. 9E-F) are referred to *Luantus propheticus* because of the following characters: molars are protohypsodont (high-crowned but retaining roots, retain flexids/fossetids, have marginal enamel that is continuous around the crown except lingually at the base of the crown in moderate stages of wear, and have wide hypoflexids with straight, V-shaped borders. In addition, the size coincides with other specimens of this taxon (Kramarz, 2006b; Pérez, 2010). The m1 or m2 (MLP 91-I-10-8c-d) have straight lingual walls, and the mesial and distal margins are slightly convex. The protoconid and hypoconid areas lack the constriction commonly observed in euhypsodont taxa, like *Eocardia*. The lingual fossetids are elongate and narrow. The mesofossetids are the smallest of the fossetids, as in other related cavioids (*e.g.*, *Neoreomys*, *Phanomys*, *Eocardia*, *Schistomys*). The anterofossetids are oriented slightly

mesiolabially, whereas the meso- and metafossetids are more transverse. The smaller of the two molars (Fig. 9E) has discontinuous enamel on most of the lingual wall. On the other molar (Fig. 9F), the enamel is interrupted only at the mesiolingual corner of the crown base.

MLP 91-I-10-8e (Fig. 9G) is a slightly-worn m3 in a small dentary fragment. The lingual flexids are still open. The enamel is continuous around the crown margins, except at the base of the mesiolingual corner. The molar is high-crowned, in lingual view, the base is wider than the apex, and the root is unformed, indicating a juvenile stage. In occlusal view, the mesial lobe is broader transversely than the distal one. The mesial margin of the hypoflexid is straight and the distal is concave mesially. The metalophid I is elongate, the hypolophid is straight and relatively wide, and the posterolophid reaches the lingual border. The antero- and mesoflexid form a unique lingual flexid because the second crest in position is lateromedially short. The posteroflexid is wide and rounded, and the deepest of the flexids. Even though this m3 is similar to both *Luantus propheticus* (*e.g.*, MACN SC 2457, MACN A 52-610?) and *L. toldensis* (*e.g.*, MACN SC 4035), its size is more similar to the type species, which justifies assigning it to *L. propheticus*,

Comments. MLP 91-I-10-8 consists of five isolated molars of different taxa. Two of them are referred here to *Eocardia montana* (MLP 91-I-10-8 a-b, see above) and the other three to *Luantus propheticus* (MLP 91-I-10-8 c-d-e). The genus has been reported for the early Miocene of Patagonia Argentina and BioBío region, Chile. *Luantus propheticus* is recorded from an unknown locality from the “Piso Astrapothericulense” (only the holotype MACN A 52-610), several localities of the Pinturas Formation (Santa Cruz Province; Kramarz, 2006b) and UFZ of the Sarmiento Formation (Chubut Province, Vucetich *et al.*, 2010).

**Rodentia/Hystricognathi/Caviomorpha/
Chinchilloidea/Chinchillidae /
Prolagostomus Ameghino, 1887
Prolagostomus pusillus Ameghino, 1887
(Fig. 9H-I)**

Referred material. See Appendix 1.

Description. The specimens assigned here to *Prolagostomus* (Appendix 1) have euhypsodont cheek teeth formed by two laminae (or lobes) connected by a narrow isthmus. The molariforms have rounded walls and the hypoflexus/id are sinuous, differing

from those of *Pliolagostomus* and *Lagostomus*, which are straight.

Comments. The genus *Prolagostomus* has been reported for the early-middle Miocene of Argentina, Chile, and Bolivia. In addition to the specimens from CBF assigned to *Prolagostomus* sp. by Vucetich (1994), we refer to *P. pusillus* two other specimens from CBF: MLP 90-III-5-14 and 91-I-10-2c.

**Rodentia/Hystricognathi/Caviomorpha/
Chinchilloidea/Chinchillidae
Pliolagostomus Ameghino, 1887
Pliolagostomus notatus Ameghino, 1887
(Fig. 9J-K)**

Referred material. See Appendix 1.

Description. These specimens (Appendix 1) are assigned to *Pliolagostomus notatus* because of their small size and having bilophodont cheek teeth with a narrow and straight hypoflexus. Moreover, as in *Pliolagostomus notatus*, the laminae of the P4 are slightly subtriangular whereas those of the M1-M2 are subrectangular (Rasia and Candela, 2019).

Comments. Three specimens from CBF referred to *Prolagostomus* sp. by Vucetich (1994) are assigned to *Pliolagostomus notatus* in this revision. The genus was recorded in the early-middle Miocene of Patagonia, Argentina.

***Pliolagostomus*? (Fig. 9L)**

Referred material. See Appendix 1.

Description. MPM-PV 19169 is a left dentary fragment with p4. The premolar is similar to that of *Pliolagostomus notatus* but at the dorso-ventral midpoint of the lateral surface of the dentary is a small mental foramen, contrasting with the condition of the type species in which the foramen is more dorsally positioned. On the other hand, *Pliolagostomus friasensis*, *Prolagostomus*, and *Lagostomus* lack the foramen (Rasia and Candela, 2019).

**Rodentia/Hystricognathi/Caviomorpha/
Chinchilloidea/Neoeuplemidae
Perimys Ameghino, 1887
Perimys sp. (Fig. 9M-N)**

Referred material. See Appendix 1.

Description. These specimens (MPM-PV 19170, MPM-PV 19172) are assigned to *Perimys* because

the cheek teeth are euhypsodont and bilophodont, with the hypoflexus/id conspicuously broader and filled with more cementum than in *Prolagostomus* and *Pliolagostomus*. As a result, the teeth of *Perimys* have a U-shape occlusal outline. The molars reported here are medium to large-sized for *Perimys* species, similar to *P. onustus* or *P. intermedius*; however, the specimens are badly damaged which prevents definite assignment to a species.

Comments. The genus was recorded in the early-middle Miocene of Patagonia, Argentina, and early-middle Miocene of Chile. Vucetich (1994: 368-369) reported six specimens of *Perimys* sp. from CBF. She considered all as belonging to the same species due to the similarity in morphology and the large size.

**Rodentia/Hystricognathi/Caviomorpha/
Octodontoidea
Acarechimys Patterson in Kraglievich, 1965
Acarechimys minutus (Ameghino, 1887)
(Fig. 9O)**

Referred material. See Appendix 1.

Description. This specimen is assigned to the type species *Acarechimys minutus* because of its small size and occlusal morphology. The m1-m2 have a reduced metalophulid II, a posteriorly extended metalophulid I, and the metaconid has a posterior arm, as distinct from *A. minutissimus*.

Comments. The genus is recorded from the late Oligocene to middle Miocene of Patagonia, Argentina, early to middle Miocene of Chile and Peru, and middle Miocene of Bolivia and Colombia. *Acarechimys minutus* has been reported from the early to middle Miocene from Sarmiento, Pinturas, Santa Cruz, and Collón Curá formations of Patagonia Argentina; early Miocene of Chile; middle Miocene Villavieja Formation of Colombia (Arnal et al., 2017). Vucetich (1994) assigned to *Acarechimys* sp. only one specimen, MLP 90-III-5-4 (field number 90-335) and another, MLP 91-I-10-5 (91-530a), as “Gen. sp. indet. B”. Both specimens are assigned here to species of *Acarechimys* (*A. minutissimus* and *A. minutus* respectively) because of their morphology and size. They are very small with brachyodont cheek teeth (very low crowns with well-developed roots), present discrete cusps and have narrow crests separated by wide flexids. The lower incisor seems to be long. The masseteric crest of the dentary is well-developed.

***Acarechimys minutissimus* (Ameghino, 1887)
(Fig. 9P)**

Referred material. See Appendix 1.

Description. MLP 90-III-5-4 is assigned to *Acarechimys minutissimus* based on its morphology and size. The molars are very small and lack metalophulid II. The posterior arm of the metaconid and posterior extension of the metalophulid I are absent, contrasting with the condition of *A. minutus*. The notch for the insertion of the tendon of nMpi is straight and located below dp4?-m1, as in *A. minutus*.

Comments. As with the type species, *A. minutissimus* presents one of the broadest geographical and temporal distribution: early to middle Miocene from Sarmiento, Pinturas, Santa Cruz, and Collón Curá Formations of Patagonia Argentina; early Miocene of Chile; middle Miocene Villavieja Formation of Colombia (Arnal *et al.*, 2017).

Acarechimys?

Referred material. See Appendix 1.

Description. The specimen (MLP 90-III-5-1) shows the nMpi placed between the dp4?-m1 on the lateral wall of the dentary. The m2 has a similar size to that of *Acarechimys minutus*; it is lower-crowned and seems to be trilophodont; however, it is too damaged to assign it at species level.

Comments. This specimen was assigned to “Gen. et sp. indet. A” by Vucetich (1994).

**Rodentia/Hystricognathi/Caviomorpha/
Octodontoidea
Stichomys Ameghino, 1887
Stichomys sp. (Fig. 9Q-S)**

Referred material. See Appendix 1.

Description. These specimens referred to *Stichomys* are larger than *Prostichomys*, and are characterized by having rooted but relatively high-crowned cheek teeth with flat occlusal surfaces and undifferentiated cusps. The deciduous premolars are retained throughout life, as in *Adelphomys*. The second crest of the m1 and/or m2 (mesolophid *sensu* Kramarz, 2001) is generally absent, unlike in *Prostichomys*; an indistinct second crest and a reduced anterofossetid in m1 and/or m2 occasionally are present (*e.g.*, MLP 91-I-10-9, Fig. 9S). *Stichomys* differs from *Adelphomys* in having a convex anterior surface of the incisors (Ameghino, 1887). However, the incisors in the new specimens

are not well enough preserved to distinguish this feature, so we agree with the assignment to *Stichomys* sp. by Vucetich (1994).

Comments. The genus was reported from the early-middle Miocene of Patagonia, Argentina, and probably early Miocene of Chile. Vucetich (1994) reported six specimens of *Stichomys* sp., but only five were reviewed here. MLP 91-I-10-17 (91-565) was not available for revision. *Stichomys* is known from Pinturas Formation, SCF, CBF, and Río Frías Formation (Vucetich, 1984; Vucetich *et al.*, 1993; Kramarz, 2005; Arnal *et al.*, 2019) of Patagonian Argentina, and the early Miocene of Pampa del Castillo, Chile (Flynn *et al.*, 2002).

**Rodentia/Hystricognathi/Caviomorpha/
Octodontoidea/Adelphominae
Adelphomyinae indet.**

Referred material. See Appendix 1.

Description. This specimen is a fragment of a small left dentary retaining an m3 with a trilophodont pattern with the oblique crests, characteristic of Adelphomyinae. However, these features alone are insufficient to assign MPM-PV 19173 at the generic level.

**Rodentia/Hystricognathi/Caviomorpha/
Octodontoidea**

Octodontoidea new taxa: Vucetich (1994) assigned MLP 90-III-5-2 (90-296), a right dentary fragment with m1-m3, and MLP 91-I-10-6 (91-530), a right M1 or M2, to “gen et sp indet. C”. MLP 90-III-5-9 (90-290), a right M1 or M2, MLP 90-III-5-27 (90-234), a left dentary fragment with incisor, m1-m3, MLP 90-III-5-24 (90-233), a left dentary fragment with m1-m2, MLP 90-III-5-32 (90-462b) to “gen. et sp. indet. A”. These specimens are new taxa of Caviomorpha, currently under study (M. Arnal, personal communication, 2021).

**Rodentia/Hystricognathi/Caviomorpha/
Erethizontoidea
Steiomys Ameghino, 1887**

Referred material. See Appendix 1.

Comments. MLP 91-I-10-14 (91-564), not reviewed here, was assigned to *Steiomys* sp. by Vucetich (1994: 368, fig.12). It consists of a left dentary fragment with m1-m2, with a conservative dental morphology

and tetralophodont pattern. *Steiromys* is slightly higher-crowned than closely related *Eosteiomys* Ameghino 1902 (Colhuehuapian). *Steiromys* was recorded in the early to middle Miocene of Patagonia Argentina, early Miocene of Chile and Peru, and middle Miocene of Colombia.

Rodentia/Hystricognathi/Caviomorpha Caviomorpha indet.

Referred material. See Appendix 1.

Comments. MLP 90-III-5-19 (90-291), a right dentary fragment with m1-m2, was reported and figured by Vucetich (1994: 369) as Gen et sp indet. D of Dasyproctidae? The nMpi is placed below m1 and joined to the masseteric crest. The cheek teeth are extremely worn and broken; only the m2 is well enough preserved, is very high-crowned, and has thick peripheral enamel. Cementum in the hypoflexid and on the external walls of the crown is very unusual in caviomorphs of the early-middle Miocene. In the lateral view, the hypoflexus is closed; in the occlusal view it is narrow and transversely reaches halfway across the crown. The labial and posterior walls are convex. This combined morphology is different from any other known caviomorph. Another specimen, MPM-PV 19174, consists of a dentary fragment with a poorly preserved m1-m3. The thick enamel layer is very similar to that of MLP 90-III-5-19.

5. Discussion

5.1. The fossil record

The number of specimens obtained from the CBF is rather limited when compared with those from the penecontemporaneous strata of the SCF (see below) at the Atlantic coast (Vizcaino et al., 2012a; Kay et al., 2012), as well as along the Río Santa Cruz (Fornicola et al., 2019a, b; Kay et al., 2021) and the Río Chalcía (Cuitiño et al., 2021). Also, the preservation of the remains is rather poor. We found only one specimen *in situ*, a partial articulated armadillo with its carapace. The cause of the poor fossil content relative to the SCF east of the Andes could be similar to that proposed for this unit at Lago Posadas, some 60 km south, that is, it may be related to the scarcity of fine-grained, especially pyroclastic, materials (see above) that could produce relatively higher preservation potential through fast

episodic burial of dead animals on the floodplains of those areas, and to rocks more resistant to erosion with a consequently lower “release rate” of fossils (Cuitiño et al., 2019a).

Among mammals, in the new collection (MPM-PV) we have not recorded metatherians, vermilinguans, astrapotheres, toxodont notoungulates (toxodontids and homalodotheriids), and macraucheniid litopterns. Carlini et al. (1993) reported the presence of a vermilinguan *Protamandua rothi*, but the specimen has not been catalogued nor further studied. Although vermilinguans, homalodotheriids and macrauchenids are usually quite rare, metatherians, astrapotheres and, particularly, toxodontids are common in other penecontemporaneous outcrops. The apparent absence of astrapotheres, toxodonts, and macrauchenids at CBF is hard to interpret. On one hand, macrauchenids tend to be uncommon and their absence could be a consequence of sampling or taphonomic conditions. But the absence of toxodonts is quite surprising, given their ubiquity and abundance in the records elsewhere in the SCF. Nevertheless, we discern no obvious climatic or vegetational implications for the absence of toxodonts (see section 5.3. Paleoenvironments).

Unfortunately, the MLP-DU collection is not completely catalogued so far and, as mentioned above, not fully available currently. It includes phorusrhacid birds, tortoises, and other major groups of mammals. Metatherians (sparassodonts and paucituberculates) counts 21 specimens that were not reviewed here, but included in the list for the record. Although there are no certain records of astrapotheres, toxodonts and macraucheniid litopterns, field observations of poorly preserved slivers of enamel of large mammals most probably represent toxodonts or astrapotheres. We had access to only some rodents and tortoises. The integrated faunal list reported here includes at least 38 taxa: one anuran, one testudines, three birds and at least 33 mammals, including metatherians, xenarthrans, litopterns, notoungulate typotheres and rodents (Table 1). Almost half the specimens are rodents, represented by all four clades of caviomorphs: Caviodea, Chinchilloidea, Erethizontoidea, and Octodontoidea. Among them, cavioids and chinchilloids are the most abundant and characterized by proto- to euhypsodont taxa (e.g., *Neoreomys*, *Eocardia*, *Luantus*, *Perimys*, and *Prolagostomus*); erethizontoids are limited to one specimen of *Steiromys*, and octodontoids (including

three new taxa; M. Arnal personal communication, 2021) seem to be the most diverse group.

A novel finding is the southernmost record of the family Testudinidae, in South America and the world, represented by *Chelonoidis* cf. *Ch. gringorum*. It confirms a more widespread and diverse distribution in Patagonia than previous mentions of testudinid specimens from Chubut and Santa Cruz provinces (see above). The species *Chelonoidis gringorum* is known from the early-middle Miocene of Chubut Province (Simpson, 1942; De la Fuente 1988, 1994; de la Fuente *et al.*, 2018; Orizabala *et al.*, 2018), but has not been recorded in the penecontemporaneous faunas of the SCF in the Santa Cruz Province. Given the large size and common occurrence of tortoises in many other localities and the vast size of the SCF fossil assemblages (Vizcaíno *et al.*, 2012a; Fernicola *et al.*, 2019a), we interpret the absence of this clade in the SCF as a real absence, not an artifact of rarity or collection bias. The southernmost occurrence of tortoises on the continent is *Chelonoidis* from the late Oligocene (Deseadan) of Cabeza Blanca (Chubut, the oldest occurrences of the family in South America) and the supposedly early Miocene (Santacrucian) of Bajo de la Oriental (Santa Cruz Province; De Broin and De la Fuente, 1993; De la Fuente *et al.*, 2018).

5.2. Correlations

Based on the available geochronological data, the CBF is correlated to the middle or upper sections of the SCF in several sites of the Austral-Magallanes Basin of southern Patagonia, including Lago Posadas, the Río Santa Cruz and Río Chalía valleys (Perkins *et al.*, 2012; Cuitiño *et al.*, 2016, 2019a, 2021), and north (e.g., Cañadón de las Vacas) and south of Río Coyle (Perkins *et al.*, 2012; Trayler *et al.*, 2020; Figs. 1 and 10). The CBF is younger than the Pinturas Formation east of the Meseta del Lago Buenos Aires (De Barrio *et al.*, 1984; Bown and Larriestra, 1990; Escosteguy *et al.*, 2003; Perkins *et al.*, 2012; Aramendía *et al.*, 2019). The lower beds of the SCF in Río Bote, near Lago Argentino, and in Sierra Baguales (Chile) are considerably older (~19–17 Ma; Cuitiño *et al.*, 2016; Bostelmann *et al.*, 2013) than the CBF, while the upper beds in those areas are of uncertain age. West of the study area in Meseta Guadal (Chile), the available ages for the lower part of the Santa Cruz (or Galeras) Formation (Encinas *et al.*, 2019) indicate that it is older than the CBF, whereas the age for its

upper part is unknown and could be, at least in part, contemporaneous with the CBF.

North of the Austral-Magallanes Basin, the CBF could be correlated to the Río Frías Formation at Río Cisnes (Chile) and Meseta Guenguel (Flynn and Swisher, 1995; De la Cruz and Cortés, 2011; Folguera *et al.*, 2018). It also shows temporal overlap with the lower part of the Collón Curá Formation, particularly with the Pilcaniyeu Ignimbrite which has a reported U-Pb zircon age of ~15.5 Ma (Bucher *et al.*, 2019; López, 2020). Finally, there is no chronostratigraphic overlap between the CBF and the older Colhué Huapi Member of the Sarmiento Formation in southern Chubut Province (Ré *et al.*, 2010; Dunn *et al.*, 2013).

As mentioned above, the fossil vertebrates have been recorded from the lower part of the stratigraphic section (representing a ~150 m-thick portion) of the CBF, between ~16 and ~15.1 Ma (late Burdigalian-early Langhian; Fig. 2). CBF vertebrates reported here mainly belong to taxa recorded in the SCF and can be considered Santacrucian *sensu lato* (Table 1). This is in accordance with the age based on the rodents proposed by Vucetich (1994), who assigned them an early Miocene age and established correlations with the Santacrucian (based on the presence of the genera *Stichomys* and *Perimys*), probably late Santacrucian (based on the presence of adult “ecardiid” rodents without fossets and fossetids). Up to now, as Vucetich (1994) mentioned for the rodents, we have not identified taxa typical of “Friasian” and Colloncuran faunas. For instance, we find no specimens of the rodents *Alloiomys*, *Protacaremys denisae*, *Maruchito trilofodonte*, *Neosteiromys? tordillense* (Vucetich *et al.*, 1993), or the primate *Proteropithecina* (Kay *et al.*, 1998). These hypotheses based on the record of rodents and primates deserve further consideration based on the new evidence available (see below).

Younger faunal correlations have been proposed for the CBF. Ugarte (1956) considered that the fauna from CBF could be correlated with the Friasian *s.l.* (middle Miocene) based on Rosendo Pascual’s comments to him about some mammals recorded in Cerro Boleadoras area. Scillato-Yané *et al.* (1993) also suggested that the xenarthrans from CBF would indicate an age similar to those of the Río Frías Formation in alto Río Cisnes, Chile. Scillato-Yané and Carlini (1998) named a new armadillo, *Stenotatus planus*, and Carlini *et al.* (2013) named a new Planopinae sloth (*Prepoplanos boleadorensis*)

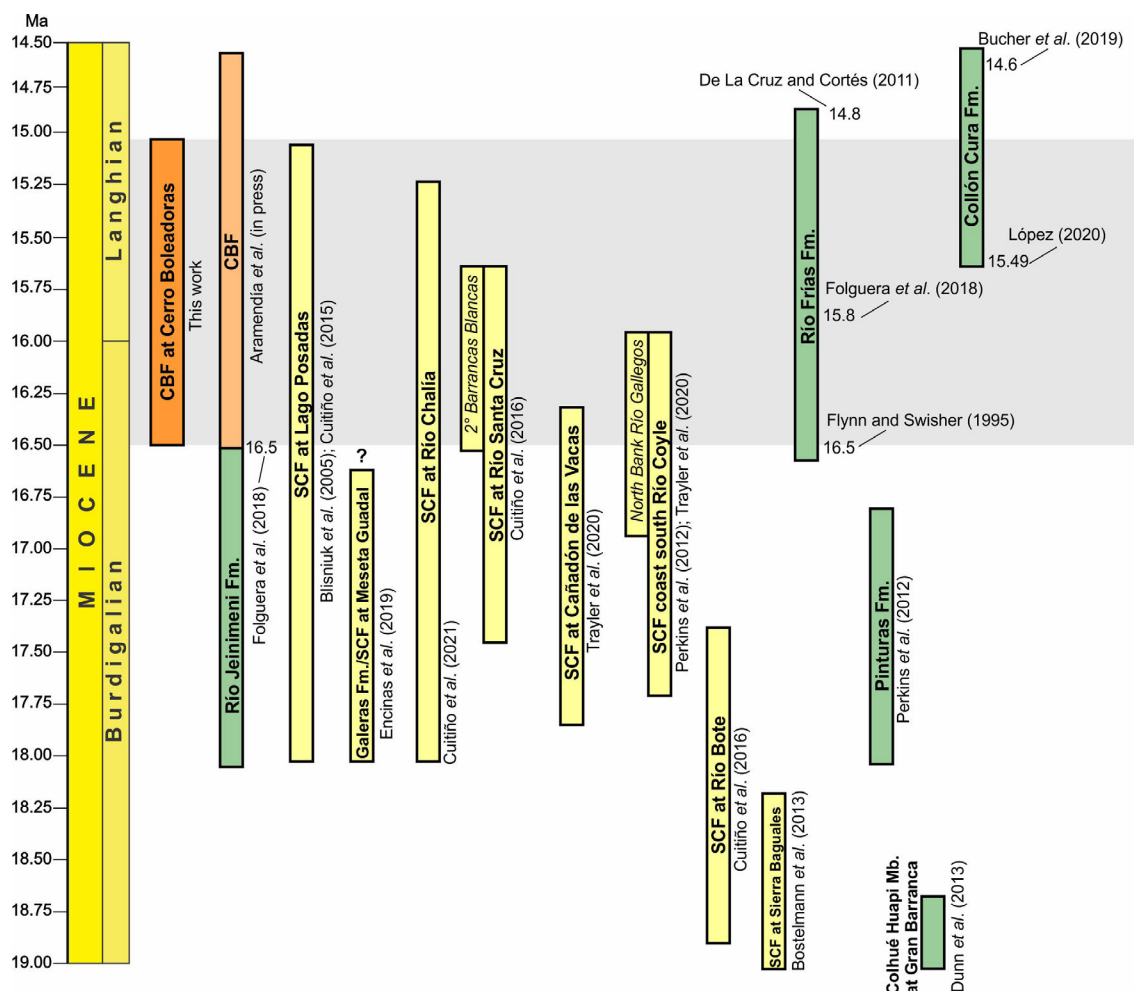


FIG. 10. Chronostratigraphic correlation scheme of Burdigalian-Langhian lithostratigraphic units rich in terrestrial fossil vertebrates from southern and central Patagonia. Orange bars correspond to the Cerro Boleadoras Formation; yellow bars correspond to several exposures of the Santa Cruz Formation; green bars correspond to other units. The source of the age for each locality is provided on the figure.

from CBF, indicating a supposed younger age for the formation, based on allegedly advanced features of the scutes of the former, and in accordance with the speculations of Scillato-Yané *et al.* (1993). Up to now, these taxa have not been reported from other localities clearly assignable to an age younger than the Santacrucian. For this reason, we consider them to be geographic or ecological variants with typical Santacrucian localities from extra-Andean Patagonia, as already proposed for other localities close to the Andes (Fericola *et al.*, 2014; Cuitiño *et al.*, 2016).

Most of the caviomorphs rodents from CBF present extensive biochrons and some taxa reviewed

here have also been reported for older and younger rocks. Vucetich (1994) considered *Stichomys* to be exclusive to the Santacrucian. Now it has a broader temporal range from the older “Pinturan” (Pinturas Formation, Santa Cruz Province) and younger Colloncuran (Río Frías Formation, Chubut Province; Arnal *et al.*, 2019). A more precise identification of the “eocardiids” studied by Vucetich allows the allocation of some of them to *Eocardia montana*, a taxon exclusive of Santacrucian age (Santa Cruz and Chinchas formations, Argentina), and others to *Luanthus propheticus*, previously recorded in the Pinturas Formation (Kramarz and Bellosi, 2005;

Kramarz, 2006b) and the uppermost level (UFZ) of the Sarmiento Formation at Gran Barranca (Kramarz *et al.*, 2010). This is the first report of the genus and species for the CBF. *Luantus* also has been reported also for the Andean Santacrucian of the Cura-Mallín Formation in Chile (Solórzano *et al.*, 2020, 2021), but not from Santacrucian localities of the SCF in extra-Andean Patagonia, east of the Andes. *Steiromys*, a porcupine reported by Vucetich (1994) is also known from “Pinturan” and Colloncuran ages (Vucetich *et al.*, 1993; Kramarz, 2004). *Acarechimys* and *Prolagostomus*, are recorded from Deseadan (Oligocene) and “Pinturan” (early Miocene) respectively, up to Laventan (middle Miocene) age. As is also the case for xenarthrans (*Stenotatus planus* and *Prepoplanops boleadorensis*), there are new rodent taxa among octodontoids of the CBF, indicating at least a certain degree of endemism (M. Arnal, personal communication, 2021).

In summary, the vertebrate assemblage of CBF resembles that of the Santacrucian age *sensu lato* (Table 1) in agreement with its likely chronological age. The record of *Luantus propheticus* indicates the persistence in the west of a taxon that appears in older rocks but had become extinct in extra-Andean Patagonia, suggesting geographic or ecological differences with Santacrucian faunas from extra-Andean Patagonia.

5.3. Paleoenvironments

Following the observations of Aramendía *et al.* (2019), the sedimentary features of the CBF near Los Antiguos-Jeinemeni Rivers suggest sediment accumulation by a mixed-load fluvial paleoenvironment that grades upward transitionally to an alluvial fan. Cuitiño *et al.* (2019a) reconstructed depositional environments and the associated fossil vertebrate fauna of the thick section of the SCF at Lago Posadas. These authors indicated that the unit accumulated in a fluvial system with extensive floodplains, occasionally interrupted by low-sinuosity, sand-dominated channels. Fine-grained sediments with dominant reddish coloration and moderate to low paleosol development, abundant crevasse splay sandstones, and lack of plant remains, suggest deposition in a low-gradient, oxygenated setting under elevated sedimentation rates. Similar sedimentary features are observed for the CBF, albeit with a higher proportion of channelized, cross-bedded sandstone deposits and

fewer paleosol horizons, resembling the upper part of the SCF at Lago Posadas. Neither plant remains nor trace fossils were observed in the CBF. North of the study area, Aramendía *et al.* (2022) recognized eolian dune deposits within the CBF that, although restricted, may suggest the occurrence of intervals of low-humidity conditions.

The records of anurans and testudines indicate the coexistence of different conditions in the landscape. The extant anuran *Calyptocephalella gayi* is an aquatic to semi-aquatic frog that dwells in lowland lakes, ponds, and slow moving streams (Cei, 1962) up to 500 m above sea level, in general associated with the *Nothofagus* forests (Muzzopappa and Báez, 2009). Thus, the record of *Calyptocephalella* indicates the presence of flooded areas and permanent body waters, possibly developed in a forested area (Fernicola and Albino, 2012; Muzzopappa, 2019).

By contrast, the extant tortoise *Chelonoidis chilensis* lives in a variety of arid environments and can tolerate seasonal temperature changes by basking or using burrows (Waller *et al.*, 1989; Richard, 1999); however, high humidity is necessary for hatching its eggs, and the sex is determined in high temperatures (30 ± 1 °C) (see Romito *et al.*, 2015 and references therein). The modern distribution of *Ch. chilensis* is controlled by warm temperatures and high precipitation, at least during the reproductive period (Ruede and Leynaud, 2015). Extant southernmost populations of *Ch. chilensis* are found in shrub-like and woody associations with diverse perennial plants, in plains and piedmont terrains (from “Chaco” plains to “Monte”; see Waller *et al.*, 1989). Thus, the record of *Chelonoidis cf. Ch. gringorum* in CBF indicates higher temperatures than today and abundant rainfall, at least seasonally. Continued cooling and aridification of the Patagonian region during the last few millions of years may have caused the retraction of tortoises into more northern latitudes (Richard, 1999).

Among birds, *Phorusrhacos*, *Patagornis* and *Psilopterus* belong to two guilds of phorusrhacids: non-volant cursorial predators (Phorusrhacinae and Patagornithinae, together with Mesembriornithinae), and predators with some flying ability (Psilopterinae). According to Degrange *et al.* (2012) these groups suggest an open habitat dominated by shrubland or grassland vegetation.

On account of the limited sample sizes and incomplete taxonomic evaluation of all the mammalian

taxa, we have not performed quantitative analyses as for Santacrucian mammal assemblages of the SCF eastward at the Atlantic Coast and the Río Santa Cruz (Kay *et al.*, 2012, 2021 respectively). However, the combined record of arboreal or semiarboreal, browsers and frugivores (*e.g.*, megatherioid sloths and the porcupine *Steiromys*) on one hand, and grazing mammals (*e.g.*, tyotheres and eocardiid rodents) on the other hand, suggest the presence of both forested and parkland vegetation for the CBF, supporting the interpretation of Vucetich (1994). As is also the case for the SCF at Lago Posadas, the available evidence does not resolve whether these two environments coexisted or alternated during the deposition of the formation, and it does not tell us about whether one environment predominated over the other. The record of conifers and Nothofagaceae in the overlying Río Correntoso Formation in this region suggests that forests persisted in the area at least until the middle Miocene (Pujana *et al.*, 2020), and that the two types of environments coexisted in the eastern areas of Patagonia, where semi-deciduous forests graded into savannas with gallery-forest components with canopy heights exceeding 20 m (Kay *et al.*, 2012, 2021). According to Kay *et al.* (2021), this range of habitats occurs today where the mesic inland Atlantic forests of southern Brazil, northeastern Argentina and eastern Paraguay give way northwestward into the more xeric Paraguayan Gran Chaco. Kay *et al.* (2021) also reconstructed the climatic condition in a suite of SCF localities (that they identified as FL 1-7) in the lower member of the SCF along the Atlantic coast, and at Barrancas Blancas and Segundas Barrancas Blancas inland along the Río Santa Cruz, as closely resembling one another. The Mean Annual Precipitation (MAP) estimates were 1,635 mm for FL 1-7, 1,451 mm for Barrancas Blancas, and 1,504 mm for Segundas Barrancas Blancas. The Mean Annual Temperature (MAT) estimates were between ~21 and ~22 °C for FL 1-7 and Segundas Barrancas Blancas, possibly lower at 16 °C for Barrancas Blancas, with the confidence intervals for the estimates overlapping widely. Temperature seasonality was modest (3 to 4 °C) and similar for all localities. However, the presence of the caviomorph rodents *Prolagostomus* and *Pliolagostomus* and the tyother *Pachyrhoxos* are also indicative of aridity. According to Kay *et al.* (2021) and Vizcaino *et al.* (2021), these genera are ground-dwelling taxa with coarse herbivorous

diets that appear in the upper parts of SCF and suggest a trend to aridification in the upper part of that formation along the Río Santa Cruz at the Segundas Barrancas Blancas locality (between ~16.5 and ~15.6 Ma) and South to the Río Coyle at Monte Tigre-Cañadón Las Totoras, and along the Río Gallegos (younger than ~17 Ma).

Vucetich (1994) also suggested that the presence of several octodontoids rodents with reduced lophs in the CBF might indicate that more arid conditions prevailed in CBF compared with the SCF in the Atlantic coastal localities. The rodent assemblage of CBF reported here includes a large proportion of protohysodont (*Neoreomys*, *Luanthus*) and euhypsodont (*Perimys*, *Prolagostomus*, *Pliolagostomus*, *Eocardia*) taxa, octodontoids with reduced occlusal cheek tooth surfaces, and very scarce erethizontids represented by *Steiromys*. This assemblage suggests habitats with open vegetation and arid environments.

6. Conclusions

This contribution provides the first comprehensive study of the paleontology and geology of the Cerro Boleadoras Formation (early-middle Miocene) in the Cerro Boleadoras and Cerro Plomo area (northwestern Santa Cruz Province). It constitutes the first effort to provide a faunal list of this area, with precise location within the stratigraphic section, and to correlate the CBF with the better known SCF in other localities of the Austral-Magallanes Basin. Together with the recent study of Lago Posadas (Cuitiño *et al.*, 2019a), it represents one of the few reports for the early-middle Miocene from the modern-day eastern slope of the Southern Patagonian Andes. The main conclusions of this contribution are:

- The sedimentary features of the CBF suggest mixed-load fluvial deposits that grade upward transitionally to an alluvial fan setting.
- The lower part of the CBF, with an estimated age between ~16.5 Ma and 15.1 Ma (late Burdigalian-early Langhian), temporally overlaps with the middle or upper sections of the SCF in many sites of the Austral-Magallanes Basin of southern Patagonia, the Río Frías Formations in Chile, and the lower Collón Curá Formation of northern Patagonia.
- Faunal differences between the vertebrate fossil content of the CBF and the mentioned

sections of the Santa Cruz, Río Frías, and Collón Curá formations may reflect ecologic, climatic and geographic differences rather than temporal ones.

- The taxa list of the vertebrate fauna of CBF includes most of the groups recorded in the SCF: one anuran, one testudines, three birds, and at least 33 mammals (metatherians, xenarthrans, litopterns, notoungulate typotheres and caviomorph rodents). Fragmentary remains of large mammals (e.g., toxodonts, astrapotheres) were present but, as well as metatherians (sparassodonts and paucituberculates), they have not yet been evaluated.
- The report of *Chelonoidis* cf. *Ch. gringorum* constitutes the southernmost record of tortoises in South America and worldwide.
- The faunal assemblage indicates a Santacrucian age *sensu lato*.
- The presence of *Luantus propheticus*, a taxon recorded in older strata from other localities, suggests geographic or ecological differences with Santacrucian faunas from extra-Andean Patagonia.
- The association of arboreal or semiarboreal, browsing, frugivorous, and grazing mammals suggests the presence of both forested and more open environments.
- The available evidence does not resolve whether these two environments coexisted or alternated or whether one environment predominated over the other.
- The presence of key taxa, such as the chinchillid rodents *Prolagostomus* and *Pliolagostomus*, and the typothere *Pachyrukhos* supports the trend to aridification previously recorded for the upper part of the Santa Cruz Formation (between ~16.5 and ~15.6 Ma) along the Río Santa Cruz and South to the Río Coyle.

Many specimens and several vertebrate groups previously recovered from the CBF remain to be studied. We expect that the updated and integrated information and conclusions provided here would serve as a framework and working hypotheses for further research on the geology and paleontology of the early to middle Miocene localities in western Patagonia. Much further field prospecting of the early to middle Miocene outcrops in and nearby the Andes is needed to envision the broad scenario of the environmental evolution of Austral South America during this crucial interval of time.

Acknowledgements

We thank the Dirección de Patrimonio, Secretaría de Cultura de Estado of the Santa Cruz Province and the Museo Regional Provincial P.M.J. Molina, Río Gallegos, for permissions and assistance for fieldwork. Also to W. Vivallo, Editor of Andean Geology, A. Encinas and an anonymous reviewer for the corrections of the manuscript. This work was supported by the Universidad Nacional de La Plata (UNLP 11/N867 to SFV); Agencia Nacional de Promoción Científica y Técnica (PICT 2017-1081 to MSB), and PICT 2016-0566 to MEP). Funds from NSF DEB-8918657 to RFK supported the MLP-Duke expeditions of 1990 and 1991.

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Manuscript received: June 17, 2021; revised/accepted: January 19, 2022; available online: May 31, 2022.

Editorial handling: Waldo Vivallo

Appendix 1

List of the referred specimens in the section 4. Paleontology.

ANURA

cf. *Calyptocephalella*. MPM-PV 19139, two partial vertebrae; MPM-PV 19140, several fragmentary bones, including skull, vertebrae, humerus and numerous unidentified elements; MPM-PV 19141, partial fragmentary unprepared skeleton; MPM-PV 19142, partial vertebra; MPM-PV 19143, three partial vertebrae and posterior portion of ilion.

TESTUDINES

***Chelonoidis* cf. *Ch. gringorum*.** MPM-PV 19144, four shell fragments; MPM-PV 19145, two shell fragments; MPM-PV 19146, nine shell fragments; MPM-PV 19148, three partial costal plates and a plastron fragment; MPM-PV 19149, left and right associated epiplastra, one plastron fragment. 10 shell fragments; MLP 90-III-5-161, one partial costal, two peripherals, two partial xiphiplastral, 18 shell fragments and a partial femur; MLP 90-III-5-156, four shell fragments.

AVES

***Phorusrhacos longissimus*.** MPM-PV 19162, ungual phalanx of the left digit II.

***Patagornis marshi*.** MPM-PV 19187, right trochlea metatarsi II.

cf. *Psilopterus lemoinei*. MPM-PV 19188, right trochlea metatarsi III.

XENARTHRA, FOLIVORA

cf. *Prepoplanops boleadorensis*. MPM-PV 19138, right calcaneum.

***Megatherioidea* indet.** MPM-PV 19132, right astragalus, partial left calcaneus, ungual phalanx, and carpals/tarsals; not associated; MPM-PV 19133, left astragalus, three partial ungual phalanges, carpal/tarsal, four vertebrae; not associated; MPM-PV 19134, three partial ungual phalanges; not associated; MPM-PV 19135, four ungual phalanges; not associated; MPM-PV 19136, proximal calcaneum, carpals/tarsals; not associated; MPM-PV 19137, partial humeral diaphysis, carpals/tarsals, ungual phalanx, vertebra; not associated.

XENARTHRA, CINGULATA

***Peltephilus* sp.** MPM-PV 17524, partial fixed osteoderm; MPM-PV 19125, two osteoderms from the carapace (fixed and movable), and two from the cephalic shield.

***Vetelia puncta*.** MPM-PV 17517, three fixed osteoderms; MPM-PV 17522, two fixed osteoderms and fragments, MPM-PV 17526, 10 fixed osteoderms, 20 fragments of fixed and movable osteoderms; MPM-PV 19127, one fixed osteoderm, and two fragments of osteoderms.

***Prozaedyus proximus*.** MPM-PV 17520, six articulated osteoderms of the pelvic shield; MPM-PV 17525 two partial osteoderms of the movable band and one fixed; MPM-PV 19126, three broken osteoderms of a movable band.

***Stenotatus* cf. *S. planus*.** MPM-PV 17514, two fragments of the pelvic shield, MPM-PV 17516, three osteoderms; MPM-PV 19118, 12 fixed osteoderms, one movable and two fragments; MPM-PV 19120 carapace and postcrania articulated; MPM-PV 19123, two osteoderms, one fixed and one movable; MPM-PV 19128, 19 fixed osteoderms, one movable and 7 fragments; MPM-PV 19130, two movable osteoderms. MPM-PV 19189, four fixed osteoderms.

***Proeutatus* cf. *Pr. oenophorus*.** MPM-PV 17513, two fixed osteoderms, and one movable; MPM-PV 17519, seven osteoderms; MPM-PV 19117, two osteoderms, one fixed and one movable; MPM-PV 19121, five fixed osteoderms.

***Propalaehoplophoridae* indet.** MPM-PV 17515, isolated osteoderms and astragalus; MPM-PV 17518, MPM-PV 17521, MPM-PV 17523, MPM-PV 19119, MPM-PV 19122, MPM-PV 19124, MPM-PV 19129, MPM-PV 19131, several isolated osteoderms.

NOTOUNGULATA

Hegetotherium mirabile. MPM-PV 19158, two specimens not associated: left dentary fragment with m2-m3; and right dentary fragment with m3; MPM-PV 19180, left dentary with m1-m2; MPM-PV 19184, associated left maxilla with P4-M3 and right maxilla with P3-M2.

Pachyrukhos cf. P. moyani. MPM-PV 19159, six fragmentary dentaries: right dentary with p4-m3, right dentary with p2-m2, right dentary with p2-m2, right dentary with m1-m2, right dentary with m2 and left dentary with p3-m2; MPM-PV 19181, left dentary fragment with p2-p3.

Protypotherium sp. MPM-PV 19152, four dentary fragments: right dentary with m2-m3, right dentary with p3-p4?, left dentary with p4-m2, left dentary with p4-m3; MPM-PV 19153, two dentary fragments: left dentary with m1-m3, right dentary with p4-m1; MPM-PV 19155, dentary and maxilla fragments: symphysis and right dentary with p2-p3 and m1-2, symphysis and right dentary with incisors, canine and p1-p2 broken, right dentary m3, right dentary with m2? broken, right dentary p2-p3?, left dentary with p2-p4 and m1, left dentary with p3-m2 broken, left dentary with m2-m3 broken, juvenile left dentary with molariforms, left maxilla with P3-M2 broken; MPM-PV 19156, left dentary fragment with p2-p3; MPM-PV 19157, mandibular symphysis with left i1-i3, and right i1-i3, c1, and p1-p4; MPM-PV 19160, left maxilla fragment with fragment of P4 and M1-M2, and postcranial elements associated; MPM-PV 19182, two dentary fragments: right dentary with m1-m2?, right dentary with premolar?; MPM-PV 19186, two dentary fragments: right dentary with p3-m2, right dentary with i1-i3, c, p1-p4 and m1 (all broken), juvenile right dentary with three molariforms (p4-m2?).

Interatherium sp. MPM-PV 19161, left dentary fragment with p2-p4; MPM-PV 19183, two right dentary fragments, one with p3 (?) and another with p1-p3 (?).

LITOPTERNA

Thoatherium minusculum. MPM-PV 19150, left mandibular fragment with dp2-dp3.

Anisolophus sp. MPM-PV 19151, left mandibular fragment with posterior roots (broken) of p4 and m1 partially preserved.

RODENTIA

Note: in order to allow direct concordance to the rodents listed by Vucetich (1994), the field catalogue numbers of the MLP-DU are included between brackets after the MLP collection numbers.

Neotomomys australis. MLP 90-III-5-5 (90-336), isolated left dp4; MLP 90-III-5-17 (90-338), right M1 or M2, right broken M1 or M2, left lower molar and left p4; MLP 90-III-5-21 (90-294), anterior portion of left p4; MLP 90-III-5-22 (90-380), left p4, two isolated left M1 or M2, and a broken incisor; MLP 90-III-5-30 (90-439), P4; MLP 90-III-5-39 (90-258), right mandibular fragment labially broken with a fragment of a p4; MLP 91-I-10-2a (91-586), right m3; MLP 91-I-10-4 (91-587), right mandibular fragment with p4-m3; MLP 91-I-10-11 (91-531), left m1; MLP 91-I-10-2b (91-586), isolated left m1 or m2; MLP 91-I-10-13 (91-596), left mandibular fragment with m2; MLP 91-I-10-19 (91-567), right upper molar; MPM-PV 19168, right mandibular fragment with p4-m3; MPM-PV 19171, right m1 or m2; MPM-PV 19175, left mandibular fragment with m1 and roots of p4; MPM-PV 19176, right maxillary fragment with M2-M3 and broken M1, MPM-PV 19177, left maxillary fragment with M2-M3; MPM-PV 19178, left mandibular fragment with m2; MPM-PV 19179, right mandibular fragment with dp4-m2.

Eocardia montana. MLP 90-III-5-12 (90-332), left dentary fragment with dp4-m1. MLP 91-I-10-1 (91-517), right dentary fragment with m1-m2; MLP 91-I-10-8a, b (91-531), a) isolated m1 or m2, and b) isolated left M1 or M2.

Luantus propheticus. MLP 91-I-10-8c, d, e (91-531), c) right m1 or m2, d) right m1 or m2, e) small right dentary fragment with m3.

Prolagostomus pusillus. MLP 90-III-5-11 (90-288), left dentary fragment with i, m1-m3; MLP 90-III-5-14 (90-343), two right p4 and m1 or m2; MLP 90-III-5-16 (90-342), right maxillary fragment with M1-M2; MLP 90-III-5-25 (90-244), left dentary fragment with i and p4; MLP 90-III-5-28 (90-254), fragment of m1 or m2; MLP 90-III-5-29 (90-440), isolated molars: a) left m1 or m2 and b) left P4?; MLP 91-I-10-2c (91-586), right dentary fragment with p4; MLP 91-I-10-54a (91-534), left dentary fragment with p4 erupting (and broken roots of dp4).

Pliolagostomus notatus. MLP 90-III-5-13 (90-341), left maxillary fragment with M1-M2; MLP 90-III-5-33 (90-465), three upper isolated molars: a) right P4, b) left M1 or M2, and c) right M1 or M2; MLP 90-III-5-34 (90-464), left dentary fragment with p4-m2; MLP 90-III-5-36 (90-403), isolated right P4?

Pliolagostomus? MPM-PV 19169, left mandibular fragment with p4.

***Perimys* sp.** MPM-PV 19170, left maxillary fragment with M1-M2; MPM-PV 19172 right m1 or m2; MPM-PV 19167, molar in concretion.

Acarechimys minutus. MLP 91-I-10-5 (91-530a), right mandibular fragment with m1-m2.

Acarechimys minutissimus. MLP 90-III-5-4 (90-335), right mandibular fragment with m1-m2.

Acarechimys? MLP 90-III-5-1 (90-287), right mandibular fragment with m2.

***Stichomys* sp.** MLP 91-I-10-9 (91-547), left dentary fragment with p4-m1; MLP 91-I-10-10 (91-547), right dentary fragment with p4-m2; MLP 91-I-10-16 (91-565), left dentary fragment with p4-m2; MLP 91-I-10-18 (91-565), left dentary fragment with m1-m3.

***Adelphomyinae* indet.** MPM-PV 19173, left dentary fragment with m3.

***Steiromys* sp.** MLP 91-I-10-14 (91-564), left dentary fragment with m1-m2.

***Caviomorpha* indet.** The specimen MLP 90-III-5-19 (90-291), a right mandibular fragment with m1-m2, MPM-PV 19174, consists in a dentary fragment with m1-m3, very deteriorated. However, the thick enamel layer is very similar to that of MLP 90-III-5-19.