

On the holotype of *Caenophilus tripartitus*Ameghino, 1903 (Interatheriidae, Notoungulata): Revision and clarification regarding its geographic and stratigraphic provenances

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ON THE HOLOTYPE OF CAENOPHILUS TRIPARTITUS AMEGHINO. 1903 (INTERATHERIIDAE, NOTOUNGULATA): REVISION AND CLARIFICATION REGARDING ITS GEOGRAPHIC AND STRATI-GRAPHIC PROVENANCES

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Abstract. In 1903, Florentino Ameghino erected the genus and species Caenophilus tripartitus based on a mandibular fragment and a lower isolated molar. The former specimen was illustrated about a decade later and it has been considered missing since, at least, 1986. The first review of the species was carried out in 2019, in which the authors presented new materials from Cerro Zeballos (Chubut Province) assigned to this taxon, a new specific description, and a discussion regarding the provenance of the type specimen, due to the contradictions perceived by them in the Ameghino's papers. Recently, the holotype of Caenophilus tripartitus was located within the Colección Nacional Ameghino at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". In this contribution, we present the first study of this holotype in more than a century, concluding that it did not come from the area of Río Fénix and Laguna Blanca, Mayo Formation, but from an uncertain stratigraphic level at the area of Colhué-Huapí, Chubut Province (Argentina). In addition, the comparison with the material from Cerro Zeballos evidences that it is not referable to C. tripartitus and would represent a second species of the genus, Caenophilus zeballensis sp. nov. In this way, the biochron of C. tripartitus is unknown, whereas that of the genus goes back at least to the late Middle Miocene (Serravallian).

Key words. Typotheria. Interatheriinae. Redescription. Colhué-Huapí. Miocene. Florentino Ameghino.

Resumen. SOBRE EL HOLOTIPO DE CAENOPHILUS TRIPARTITUS AMEGHINO, 1903 (INTERATHERIIDAE, NOTOUNGULATA): REVISIÓN Y ACLARACIONES RESPECTO A SUS PROCEDENCIAS GEOGRÁFICA Y ESTRATIGRÁFICA. En 1903, Florentino Ameghino fundó el género y especie Caenophilus tripartitus a partir de un fragmento mandibular y un molar inferior aislado. El primero fue ilustrado alrededor de una década más tarde y se consideraba como perdido desde, al menos, 1986. La primera revisión de la especie se llevó a cabo en 2019, en la cual los autores presentaron nuevos materiales de Cerro Zeballos (provincia de Chubut) asignados a este taxón, una nueva descripción específica y se brindó una discusión respecto a la procedencia del ejemplar tipo debido a las contradicciones percibidas por ellos en las publicaciones de Ameghino. Recientemente, el holotipo de Caenophilus tripartitus fue localizado dentro de la Colección Nacional Ameghino del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". En esta contribución presentamos el primer estudio de este holotipo en más de un siglo, concluyendo que éste no provendría del área de Río Fénix y Laguna Blanca, Formación Mayo, sino de un nivel estratigráfico desconocido del área de Colhué-Huapí, en la provincia del Chubut (Argentina). Además, la comparación con el material de Cerro Zeballos evidencia que éste no es referible a C. tripartitus y representaría una segunda especie del género, Caenophilus zeballensis sp. nov. De esta manera, se desconoce el biocrón de C. tripartitus, mientras que el del género se remontaría como mínimo al Mioceno Medio tardío (Serravalliense).

Palabras clave. Typotheria. Interatheriinae. Redescripción. Colhué-Huapí. Mioceno. Florentino Ameghino.

ONE OF the main collections of Tertiary fossil mammals was created by brothers Florentino and Carlos Ameghino, which is mostly based on fossils collected by the latter in fifteen expeditions, between 1887 and 1903, in diverse

fossiliferous outcrops of the Argentinian Patagonia. Carlos was responsible for recovering specimens and obtaining any other relevant data in the field, such as the stratigraphic and/or geographic information of each specimen. For more



than a decade, Florentino used these remains to erect and describe a remarkable number of mammal taxa that in the case of the order Notoungulata surpasses the 200 species (Fernández *et al.*, 2018, 2019). Most of these taxa were rarely accompanied by illustrations and adequate diagnosis and never published with collection numbers, complicating the identification of the type materials.

The private collection constructed by the Ameghino brothers is housed at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN) since the 1930s, currently known as the Colección Nacional Ameghino (MACN-A), along with Florentino's handwritten catalog (Bordas, 1936; Simpson, 1984; Bond, 2000; Fernicola, 2011; Fernández et al., 2018, 2019). This catalogued information was directly transferred to the MACN catalog. Florentino provided the inventory number of each specimen (up to 10,316), its taxonomic assignment, a short description, its geographic provenance, the year of collection, and any other information he thought was relevant. It is worth mentioning that materials within the collection not cataloged by Florentino, due to his death in 1911, range from specimen numbers 10,317 to 12,700. These numbers were given by diverse curators in charge of the MACN collection (Fernández et al., 2019).

Among the numerous notoungulates within the MACN-A, the typothere family Interatheriidae (late Paleocene-Early Pliocene) particularly stands out, given its diversity and abundance of specimens. One of the least known taxa within the interatheres is the monospecific genus Caenophilus Ameghino, 1903 (with C. tripartitus), which was erected from a left mandibular fragment and an isolated lower molar, both most likely from the same individual. As commented above, Ameghino (1903) did not provide any collection number of these specimens; nevertheless, the mandibular fragment was later illustrated by Rovereto (1914, figs. 3-4). According to Ameghino (1903, p. 207) and the MACN-A catalog, these materials come from Colhué-Huapí, Chubut Province (Argentina), from levels he called 'upper Tehuelche', and 'Tehuelche formation'. In addition, Ameghino (1906) established that Caenophilus tripartitus was an exclusive taxon of the 'Rionegrense' stage, 'Araucana formation'. Recently, Vera et al. (2019) presented new specimens from Cerro Zeballos (Chubut Province) assigned to *C. tripartitus* based on Rovereto's (1914) illustration and provided an emended diagnosis of the taxon. In addition, these authors considered that the information given by Ameghino (1903, 1906) on the provenance of the holotype was contradictory and stated that it most likely came from the area of Río Fénix and Laguna Blanca (Chubut). These authors based their conclusion on the fact that Ameghino (1906) (which was the latest paper of the author) referred the provenance of the holotype to Lago Blanco (= Laguna Blanca) instead of Colhué-Huapí, as stated by Ameghino (1903), and that the new remains identified by them as *Caenophilus* came from younger sediments than those of Colhué-Huapí.

This contribution aims to present the first direct study of the holotype of *Caenophilus tripartitus* since its rediscovery. We revise and discuss the assigned materials to this species. We also discuss the geographic and stratigraphic provenance of the type material and the biochron of the genus (and species).

MATERIAL AND METHODS

The present study was performed through comparative morphometric and morphologic studies of the holotype of C. tripartitus and other interatheriine taxa. Data mostly come from direct observation of the type and referred materials, either published and unpublished, housed at diverse national and foreign institutions. In addition, we also got information from photographs kindly provided by colleagues and from the scientific literature. Along the text, the names/terms concerning ages, stages, and formations that are indicated with single quotation marks represent informal names/ terms and/or old names/terms no longer used and/or with a current different meaning. The measurements were taken with a Wembley digital caliper (0.02 mm). The photographs were taken with Kodak Digital AZ651 camera. All the nomenclatural acts follow the regulations established by the International Code of Zoological Nomenclature (2000). The dental terminology follows Hooker (1986) and Smith & Dodson (2003), with some considerations from Reguero et al. (2003) for the upper dentition, and Fernández et al. (2021a, 2021b, 2023a, 2023b, 2023c) for upper and lower dentitions.

Institutional abbreviations. MACN-A, Colección Nacional

Ameghino, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad Autónoma de Buenos Aires, Argentina; **LIEB-PV**, Colección Paleovertebrados, Laboratorio de Investigaciones en Evolución y Biodiversidad, Esquel, Chubut, Argentina.

Anatomical abbreviations. C/c, upper/lower canine; dP/dp, upper/lower deciduous premolar; I/i, upper/lower incisor; M/m, upper/lower molar; P/p, upper/lower permanent premolar. Other Abbreviations. Fm., Formation; SALMA, South American Land Mammal Age.

SYSTEMATIC PALEONTOLOGY

Order NOTOUNGULATA Roth, 1903
Suborder TYPOTHERIA Zittel, 1893
Family INTERATHERIIDAE Ameghino, 1887
Subfamily INTERATHERIINAE Ameghino, 1887

Genus Caenophilus Ameghino, 1903

Type species. *Caenophilus tripartitus* Ameghino, 1903. Uncertain stratigraphic occurrence, Colhué-Huapí, Chubut Province, Argentina. **Included species.** *Caenophilus tripartitus* Ameghino, 1903 and *Caenophilus zeballensis* sp. nov.

Amended diagnosis. Interatheriinae of medium size, like Choichephilum, Cochilius, Progaleopithecus tournoueri, Protypotherium praerutilum, and P. claudum. Presence of the postero-dorsal process of the premaxilla as in Santiagorothia, Argyrohyrax, and Protypotherium. Cementum covering the teeth unlike Eopachyrucos and Santiagorothia. Upper canine always present, in contrast to *Interatherium*, and with a distinctive mesio-labial groove unlike Cochilius and Interatherium. Cheek teeth euhypsodont unlike Eopachyrucos, Santiagorothia, Proargyrohyrax, Argyrohyrax, Federicoanaya, and Brucemacfaddenia (protohypsodont). The dP1 lacking a conspicuous parastylar groove as in some specimens of Protypotherium. Upper cheek teeth with a persistent lingual groove between the protoloph and metaloph as in Neoicochilus, Archaeophylus, Choichephilum, Argyrohyrax, Protypotherium, Miocochilius, Interatherium, Cochilius, and Progaleopithecus; without a mid-lingual lobe in contrast to Santiagorothia, Proargyrohyrax, Argyrohyrax, Cochilius, and Brucemacfaddenia; sub-triangular P3-4 shorter than wide as in *Protypotherium*; entoflexus mesially located as in *Miocochilius* and *Protypotherium*. The i1–3 without diastemas in contrast to *Miocochilius* and *Patriarchus*; i3 larger than i2 in contrast to *Cochilius*, *Miocochilius*, *Interatherium*, and *Patriarchus*; p3 exhibits the entoflexid oriented distally to the ectoflexid as in *Eopachyrucos*, *Santiagorothia*, *Proargyrohyrax*, *Argyrohyrax*, and *Brucemacfaddenia*; p3–4 with trigonid longer than talonid as in *Eopachyrucos*, *Santiagorothia*, *Proargyrohyrax*, *Miocochilius*, *Federicoanaya*, and *Protypotherium*; and trigonid with a conspicuous mesio-labial groove unlike other interatheriines.

Stratigraphic occurrence. At least from the late Middle Miocene (Serravallian). Known from, at least, the Collón Curá Fm. of Chubut Province (Argentina).

Caenophilus tripartitus Ameghino, 1903 Figure 1.1–6; Table 1

Holotype. MACN-A 10428 left mandibular fragment with the base of dp1, alveolus of p2, and complete p3-4 (Fig. 1.1-3), and isolated m1 (lost) assumed to belong to the same individual.

Comments about the holotype. Ameghino (1903) erected and described this species without illustrating the holotype or providing a collection number, based on a left mandibular fragment with part of the dentition plus and isolated lower molar. Rovereto (1914, figs. 3-4) illustrated the mandibular fragment (Fig. 1.4-5), but omitted the molar and any description of any of these materials. No specimen is indicated as the type in Ameghino's catalog or in Mones (1986, p. 152); the latter only indicated "MACN (-)", which means that the holotype was already supposed to be missing at that time. According to Ameghino's catalog, the only specimen listed under C. tripartitus is MACN-A 10428, identified as a mandibular fragment. Vera et al. (2019) recognized that MACN-A 10428 was lost. Fortunately, this specimen has been recently located within the Colección Nacional Ameghino. It matches the original description and measurements given by Ameghino (1903, p. 106-107), allowing its confirmation as part of the holotype of C. tripartitus (Fig. 1.1-3). In addition, we confirm that the illustrations made by Rovereto (1914, figs. 3-4), and herein



reproduced in Figure 1.4–5, are based on the holotype of this species. However, there is no evidence of the lower molar that completes the holotype and we assume that it has been lost since at least the early 1910s, before Rovereto's work.

Referred material. The type specimen only.

Amended diagnosis. Caenophilus tripartitus presents a continuous lower dentition, in contrast to C. zeballensis sp. nov., which exhibits a diastema between dp1 and p2; dp1 shorter than p2 and with a shallow ectoflexid that labially separates the trigonid from the talonid, resulting in a bilobed tooth in oclusal view, in contrast to C. zeballensis sp. nov., in which dp1 is longer, has a flat labial face, and lacks a distinctive talonid; lingual face of p2 almost flat, whereas C. zeballensis sp. nov. presents a transversally shallow entoflexid; p3–4 with conspicuous, but small mesio-labial lobe, more developed in C. zeballensis sp. nov.; and the entoflexid and the ectoflexid of p4 are opposite to each other, whereas in C. zeballensis sp. nov. the entoflexid is distal to the ectoflexid.

Description. The permanent lower cheek teeth of MACN-A 10428 are euhypsodont and covered with a thin layer of cementum, with continuous enamel, being thinner in the mesial and, to a lesser degree, the distal regions of p3-4. The dp1 and p2-4 are longer than wide and increase in length antero-posteriorly. The canine is not preserved, but its presence is indicated by the distal region of its alveolus; no diastema is observed between c and dp1. The latter is not mesially nor distally imbricated; the labial face of dp1 bears a transversally shallow ectoflexid that separates the trigonid from the talonid resulting in a labially bilobed tooth in oclusal view, the distal lobe being shorter than the mesial one. The lingual face of dp1 is almost flat. The p2-4 are labially imbricated, so that the mesial region of the paralophid of the posterior cheek tooth overlaps the distal region of the hypolophid region of the anterior tooth. The alveolus of the p2 allows recognizing a shallow ectoflexid, distally placed; there is a transversally shallow but longitudinally deep (i.e., persistent) labio-mesial groove; there are no traces of an entoflexid, thus, the lingual face of the tooth is almost flat. The p3 has both sub-triangular trigonid and talonid, although the latter is more subrounded; the trigonid is wider and longer than the talonid. These are well defined and separated by both persistent entoflexid and ectoflexid, the former being much shallower transversally and distally located than the latter. The lingual region of the trigonid of p3 is flat and convex. The labial region of the trigonid exhibits a persistent mesial groove that is transversally shallow, but deeper than the entoflexid. The presence of this groove develops a small mesio-lingual lobe. The p4 exhibits the same features as p3, except for the following differences: p4 is wider and longer than p3; the entoflexid is transversally deeper and it is more mesially placed than that of the p3, being located at almost the same level as the ectoflexid, reason why both are opposite; the mesio-labial groove of the trigonid is transversely deeper; the mesio-lingual lobe is bigger and labially projected; and there are traces of the metalophid-paralophid groove, which is transversally shallow but persistent. Not much can be described from the mandible due to its fragmentary nature, except for the following: the mandibular symphysis is inferred to begin at the same level as p2; the horizontal ramus is high, slightly more than five times the height of p4; and the mandibular foramen (here recognized as the posterior one) is elliptical in shape, being antero-posteriorly elongated and located below p3.

Geographic and stratigraphic occurrence. Area of Colhué-Huapí, Chubut Province (Argentina). Uncertain stratigraphic provenance.

Caenophilus zeballensis sp. nov.

Figure 1.7-8

LSID urn:lsid:zoobank.org:act:40AB9EDA-F466-4069-9174-C6330D5CE757

Derivation of the specific epithet. The name "zeballensis" refers to the geographic provenance (Cerro Zeballos) of the materials that helped to erect this species.

Holotype. LIEB-PV 7084, right mandibular fragment with right i1 (broken)-p4.

Referred material. LIEB-PV 7068, left mandibular fragment with left c-p4; and LIEB-PV 7083, right maxillary fragment with right C-P4.

Diagnosis. Caenophilus zeballensis sp. nov. presents discontinuous dentition due to the presence of a diastema between dp1 and p2, in contrast to *C. tripartitus*; dp1 is longer than p2, it exhibits a flat labial face, and lacks a distinctive talonid, whereas in *C. tripartitus* dp1 is shorter

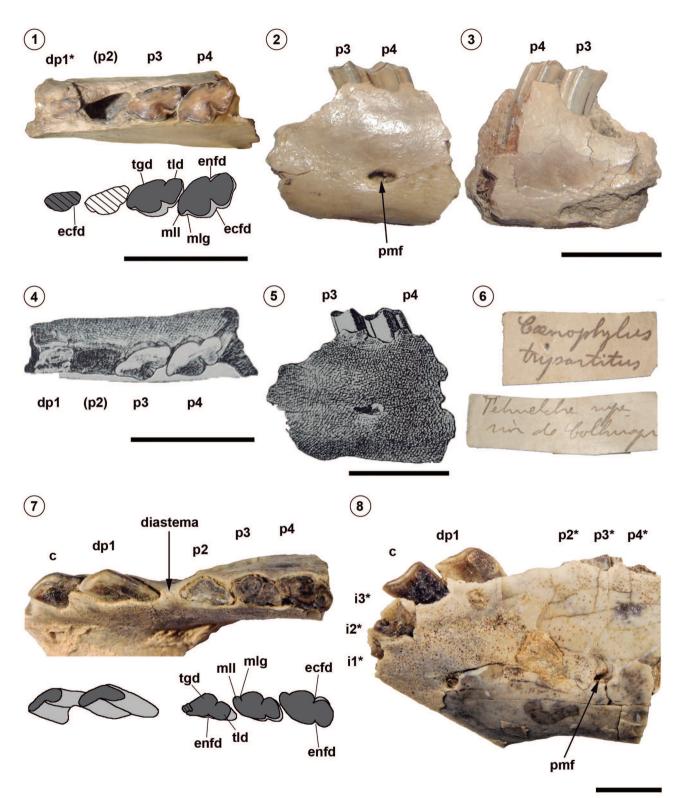


Figure 1. 1–6, *Caenophilus tripartitus*, MACN-A 10428, left mandibular fragment with the base of dp1, alveolus of p2, and complete p3–4; 1, occlusal view; 2, labial view; 3, lingual view; 4–5, modified reproductions of figures 4 and 3, respectively, of Rovereto (1914); 6, paper fragments with Florentino Ameghino's handwriting indicating the name of the species (above) and its provenance (below). 7–8, *Caenophilus zeballensis* sp. nov., LIEV-PV 7084, right mandibular fragment with right i1 (broken)–p4, modified from Vera *et al.* (2019, fig. 3C, F); 7, occlusal view; 8, labial (inverted) view. Abbreviations: ecfd, ectoflexid; enfd, entoflexid; mlg, mesio-labial groove; mll, mesio-labial lobe; pmf, posterior mandibular foramen; tgd, trigonid; tld, talonid. * indicates broken tooth and () indicates the alveolus of the tooth. Scale bars=10 mm.



TABLE 1 - Measurements (in mm) of MACN-A 10428, holotype of Caenophilus tripartitus

	dp1		p2		рЗ		p4	
	L	W	L	W	L	W	L	W
MACN-A 10428	(2.97)	(1.61)	(3.82)	(2.30)	4.56	2.58	4.98	3.13

Abbreviations: (), values measured at the alveolar level; L, maximum length of the tooth; W, maximum width of the tooth

than p2 and presents a shallow ectoflexid that labially separates the trigonid from the talonid, resulting in a bilobed tooth in occlusal view; lingual face of p2 with a transversally shallow entoflexid, whereas in *C. tripartitus* it is flat; p3–4 with a well-developed mesio-labial lobe, which is smaller in *C. tripartitus*; and p4 with the entoflexid distal to the ectoflexid, whereas in *C. tripartitus* both are opposite to each other. **Geographic and stratigraphic occurrence.** Cerro Zeballos, Chubut Province (Argentina); Collón Curá Fm. (late Middle Miocene; Serravallian).

DISCUSSION AND CONCLUSIONS

Taxonomic analysis. The comparison between the holotype of *C. tripartitus* (MACN-A 10428) and the assigned materials presented by Vera et al. (2019) as C. tripartitus allows us to establish that the latter materials belong to the genus Caenophilus; they share many features that differentiate them both from the remaining Interatheriinae (see the Amended diagnosis of the genus). Nevertheless, we reject the recent referral of specimens to this species made by Vera et al. (2019) since both sets of materials present differences that allow them to be recognized as two specific entities, as summarized in the amended diagnoses of C. tripartitus and C. zeballensis sp. nov., the former represented only by its type material MACN-A 10428, and the latter represented by the sample presented by Vera et al. (2019). Geographic provenance of the holotype of Caenophilus tripartitus. Up to this contribution, the collection unit of C. tripartitus (i.e., its holotype plus its attached data) was considered lost. The only reference concerning its geographic provenance was associated with Ameghino's original publication (Ameghino, 1903, p. 107), in which the author indicated that the type specimen of C. tripartitus came from "Formación Tehuelche de Patagonia. De un depósito aislado, en forma de cuenca, en la cumbre de la formación cretácea de Colhué-Huapí; probablemente Tehuelche superior" (Tehuelche formation from Patagonia. From an isolated deposit at the summit of the Cretaceous formation from Colhué-Huapí; probably from upper Tehuelche). This information is reproduced in the MACN-A catalog, with "Colhué-Huapí" indicated as the geographic provenance of MACN-A 10428. However, as mentioned in the Introduction, the information concerning specimens labeled MACN-A 10317 onwards was written by diverse curators in charge of the MACN collection (Fernández et al., 2019), based on Ameghino's personal information and bibliography, and/or any data attached to the material, among other sources.

Fortunately, the vial with the part of the holotype of *C. tripartitus* that we were able to locate (MACN-A 10428) contained a piece of paper with "Tehuelche superior de Colhué-Huapí" written in Florentino's handwriting, reproduced herein in Figure 1.6. This historical reference reinforces the geographic origin published by Ameghino (1903) that was transcribed in the MACN-A catalog. This information allows us to conclude that Ameghino (1903) was certain enough about the geographic provenance of the holotype to reproduce it. In this context, we reject the proposal of Vera et al. (2019) that postulates the area of Río Fénix and Laguna Blanca as the holotype's provenance because, in light of the new evidence, the holotype MACN-A 10428 undoubtedly comes from the area of Colhué-Huapí.

It is worth mentioning that 'Colhué-Huapí' is a common geographical reference used by Ameghino in multiple publications (*e.g.*, Ameghino, 1903, 1904, 1906). This region includes the Colhué-Huapí and Musters lakes plus all the territory surrounding these water bodies (see Simpson, 1967), so Ameghino's 'Colhué-Huapí' is an extensive area, which limits cannot be established with certainty.

Stratigraphic provenance of the holotype of *Caenophilus tripartitus*. In contrast to what was mentioned above, Ameghino (1903, p. 107) was not able to confirm the stratigraphic provenance of the holotype of the species, so he included the word 'probably' in his original description. This is quite striking because the author was explicit about both geographic and stratigraphic provenances in the same work in most cases (see Appendix 1). Consequently, Ameghino (1903) referred the species, with doubts, to the 'upper Tehuelche stage', and later (Ameghino, 1906), to the 'Rionegrense stage'.

Ameghino (1903, p. 107) mentioned that the holotype came from an isolated deposit above the Cretaceous formation at Colhué-Huapí. Up to that moment, the upper Cretaceous formation was the 'Guaranítica formation', from the 'Pehuechense' (older) to the 'Piroteriense' (younger) subaerial stages. This means that the specimen was unconformably placed within an isolated deposit above the 'Guaranítica formation' and, more precisely, above the 'Piroteriense'. Therefore, the specimen came from levels younger than those of the 'Piroteriense' (=Deseadan SALMA; late Oligocene), but we cannot state how much younger it would be. It is worth highlighting that the recognition of the discontinuity between the isolated deposits and the 'Piroteriense' indicates that Florentino (based on the observations made by Carlos in the field) did not recognize his 'Colpodonense' (=Colhuehuapian SALMA; Early Miocene) in that area. Therefore, the specimen would have been collected from a sequence outside Gran Barranca, south of Colhué-Huapí Lake (see Madden et al., 2010 for the exhaustive paleontological study of this area). This discards the hypothesis of Vera et al. (2019, p. 8) that the isolated deposits from where C. tripartitus came, following Ameghino (1903), could correspond to the Upper Fossil Zone of Kramarz et al. (2010). In addition, this is a mammal-bearing level located at the top of the Colhué-Huapí Member section of the Sarmiento Fm. at the Gran Barranca, which was discovered between 2000 and 2010 after diverse field works took place in the region (Kramarz et al., 2010).

Unfortunately, we cannot solve the cause (or causes) of Ameghino's doubt with the available information, but we can make some assumptions. Until 1906, Ameghino's

stratigraphic scheme of Patagonia involved diverse modifications through the years, which led to changes in the definitions of many of his 'formations' and 'stages'. Initially, Ameghino (1897) defined the marine 'Tehuelche formation', divided into three stages: the lower 'Rionegrense', the 'Fairweatheriense', and the upper 'Tehuelche' or 'Tehuelchense'. The author stated than the latter covered almost the entire Patagonia from the Río Negro to the Magallanes region and even recognized the absence of vestiges of seashells and the presence of many large mammalian fossils in the uppermost part.

Later, Ameghino (1902) restructured his scheme by, for example, relocating the marine 'Rionegrense' stage at the top of the older 'Entrerriana formation' and dividing the remaining of the marine 'Tehuelche formation' into two: the 'ancient Tehuelche formation' (correlated with the subaerial 'Araucana formation' from northwestern Argentina) and the 'modern Tehuelche formation' (correlated with the subaerial 'Pampeana' and 'post-Pampeana' formations). Ameghino (1902) mentioned that the 'Pampeana formation' was represented in Patagonia by small and isolated deposits, supported by the presence of many mammal genera and species characteristic of the Pampean Region. In this context, the author recognized a continental 'upper Techuelche' in southern Patagonia, included within the 'Pampeana formation' as part of the 'Ensenadense' subaerial stage, by the presence of, among other taxa, the notoungulate Typotherium (=Mesotherium) and the litoptern Macrauchenia.

A few years later, Ameghino (1906) abandoned the term 'Tehuelche' as well as 'ancient' and 'modern', leaving the concept to what is currently known as "rodados Patagónicos" (see Martínez et al., 2009). The subaerial 'upper Tehuelche' was completely absorbed by the 'Ensenadense' and the marine 'Rionegrense' stage became part of the 'Araucana formation' (located between the older 'Entrerriana' and the younger 'Pampeana' formations). The marine 'Rionegrense' was correlated with a new subaerial stage named also as the 'Rionegrense'. Ameghino (1906) listed *C. tripartitus* as an exclusive taxon of the 'fauna Rionegrense', a new faunal assemblage created from the materials collected between 1901–1902 by Carlos in Patagonia, mostly—but not exclusively—from the area of Río Fénix and Laguna Blanca (see Appendix 1). Based on the



data provided by Carlos, Florentino (Ameghino, 1906, fig. 61) presented the geographical distribution of the fluvial gray or blue sandstones of the continental 'Rionegrense' stage (Appendix 2) and provided a general description of this area. The 'Rionegrense' could be identified in northern Patagonia, around the San Antonio Gulf, in the Valdés Peninsula, and in central Patagonia, where the valley of the Chico River extends up to the coast, and the Santa Cruz River (Rovereto, 1914). In addition, among the many profiles given by Ameghino (1906) regarding Colhué-Huapí, the 'Rionegrense' was only indicated in one profile made by Carlos in the south of Colhué-Huapí, across the Cañadón de Pietrobelli (Ameghino, 1906, fig. 9; see Appendix 3).

In the framework explained above, Caenophylus was described during the shaping of Ameghino's scheme of Patagonia. Following the information provided by Ameghino (1903) and Florentino's handwritten paper, if C. tripartitus was, in fact, collected from levels that he considered as part of the 'upper Tehuelche', its stratigraphic provenance would be associated to the 'Pampeana formation'; however, the author rejected this when including the species within the 'fauna Rionegrense'. It is not clear why Ameghino (1906) did it, particularly considering that, as explained above, the 'Rionegrense' stage is not the Ameghino's 'upper Tehuelche' nor the 'Tehuelche formation' as stated by Vera et al. (2019). However, it is highly probable that Florentino Ameghino did not truly believe that C. tripartitus could be associated with the megafauna of the 'Pampeana formation' as he conceived it and, perhaps, with any other established terrestrial stage above the 'Cretaceous formation' such as the 'Colpodonense' (= Colhuehuapian), based on the species morphology and/or size. As a result, he could have decided to include C. tripartitus within a new continental fauna, the 'Rionegrense', together with another interathere, Epipatriarchus bifidens (= Protypotherium australe; see Fernández et al., 2023b, 2023c) that resembles C. tripartitus in general size and morphology. Therefore, the stratigraphic provenance of the holotype of C. tripartitus and its association with the 'Rionegrense' is rather a consequence of a faunal analysis made by Florentino.

In summary, the information in Ameghino (1903) and Ameghino (1906) is not contradictory in terms of the geographic and stratigraphic provenance of the holotype of C. tripartitus as stated by Vera et al. (2019), because it adjusted to his changing stratigraphic scheme regarding the levels that were discordantly deposited above the 'Cretaceous formation'. There is no doubt that the holotype was collected from an isolated deposit in Colhué-Huapí (Chubut) and not from the Mayo Fm. in the area of Río Fénix and Laguna Blanca. Nevertheless, the stratigraphic level is still uncertain based on current data. All that is known for certain is that C. tripartitus comes from levels younger than those of the 'Piroteriense' (=Deseadan, late Oligocene), but we cannot state how much younger.

Finally, according to all previously mentioned, the biochron of *C. tripartitus* is unknown. Instead, as the material from Cerro Zeballos is confirmed to belong to *Caenophilus* and comes from the Collón Curá Fm. (late Middle Miocene; Serravallian), the biochron of the genus is at least the late Middle Miocene, but it could extend earlier or later.

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APPENDIX 1. List of species erected by Ameghino (1903, 1904) with the corresponding origin established by the author (literal translation), only in two cases it is considered as probable. The order of the species is the same as that of the publications. *Indicates the species mentioned as exclusive from the 'Rionegrense stage' by Ameghino (1906).

Species	Provenance	Paper
Epipithecus confluens	Upper Cretaceous of Patagonia [notostylopense (sic)]	Ameghino (1903)
Acropithecus tersus	Upper Cretaceous of Patagonia [notostylopense (sic)]	Ameghino (1903)
Antepithecus innexus	Upper Cretaceous of Patagonia [notostylopense (sic)]	Ameghino (1903)
Antepithecus interrasus	Upper Cretaceous of Patagonia [notostylopense (sic)]	Ameghino (1903)
Antepithecus gradatus	Upper Cretaceous of Patagonia [notostylopense (sic)]	Ameghino (1903)
Gonopithecus trigonodontoides	Upper Cretaceous of Patagonia [notostylopense (sic)]	Ameghino (1903)
Henricosbornia alouatina	Upper Cretaceous of Patagonia [notostylopense (sic)]	Ameghino (1903)
Henricosbornia subconica	Upper Cretaceous of Patagonia [notostylopense (sic)]	Ameghino (1903)
Oldfieldthomasia plicata	Upper Cretaceous of Patagonia [notostylopense (sic)]	Ameghino (1903)
Eohyrax platyodus	Upper Cretaceous of Patagonia [astraponotense (sic)]	Ameghino (1903)
Eohyrax isotemnoides	Upper Cretaceous of Patagonia [notostylopense (sic)]	Ameghino (1903)
Phanophilus dorsatus	Uppermost Cretaceous of Patagonia [pyrotheriense (sic)]	Ameghino (1903)
Epipatriarchus bifidens*	Tehuelche formation of Patagonia	Ameghino (1903)
Epipatriarchus innexus*	Tehuelche formation of Patagonia	Ameghino (1903)
Caenophilus tripartitus*	Tehuelche formation of Patagonia. From an isolated deposit at the summit of the Cretaceous formation from Colhué-Huapí; <u>probably</u> from upper Tehuelche	Ameghino (1903)
Getohetherium tournoueri	Santa Cruz formation of southern Patagonia [horizon santacruzense (sic)]	Ameghino (1903)
Tegehotherium burmeisteri	Found by Carlos Burmeister on the Chubut River, <u>probably</u> in the upper Patagonian	Ameghino (1903)
Pseudotypotherium pulchrum	Upper Miocene of Monte Hermoso	Ameghino (1904)
Trachytypotherium superans*	Tehuelche formation of Patagonia [middle tehuelche (sic) of Laguna Blanca]	Ameghino (1904)
Trachytypotherium rectum*	Tehuelche formation of the Río Fénix and Laguna Blanca at Patagonia	Ameghino (1904)
Trachytypotherium disparile*	Tehuelche formation of Patagonia [middle tehuelche (sic) of Laguna Blanca]	Ameghino (1904)
Trachytypotherium vietum*	Tehuelche formation of Patagonia [middle tehuelche (sic) of Laguna Blanca]	Ameghino (1904)
Xenotherium immersum	Upper Miocene of Monte Hermoso	Ameghino (1904)
Typotherium pseudopachygnathum	Monte Hermoso	Ameghino (1904)
Typotherium eguiai	This species is exclusive of the lower Pampeano (sic)	Ameghino (1904)
Progaleopithecus fissurellatus	Upper Cretaceous of Patagonia [lower pyrotheriense (sic) of Chubut]	Ameghino (1904)
Progaleopithecus tournoueri	Uppermost Cretaceous of Patagonia [upper pyrotheriense (sic) of Deseado]	Ameghino (1904)
Stereotoxodon tehuelche*	Tehuelche formation of Patagonia (Arroyo Chalía, Laguna Blanca)	Ameghino (1904)
Nesohippus insulatus	Upper Cretaceous of Patagonia [pyrotheriense (sic)]	Ameghino (1904)
Interhippus phorcus	Upper Cretaceous of Patagonia [upper pyrotheriense (sic) of Deseado]	Ameghino (1904)
Stilhippus deterioratus	Lower Eocene of Patagonia [colpodonense (sic)]	Ameghino (1904)
Perhippidion tetragonoides	Lower Eocene of Patagonia [colpodonense (sic)]	Ameghino (1904)
Didolodus dispar	Upper Cretaceous of Patagonia [notostylopense (sic)]	Ameghino (1904)
Argyrolambda conidens	Upper Cretaceous of Patagonia [notostylopense (sic)]	Ameghino (1904)
Heterolambda lunulata	Upper Cretaceous of Patagonia [notostylopense (sic)]	Ameghino (1904)
Adiantus patagonicus	Lower Terciary of Patagonia [colpodonense (sic) of Colhué-Huapí]	Ameghino (1904)
Theosodon karaikensis	Upper Eocene of Patagonia [notohippidense (sic) of Karaiken]	Ameghino (1904)

APPENDIX 1. Continuation

Species	Provenance	Paper
Phoenixauchenia tehuelcha*	Tehuelche formation of the Río Fénix in southern Patagonia	Ameghino (1904)
Eoprotherotherium inaequifacies	Uppermost Cretaceous [pyrotheriense (sic)] of Río Chico, Chubut	Ameghino (1904)
Proterotherium karaikense	Santacrucian formation [notohippidense (sic) of Karaiken] of southern Patagonia	Ameghino (1904)
Proterotherium dichotomum	Santacrucian formation [horizon santacrucense (<i>sic</i>) of Monte Observación] of southern Patagonia	Ameghino (1904)
Proterotherium politum	Santacrucian formation [horizon santacrucense (sic)] of southern Patagonia	Ameghino (1904)
Lophogododon paranensis	Upper Oligocene [mesopotamiense (sic)] of the surroundings of Paraná	Ameghino (1904)
Licaphrium pyramidatum	Santacrucian formation [stage santacrucense (sic)] of southern Patagonia	Ameghino (1904)
Licaphrium proximun	Santacrucian formation [stage santacrucense (<i>sic</i>) of Monte Observación] of southern Patagonia	Ameghino (1904)
Licaphrops coalescens	Santacrucian formation [stage santacrucense (sic) from southern Patagonia]	Ameghino (1904)
Prothoatherium plicatum	Lower Eocene [stage colpodonense (<i>sic</i>) of the Patagonian formation] of Colhué-Huapí	Ameghino (1904)
Thoatherium velatum	Santacrucian formation [stage santacrucense (sic)] of Río Santa Cruz	Ameghino (1904)
Thoatherium karaikense	Santacrucian formation [stage notohippidense (<i>sic</i>) of Karaiken] of southern Patagonia	Ameghino (1904)
Thoatherium bilobatum	Santacrucian formation [stage santacrucense (sic)] of southern Patagonia	Ameghino (1904)
Dudiaphorus coelops	Santacrucian formation [stage santacrucense (sic)] of southern Patagonia	Ameghino (1904)
Proectocion argentinus	Upper Cretaceous of Patagonia [notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Proectocion precisus	Upper Cretaceous of Patagonia [horizon notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Anagonia insulata	Upper Cretaceous of Patagonia [upper notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Listriodon bonaerensis	Upper Pampeano (sic) [horizon bonaerense (sic)] from the same Buenos Aires city	Ameghino (1904)
Listriodon tarijensis	It comes from the Pampeano (sic) of Tarija	Ameghino (1904)
Catagonus metropolitanus	Lower Pampeano (sic) [horizon bonaerense (sic)] of Buenos Aires city	Ameghino (1904)
Dicotyles platensis	Postpampeano (sic) formation [horizon querandinense (sic)] of La Plata city	Ameghino (1904)
Microtragulus argentinus	Upper Miocene of Monte Hermoso. Collections of the Museo Nacional	Ameghino (1904)
Trigonostylops columnifer	Upper Cretaceous of Patagonia [horizon notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Trigonostylops coryphodontoides	Upper Cretaceous of Chubut [horizon notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Trigonostylops germinalis	Upper Cretaceous [horizon notostylopense (sic)] of Chubut	Ameghino (1904)
Scabellia cyclogona	Upper Cretaceous of Patagonia [notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Albertogaudrya oxygona	Upper Cretaceous of Patagonia [upper notostylopense (sic) of Colhué-Huapi]	Ameghino (1904)
Albertogaudrya separata	Upper Cretaceous of Chubut [upper notostylopense (sic) of Colhué-Huapi]	Ameghino (1904)
Astrapotherium karaikense	Santacrucian formation of southern Patagonia [notohippidense (sic) of Karaiken]	Ameghino (1904)
Astrapothericulus emarginatus	Middle Eocene of southern Patagonia, [horizon astrapothericulense (<i>sic</i>)] of the Patagonian formation)	Ameghino (1904)
Astrapothericulus peninsulatus	Upper Eocene of southern Patagonia [notohippidense (<i>sic</i>) of the Santacrucian formation at Karaiken]	Ameghino (1904)
Colpodon plicatus	Lower Eocene of Chubut [horizon colpodonense (sic) of Colhué-Huapí]	Ameghino (1904)
Henricofilholia intercincta	Uppermost Cretaceous of Patagonia [horizon pyrotheriense (sic) of Monte Espejo]	Ameghino (1904)
Pyralophodon pyriformis	Uppermost Cretaceous of Patagonia [horizon pyrotheriense (sic) of Mazaredo]	Ameghino (1904)
Amphitemnus nucleatus	Upper Cretaceous of Chubut [notostylopense (<i>sic</i>) of Colhué-Huapí]	Ameghino (1904)



APPENDIX 1. Continuation

Species	Provenance	Paper
Amphitemnus transitorius	Upper Cretaceous of Patagonia [notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Dialophus recticrista	Upper Cretaceous of Patagonia [notostylopense (sic) of Río Chico from Chubut]	Ameghino (1904)
Plexotemnus complicatissimus	Upper Cretaceous of Patagonia [notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Pleurostylodon irregularis	Upper Cretaceous of Patagonia [notostylopense (sic) of Chubut]	Ameghino (1904)
Pleurostylodon limpidus	Upper Cretaceous of Patagonia [notostylopense (sic) of Chubut]	Ameghino (1904)
Pleurostylodon obscurus	Upper Cretaceous of Patagonia [notostylopense (sic) of Chubut]	Ameghino (1904)
Pleurostylodon bifidus	Upper Cretaceous of Patagonia [notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Pleurostylodon neglectus	Upper Cretaceous of Patagonia [notostylopense (sic) of Chubut]	Ameghino (1904)
Paratemnus geminatus	Upper Cretaceous of Patagonia [notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Tychostylops simus	Upper Cretaceous of Patagonia [notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Lophocoelus macrostomus	Uppermost Cretaceous of Patagonia [pyrotheriense (sic) of Mazaredo]	Ameghino (1904)
Notostylops brachycephalus	Upper Cretaceous of Patagonia [notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Notostylops promurinus	Upper Cretaceous of Patagonia [notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Catastylops deflexus	Upper Cretaceous of Patagonia [notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Eosteiromys medianus	Uppermost Cretaceous of Patagonia [pyrotheriense (sic) of Deseado]	Ameghino (1904)
Parasteiromys uniformis	Lower Eocene of Patagonia [colpodonense (sic) of Colhué-Huapí]	Ameghino (1904)
Protoacaremys amplus	Lower Eocene of Patagonia [colpodonense (sic) of Chubut]	Ameghino (1904)
Disteiromys graciloides*	Lower tehuelche formation of Laguna Blanca of Chubut	Ameghino (1904)
Paramyocastor intactus	Upper Eocene of Patagonia [santacrucense (sic) of Monte Observación]	Ameghino (1904)
octodon crassiusculus	Lower Eocene of Patagonia [colpodonense (sic) of Colhué-Huapí]	Ameghino (1904)
Sigmomys oppositus*	Lower tehuelche formation of Río Fénix from southern Patagonia	Ameghino (1904)
Simplimus indivisus*	Ancient tehuelche formation of Laguna Blanca in the territory of Chubut	Ameghino (1904)
Tetrastylus araucanus	Found in Toay (Central Pampa) while digging a well at 51 meters deep, in the araucana (<i>sic</i>) formation (Upper Miocene). Collections of the Museo Nacional	Ameghino (1904)
Tetrastylus giganteus	Upper Miocene of Monte Hermoso. Collections of the Museo Nacional	Ameghino (1904)
Archaeocardia mustersiana	Lower Eocene of Patagonia [colpodonense (sic) of Colhué-Huapí]	Ameghino (1904)
Argyrolagus palmeri	Upper Miocene of Monte Hermoso	Ameghino (1904)
Polidolops simplex	Upper Cretaceous of Patagonia [notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Orthodolops sciurinus	Upper Cretaceous of Patagonia [notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Anadolops thylacoleoides	Upper Cretaceous of Patagonia [notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Pilchenia lucina	Uppermost Cretaceous of Patagonia [pyrotheriense (sic)]	Ameghino (1904)
Pilchenia lobata	Upper Eocene [notohippidense (sic)] of Karaiken from southern Patagonia	Ameghino (1904)
Progarzonia notostylopense	Upper Cretaceous of Patagonia [notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Clenia minuscula	Lower Eocene of Patagonia [colpodonense (sic) of Colhué-Huapí]	Ameghino (1904)
Didelphys abrupta	Upper Miocene of Monte Hermoso. Collections of the Museo Nacional	Ameghino (1904)
Didelphys biforata	Upper Miocene of Monte Hermoso. Collections of the Museo Nacional	Ameghino (1904)
Didelphys perplana	Upper Miocene of Monte Hermoso	Ameghino (1904)
Hyperdidelphys acutidens	Upper Miocene of Monte Hermoso	Ameghino (1904)

APPENDIX 1. Continuation

Species	Provenance	Paper
Paradidelphys nodosa	Upper Miocene of Monte Hermoso. Collections of the Museo Nacional	Ameghino (1904)
Cladodidelphys crucialis	Upper Miocene of Monte Hermoso. Collections of the Museo Nacional	Ameghino (1904)
Arminhieringia contigua	Upper Cretaceous of Patagonia [notostylopense (sic) of Colhué-Huapí]	Ameghino (1904)
Parahyaenodon argentinus	Upper Miocene of Monte Hermoso. Collections of the Museo Nacional	Ameghino (1904)
Acrohyaenodon pungens	Upper Miocene of Monte Hermoso. Collections of the Museo Nacional	Ameghino (1904)
Pachynasua clausa	Upper Miocene of Monte Hermoso. Collections of the Museo Nacional	Ameghino (1904)
Pararctotherium enectum	Middle Pampeana (<i>sic</i>) formation [lower section of the horizon bonaerense (<i>sic</i>)] from Buenos Aires city. Collections of the Museo Nacional	Ameghino (1904)
Pararctotherium pamparum	Pampeana (<i>sic</i>) formation [upper section of the stage bonaerense (<i>sic</i>)] of Mercedes, Buenos Aires Province. Collections of the Museo Nacional	Ameghino (1904)
Amphicyon argentinus	Upper Miocene of Monte Hermoso	Ameghino (1904)
Notoamphicyon paranensis	Upper Oligocene [stage mesopotamense (sic)] of Paraná	Ameghino (1904)
Smilodon crucians	Lower Pampeano (<i>sic</i>) [stage ensenadense (<i>sic</i>)] of Buenos Aires city. Collections of the Museo Nacional	Ameghino (1904)
Felis propuma	Lower Pampeano (sic) [stage ensenadense (sic)] of Mar del Plata	Ameghino (1904)
Feliz proplatensis	Lower Pampeano (<i>sic</i>) [stage ensenadense (<i>sic</i>)] of Buenos Aires city. Collections of the Museo Nacional	Ameghino (1904)
Rathymotheriom perfectum	Upper Miocene of Monte-Hermoso. Collections of the Museo Nacional.	Ameghino (1904)
Protamandua rothi	Upper Eocene [santacrucense (<i>sic</i>)] of southern Patagonia. Collections of the Museo de La Plata	Ameghino (1904)
Promyrmephagus euryarthrus	Upper Eocene [santacrucense (sic)] of southern Patagonia	Ameghino (1904)
Promyrmephagus dolichoarthrus	Upper Eocene [santacrucense (<i>sic</i>)] of southern Patagonia. Collections of the Museo de La Plata	Ameghino (1904)
Argyromanis patagónica	Upper Eocene [santacrucense (sic)] of southern Patagonia	Ameghino (1904)
Orthoarthrus mixtus	Upper Eocene [santacrucense (<i>sic</i>)] of southern Patagonia. Collections of the Museo de La Plata	Ameghino (1904)
Proprepotheriun deseadense	Middle Eocene [astrapothericulense (sic)] of southern Patagonia	Ameghino (1904)
Prepotheriops meaatheroides	Upper Eocene [horizon santacrucense (sic)] of southern Patagonia	Ameghino (1904)
Megathericulus patagonicus*	Ancient tehuelche of Chubut (Laguna Blanca)	Ameghino (1904)
Neonematherium flabellatum*	Ancient tehuelche formation of Río Fénix of southern Patagonia	Ameghino (1904)
Scelidotheriops avunculus	Upper Eocene [santacrucense (sic)] of southern Patagonia	Ameghino (1904)
Eumylodon bonaerensis	Upper Pampeana (<i>sic</i>) formation [stage bonaerense (<i>sic</i>)] of Buenos Aires Province. Collections of the Museo Nacional	Ameghino (1904)
Octomylodon aversus	Upper Oligocene [mesopotamiense (sic)] of Paraná	Ameghino (1904)
Palaehoplophorus meridionalis*	Ancient tehuelche formation of central Patagonia	Ameghino (1904)
Plohophorus cuneiformis	Upper Miocene of Monte Hermoso. Collections of the Museo Nacional	Ameghino (1904)
Plohophorus araucanos	Araucana (<i>sic</i>) formation. Upper Miocene of pampa central. Collections of the Museo Nacional	Ameghino (1904)
Doedicurus ensenadensis	Lower Pampeana (sic) formation [horizon ensenadense (sic)] of La Plata	Ameghino (1904)
Eutatus praepampaeus	Upper Miocene of Monte Hermoso. Collections of the Museo Nacional	Ameghino (1904)
Epipeltephilus recurvus*	Ancient tehuelche formation of Laguna Blanca from central Patagonia	Ameghino (1904)



APPENDIX 2. Maps from the main areas discussed in the manuscript.

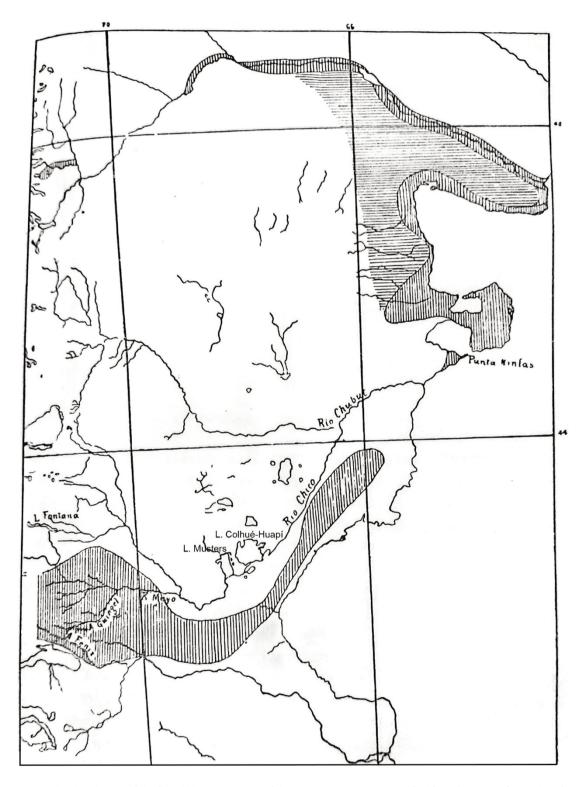
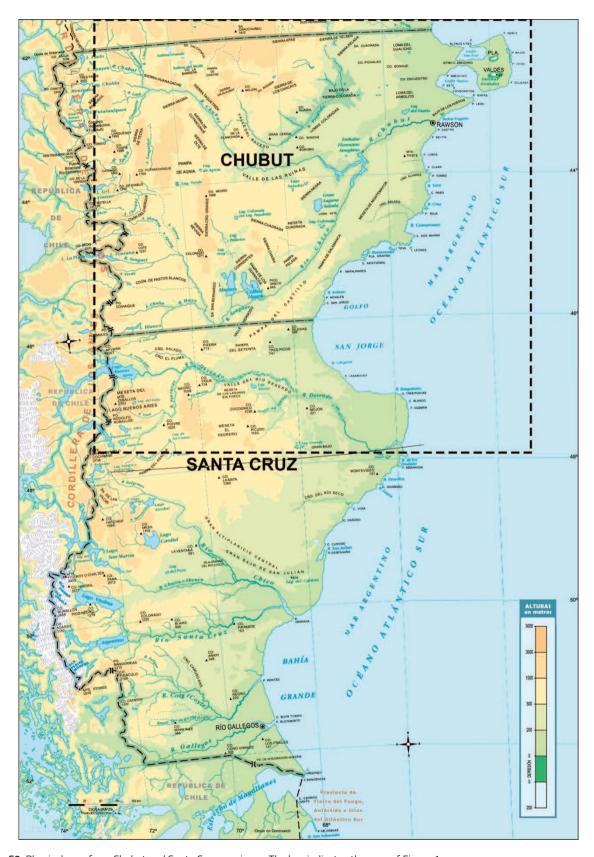
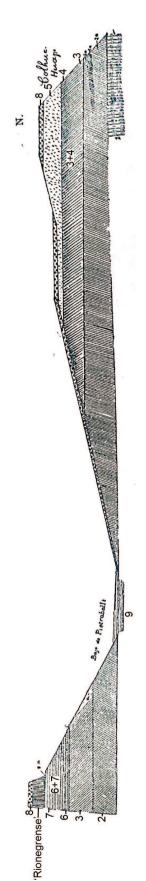


Figure S1. Geographic distribution of the fluvial blue sandstones of the 'Rionegrense' stage, modified from figure 61 of Ameghino (1906). The vertical lines represent the outcrops and horizontal lines represent the connections.



 $\textbf{Figure S2.} \ Physical \ map \ from \ Chubut \ and \ Santa \ Cruz \ provinces. \ The \ box \ indicates \ the \ area \ of \ Figure \ 1.$



2, red sandstones with dinosaurs; 3, 'Notostilopense'; 4, 'Piroteriense'; 3+4, continental layers with *Notostylops* and *Pyrotherium*; 5, 'Colpodonense'; 6, 'Patagónico'; 7, 'Superpatagónico'; 6+7, marine 'Patagónico' and 'Superpatagónico'; 8, 'guijarros rodados tehuelches'; 9, recent clay deposits, probably 'Pampeano'. Figure S3. Carlos Ameghino's profile south of the area of Colhué-Huapí through the Cañadón de Pietrobelli, modified from Ameghino (1906, fig. 9). References: 1, variegated sandstones;