

FOSSIL MARSUPIALIA FROM THE TYPE FRIASIAN LAND MAMMAL AGE (MIOCENE), ALTO RIO CISNES, AISEN, CHILE

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ABSTRACT

The type fauna for the Friasian Land Mammal Age (Middle Miocene, about 15-12 Ma) is from the Río Frías Formation along the Alto Río Cisnes, Aisén, southern Chile. A recent two year program to restudy the geology, geochronology and vertebrate paleontology of this important but poorly known locality has resulted in the recovery of 49 specimens of marsupials which include 11 species, 9 genera and 6 families: Microbiotheriidae (*Microbiotherium tehuelchum*), Hathliacynidae (*Sipalocyon gracilis*, *Cladosictis patagonica*), Borhyaenidae (*Borhyaena tuberata*, *Prothylacynus patagonicus*), Caenolestidae (*Pichipilus halleuxi* sp. nov.), Palaeothentidae (*Palaeothentes minutus*, *P. intermedius*, *P. lemoinei*) and Abderitidae (*Abderites meridionalis*, *Pitheculites rothi* sp. nov.). Nine of these taxa are indistinguishable from species previously known only from the Santa Cruz Formation of southern Argentina (600-800 km S-SE of the Alto Río Cisnes) which is the type formation and fauna of the Santacrucian Land Mammal Age (late Early Miocene, about 18-15 Ma). Thus, the age of the Alto Río Cisnes fauna may be Santacrucian and the Friasian Land Mammal Age (*sensu stricto*) could represent a time equivalent of the Santacrucian Land Mammal Age. If this equivalence is substantiated by other ongoing studies on the geochronology and vertebrate paleontology of the Alto Río Cisnes, then the Colloncuran (*sensu* Kraglievich, 1930) can both conceptually and operationally be used for the land mammal age between Santacrucian and Chasicooan. The Collón Curá Formation at Pilcaniyeu Viejo, Río Negro Province, Argentina could serve as the type fauna and locality for the Colloncuran Land Mammal Age.

Key words: Fossil Marsupialia, Friasian Land Mammal Age, Río Frías Formation, Miocene, Chile.

RESUMEN

La fauna tipo de la Edad-mamífero Friasense (Mioceno Medio, 15-12 Ma) proviene de rocas de la Formación Río Frías, Alto Río Cisnes, Aisén, Chile. Del presente estudio (dos años de trabajo geológico, geocronológico y paleontológico) de esta importante pero pobremente conocida localidad, ha resultado la recuperación de 49 especímenes de marsupiales, donde se incluyen 11 especies, 9 géneros y 6 familias: Microbiotheriidae (*Microbiotherium tehuelchum*), Hathliacynidae (*Sipalocyon gracilis*, *Cladosictis patagonica*), Borhyaenidae (*Borhyaena tuberata*, *Prothylacynus patagonicus*), Caenolestidae (*Pichipilus halleuxi* sp. nov.), Palaeothentidae (*Palaeothentes minutus*, *P. intermedius*, *P. lemoinei*) y Abderitidae (*Abderites meridionalis*, *Pitheculites rothi* sp. nov.). Nueve de estos taxa son indistinguibles de especies antes conocidas sólo en la Formación Santa Cruz del sur de Argentina (600-800 km, S-SE del Alto Río Cisnes), siendo esta formación la que incluye la fauna tipo de la Edad-mamífero Santacrucense (parte alta del Mioceno Inferior, 18-15 Ma). De este modo, la fauna del Alto Río Cisnes sería Santacrucense y la Edad Friasense (*sensu stricto*) podría ser equivalente a la Edad Santacrucense. Si esta equivalencia es verificada por los estudios en curso de geocronología y paleontología de vertebrados del Alto Río Cisnes, el Colloncurense (*sensu* Kraglievich, 1930) podría ser usado conceptual y operacionalmente para denominar la Edad-mamífero entre el Santacrucense y Chasicooense. La Formación Collón Curá, de Pilcaniyeu Viejo, Provincia de Río Negro, Argentina, podría servir como localidad tipo de la Edad-mamífero Colloncurense.

Palabras claves: Fósiles Marsupialia, Edad-mamífero Friasense, Formación Río Frías, Mioceno, Chile.

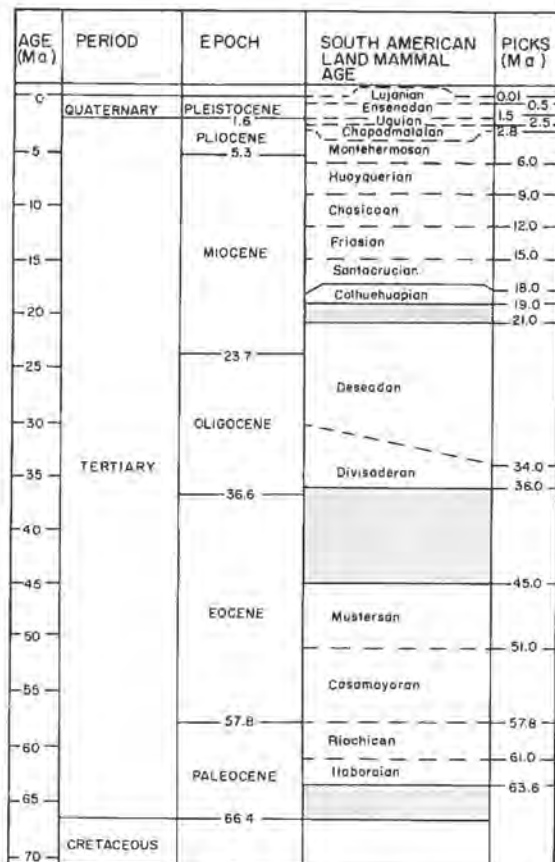
INTRODUCTION

The fossil record of Cenozoic age land mammals in South America is one of the most complete sequences of its kind in the world (Patterson and Pascual, 1972). In fact, it is so complete that geologists and vertebrate paleontologists have long used fossil land mammals to subdivide geologic time. The occurrence of unique associations of taxa that are inferred to have existed during a restricted interval of time has resulted in recognition of discrete intracontinental time units called Land Mammal Ages (Simpson, 1971; Pascual and Odreman Rivas, 1971; Marshall *et al.*, 1983; Marshall, 1985). These South American Land Mammal Ages (SALMA) were established on the basis of knowledge of stage of evolution of the taxa, on their time of first and of last appearance in the fossil record, and on changing faunal associations

through time. When these ages were first erected by the Argentine paleontologist Florentino Ameghino in the early part of the 20th century (*e.g.* Ameghino, 1906) they were comparatively ranked into general categories of 'older than' and 'younger than', an arrangement that resulted in recognition of a relative time sequence for mammalian evolution within South America. By the 1970's a consensus existed for an approximate correlation of these SALMA's with the geologic time scale (see Patterson and Pascual, 1972).

In 1975 a geochronologic program was initiated to establish an absolute time scale for Cenozoic Land Mammal Ages in South America. This interdisciplinary effort involved: radioisotopic (potassium-argon) dating of volcanic rocks (*i.e.* basalts, tuffs, ignimbrites) associated with land mammal faunas (Robert Drake and Garniss Curtis, Berkeley Geochronology Center at the Institute of Human Origins, Berkeley); magnetostratigraphic studies of the fossiliferous rock units themselves (Robert Butler, University of Arizona, Tucson); and restudy of fossil land mammal faunas to permit better biostratigraphic control (the author and Argentine colleagues). As a result of this work many 'key' land mammal age faunas in South America are now securely calibrated with the geologic time scale, and our present concept of SALMA boundaries and durations is, in places, considerably more refined than what it was 10 years ago (Text-Fig. 1).

The most complete and best studied sequence of land mammal faunas in South America is from Argentina, and these faunas represent both the conceptual and operational basis for establishment of a Land Mammal Age chronology on that continent. Our knowledge of these faunas is largely due to the efforts of Florentino and Carlos Ameghino in the latter part of the 19th century and early part of the 20th century. Because of the wealth of fossils in Argentina and of the active school of paleontologists in that country during the last 100 years, it is not surprising that all but two of the type SALMA's presently recognized are based on Argentine rocks and faunas. The exceptions are the Itaboraian Land Mammal Age (Middle Paleocene) based on the fauna from São José de Itaboraí in Brazil, and the Friasian Land Mammal Age (Middle Miocene) based on the fauna from the Alto Río Cisnes in Aisén, southern Chile.



Text-Fig. 1. Geological time scale for the Cenozoic showing South American Land Mammal Ages (after Marshall, 1985).

FRIASIAN LAND MAMMAL AGE

The type Friasian Land Mammal Age is located along the Alto Río Cisnes in Aisén, southern Chile, at Lat. 44°34-39'S, Long. 71°13-15'W, about 11-16 km southeast of the Estancia Río Cisnes (Text-Fig. 2). A map showing the locality is given by Feruglio (1950, Fig. 266) and Ramos (1981, Fig. 12), and photographs are provided by Roth (1908, Pl. 17) and Ramos (1981, Pl. 6).

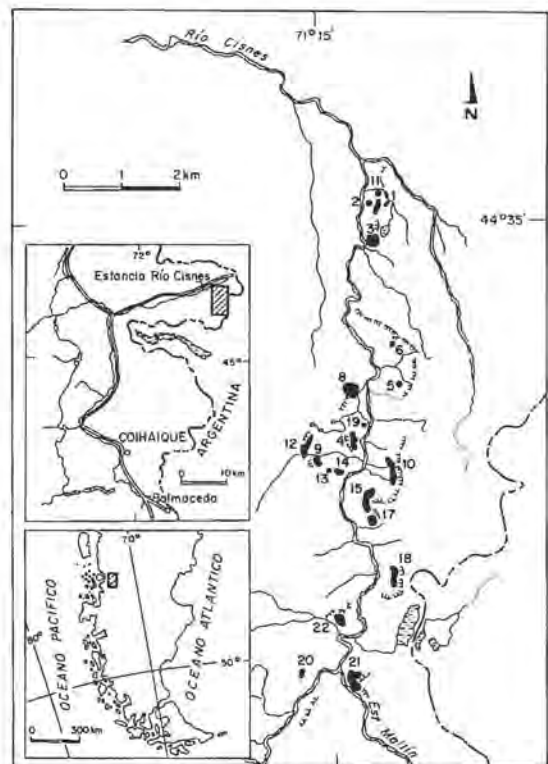
The area was discovered in 1897-1898 by Santiago Roth, a Swiss immigrant to Argentina, who was employed by F. Moreno, Director of the Museo de La Plata, to survey the Argentina-Chile frontier in Patagonia. Roth believed that the locality was in Argentina and applied the name Río Frías to the small river along which he collected the fossils. Subsequent surveys showed that the 'Río Frías' of Roth is in fact the headwaters of the Río Cisnes and is thus within Chile.

Roth apparently spent only a few days in this area and made a small collection of fossil mammals which is now deposited in the Museo de La Plata. Preliminary lists of the fossils were published by Ameghino (1906) and Roth (1908), and specimens were later described in more detail by Kraglievich (1930), Cabrera (1940), and Vucetich (1984). The fossils came from what Roth (1908) called the 'Río Frías Stufe' which is now recognized as the Río Frías Formation (Ploszkiewicz and Ramos, 1977; Ramos, 1981).

The concept of a Friasian Land Mammal Age stems from Ameghino (1906) who applied the term 'étage friaséen' to the as yet undescribed fauna collected by Roth which appeared to be slightly younger or more advanced than the fauna from the Santa Cruz Formation (*i.e.* Santacrucian Land Mammal Age) of southern Argentina. Roth's fauna, however, was poorly known and was not sampled again until 1987 (see below). The specimens in the Roth collection in the Museo de La Plata include: Dasypodidae (*Prozaedius* sp.), Glyptodontidae (?*Propalaeohoplophorus* sp., ?*Palaeohoplophorus* sp.), Megatheriidae (*Megathericulus friasensis* Kraglievich, 1930), Mylodontidae (*Neonematherium* sp.), Macraucheniiidae (*Theosodon* sp., *Phoenixauchenias* sp.), Homalodotheriidae (*Homalodotherium*, sp.), Mesotheriidae (*Eutypotherium* sp.), Intertheriidae (*Protypotherium* sp.), Hegetotheriidae (*Pachyrukhos* sp.), Toxodontidae (*Nesodon* sp., *Andinotherium* sp.,

Prototrigodon rothi Kraglievich, 1930), Astrapotheriidae (*Astrapotherium hesperinum* Cabrera, 1940), and Dasyproctidae (*Alloiomys friasensis* Kraglievich, 1930; Vucetich, 1984) (Bondesio *et al.*, 1980).

Much of our present concept and knowledge of Friasian age faunas is based on those from Argentina which were originally described by Roth (1899, 1908, 1920, 1925), Ameghino (1904, 1906), and Kraglievich (1930) (see Bondesio *et al.*, 1980; Marshall *et al.*, 1983). These faunas are from scattered localities of the Collón Curá Formation in the provinces of Río Negro and Neuquén (Roth, 1899; Bondesio *et al.*, 1980; Pascual *et al.*, 1978, 1984); from scattered localities in what is mapped as the Río Frías or Río Mayo Formation in south-west Chubut (*i.e.* Río Huemules, Río Mayo, Río Guenguel, Río Senguerr, Laguna Blanca = Lago Blanco) and north-west Santa Cruz Province (*i.e.* Río Fénix) (see González, 1967; Bondesio *et al.*, 1980; Riccardi and Roller, 1980; Vucetich, 1984).



Text-Fig. 2. Map of the Alto Río Cisnes, Aisén, southern Chile showing localities where fossil vertebrates were collected during the course of this study.

These faunas along with that from the Alto Río Cisnes of Chile are currently placed within the Friasian Land Mammal Age which based on geochronological data presented in Marshall *et al.* (1977, 1986), Marshall (1985), and Bondesio *et al.* (1980) is believed to range from about 15-12 Ma (Text-Fig. 1). Land mammal faunas of possible Friasian age from elsewhere in South America are discussed by Marshall *et al.* (1983).

There are some debated points about the Friasian Land Mammal Age. First, the scattered faunas are in dire need of systematic treatment and the relative ages of each have yet to be firmly established. The only group to receive monographic treatment is the Rodentia (Vucetich, 1984). Second, Pascual (*in* Patterson and Pascual, 1972, p. 251) doubted the

validity of a Friasian age, implying that faunas presently placed in it may better be regarded as Late Santacrucian. Third, Charrier *et al.* (1976, p. 437) noted that "along the Argentina-Chile border between Lat. 45° and Lat. 47°S, there are no lithologic criteria to differentiate the Friasian from the Santacrucian deposits. Considering that the stratigraphic position of the Santacrucian deposits in the region of Pueyrredón Lake... is similar to that of the Friasian deposits in the region of Meseta Buenos Aires, it is highly probable that both stages are of the same age". And fourth, Pascual *et al.* (1984, p. 551) cautioned that "... no es improbable que la parte inferior de unidades mamíferas asignadas a la Edad Friasense... puedan representar realmente la Edad Santacrucense..."

PRESENT STUDY

In view of the importance of the Alto Río Cisnes as the type fauna and locality of the Friasian Land Mammal Age, that it was sampled only once by Roth in the late 1890's, and of the debates regarding the absolute and relative age of Friasian faunas in general, a geochronologic-paleontologic program was begun in 1987 to revisit this area and to undertake a definitive study of the type Río Frías Formation and its vertebrate fauna. This program, undertaken in December 1987 and January-February 1989, was carried out under the auspices of the Museo Nacional de Historia Natural in Santiago, and the direction of Patricia Salinas of the Sección de Geología of that institution. Studies of the geology and geochronology were made by Patricia Salinas, John Flynn (Field Museum of Natural History, Chicago) and the author; and fossil vertebrates were collected by Richard Kay and Rick Madden (Duke University), Richard Cifelli (University of Oklahoma) and Annie Walton (Southern Methodist University, Dallas, Texas).

This is the first of a series of papers that will be published on aspects of the geology, geochronology and vertebrate paleontology of this important area. In this paper the fossil Marsupialia which prior to this study were not known from this fauna are described. In fact, marsupials have not yet been described or figured from any Friasian age fauna in Argentina although there are reports of their existence. For example, Borhyaenidae indet. are reported from the Collón Curá Formation at Quebrada Azul, Cerro Las

Buitreras in Neuquén Province (Pascual *et al.*, 1978); *Abderites?* sp. and *Borhyaena?* sp. are reported from the Río Frías Formation at Río Senguerr in Chubut Province (Kraglievich, 1930, p. 140; Bondesio *et al.*, 1980); Pascual *et al.* (1984) report *Prothylacynus* sp. (at Pilcaniyeu Viejo, Valle Huahuel Niyen, Cantera Lif Mahuida) from the Collón Curá Formation, and *Palaeotheres* sp. (at Puesto Marileo) from the ?Collón Curá Formation in Río Negro Province; while Bondesio (1986) records *Borhyaena?* sp., *Prothylacynus* sp., *Palaeotheres* sp., and *Abderites?* sp. in Friasian age faunas in Argentina. These reports suggest that marsupials may be rare in faunas of this age in Argentina, while at the Alto Río Cisnes they are extremely abundant, particularly in small size taxa.

Elsewhere in South America marsupials of reputed Friasian age have been described from the La Venta fauna of Colombia (*i.e.* Borhyaenidae, *Lycopsis longirostris*, gen. et sp. indet.; Hondadelphidae, *Hondadelphys fieldsi*; Didelphidae, *Marmosa laventica*, *Marmosasp.*; Marshall, 1976a, 1977). However, work now in progress suggests that the La Venta fauna may be Santacrucian partly or totally in age. Marsupials (*i.e.* Borhyaenidae; Caenolestidae; Argyrolagidae, *Hondalagus altiplanensis*; see MacFadden and Wolff, 1981; Villarroel and Marshall, 1988) are also known from the fauna at Quebrada Honda in southern Bolivia which was originally assigned a Friasian age (Hoffstetter, 1977) but which is now regarded as Santacrucian (Frailey, 1988).

SYSTEMATIC PALEONTOLOGY

Use and chronology of South American Land Mammal Ages follows Marshall (1985; see Text-Fig. 1); known fossil localities along the Alto Río Cisnes are shown in Text-Fig. 2 and Pl. 1; suprageneric classification of Marsupialia follows Marshall *et al.* (1989); and the permanent adult cheek tooth formula is based on the serial designation of P1, P2, P3, M2, M3, M4, M5, the deciduous 'premolar' is the M1 (*vide* Archer, 1978) while in earlier literature referenced in this study the adult formula is numbered P1, P2, P3, M1, M2, M3, M4, and the deciduous tooth is the dP4. All specimens are deposited in the Sección de Geolo-

gía, Museo Nacional de Historia Natural, Santiago, Chile. The stratigraphic position of the fossils described in this study are documented in the paper on the geology of the Alto Río Cisnes area (Marshall and Salinas, 1990.). As shown in that study, all of the fossil Marsupialia were collected within ca. 10 m of the guide level.

The following abbreviations are used; C. canine; I. lower incisor; I. upper incisor; L. length; m. lower molar; M. upper molar; mm, millimeters; MNHN. Museo Nacional de Historia Natural, Santiago; p. lower premolar; P. upper premolar; W. width.

Supercohort Marsupialia
Order Microbiotheria
Superfamily Microbiotheroidea
Family Microbiotheriidae
Genus *Microbiotherium* Ameghino, 1887
***Microbiotherium tehuelchum* Ameghino, 1887**
(Pls. 2, 3; Table 1)

Specimens: MNHN 524, posterior half of left dentary with complete m3-5 (locality 4); MNHN 525, part of left dentary with m4 missing protoconid and basolabial edge, and complete m5 (locality 8); MNHN 526, isolated right m2 (locality 4); MNHN 527, anterior part of right dentary with alveoli of i1-4 and C, complete p1-2, and anterior root and posterior alveolus of p3 (locality 4); MNHN 528, anterior part of right dentary with alveoli of i1-4, root of C, base of p1, complete p2, and anterior root and posterior alveolus of p3 (locality 4); MNHN 537, an isolated C (locality 4); MNHN 538, an isolated C (locality 4); MNHN 539, an isolated C (local-

ity 3); MNHN 540, an isolated C (locality 8); MNHN 545, part of a left dentary with complete C, p1 and p3, and broken base of p2 (locality 14); MNHN 547, part of a left dentary with alveoli of p3, complete m2, and alveoli of m3-4 (locality 15); MNHN 548, part of left dentary with complete but worn m2-4 (locality 14); MNHN 549, an isolated C (locality 3).

Measurements: Table 1.

Previous known occurrences and age: Known previously only from the Santa Cruz Formation in Santa Cruz Province, southern Argentina, which is the type fauna and formation of the Santacrucian

TABLE 1. MEASUREMENTS (in mm) OF LOWER CHEEK-TEETH OF *Microbiotherium tehuelchu*

Specimen	P3		M2		M3		M4		M5	
	L	W	L	W	L	W	L	W	L	W
MNHN 524	---	---	---	---	2.0	1.4	1.9	1.3	1.4	1.0
MNHN 525	---	---	---	---	---	---	1.9	1.2	1.4	0.9
MNHN 526	---	---	2.0	1.4	---	---	---	---	---	---
MNHN 545	1.3	0.8	---	---	---	---	---	---	---	---
MNHN 547	---	---	1.9	1.3	---	---	---	---	---	---
MNHN 548	---	---	2.0	1.3	1.9	1.5	1.9	1.2	---	---

Land Mammal Age (see Marshall, 1982, p. 26).

Comments: A systematic revision of *Microbiotherium tehuelchum* is provided by Marshall (1982, p. 26). This is the most common and best represented species of *Microbiotherium* known, and several dozen specimens have been collected from at least seven localities of the Santa Cruz Formation in southern Argentina. In both size (compare Table 1 with Tables 6 and 7, in Marshall, 1982) and structure, the specimens from the Alto Río Cisnes are inseparable from the large sample of *M. tehuelchum* known from the Santa Cruz Formation. Based on alveoli, as pre-

served in MNHN 527 and 528, the i1-4 are apparently subequal in size. In MNHN 528 the p1-2 are two-rooted, in MNHN 527, p1 is either one or weakly two-rooted while p2 is definitely two-rooted, and in MNHN 545, p1 and p2 appear to be one-rooted. This same variation in the number of roots of p1 and p2 occurs in the sample of *M. tehuelchum* from the Santa Cruz Formation (see Marshall, 1982). The isolated canines are referred to *M. tehuelchum* based on the fact that this species is the only marsupial known from the Alto Río Cisnes which has canines of this relative size and structure.

Order Sparassodonta
Superfamily Borhyaenoidea
Family Hathliacynidae
Genus *Sipalocyon* Ameghino, 1887

***Sipalocyon gracilis* Ameghino, 1887**
(Pl. 4, Figs. 1, 2)

Specimens: MNHN 541, part of a right maxilla with worn M2-3 and anterior root of M4 (locality 13).

Measurements: M2 L = 6.4 mm, W = 3.8 mm; M3 L = 6.4 mm, W = 4.8 mm.

Previous known occurrences and age: Known previously only from the Santa Cruz Formation in Santa Cruz Province, southern Argentina (see Marshall, 1981, p. 44).

Comments: A systematic revision of *Sipalocyon gracilis* is provided by Marshall (1981, p. 44). This is

the most common and best represented of the two species of *Sipalocyon* known in the Santa Cruz Formation, the other being *S. obusta* Ameghino, 1891 (see Marshall, 1981, p. 60). The only known specimen of *S. gracilis* from the Alto Río Cisnes is indistinguishable in size (compare measurements above with Tables 10 and 11 in Marshall, 1981) and structure from the sample of this species from the Santa Cruz Formation.

Genus *Cladosictis* Ameghino, 1887

***Cladosictis patagonica* Ameghino, 1887**
(Pl. 4, Figs. 3, 4)

Specimens: MNHN 501, an isolated right m4 missing posterior base of talonid (locality 8); MNHN 502, paraconid and anterior edge of protoconid of a left m5 (locality 3); MNHN 503, paraconid and anterior-most edge of protoconid of a right m3 or m4 (locality 8); MNHN 504, anterior part of a left dentary with nearly complete symphysis, alveoli of I1-3, broken base of C, and roots of p1 (locality 1).

Measurements: MNHN 501, m4 L = 8.0 mm, W = 4.2 mm; MNHN 502, m5 W = 4.6 mm; MNHN 504, p1 L (measured at base of alveoli) = ca. 5.7 mm, diastema between C-p1 L = ca. 3.2 mm, diastema between p1-2 L = ca. 2.0 mm.

Previous known occurrences and age: Known previously only from the Santa Cruz Formation in Santa Cruz Province, southern Argentina (see Marshall, 1981, p. 79).

Comments: A systematic revision of *Cladosictis patagonica* is provided by Marshall (1981, p. 79). This is the only known species of *Cladosictis* recognized in the Santa Cruz Formation where it is extremely abundant and known from at least 15 localities (Marshall, 1981, p. 89). The three partial lower molars from the Alto Río Cisnes (MNHN 501, 502, 503) are indistinguishable in size (compare measurements above with Table 21 in Marshall, 1981) and structure

from the Santa Cruz Formation sample. The partial dentary (MNHN 504) from the Alto Río Cisnes is assigned to *C. patagonica* by the large size of p1 (L = ca. 5.7 mm) which is considerably larger than p1 in

Sipalocyon gracilis (in *C. patagonica* the length of p1 ranges from 5.1-5.9 mm, while in *Sipalocyon gracilis* it ranges from 4.0-4.4 mm (see Tables 13 and 22 in Marshall, 1981).

Family Borhyaenidae
Subfamily Borhyaeninae
Genus *Borhyaena* Ameghino, 1887

***Borhyaena tuberata* Ameghino, 1887**
(Pl. 5, Figs. 1, 2)

Specimens: MNHN 505, greater part of protoconid and complete talonid of a left m3 (locality 3).

Measurements: m3 W = 7.0 mm

Previous known occurrences and age: This species was known previously only from the Santa Cruz Formation of southern Argentina (see Marshall, 1978, p. 43). *Borhyaena* ? is also reported from the Río Frías Formation at Río Senguerr in Chubut Province, Argentina (see above; Bondesio *et al.*, 1980).

Comments: A systematic revision of *Borhyaena tuberata* is provided by Marshall (1978, p. 43). This is the only species of *Borhyaena* recognized in the rich fauna of the Santa Cruz Formation, where it is quite

abundant and known from at least 14 localities. The only known specimen from the Alto Río Cisnes is indistinguishable in size (W = 6.7-7.8 mm based on 9 specimens from Santa Cruz Formation; see Marshall, 1978, Table 7A) and structure from the large sample studied by Marshall (1978). In MNHN 505 the protoconid is worn flat with a blunt horizontal surface, on the posterior surface of the protoconid is a narrow vertical keel which, on the talonid, terminates as a small cuspule; the posterior edge of the talonid is elevated into a distinct ridge which extends lingually to enclose a very small talonid basin, and extends labially as a strong ventro-ventroanteriorly directed ridge.

Subfamily Prothylacyninae
Genus *Prothylacynus* Ameghino, 1891

***Prothylacynus patagonicus* Ameghino, 1891**
(Pl. 5, Figs. 3, 4)

Specimens: MNHN 506, part of a right dentary with posterior root of m2, base of m3 (anterior half is broken, talonid is complete), and roots of m4 (locality 8).

Measurements: m3 L = ca. 11.0 mm, W = ca. 5.7 mm.

Previous known occurrences and age: This species has been recorded previously only from the Santa Cruz Formation of southern Argentina (see Marshall, 1979, p. 8). *Prothylacynus* sp. is reported from the Collón Curá Formation of Argentina (see above; Pascual *et al.*, 1984).

Comments: A systematic revision of *Prothylacynus patagonicus* is provided by Marshall (1979, p. 8). This species was previously known by only 13 specimens, some complete skulls, collected from five localities of

the Santa Cruz Formation. The only known specimen from the Alto Río Cisnes is indistinguishable in size (compare measurements above with Table 4 in Marshall, 1979) and structure from the sample described by Marshall (1979). This species is distinguished by the moderately well developed talonid which is higher lingually and slightly lower labially, and the position of the anterior root of m4 which is set slightly lingual of the posterior root of m3. It differs from the similar size *Lycopsis torresí* Cabrera, 1927 (see Marshall, 1979, p. 23) in which the talonid is relatively larger, distinctly basined, and has a distinct lingual cusp (absent in *P. patagonicus*), and in the anterior root of m4 being set directly posterior to the posterior root of m3.

Order Paucituberculata
 Superfamily Caenolestoidea
 Family Caenolestidae
 Genus *Pichipilus* Ameghino, 1890

Pichipilus halleuxi sp. nov.

(Pl. 6, Figs. 1-3)

Etymology: *halleuxi*, named in honor of Pablo Raty de Halleux, manager of the Estancia Río Cisnes in recognition for his support of the paleontological program at the Alto Río Cisnes.

Type specimen: MNHN 534, part of a right dentary with posterior half of p3 and complete m2 (locality 4).

Hypodigm: Type only.

Measurements: p3 L = ca. 1.0 mm, W = 0.6 mm; m2 L = 1.7 mm, W = 1.3 mm.

Diagnosis: Similar in size to *Pichipilus centinelus*, but differs from that species, the smaller *P. riggsi* and larger *P. osborni*, in having the labial side of the tooth elevated relative to the lingual side, and in the smaller size of the metaconid and entoconid.

Description: A very large mental foramen occurs ventral to anterior root of m2; as evidenced by swelling of the ventral edge of the dentary, the root of the large procumbent I1 extended posteriorly to a point ventral to the center of m2; p3 is well developed and two-rooted, the tip of the crown is about the same height as the m2 paraconid, and a transversely broad posterobasal heel is higher labially and lower lingually; m2 trigonid is narrower and only slightly higher than talonid; there is a well developed anterobasal cingulum and a small labial cuspule at the base of the hypoflexid; protoconid is highest of trigonid cusps and it is connected by a high blade-like paracristid with the lower paraconid which is situated at the anterolingual edge of the tooth; metaconid is subequal in height to paraconid and is situated directly linguad of protoconid; metaconid is small, isolated and not joined with protoconid by a protocristid; talonid is broad and deeply basined; hypoconid is largest of talonid cusps and is much higher than entoconid and hypoconulid; entoconid is slightly higher than hypoconulid; hypoconulid is set lingually on posterior edge of tooth, closer to entoconid than to

hypoconid; labial side of m2 crown is considerably higher than lingual side, and is dominated by a crest-like structure involving the hypoconid-elevated crista obliqua (which connects with posterolabial side of protoconid)-protoconid-blade like paracristid-and paraconid.

Comments: MNHN 534 from the Alto Río Cisnes is referable to *Pichipilus* based on size and structure of the p3 (*i.e.* it is two-rooted, about same height as m2 paraconid, and has a transversely broad posterobasal heel), the broad anterobasal cingulum on m2, and the trigonid being only slightly higher than the talonid. The combination of these features serve to distinguish species of *Pichipilus* from species of *Stilotherium* and *Phonocdromus* which occur in rocks of similar age (see Marshall, 1976c, 1980; Marshall and Pascual, 1977).

Three species of *Pichipilus* were previously known: *P. riggsi* of Colhuehuapian age from Argentina; *P. centinelus* of Early Santacrucian age from Argentina; and *P. osborni* of Santacrucian age from Argentina (see Marshall, 1976c, 1980; Marshall and Pascual, 1977). Of these three species, *P. halleuxi* agrees best in size and structure with *P. centinelus*, particularly in the p3. *P. halleuxi* differs from this and the other two species in the m2 crown being elevated labially, and in the smaller size of the metaconid and entoconid. In the elevated structure of the labial side of m2, *Pichipilus halleuxi* resembles specimens of *Pliolestes* from beds of Chasicuan and Montehermosan age in Argentina in which the m2 is high crowned, both labially and lingually. *P. halleuxi* thus supports the prediction by Marshall and Pascual (1977) that a species of *Pichipilus* was probably involved in the ancestry of *Pliolestes*. In fact, of the four species of *Pichipilus* now known, *P. halleuxi* most closely approximates the ancestor of *Pliolestes*.

Family Palaeothentidae

Genus *Palaeothentes* Ameghino, 1887

There are four species of *Palaeothentes* known in the Santa Cruz Formation of southern Argentina (see Marshall, 1980) and three of these are present at the

Alto Río Cisnes. *Palaeothentes* sp. is also recorded from the Friasian age Collón Curá Formation of Argentina (see above; Pascual *et al.*, 1984).

***Palaeotheres minutus* Ameghino, 1887**

(Pl. 6, Figs. 4-9, Table 2)

Specimens: MNHN 531, part of a right dentary with complete m2-3 (locality 4); MNHN 532, part of a right dentary with a complete p3 (locality 4); MNHN 533, an isolated left M2 (locality 4); MNHN 536, talonid of a left m2 (locality 4).

Measurements: Table 2; MNHN 533 M2 L = 2.1 mm, W = 1.9 mm.

Previous known occurrences and age: Known previously only from the Santa Cruz Formation of southern Argentina (see Marshall, 1980, p. 55).

Comments: A systematic revision of *Palaeotheres*

minutus is provided by Marshall (1980, p. 55). This taxon is known from over 50 specimens collected from at least eight localities in the Santa Cruz Formation. The specimens from the Alto Río Cisnes are indistinguishable in size (compare measurements above and in Table 2 with Tables 3-5 in Marshall, 1980) and structure from those in the large sample studied by Marshall (1980). This is the smallest species of *Palaeotheres* known from the Alto Río Cisnes.

***Palaeotheres intermedius* Ameghino, 1887**

(Pl. 6, Figs. 10-12; Table 2)

Specimens: MNHN 530, part of a right dentary with complete m2-3 (locality 8); MNHN 543, part of a left dentary with roots of p3, alveoli of m2, and complete m3 (locality 5).

Measurements: Table 2.

Previous known occurrences and age: Known previously only from the Santa Cruz Formation in southern Argentina (see Marshall, 1980, p. 72).

Comments: A systematic revision of *Palaeotheres*

intermedius is given by Marshall (1980, p. 72). This taxon was previously known from about 25 specimens collected from six localities of the Santa Cruz Formation. The two specimens from the Alto Río Cisnes are indistinguishable in size (compare measurements in Table 2 with those in Tables 8-9 in Marshall, 1980) and structure from those studied by Marshall (1980). This is the medium size species of *Palaeotheres* known from the Alto Río Cisnes.

***Palaeotheres lemoinei* Ameghino, 1887**

(Pl. 7, Figs. 1-3; Table 2)

Specimens: MNHN 529, greater part of a right dentary with complete p3 and m3-4, and alveoli of p2, m2

and m5 (locality 8); MNHN 546, part of a left dentary with complete m3 and alveoli of m4 (locality 14).

TABLE 2. MEASUREMENTS (in mm) OF LOWER CHEEK-TEETH OF SPECIES OF *Palaeotheres*

Specimen	P3		M2		M3		M4	
	L	W	L	W	L	W	L	W
<i>P. minutus</i>								
MNHN 531	---	---	2.3	1.2	1.8	1.3	---	---
MNHN 536	---	---	---	1.2	---	---	---	---
<i>P. intermedius</i>								
MNHN 530	---	---	3.3	1.8	2.4	1.9	---	---
MNHN 543	---	---	---	---	2.5	1.9	---	---
<i>P. lemoinei</i>								
MNHN 529	2.2	1.5	---	---	3.5	2.4	2.5	1.9
MNHN 546	---	---	---	---	3.3	2.2	---	---

Measurements: Table 2.

Previous known occurrences and age: Known previously only from the Santa Cruz Formation of southern Argentina (see Marshall, 1980, p. 80).

Comments: A systematic revision of *Palaeothentes lemoinei* is provided by Marshall (1980, p. 80). This species was previously known from about 25 specimens collected from 10 localities in the Santa Cruz Formation. The Alto Río Cisnes specimens are indistinguishable in size (compare measurements in Table

2 with Tables 11-13 in Marshall, 1980) and structure from those monographed by Marshall (1980). This is the largest of the three known species of *Palaeothentes* at the Alto Río Cisnes. The only other species of *Palaeothentes* known from the Santa Cruz Formation which is not represented at the Alto Río Cisnes is *P. aratae* Ameghino, 1887, which is the largest of the four species of this age and is rare (see Marshall, 1980, p. 87).

Family Abderitidae
Genus *Abderites* Ameghino, 1887

***Abderites meridionalis* Ameghino, 1887**
(Pls. 8-10, Table 3)

Specimens: MNHN 507, an isolated right M2 missing anterior root (locality 3); MNHN 508, isolated right M2 missing anterior root (locality 3); MNHN 509, isolated left M2 (locality 3); MNHN 510, isolated right M2 (locality 8); MNHN 511, isolated right M2 (locality 5); MNHN 512 part of right maxilla with worn M2-4 (locality 8); MNHN 513, part of right dentary with complete m3 and alveoli of m4-5 (locality 3); MNHN 514, part of a right dentary with complete m3 (locality 3); MNHN 515,

isolated left m2 (locality 3); MNHN 516, isolated right m3 (locality 8); MNHN 517, isolated right m3 (locality 4); MNHN 518, isolated right m2 (locality 3); MNHN 519, relatively complete left dentary with complete m2-3 and alveoli of m4-5 (locality 5); MNHN 520, part of a right dentary with talonid of m2, m3-4 present but very worn and chipped, and alveoli of m5 (locality 8); MNHN 521, trigonid of a left m2 (locality 3); MNHN 522, greater part of a left I1 (locality 3); MNHN 523, basal

TABLE 3. MEASUREMENTS (in mm) OF CHEEK-TEETH OF *Abderites meridionalis*

Specimen	M2		M3		M4	
	L	W	L	W	L	W
Upper Cheek-Teeth						
MNHN 507	4.3	2.2	---	---	---	---
MNHN 508	4.1	2.2	---	---	---	---
MNHN 509	4.1	2.2	---	---	---	---
MNHN 510	4.5	2.1	---	---	---	---
MNHN 511	4.1	2.2	---	---	---	---
MNHN 512	4.4	2.3	2.8	3.0	2.8	3.0
Lower Cheek-Teeth						
MNHN 513	---	---	3.5	2.4	---	---
MNHN 514	---	---	3.5	2.5	---	---
MNHN 515	4.8	2.1	---	---	---	---
MNHN 516	---	---	3.7	2.7	---	---
MNHN 517	---	---	3.4	2.6	---	---
MNHN 518	5.0	2.2	---	---	---	---
MNHN 519	5.0	2.1	3.5	2.5	---	---
MNHN 520	---	---	3.6	2.8	3.0	2.5
MNHN 521	---	2.1	---	---	---	---
MNHN 542	---	---	3.6	2.7	3.1	2.5

part of a right I1 (locality 3); MNHN 542, part of a right dentary with base of posterior root of m2, complete m3-4, and alveoli of m5 (locality 17); MNHN 544, anterior part of a right dentary with base of I1 followed by four small alveoli (locality 5).

Measurements: Table 3.

Previous known occurrences and age: Known previously only from the Santa Cruz Formation of southern Argentina (see Marshall, 1976d, p. 64). *Abderites?* sp. is also recorded from the Río Frías Formation at Río Senguerr (Bondesio *et al.*, 1980).

Comments: A systematic revision of *Abderites meridionalis* is presented by Marshall (1976d, p. 64). This species was previously known from about 25 speci-

mens collected from seven localities of the Santa Cruz Formation. The specimens from the Alto Río Cisnes are virtually indistinguishable in size (compare Table 3 with Tables 2-3 in Marshall, 1976d) and structure from the sample studied by Marshall (1976d). The only observed difference is that the Alto Río Cisnes specimens tend to have relatively broader trigonids on m3-4 than do the specimens from the Santa Cruz Formation, and that m4 appears to be relatively broader and more robust. However, these differences do not appear to be great nor do they warrant specific recognition, and the Alto Río Cisnes specimens are confidently referred to *Abderites meridionalis*.

Genus *Pitheculites* Ameghino, 1902

Pitheculites rothi sp. nov.

(Pl. 7, Figs. 4-7)

Etymology: *rothi*, named in honor of Santiago Roth, who discovered and first collected fossils from the Alto Río Cisnes.

Type specimen: MNHN 535, part of a left dentary with complete m3-4 and alveoli of m5 (locality 4).

Hypodigm: Type only.

Measurements: m3 L = 1.8 mm, W = 1.3 mm; m4 L = 1.5 mm, W = 1.1 mm.

Diagnosis: Differs from *Pitheculites minimus* in having trigonid and talonid of m3-4 better differentiated due to presence of distinct hypoflexid (trigonid and talonid poorly differentiated in *P. minimus*); in having only two talonid cusps lingually (there are three in *P. minimus*); in having small posterobasal cingulum which encloses a small basin (absent in *P. minimus*); in having two transverse crests (absent in *P. minimus*); and in m4 being distinctly longer than wide (in *P. minimus* m4 is subequal in length and breadth, and nearly quadrate in shape in occlusal view).

Description: Relative to size of the molars the dentary is very deep; masseteric fossa very deep; molars are bunodont and decrease in size (both length and width) from m3 to m5; trigonid and talonid are well differentiated on m3 and m4 by presence of distinct hypoflexid, and are subequal in breadth; on both m3 and m4 trigonid has two labial cusps (posterior one is larger) and one lingual cusp which has a distinct crest extending posteriorly; lingual cusp and posterior labial cusp on trigonid are subequal in size and connected by a transverse crest; talonid has two labial and two lingual cusps which are connate basally, anterior

cusp on labial side is smaller than posterior cusp while two lingual cusps are subequal in size; the posterior labial and posterior lingual cusp on the talonid are connected by a transverse crest, posterior to which is a small basin enclosed by a posterobasal cingulum; m4 differs from m3 in that the three trigonid cusps are closer together, in having a smaller posterior basin which is developed only on lingual side, and in the two lingual talonid cusps being set anterior relative to the two labial cusps (on m3 the labial and lingual cusps are directly across from each other); m5 is two-rooted and smaller than m4.

Comments: A systematic revision of *Pitheculites* is provided by Marshall (1976d, p. 72) which previously was known by a single species, *P. minimus* Ameghino, 1902, represented by six specimens collected from the Colhué Huapi Formation at the Gran Barranca south of Lago Colhué-Huapi in Chubut Province, Argentina, which is the type formation and fauna of the Colhuehuapian Land Mammal Age (see Fext-Fig. 1). *Pitheculites minimus* and *P. rothi* are similar in size (compare measurements of *P. rothi* above with those of *P. minimus* in Marshall, 1976d, Table 4) although the molars of *P. minimus* are shorter and wider than those of *P. rothi*. Other differences between these species are noted in the diagnosis above. All of the features seen in *P. rothi* (*i.e.* trigonid and talonid better differentiated, talonid with only two lingual cusps, molars less quadrate, etc.) indicate that overall this taxon is less derived than *P. minimus*.

DISCUSSION

Forty nine specimens of fossil marsupials were collected from nine localities of the Río Frías Formation along the Alto Río Cisnes in Aisén, southern Chile. The known taxa include representatives of 3 orders, 6 families, 9 genera and 11 species (Table 4). The majority (about 64%) of the 49 specimens are referable to two species: *Abderites meridionalis* (about 38%) and *Microbiotherium tehuelchum* (about 26%). *Palaeothentes minutus* and *Cladosictis patagonica* are each represented by about 8% of the specimens (4 each); *Palaeothentes intermedius* and *P. lemoinei* are each represented by about 4% of the specimens (2 each); while *Sipalocyon gracilis*, *Prothylacynus*

patagonicus, *Borhyaena tuberata*, *Pichipilus halleuxi* and *Pitheculites rothi* are each represented by about 2% of the specimens (1 each). In view of the fact that seven of the species are represented by only 1 or 2 specimens, future collecting will almost certainly result in recovery of additional taxa. Moreover, of the 11 known species, 7 (*Microbiotherium tehuelchum*, *Pichipilus halleuxi*, *Palaeothentes minutus*, *P. intermedius*, *P. lemoinei*, *Abderites meridionalis*, *Pitheculites rothi*) are of small to very small size and these account for about 86% of the marsupial specimens; the other 4 taxa (*Sipalocyon gracilis*, *Cladosictis patagonica*, *Prothylacynus patagonicus*, *Borhyaena tu-*

TABLE 4. SYSTEMATIC LIST OF MARSUPIALS KNOWN FROM THE RIO FRIAS FORMATION ALONG THE ALTO RIO CISNES

Taxon	Known localities (see Text-Fig. 2)	Number of specimens
Order Microbiotheria		
Superfamily Microbiotheroidea		
Family Microbiotheriidae		
<i>Microbiotherium tehuelchum</i>	3, 4, 8, 14, 15	13
Order Sparassodonta		
Superfamily Borhyaenoidea		
Family Hathliacynidae		
<i>Sipalocyon gracilis</i>	13	1
<i>Cladosictis patagonica</i>	1, 3, 8	4
Family Borhyaenidae		
<i>Borhyaena tuberata</i>	3	1
<i>Prothylacynus patagonicus</i>	8	1
Order Paucituberculata		
Superfamily Caenolestoidea		
Family Caenolestidae		
<i>Pichipilus halleuxi</i> sp. nov.	4	1
Family Palaeothentidae		
<i>Palaeothentes minutus</i>	4	4
<i>Palaeothentes intermedius</i>	5, 8	2
<i>Palaeothentes lemoinei</i>	8, 14	2
Family Abderitidae		
<i>Abderites meridionalis</i>	3, 4, 5, 8, 17	19
<i>Pitheculites rothi</i> sp. nov.	4	1

berata) are of medium to large size by marsupial standards and collectively represent only about 14% of the known specimens. Thus, the marsupial fauna from the Alto Río Cisnes is clearly biased in favor of small to very small size taxa, while large size forms are under represented. The medium to large size taxa represent carnivores, while the small to very small size taxa have dental specializations suggesting they were insectivorous and/or omnivorous.

Two new species are recognized: *Pichipilus halleuxi* is referable to a genus known previously from only one species of Colhuehuapian age and two species of Santacrucian age; and *Pitheculites rothi* is referable to a genus known previously by only a single species of Colhuehuapian age. These taxa are of biostratigraphic importance for indicating that the fauna from the Alto Río Cisnes is of Colhuehuapian and Santacrucian aspect. The remaining 9 taxa are indistinguishable from species previously known only from the Santa Cruz Formation of southern Argentina (located 600-800 km S-SE of the Alto Río Cisnes) which is the type formation and fauna of the Santacrucian Land Mammal Age (Text-Fig. 1). The overall taxonomic similarity of the Alto Río Cisnes fauna with that from the Santa Cruz Formation is thus striking, a feature which strongly suggests that it is Santacrucian in age.

Unfortunately, it is not possible to compare directly the Alto Río Cisnes marsupials with those from reputed Friasian age localities in Argentina because marsupials appear to be rare in those faunas and the specimens upon which reports of *Abderites?*, *Palaeotheres*, *Borhyaena?* and *Prothylacynus* have been based (see above) have neither been described nor figured and these identifications remain preliminary. It is important to note that among Tertiary land mammal age faunas in South America, the same species of marsupials have never been reported in sequential ages. This feature and the common occurrence of 9 species between the Río Frías Formation at the Alto Río Cisnes and the Santa Cruz Formation in southern Argentina thus suggest that they are time equivalents, or near so, and are referable to the Santacrucian Land Mammal Age (i.e. 18-15 Ma; Text-Fig. 1). In fact, the presence of *Pichipilus halleuxi* and *Pitheculites rothi* suggests reference to the early part of Santacrucian time (i.e. the Notohipidense horizon, see Marshall and Pascual, 1977).

The possibility that the Alto Río Cisnes fauna is of Santacrucian age is not surprising given the concep-

tual and operational history of the Friasian Land Mammal Age. This age was based on the small and fragmentary collection of fossil mammals made by Santiago Roth from the Río Frías Formation along the Alto Río Cisnes in Chile. The Friasian Land Mammal Age conceptually included faunas that were slightly more progressive in their stage of evolution than those from the Santa Cruz Formation of southern Argentina. Numerous faunas which 'fitted' this concept have been described from Argentina, the taxonomically most abundant of them are from the Collón Curá Formation in the provinces of Río Negro and Neuquén (see above). As a result of numerous active paleontologists in Argentina, the fauna from the Collón Curá Formation has been well sampled and this fauna has come to serve as the operational basis of the Friasian Land Mammal Age. There is thus good evidence based on the Argentine faunas to support the existence of a Land Mammal Age between the Santacrucian and Chasicuan (see Text-Fig. 1). However, the fauna from the Alto Río Cisnes has been virtually ignored for the past 90 years and its absolute age relative to the land mammal sequence in Argentina has remained undocumented. Thus, a Friasian age for the type fauna along the Alto Río Cisnes has been, for these historical reasons, assumed but never securely demonstrated.

At the present time there are numerous ongoing studies of the geology, and geochronology (by J. Flynn, P. Salinas and the author), and vertebrate paleontology (by R. Cifelli, R. Kay, R. Madden, P. Salinas, G.J. Scillato Yané and the author) of the Río Frías Formation along the Alto Río Cisnes. This study on the marsupials is the first of a series of papers that will appear on this formation and fauna, and because of this the conclusions reached here about its age must be regarded as preliminary. Nevertheless, based on knowledge of the marsupials it appears possible that this formation and fauna along the Alto Río Cisnes are of Santacrucian age. If this age assignment is supported by the other ongoing studies, then the Friasian Land Mammal Age (*sensu stricto*) will have to be regarded as a junior synonym of the Santacrucian Land Mammal Age which based on the date of publication has priority.

There are, however, land mammal faunas which are securely of post-Santacrucian and pre-Chasicuan aspect known from the Collón Curá Formation in Argentina, and these are conceptually and operationally equivalent to the 'Friasian' Land Mammal

Age as shown in Text-Fig. 1. The possibility thus exists that the Colloncuran Land Mammal Age (*sensu* Kraglievich, 1930) may warrant recognition in future studies in place of the Friasian Land Mammal Age. If this proves to be true, then the fauna from the Collón Curá Formation at Pilcaniyeu Viejo in Río Negro Province, Argentina, as summarized by Bonde-

sio *et al.* (1980) may serve as the type for the Colloncuran Land Mammal Age. Future studies are needed to clarify the age of known Argentina faunas which are from rocks mapped as the Río Frías and Río Mayo formations. It is possible that at least some of these faunas may prove to be Santacrucian in age.

ADDENDUM

Subsequent to completion of this paper, the author was able to identify another marsupial specimen (MNHN 550) in the collection which consists of a partial right dentary with alveoli of m3-5 (locality 05). This specimen is indistinguishable from *Parabderites bicristatus* Ameghino, 1902 (family Abderitidae, subfamily Parabderitinae) which was previously known only

from rocks of Colhuehuapian and Early Santacrucian age (Notohipidense horizon at Lago Argentino) in Argentina (see Marshall, 1976d; Marshall and Pascual, 1977). The presence of this taxon lends further support for a possible Early Santacrucian age for the vertebrate fauna from the Río Frías Formation along the Alto Río Cisnes.

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REFERENCES

- Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de la Patagonia austral y depositados en el Museo de La Plata. *Museo de La Plata, Boletín*, Vol. 1, p. 1-26.
- Ameghino, F. 1890. Los plagiaulacéidos argentinos y sus relaciones zoológicas, geológicas y geográficas. *Instituto Geográfico Argentino, Boletín*, Vol. 11, p. 143-201.
- Ameghino, F. 1891. Nuevos restos de mamíferos fósiles descubiertos por Carlos Ameghino en el Eoceno inferior de la Patagonia austral. Especies nuevas, adiciones y correlaciones. *Revista Argentina de Historia Natural*, Vol. 1, No. 5, p. 289-328.
- Ameghino, F. 1902. Première contribution à la connaissance de la faune mammalogique des couches à *Colpodon*. *Academia Nacional de Ciencias de Córdoba, Boletín*, Vol. 17, 71-141.
- Ameghino, F. 1904. Nuevas especies de mamíferos cretácicos y terciarios de la República Argentina. *Anales de la Sociedad Científica Argentina*, Vol. 56, p. 193-208 (1903); Vol. 57, p. 162-175, 327-341 (1904); Vol. 58, p. 35-71, 182-192, 225-291 (1904).
- Ameghino, F. 1906. Les formations sédimentaires du Crétacé supérieur et du Tertiaire de Patagonie avec un parallèle entre leurs faunes mammalogiques et celles de l'ancien continent. *Anales del Museo Nacional, Serie 3*, Vol. 15, No. 8, 568 p.
- Archer, M. 1978. The nature of the molar-premolar boundary in marsupials and reinterpretation of the homology of marsupial cheekteeth. *Queensland Museum, Memoirs*, Vol. 18, p. 157-164.
- Bondesio, P. 1986. Lista sistemática de los vertebrados terrestres del Cenozoico de Argentina. Evolución de Vertebrados Cenozoicos. *In Congreso Argentino de Paleontología y Bioestratigrafía, No. 4, Actas*, Vol. 2, p. 187-190. Mendoza.
- Bondesio, P.; Rabassa, J.; Pascual, R.; Vucetich, M.G.; Scillato Yané, G.J. 1980. La Formación Collón-Curá de Pilcaniyeu Viejo y sus alrededores (Río Negro, República Argentina). Su antigüedad y las condiciones ambientales según su distribución, su litogénesis y sus vertebrados. *In Congreso Argentino de Paleontología y Bioestratigrafía, No. 2, y Congreso Latinoamericano de Paleontología, No. 1, Actas*, Vol. 3, p. 85-99. Buenos

- Aires.
- Cabrera, A. 1927. Datos para el conocimiento de los dasiuroideos fósiles argentinos. *Museo de La Plata, Revista*, Vol. 30, p. 271-315.
- Cabrera, A. 1940. Sobre dos grandes mamíferos friasenses. *Museo de La Plata, Notas, Paleontología*, Vol. 5, No. 24, p. 241-250.
- Charrier, R.; Linares, E.; Niemeyer, H.; Skarmeta, J. 1979. K-Ar ages of basalt flows of the Meseta Buenos Aires in southern Chile and their relation to the southeast Pacific triple junction. *Geology*, Vol. 7., p. 436-439.
- Feruglio, E. 1950. Descripción geológica de la Patagonia. *Ministerio de Industria y Comercio Nacional, División General de Yacimientos Petrolíferos Fiscales*, Vol. 3, 431 p. Buenos Aires.
- Frailey, C.D. 1988. The Miocene vertebrates of Quebrada Honda, Bolivia. Part 2. Edentata. *The University of Kansas, Museum of Natural History, Occasional Papers*, Vol. 123, p.1-13.
- González, R.R. 1967. Geología de la región del Lago Blanco y Paso Río Mayo (Chubut). *Acta Geológica Lilloana*, Vol. 9, p. 45-65.
- Hoffstetter, R. 1977. Un gisement de mammifères miocènes à Quebrada Honda (Sud-Bolivien). *Comptes rendus hebdomadaires des séances de l'Académie des Sciences, Séries D*, Vol. 284, p. 1517-1520. Paris.
- Kraglievich, L. 1930. La Formación Friaseana del Río Frías, Río Fénix, Laguna Blanca, etc., y su fauna de mamíferos. *Physis*, Vol. 10, p. 127-161.
- MacFadden, B.J.; Wolff, R.G. 1981. Geological investigations of late Cenozoic vertebrate-bearing deposits in southern Bolivia. *In Congreso Latinoamericano de Paleontología, No. 2, Actas*, Vol. 2, p. 765-778. Porto Alegre.
- Marshall, L.G. 1976a. New didelphine marsupials from the La Venta fauna (Miocene) of Colombia, South America. *Journal of Paleontology*, Vol. 50, No. 3, p. 402-418.
- Marshall, L.G. 1976b. Fossil localities for Santacrucian (Early Miocene) mammals, Santa Cruz Province, southern Patagonia, Argentina. *Journal of Paleontology*, Vol. 50, No. 6, p. 1129-1142.
- Marshall, L.G. 1976c. On the affinities of *Pichipilus orborni* Ameghino, 1890 (Marsupialia, Caenolestidae) from the Santa Cruz Beds of southern Patagonia, Argentina. *Ameghiniana*, Vol. 13, No. 1, p. 56-64.
- Marshall, L.G. 1976d. Revision of the South American fossil marsupial subfamily Abderitinae (Mammalia, Caenolestidae). Museo Municipal de Ciencias Naturales de Mar del Plata 'Lorenzo Scaglia', Publicaciones, Vol. 2, No. 3, p. 57-90.
- Marshall, L.G. 1977. A new species of *Lycopsis* (Borhyaenidae: Marsupialia) from the La Venta fauna (Miocene) of Colombia, South America. *Journal of Paleontology*, Vol. 51, No. 3, p. 633-642.
- Marshall, L.G. 1978. Evolution of the Borhyaenidae, extinct South American predaceous marsupials. *University of California Publications in Geological Sciences*, Vol 117, p. 1-89.
- Marshall, L.G. 1979. Review of the Prothylacyninae, an extinct subfamily of South American 'dog-like' marsupials. *Fieldiana: Geology new series*, Vol. 3, 50 p.
- Marshall, L.G. 1980. Systematics of the South American marsupial family Caenolestidae. *Fieldiana: Geology new series*, Vol. 5, 145 p.
- Marshall, L.G. 1981. Review of the Hathlyacyninae, an extinct subfamily of South American 'dog-like' marsupials. *Fieldiana: Geology new series*, Vol. 7, 120 p.
- Marshall, L.G. 1982. Systematics of the South American marsupial family Microbiotheriidae. *Fieldiana, Geology new series*, Vol. 10, 75 p.
- Marshall, L.G. 1985. Geochronology and land-mammal biochronology of the transamerican faunal interchange. *In The Great American Biotic Interchange* (Stehli, F.G.; Webb, S.D.; editors). *Plenum Press*, p. 49-85. New York.
- Marshall, L.G.; Pascual, R. 1977. Nuevos marsupiales Caenolestidae del 'Piso Notohipidense' (SW de Santa Cruz, Patagonia) de Ameghino. Sus aportaciones a la cronología y evolución de las comunidades de mamíferos sudamericanos. *Museo Municipal de Ciencias Naturales de Mar del Plata 'Lorenzo Scaglia', Publicaciones*, Vol. 2, No. 4, p. 91-122.
- Marshall, L.G.; Pascual, R.; Curtis, G.H.; Drake, R.E. 1977. South American geochronology: radiometric time scale for Middle to Late Tertiary mammal-bearing horizons, Patagonia. *Science*, Vol. 195, p. 1325-1328.
- Marshall, L.G.; Hoffstetter, R.; Pascual, R. 1983. Mammals and stratigraphy: Geochronology of the continental mammal-bearing Tertiary of South America. *Palaeo-vertebrata, Mémoire Extraordinaire*, 93 p.
- Marshall, L.G.; Drake, R.E.; Curtis, G.H.; Butler, R.F.; Flanagan, F.M.; Naeser, C.W. 1986. Geochronology of type Santacrucian (Middle Miocene) land mammal age, Patagonia, Argentina. *Journal of Geology*, Vol. 94, p. 449-457.
- Marshall, L.G.; Case, J.A.; Woodburne, M.O. 1989. Phylogenetic relationships of the families of marsupials. *Current Mammology*, Vol. 2, p. 433-502.
- Marshall, L.G.; Salinas, P. 1990. Stratigraphy of the Río Frías Formation (Miocene), along the Alto Río Cisnes, Aisén, Chile. *Revista Geológica de Chile*, Vol. 17, No. 1, p. 57-87.
- Pascual, R.; Odreman Rivas, O.E. 1971. Evolución de las comunidades de los vertebrados del Terciario Argentino. Los aspectos paleozoogeográficos y paleoclimáticos relacionados. *Ameghiniana*, Vol. 8, Nos. 3-4, p. 372-412.
- Pascual, R.; Bondesio, P.; Scillato Yané, G.J.; Vucetich, M.G.; Gasparini, Z.B. 1978. Vertebrados. *In Geología y Recursos Naturales del Neuquén, Congreso Geológico Argentino, No. 7, Relatorio*, Vol. 1, p. 177-185. Buenos Aires.
- Pascual, R.; Bondesio, P.; Vucetich, M.G.; Scillato Yané,

- G.J.; Bond, M.; Tonni, E.P. 1984. Vertebrados fósiles cenozoicos. In *Geología y Recursos Naturales de la Provincia de Río Negro, Congreso Geológico Argentino, No. 9, Relatorio*, Vol. 2, p. 439-461.
- Patterson, B.; Pascual, R. 1972. The fossil mammal fauna of South America. In *Evolution, Mammals and Southern Continents* (Keast, A.; Erk, F.C.; Glass, B.; editors). *The University of New York Press*, p. 247-309. Albany.
- Ploszkiewicz, J.V.; Ramos V.A. 1977. Estratigrafía y tectónica de la Sierra Payaniyeu (Provincia del Chubut). *Asociación Geológica Argentina, Revista*, Vol. 32, No. 3, p. 209-226.
- Ramos V.A. 1981. Descripción geológica de la Hoja 47ab-'Lago Fontana', Provincia del Chubut. *Servicio Geológico Nacional, Boletín*, Vol. 183, 135 p. Buenos Aires.
- Riccardi, A.C.; Roller, E.O. 1980. Cordillera Patagónica Austral. In *Geología Regional Argentina. Academia Nacional de Ciencias*, Vol. 2, p. 1173-1306. Córdoba.
- Roth, S. 1899. Apuntes sobre la geología y paleontología de los territorios de Río Negro y Neuquén. *Museo de La Plata, Revista*, Vol. 9, p. 141-172.
- Roth, S. 1908. Beitrag zur Gliederung der Sedimentablagerungen in Patagonien und der Pampasregion. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, Vol. 26, p. 119-150.
- Roth, S. 1920. Investigaciones geológicas en la llanura pampeana. *Museo de La Plata, Revista*, Vol. 25, p. 135-313.
- Roth, S. 1925. Investigaciones geológicas en la región norte de la Patagonia durante los años 1897 a 1899. *Museo de La Plata, Revista*, Vol. 27, p. 146-180.
- Simpson G.G. 1971. Clasificación, terminología y nomenclatura provinciales para el Cenozoico mamífero. *Asociación Geológica Argentina, Revista*, Vol. 26, No. 3, p. 281-297.
- Villarroel C.; Marshall, L.G. 1988. A new argyrolagoid (Mammalia: Marsupialia) from the Middle Miocene of Bolivia. *Journal of Paleontology*, Vol. 62, p. 463-467.
- Vucetich, M.G. 1984. Los roedores de la edad Friasense (Mioceno Medio) de Patagonia. *Museo de La Plata, Revista, (Nueva Serie), Paleontología*, Vol. 50, No. 8, p. 47-126.

PLATES 1 - 10

PLATE 1**Figures**

Photographs of the Río Frías Formation along the Alto Río Cisnes showing various vertebrate-bearing localities (see Text-Fig. 2 for reference)

- 1 View looking S-SW from above (north side of) locality 06, showing valley of the Alto Río Cisnes and localities 8, 9 and 12 on the right side of the photo.
- 2 View looking eastward from east bank of Río Cisnes toward locality 1.
- 3 View of locality 4, looking north. The level from which fossil marsupials were collected is indicated by the person in the center of the photo.
- 4 View looking north toward locality 5.
- 5 View looking east across Río Cisnes toward locality 15.

PLATE 1



PLATE 2

Figures

Microbiotherium tehuelchum Ameghino, 1887
p. 23

- 1 - 3 MNHN 524, posterior half of left dentary with complete m3-5 (1. labial; 2. occlusal; 3. lingual views); x 15.
- 4 - 6 MNHN 548, part of left dentary with complete but worn m2-4 (4. labial; 5. occlusal; 6. lingual views); x 15.

PLATE 2

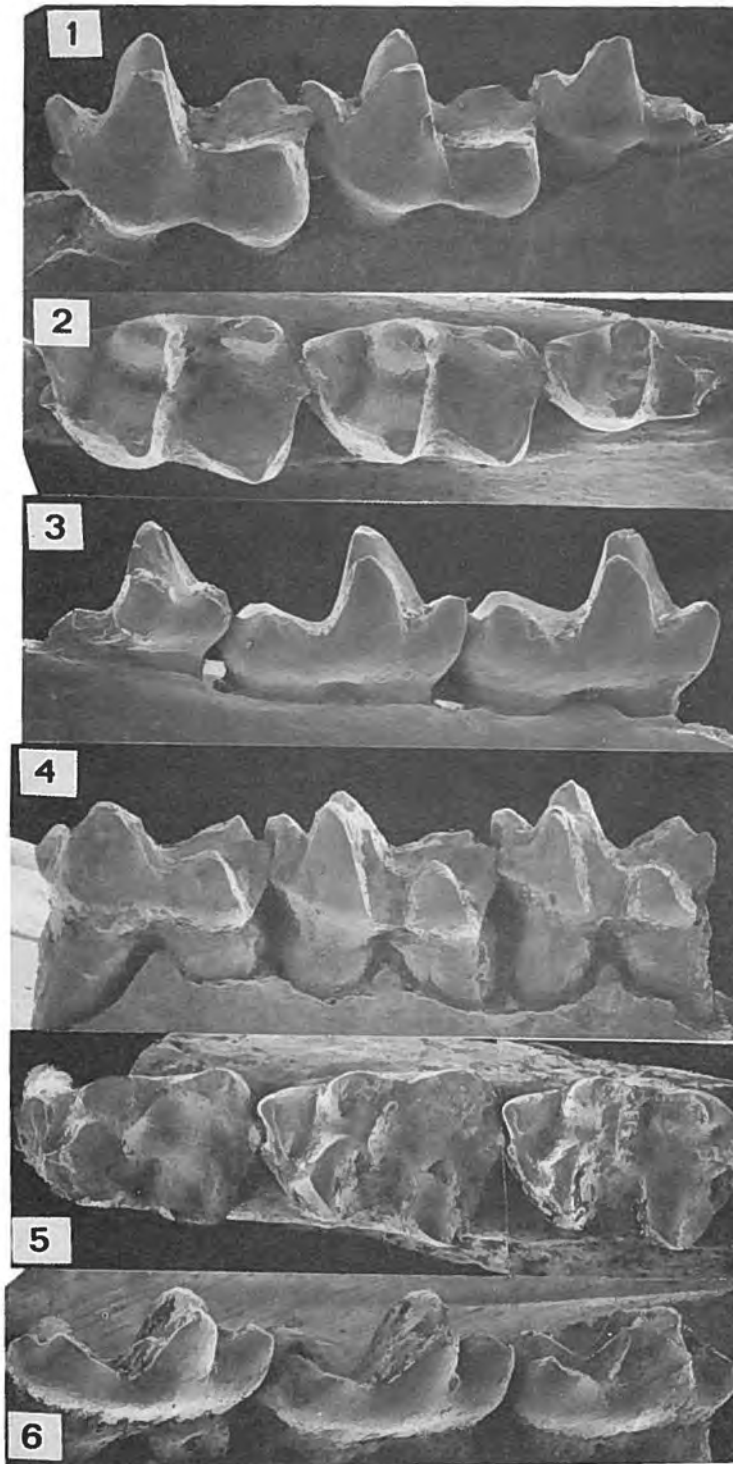


PLATE 3**Figures**

Microbiotherium tehuelchum Ameghino, 1887
p. 23

- 1 - 2 MNHN 527, anterior part of right dentary with alveoli of I1-4 and C, and complete p1-2. (1. occlusal; 2. labial views); x 15.
- 3 - 4 MNHN 545, part of a left dentary with complete C, p1 and p3, and broken base of p2. (3. occlusal; 4. labial views); x 15.

PLATE 3

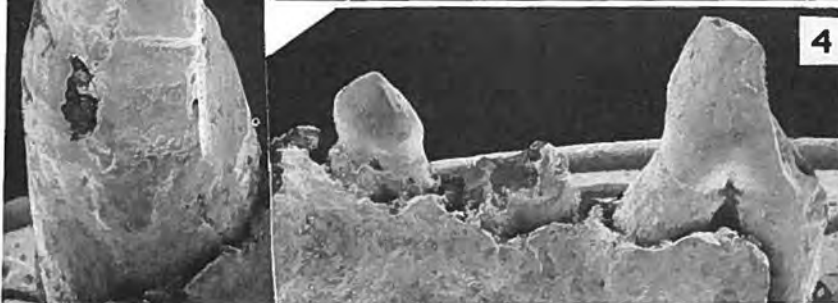
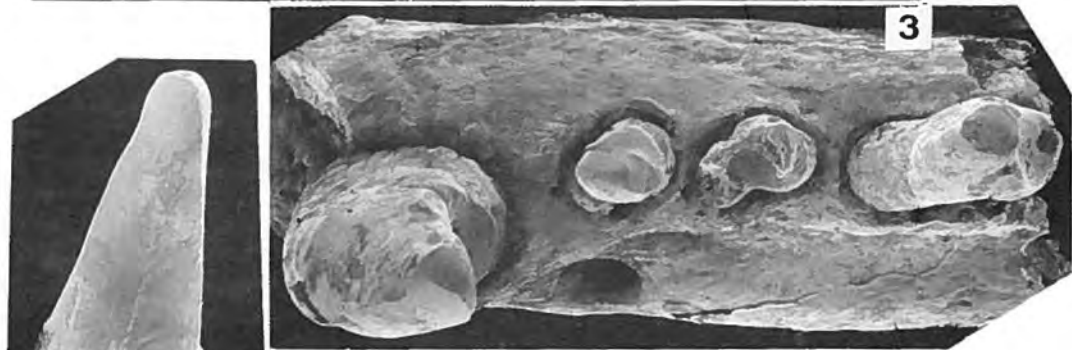
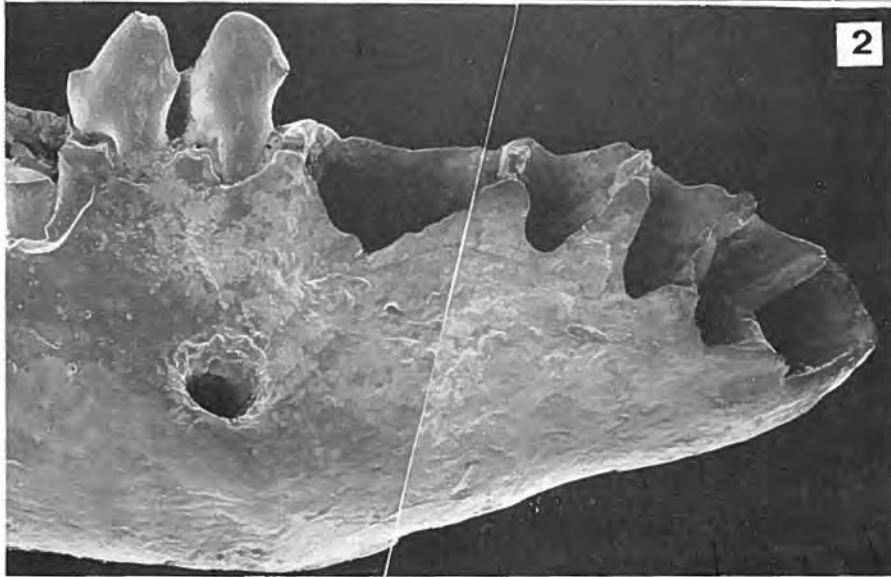
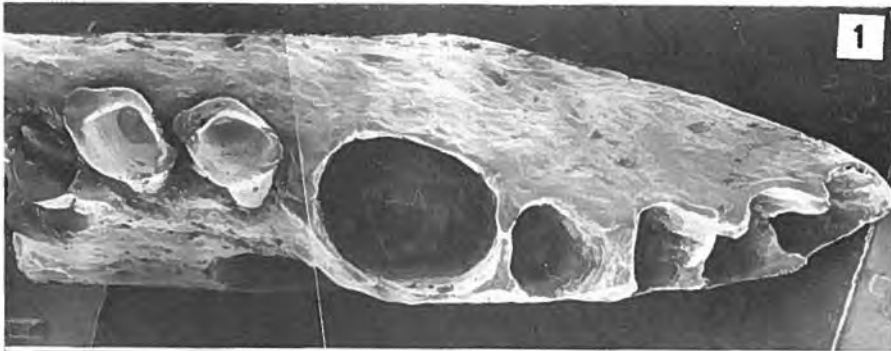


PLATE 4

Figures

- 1 - 2 *Sipalocyon gracilis* Ameghino, 1887. MNHN 541, part of a right maxilla with worn M2-3 and anterior root of M4 (1. occlusal ; 2. lingual views). Stereophotos x 3; p. 24.
- 3 - 4 *Cladosictis patagonica* Ameghino, 1887. MNHN 501, an isolated right m4 missing posterior base of talonid (3. occlusal; 4, lingual views). Stereophotos x 4; p. 24.

PLATE 4

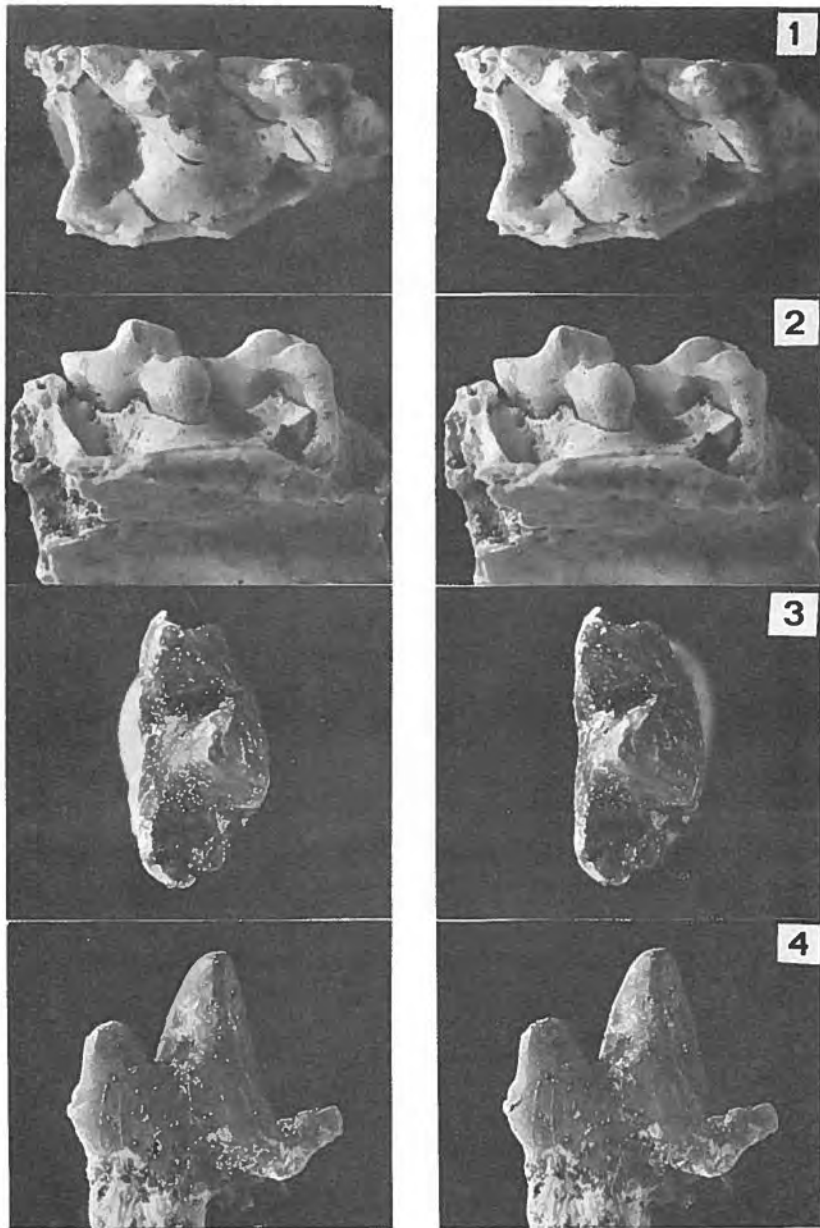


PLATE 5

Figures

- 1 - 2 *Borhyaena tuberata* Ameghino, 1887. MNHN 505, greater part of protoconid and complete talonid of a left **m3** (1. labial; 2. posterior views). Stereophotos x 4; p. 25.
- 3 - 4 *Prothylacynus patagonicus* Ameghino, 1891. MNHN 506, part of right dentary with posterior root of **m2**, base of **m3** (anterior half broken, talonid complete), and roots of **m4** (3. occlusal view, anterior is toward top; 4. labial view, anterior is toward right). Stereophotos x 2; p. 25.

PLATE 5

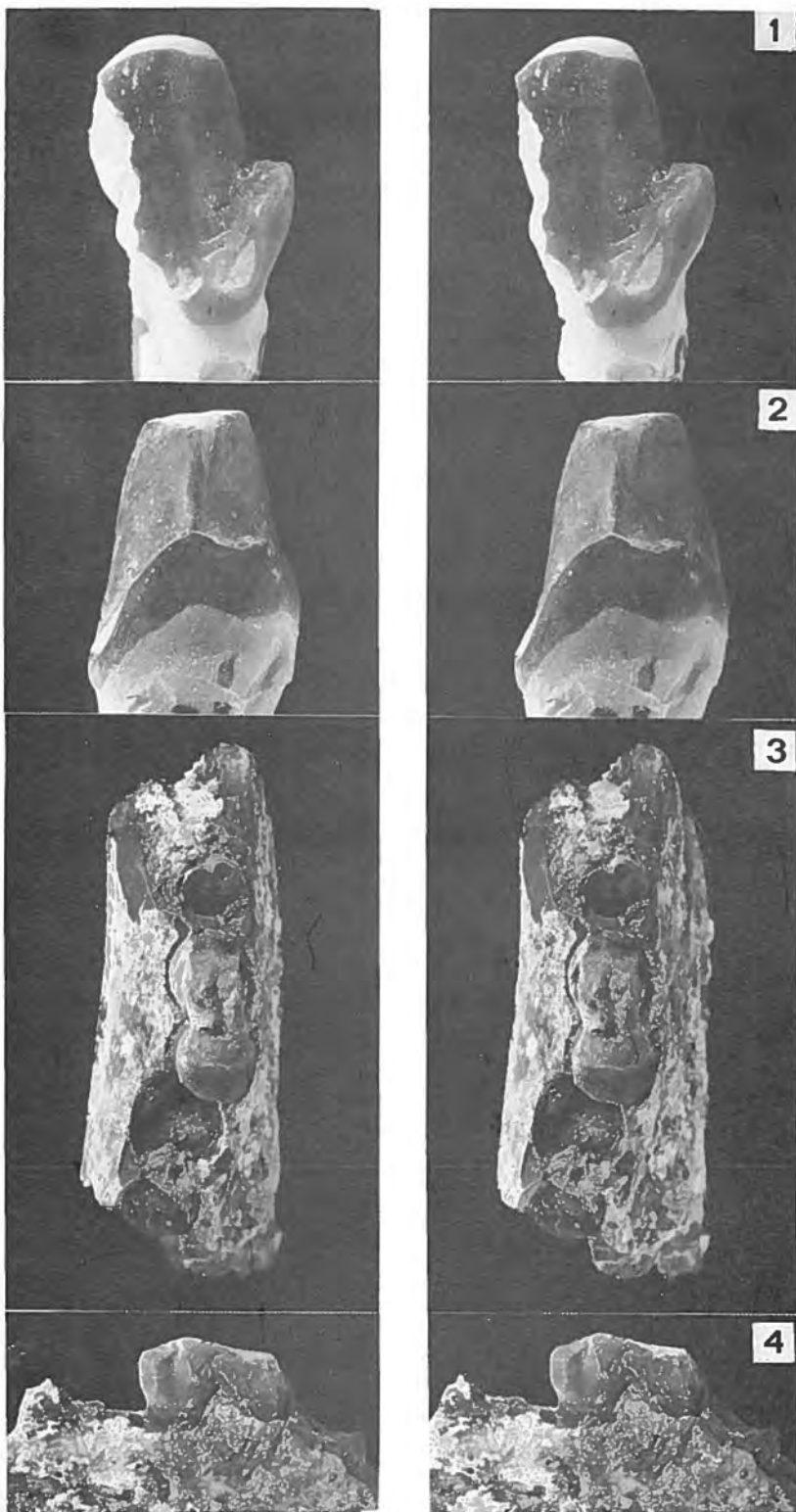


PLATE 6

Figures

- 1 - 3 *Pichipilus halleuxi* sp. nov. MNHN 534 (type), part of a right dentary with posterior half of p3 and complete m2 (1. labial; 2. occlusal; 3. lingual views); x 15; p. 26.
- 4 - 6 *Palaeothentes minutus* Ameghino, 1887. MNHN 531, part of right dentary with complete m2-3 (4. labial; 5. occlusal; 6. lingual views); x 15; p. 27.
- 7 - 9 *Palaeothentes minutus* Ameghino, 1887. MNHN 533, an isolated left complete M2 (7. labial; 8. occlusal; 9. lingual views); x 15; p. 27.
- 10 - 12 *Palaeothentes intermedius* Ameghino, 1887. MNHN 530, part of a right dentary with complete m2-3 (10. labial; 11. occlusal; 12. lingual views); x 15; p. 27.

PLATE 6

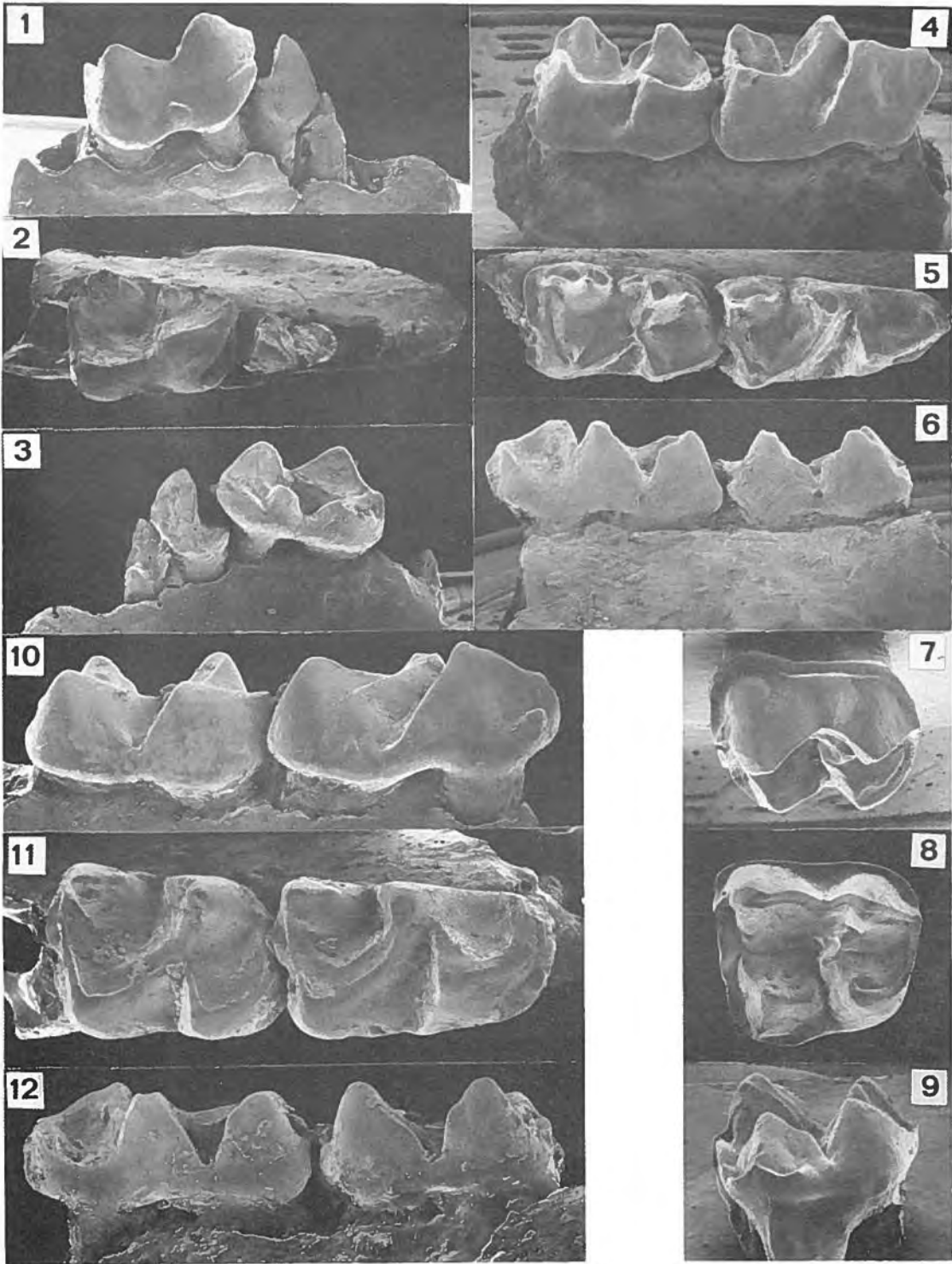


PLATE 7

Figures

- 1 - 3 *Palaeothentes lemoinei* Ameghino, 1887. MNHN 529, right dentary with complete m3-4 (1. labial; 2. occlusal; 3. lingual views); x 15; p. 27.
- 4 - 7 *Pitheculites rothi* sp. nov. MNHN 535 (type), part of left dentary with complete m3-4 and alveoli of m5 (4. labial; 5. lingual; 6. occlusal; 7. posterior views); x 15; p. 29.

PLATE 7

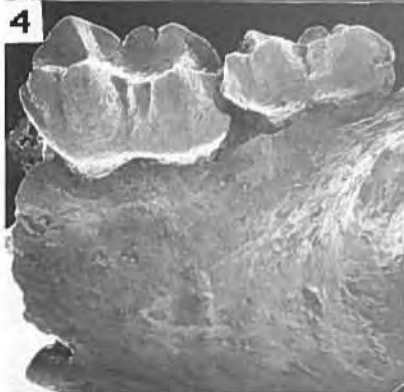
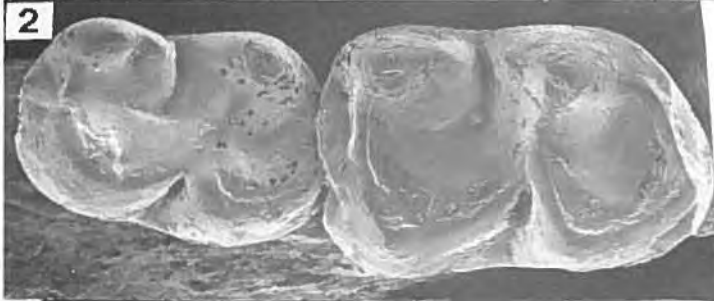


PLATE 8

Figures

Abderites meridionalis Ameghino, 1887
p. 28

1 - 3 MNHN 542, part of right dentary with complete m3-4 (1. labial; 2. occlusal; 3. lingual views); x 15.

PLATE 8

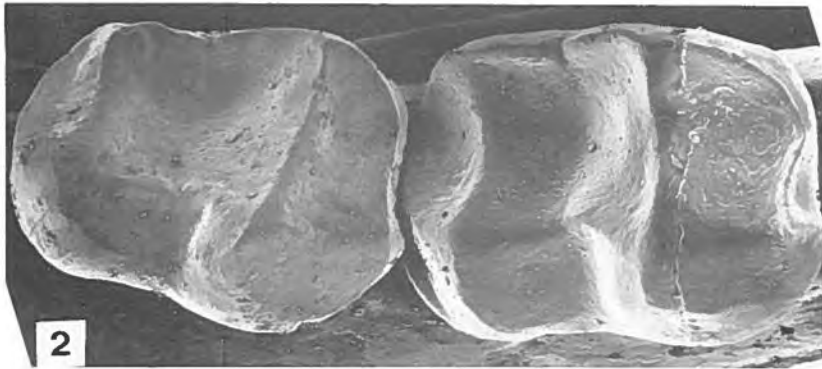
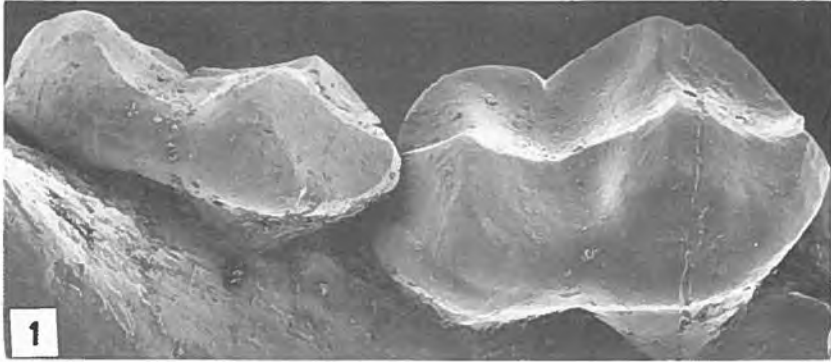


PLATE 9**Figures**

Abderites meridionalis Ameghino, 1887
p. 28

1 - 3

MNHN 519, left dentary with complete m2-3 (1. lingual; 2. occlusal; 3. labial views); x 15.

PLATE 9

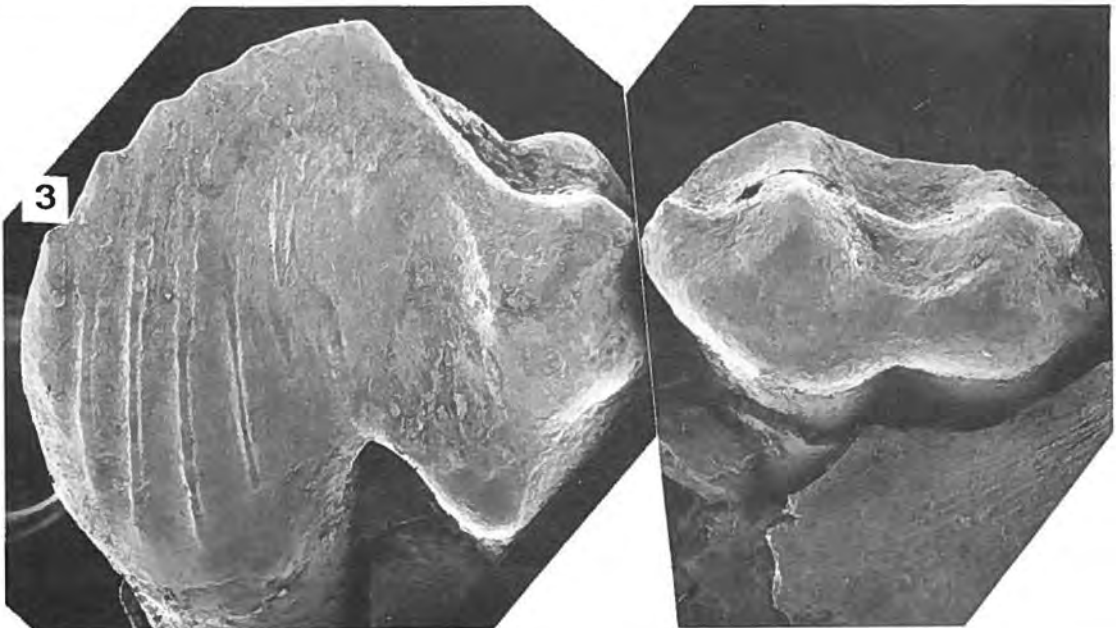
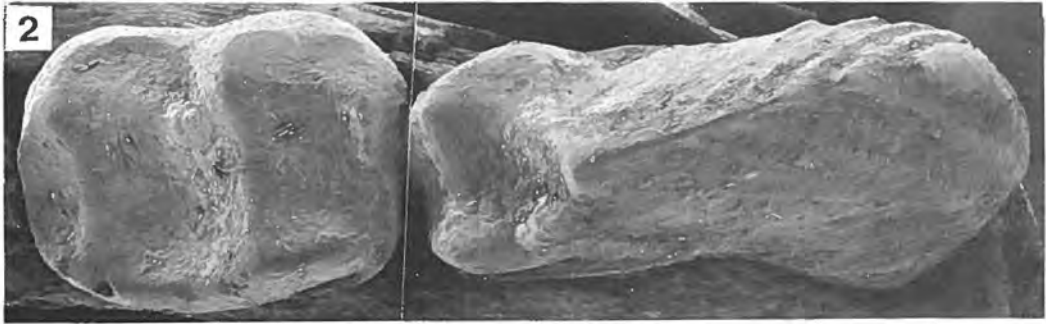


PLATE 10**Figures**

Abderites meridionalis Ameghino, 1887
p. 28

- 1 - 3 MNHN 512, part of right maxilla with worn and slightly broken M2-4 (1. lingual;
2. occlusal; 3. labial views); x 15.

PLATE 10

