FIELDIANA
Geology

Published by Field Museum of Natural History

New Series, No. 3 December 5, 1979

Review of the Prothylacyninae, an Extinct Subfamily of South American "Dog-like" Marsupials

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INTRODUCTION

In South America and Australia marsupials evolved to fill the ecological role of terrestrial mammalian carnivores. On northern continents and Africa these same niches were filled by placental carnivores; first by certain creodonts and members of other orders, and later by members of the Carnivora. These faunal differences are clearly related to the long isolation of the South American continent and to the initial presence of marsupials and absence of placental carnivores.

The South American group which filled this role is classified into two families—the dog-like Borhyaenidae and the saber-tooth Thylacosmilidae (Marshall, 1976a)—in the superfamily Borhyaenoidea. The group is known from beds of Riochican (late Paleocene) through Montehermosan (Pliocene) age. Four subfamilies of Borhyaenidae are recognized: The Hathlyacyninae, which includes small-to-medium-sized omnivores and carnivores which were in part semiarboreal; the Borhyaeninae and Proborhyaeninae, which included large terrestrial carnivores; and the Prothylacyninae, which included both large terrestrial carnivores and omnivores. These subfamilies are distinguished on the basis of a large number of dental and cranial characters (see Marshall, 1978).

Library of Congress Catalog Card No.: 79-51546
ISSN 0096-2651

A review of the Borhyaenidae in general and Borhyaeninae in particular is given by Marshall (1978). The purpose of this paper is to review, in detail, the taxonomic history of the Prothylacyninae, to discuss the possible phylogenetic relationships of the included taxa, and to stabilize the group's taxonomy at the generic and specific levels.

During the course of this study, I was able to examine, firsthand, all pertinent materials, including type and referred specimens. This work includes discussion and description of some new materials, but is essentially based on a reappraisal of previously known specimens and literature. All diagnoses of the subfamily, genera, and species have been revised and enlarged upon those of previous workers. This study represents an attempt to bring together in one place a modern and expanded treatment of these animals, the relationships of which are now better understood only in hindsight and through the pioneering efforts of a multitude of earlier workers.

The fossil localities mentioned below are shown on maps and are discussed in detail in Marshall (1976a, b, c, d; 1977; 1978). The chronology and usage of South American Land Mammal Ages follows Marshall et al. (1977) for the early Tertiary and Marshall et al. (1979) for the later Tertiary.

All measurements are in millimeters (mm).

Abbreviations

Abbreviations used in the text, figure captions, and tables of measurements are as follows: C, canine; ca, approximate measurement; I, incisor; L, length; M, molar; P, premolar; W, width.

The following abbreviations are used for specimens from institutional collections: AMNH, American Museum of Natural History, New York; BM(NH), British Museum (Natural History), London; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires; MLP, Museo de Ciencias Naturales de La Plata, Argentina; MNHN, Muséum National d'Histoire Naturelle, Paris; PU, Princeton University, Princeton, New Jersey; UCMP, University of California Museum of Paleontology, Berkeley.

SYSTEMATICS

Superfamily Borhyaenoidea (Ameghino, 1894) Simpson, 1930

Diagnosis.—Dental formula I0-4/0-3 C1/1 P2-3/2-3 M4/4. Extinct South American "dog and cat-like" marsupials of small-to-large

size. Lack palatal vacuities. Transverse canal either rudimentary or absent. Strong sagittal and nuchal crests. Lunar small and in contact with large magnum. Lacrimal bone extends onto rostrum and usually has large tuberosity developed above lacrimal canal which opens within orbit.

Known range.—Riochican through Montehermosan.

Family Borhyaenidae Ameghino, 1894

Diagnosis.—Dental formula I3-4/2-3 C1/1 P3/3 M4/4. Small-to-large size. Skull dolichocephalic to brachycephalic, rostrum robust and well developed. Upper and lower canines *usually* large, laniary, and with closed roots in adults. Mandibular symphysis typically shallow (may be fused or unfused in adult) and without flange. Mandibular ramus of subequal depth and breadth below molar series, and without distinct labial bend posteriorly along ventral edge as in thylacosmilids. Masseteric fossa usually shallow. Premolars double rooted. Molars increase gradually or rapidly in size from M1/1 to M3/4. Protocone large to very reduced. Paracone often reduced. Paracone and metacone approximated on M^{1-3}. Stylar shelf reduced. Talonids large or reduced, and often imperfectly or not basined. Metaconids often absent; if present always smaller than paraconids. Nasals large and expanded posteriorly. Distinct nasal-lacrimal contact. No postorbital bar. Basicranial and basifacial planes parallel. Basisphenoid and basioccipital processes increase in width posteriorly, neither has a distinct medial keel and both are relatively flat transversely; at suture they form a fairly prominent transverse ridge. Pars petrosa of periotic lacks a tympanic process. Large hypoglossal, postsquamosal and postglenoid foramina present.

Known range.—Riochican through Montehermosan.

Subfamily Prothylacyninae (Ameghino, 1894) Trouessart, 1898

Diagnosis.—Dental formula I4/3 C1/1 P3/3 M4/4. Borhyaenids of medium-to-large size. Mandibular symphysis either ligamentous (*Lycopsis*, *Stylocynus*), or ankylosed (i.e., immovably united) and rami unfused in adult (*Pseudothylacynus*) or tightly fused in adult (*Prothylacynus*). Symphysis extends posteriorly to a point below P_3. Large mental foramen below P_2. Canine moderately developed, usually not large as in Borhyaeninae or Proborhyaeninae; roots closed in adult (not open as in Proborhyaeninae or Thylacosmilidae). Lower premolars with posterobasal cusp (heel), increasing in size from P_1 to P_3. P_1 set obliquely in jaw; P_{2-3} are set straight in jaw. P_3 usually

only moderately well developed, and usually similar in size to M_1. Lower molars increase rapidly in size from M_1 to M_4. Weak anterobasal cingulum on M_{2-4}; absent on M_1. Lower molars, except in *Stylocynus*, lack metaconid. Well-developed talonids on M_{1-3}, M_4 talonid usually reduced. M^{1-3} with large protocone and parastyle. Metacrista moderately well developed. Skull dolichocephalic (*Lycopsis*) or brachycephalic (*Prothylacynus*). Paroccipital process large. No trace of an ossified auditory bulla. Tympanic process of alisphenoid, tympanic process of pars petrosa and epitympanic sinuses lacking. Shallow floccular fossa on periotic. Foramen lacerum medium rudimentary. Foramen lacerum anterium and posterium large. Foramen ovale large (*Prothylacynus*) or small (*Lycopis longirostrus*). Terminal phalanges laterally compressed, sharply pointed, and slightly cleft.

Known range.—Colhuehuapian (late Oligocene) through Huayquerian.

Pseudothylacynus Ameghino, 1902

Pseudothylacynus Ameghino, 1902, p. 127.

Type.—*Pseudothylacynus rectus* Ameghino, 1902.

Distribution.—Colhué-Huapí Formation, Chubut Province, Argentina.

Diagnosis.—As for type and only known species.

Pseudothylacynus rectus Ameghino, 1902. Figures 1, 2; Table 1.

Pseudothylacynus rectus Ameghino, 1902, p. 127.

Type.—MACN 52-369, a nearly complete left mandibular ramus with P_1-M_4.

Hypodigm.—Type and MNHN Col. 5, a left mandibular ramus with P_3-M_4.

Horizon and Locality.—Both specimens are from the Great Barranca south of Lago Colhué-Huapí, Colhué-Huapí Formation, Chubut Province, Argentina. The type was collected by Carlos Ameghino and the MNHN specimen was collected by André Tournouër.

Age.—Colhuehuapian.

Diagnosis.—Medium-sized borhyaenid. Lower premolars increase in size from P_1 to P_3. P_1 set diagonally in jaw at 25° angle relative to rest of tooth row. Tooth row tight but not packed, small diastema

FIG. 1. *Pseudothylacynus rectus* Ameghino, 1902. MACN 52-369 (type), a nearly complete left mandibular ramus with P_1-M_4; **a**, left lateral and **b**, occlusal views. Scale = 5 cm.

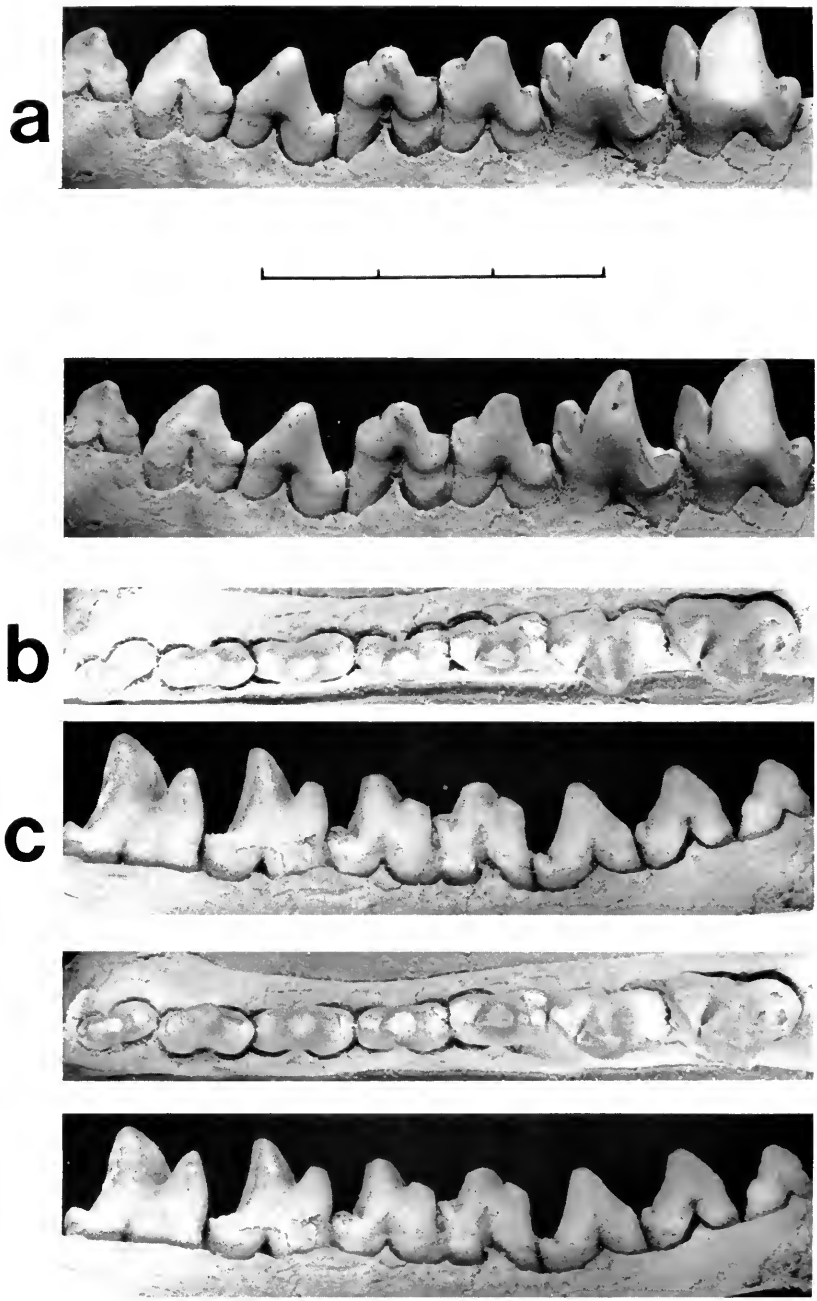

FIG. 2. *Pseudothylacynus rectus* Ameghino, 1902. Stereopairs of MACN 52-369 (type), a nearly complete left mandibular ramus with P_1-M_4: **a**, labial; **b**, occlusal; and **c**, lingual views. Scale = 3 cm.

TABLE 1. Measurements of lower cheek teeth of *Pseudothylacynus rectus*.

Specimen	P1		P2		P3		M1		M2		M3		M4		P_1-M_4	M_{1-4}
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	L
MACN 52-369	6.7	3.0	8.3	3.8	9.9	4.4	8.9	4.5	9.7	5.2	11.3	6.1	12.7	7.1	66.8	41.4
MNHN Col. 5	....	....	....	....	10.0	4.6	9.1	4.7	10.2	5.8	11.8	6.9	12.7	7.3	....	42.7

between C and P_1. Lower molars lack metaconid. Moderately developed talonid on M_{1-3}, basined lingually but cuspate labially. M_4 talonid relatively and absolutely smaller than on M_{1-3} and basined throughout its length (no labial cusp).

Measurements of MACN 52-369, depth of mandibular ramus below labial side of P_3 = 22.5 mm., breadth of same = 10.0 mm.; depth of mandibular ramus below labial side of M_3 = 25.0 mm., breadth of same = 12.0 mm.

Comments.—Pseudothylacynus rectus is possibly involved in the ancestry of *Lycopsis torresi*, but more probably in the ancestry of *Prothylacynus patagonicus.* The principal changes involved in such a lineage include increase in body size and slight reduction in size of talonid and protocone. A detailed discussion of the relationships of these taxa is given in the "Comments" section of *P. patagonicus.* Ameghino (1902, p. 127) was well aware of the similarity of these taxa as he made his comparison of *P. rectus* with *Prothylacynus* in the original description of that species. *Lycopsis* was not recognized as such by Ameghino.

Prothylacynus Ameghino, 1891b

Prothylacynus Ameghino, 1891b, p. 312.

Napodonictis Ameghino, 1894, p. 380.

Prothylacocyon Winge, 1923, p. 67.

Type.—Prothylacynus patagonicus Ameghino, 1891b.

Distribution.—Santa Cruz Formation, Santa Cruz Province, Argentina.

Diagnosis.—As for type and only known species.

Prothylacynus patagonicus Ameghino, 1891b. Figures 3-8; Tables 2-5.

Prothylacynus patagonicus Ameghino, 1891b, p. 312; 1894, p. 380, figs. 47-49; 1898, p. 191, figs. 56, 57a; 1904, p. 21, fig. 9; 1906, fig. 185; Sinclair, 1905, p. 75, pl. II; 1906, p. 372 (with numerous plates and figures); Piveteau, 1961, figs. 21, 22.

Agustylus carnifex Mercerat, 1891, p. 54.

Prothylacynus carnifex Cabrera, 1927, p. 300, figs. 13, 14.

Borhyaena excavata Ameghino, 1894, p. 377 (*partim*).

Prothylacynus brachyrhynchus Ameghino, 1894, p. 380; 1898, p. 189.

Napodonictis thylacynoides Ameghino, 1894, p. 381; 1898, p. 189.

Type.—Prothylacynus patagonicus: MACN 706-720, a nearly

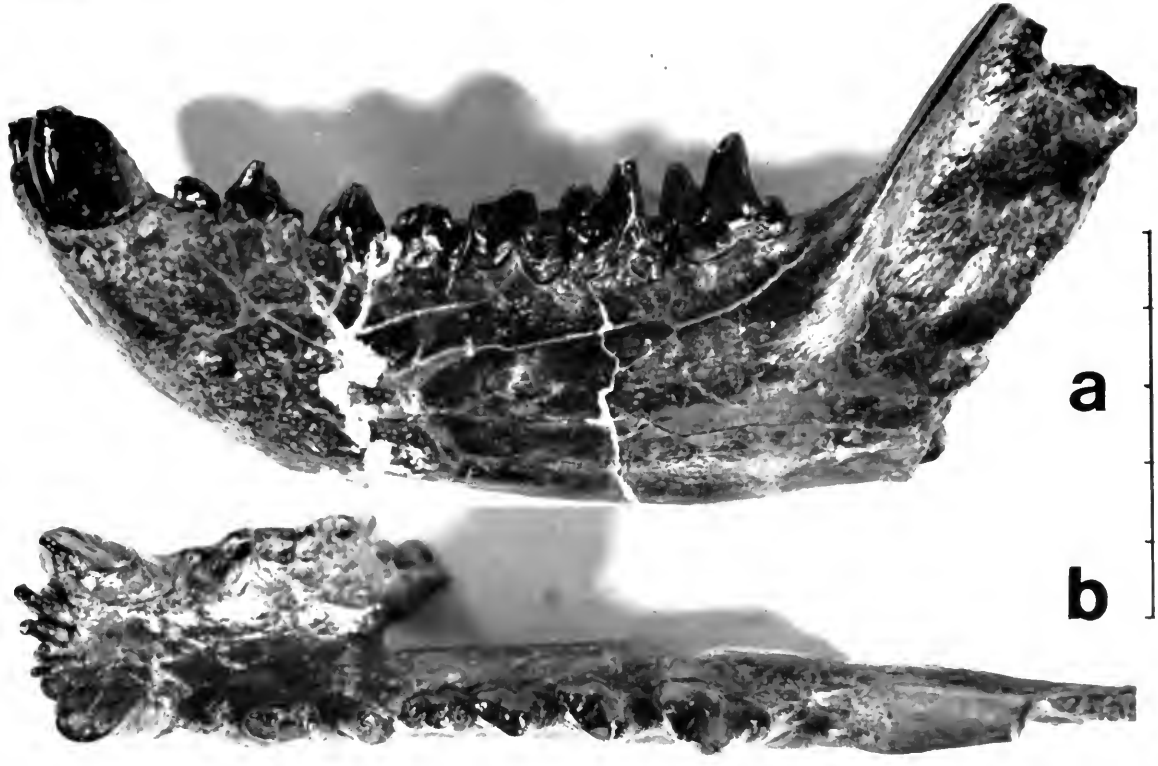

FIG. 3. *Prothylacynus patagonicus* Ameghino, 1891b. MACN 706 (type), a nearly complete left mandibular ramus and attached portion of right symphysis with left I_1-M_4 and right I_1-C: a, left lateral and b, occlusal views. Scale = 5 cm.

complete left mandibular ramus and attached portion of right symphysis with left I_1-M_4 and right I_1-C (706); a left maxillary with M^{1-4} (707); and associated postcranial remains (708-720), all of a single individual. Figured by Ameghino (1894, figs. 47-49; 1898, figs. 56, 57a; 1904, fig. 9; 1906, fig. 185).

Type.—Prothylacynus carnifex: MLP 11-38, a nearly complete mandible with most of dentition present, but broken. Figured by Cabrera (1927, figs. 13, 14).

Type.—Prothylacynus brachyrhynchus: MACN 5926, portion of a mandible with left and right rami fused, with left C, alveoli of P_1, P_2 complete, alveoli of P_3, M_{1-4} complete; and right P_2 complete, alveoli of P_3-M_1, M_{2-4} complete.

Lectotype.—Borhyaena excavata: MACN 649, a right lower canine.

Type.—Napodonictis thylacynoides: MACN 5931-5937, a complete skull with dentition (M^4 and P^3 erupting; 5931); greater part of a broken right mandibular ramus with dentition (M_4 erupting; 5932); and part of an associated and fragmentary skeleton (5933-5937), all of a single individual.

Hypodigm.—The five types and PU 15700, an associated partial skull, mandible, and partial skeleton; MACN 189, a fragment of a right mandibular ramus with roots of M_{2-3}, trigonid and posterior root of M_4; MACN 670, isolated right M^2 missing parastyle; MACN 11640, posterior half of a left and right mandibular ramus, both with M_{2-4} present, but partially broken; MACN 14453, greater part of a skull with most of dentition; AMNH 9561, right maxillary fragment with M^{2-4} (occlusal surfaces of M^{2-3} are heavily worn and small protocone of M^2 and part of that of M^3 are missing); BM(NH) M8075, part of a maxilla with teeth; BM(NH) M9178, posterior part of a mandibular ramus with teeth.

Horizon and Locality.—All specimens are from the Santa Cruz Formation, Santa Cruz Province, Argentina, and their specific localities of collection are as follows: *Monte Observación* MACN 649,

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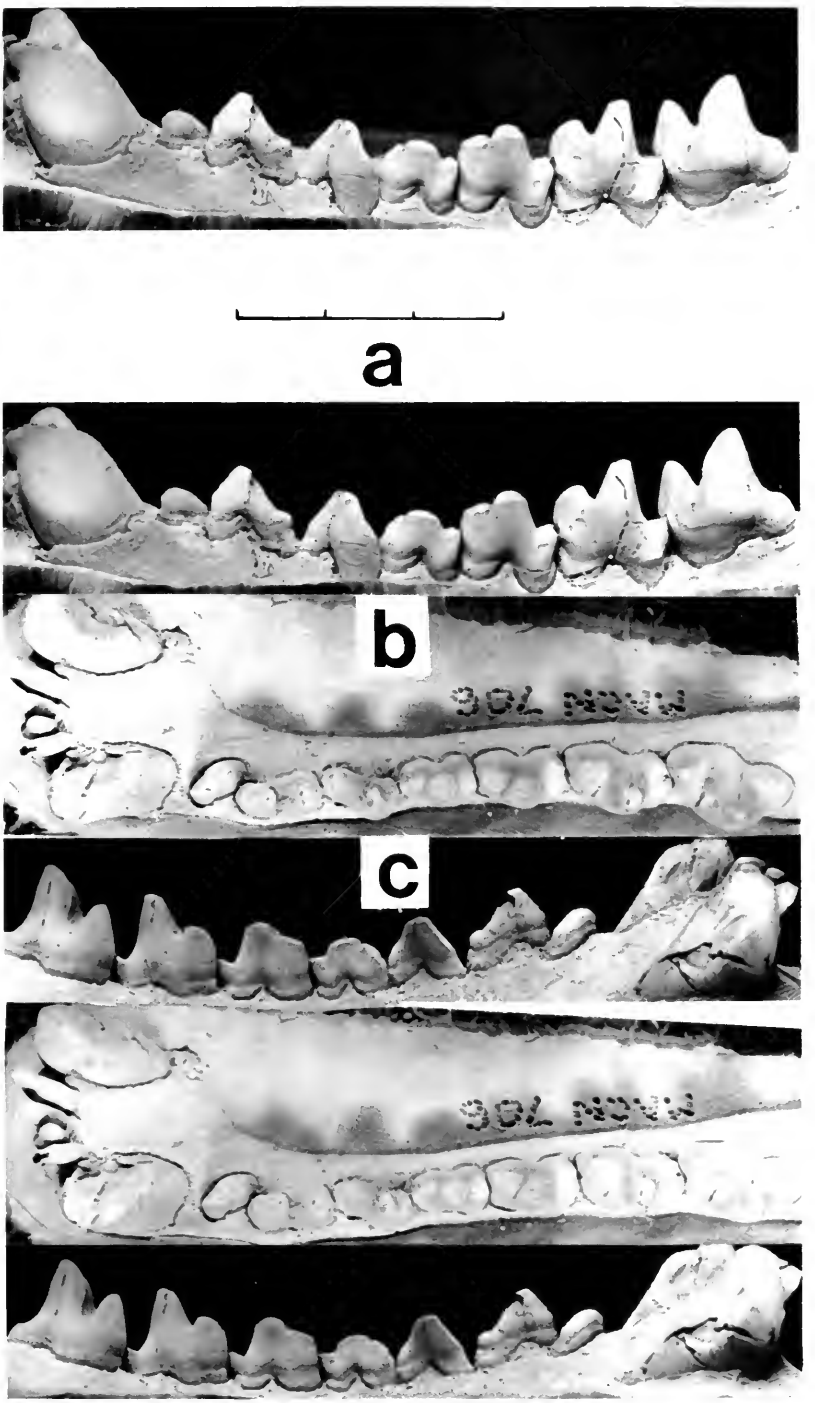
Opposite:

FIG. 4. *Prothylacynus patagonicus* Ameghino, 1891b. Stereopairs of MACN 706 (type), a nearly complete left mandibular ramus and attached portion of right symphysis with left I_1-M_4 and right I_1-C: **a**, labial; **b**, occlusal; and **c**, lingual views. Scale = 3 cm.


a
b
c

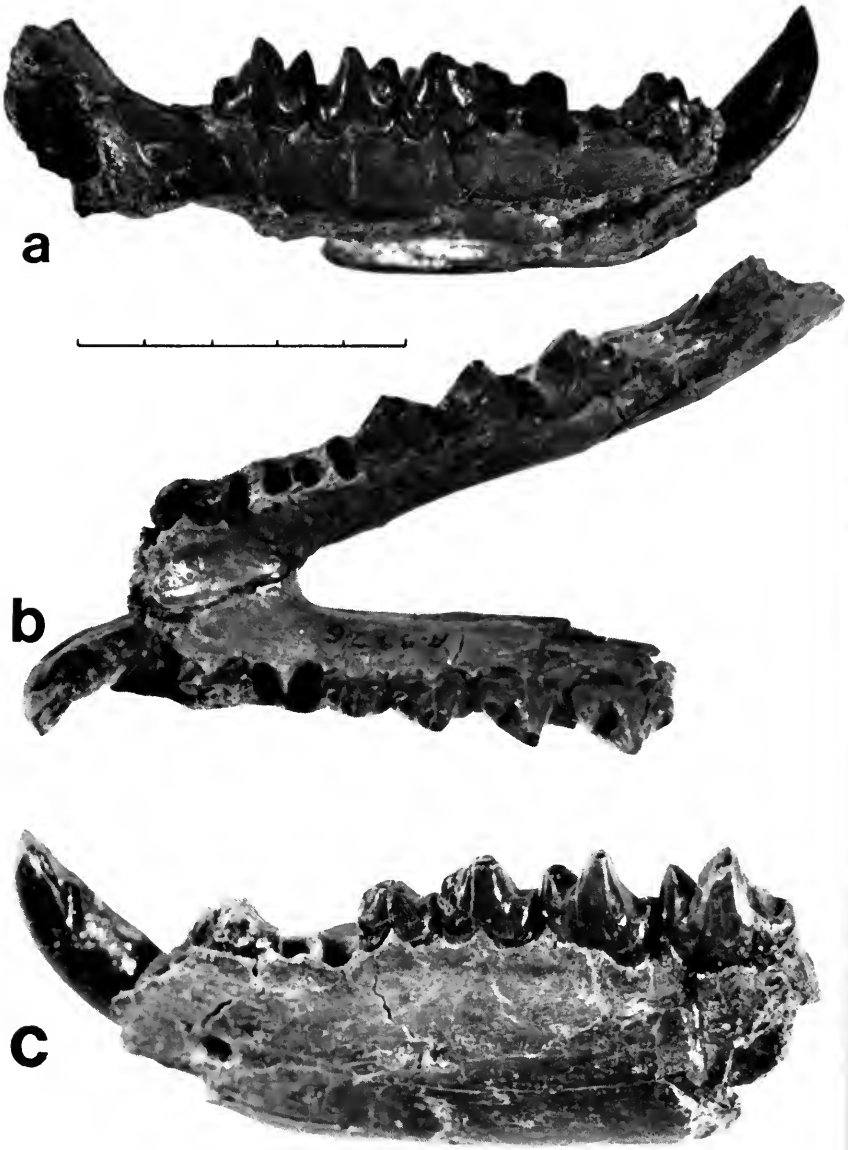


FIG. 5. *Prothylacynus patagonicus* Ameghino, 1891b. MACN 5926, portion of a mandible with left and right rami fused, with left C, alveoli of P_1, P_2 complete, alveoli of P_3, M_{1-4} complete; and right P_2 complete, alveoli of P_3-M_1, M_{2-4} complete: a, right lateral; b, occlusal; and c, left lateral views. Scale = 5 cm.

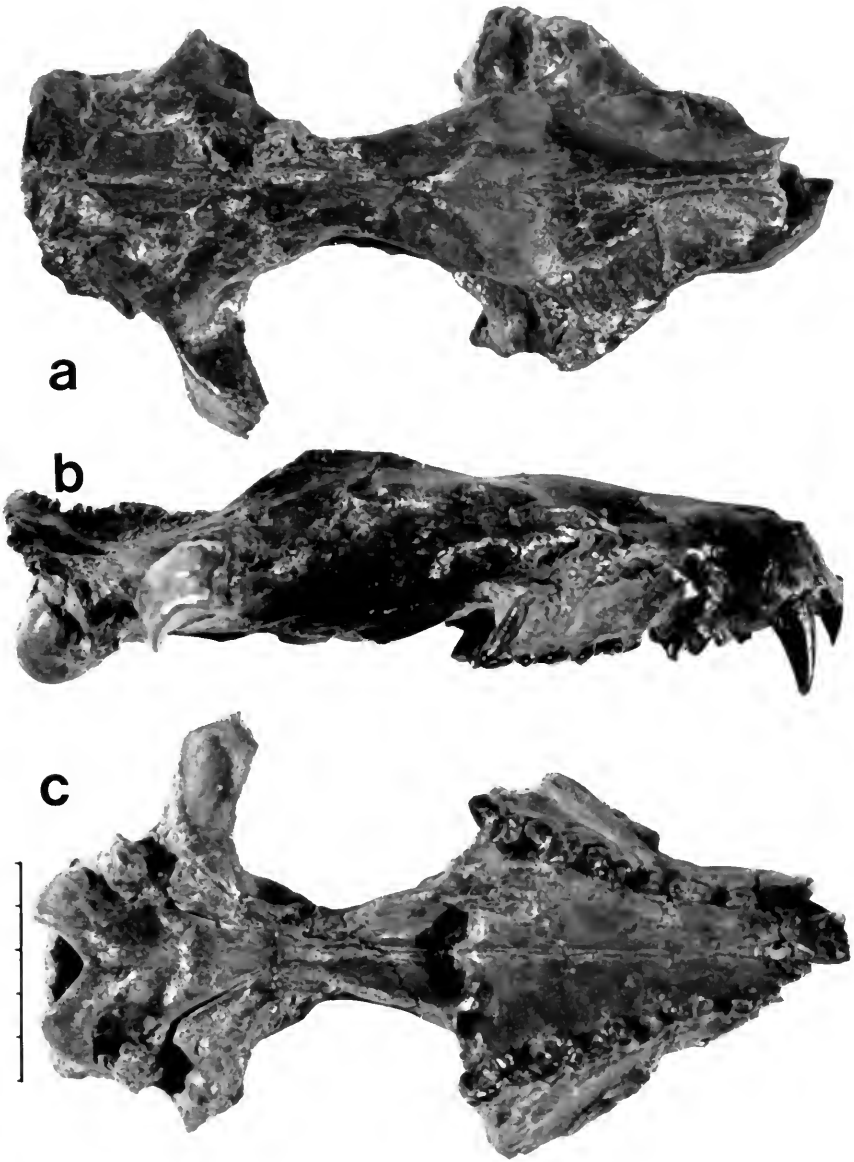


FIG. 6. *Prothylacynus patagonicus* Ameghino, 1891b. MACN 5931, a nearly complete skull of a young adult with most of dentition (M^4 and P^3 are erupting): **a**, dorsal; **b**, right lateral; and **c**, ventral views. Scale = 5 cm.

670 (collected by C. Ameghino 1890-1891); *Corriquen-Kaik* MACN 706-720, 5926, 5931-5937 (collected by C. Ameghino 1890-1891); *Santa Cruz* MACN 189, MLP 11-38; *Cañadón de las Vacas* MACN 14453 (collected by A. Bordas 1941-1942); *Felton's Estancia* BM(NH) M9178 (collected by H. T. Martin in 1903 and sold to BM(NH) in 1905), PU 15700 (collected by J. B. Hatcher in 1896), AMNH 9561 (collected by B. Brown in 1899); MACN 11640 and BM(NH) M8075 (presented by C. Arthur Pearson, June 1902) are without specific locality data.

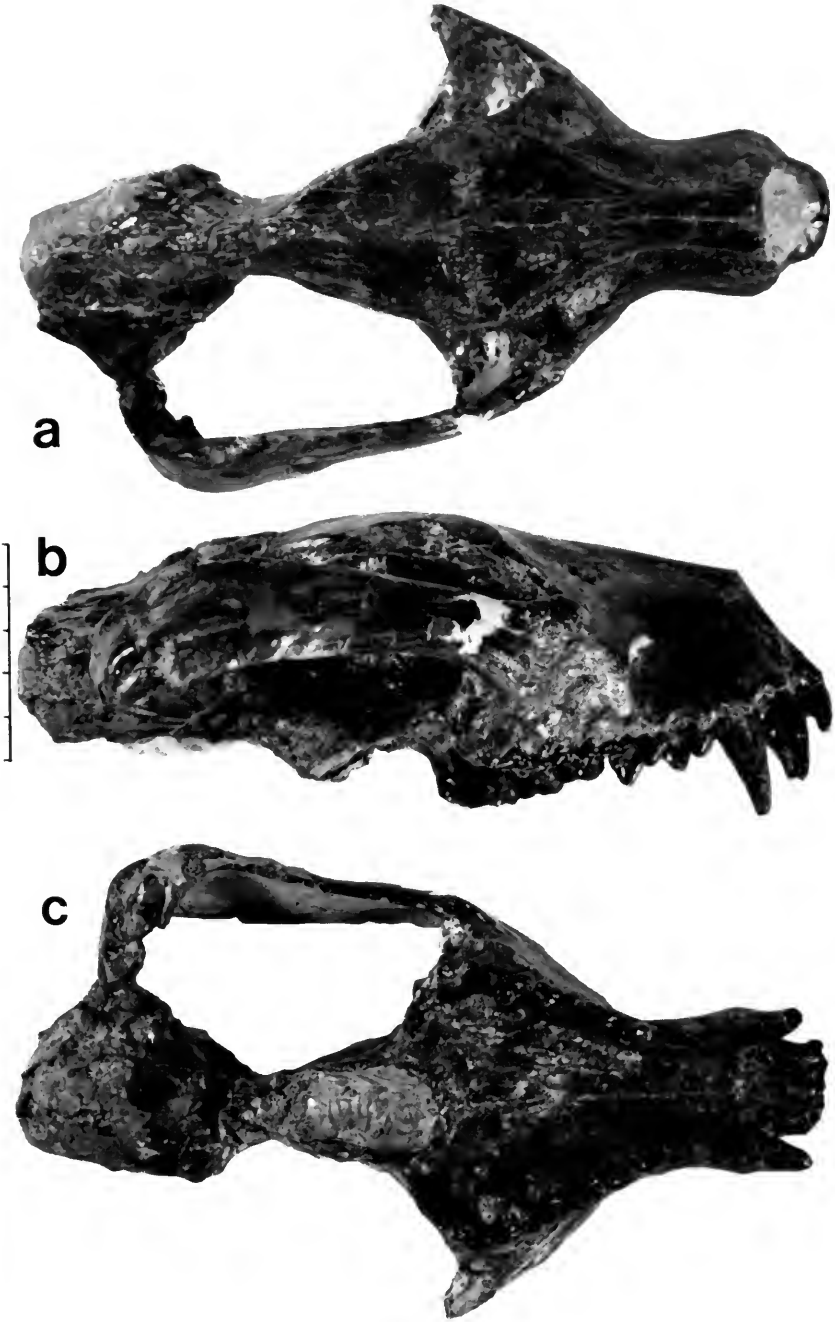
Age.—Santacrucian (early Miocene).

Diagnosis.—Medium-sized borhyaenid. Mandibular symphysis ankylosed and both rami tightly fused in adult. P_1 set at 30° oblique angle relative to rest of tooth row. P_3 large, but not prominent as in species of *Cladosictis* and *Borhyaena*. P_{1-3} relatively shorter and more robust than in other Prothylacyninae. M^{1-3} with large protocone which is cuspate and never basined as in other Prothylacyninae. Skull brachycephalic. Foramen ovale large.

Description.—Symphysis of jaw extends posteriorly to point below P_3-M_1 contact. Lower incisors increase slightly in size from I_1 to I_3. Cheek tooth row relatively short and more packed than in *Pseudothylacynus rectus*. In length $P_1 < P_2 > P_3$, in width $P_1 < P_2 = P_3$. M_{1-4} are proportionately shorter and more robust than in *P. rectus*. M_{1-3} with small to moderately well developed talonid which is flat or slightly cuspate but never basined. Talonid as wide as trigonid on M_{1-2}, narrower on M_3. Small but distinct talonid present on M_4 which is always basined and never cuspate. Weak anterobasal cingula present on M_{2-4}, but not on M_1. Upper incisors increase in size from I^1 to I^4; increase in size from I^1 to I^3 gradually, I^4 much larger than I^3. In length and breadth $P^1 < P^2 < P^3$. Premolars are separated from each other and adjacent teeth by small diastems. P^{1-3} have large posterobasal heel which increases in size from P^1 to P^3 and is best developed on P^{2-3}. P^1 is set obliquely in jaw relative to rest of tooth row. P^{1-3} are markedly shorter and more robust than in other Prothylacyninae but less so than in Borhyaeninae. In length $M^1 < M^2 > M^3$, in width $M^1 < M^2 < M^3$. M^4 protocone reduced but larger than occurs in *Borhyaena tuberata*. No trace of para- or meta-

Opposite

FIG. 7. *Prothylacynus patagonicus* Ameghino, 1891b. MACN 14453, greater part of skull with most of dentition: **a**, dorsal; **b**, right lateral; and **c**, ventral views. Scale = 5 cm.


a
b
c

conules on M^{1-4}. Paracone smaller than metacone and becoming proportionately smaller from M^1 to M^3. Metacone becomes relatively and absolutely larger from M^1 to M^3. Paracone and metacone connate basally. Paracone dominant cusp on M^4. Very large parastyle present on M^{1-3} which is separated from paracone and not connected to it by a paracrista. A distinct ectocingulum is developed posterior to metacone on M^{1-3} which encloses pocket between it and metacrista. Metacrista is well developed and forms major shear surface on M^{1-3}. A small, but distinct, ectoflex is present on M^{2-3} but not on M^1.

Skull is brachycephalic. Infraorbital foramen is rather small (diameter = 9.0 mm.; depth = 4.5 mm. on right side of MACN 14453) and opens over point between P^3-M^1 contact. Anterior edge of orbit extends to point above M^2. Postorbital process weak and poorly defined.

Recess for external auditory meatus is a large shallow U-shaped trough, upper border of which is on line with dorsal edge of occipital condyles; it is bordered posteriorly by a large massive mastoid process, the ventral edge of which reaches a point corresponding to middle of occipital condyle. Ventral edge of mastoid process does not extend forward toward glenoid area of zygomatic arch as in *Lycopsis longirostrus.* No trace of distinct paroccipital process, nor of a tympanic process of alisphenoid. No evidence of an ossified auditory bulla. A rather ill-defined anterior epitympanic sinus is present; no trace of posterior epitympanic sinus.

A large postsquamosal foramen opens directly above dorsal edge of recess for external auditory meatus. A large postglenoid foramen opens onto posterior surface of zygomatic arch just behind and at medialmost edge of postglenoid process near anterodorsal edge of recess for external auditory meatus. A large hypoglossal foramen opens just medial to each occipital condyle, and a very tiny foramen occurs 4.0 mm. anteromedial to latter. A large foramen ovale opens within alisphenoid midway between innermost edge of postglenoid process and outer edge of basioccipital-basisphenoid contact. A very tiny foramen lacerum medium opens 14.5 mm. anteromedial to foramen ovale. Body of petrosal is bulbous and pea-shaped on outer

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Opposite:

FIG. 8. *Prothylacynus patagonicus* Ameghino, 1891b. Stereopairs of MACN 707 (type), a left maxillary with M^{1-4}: **a**, labial; **b**, occlusal; and **c**, lingual views. Scale = 3 cm.

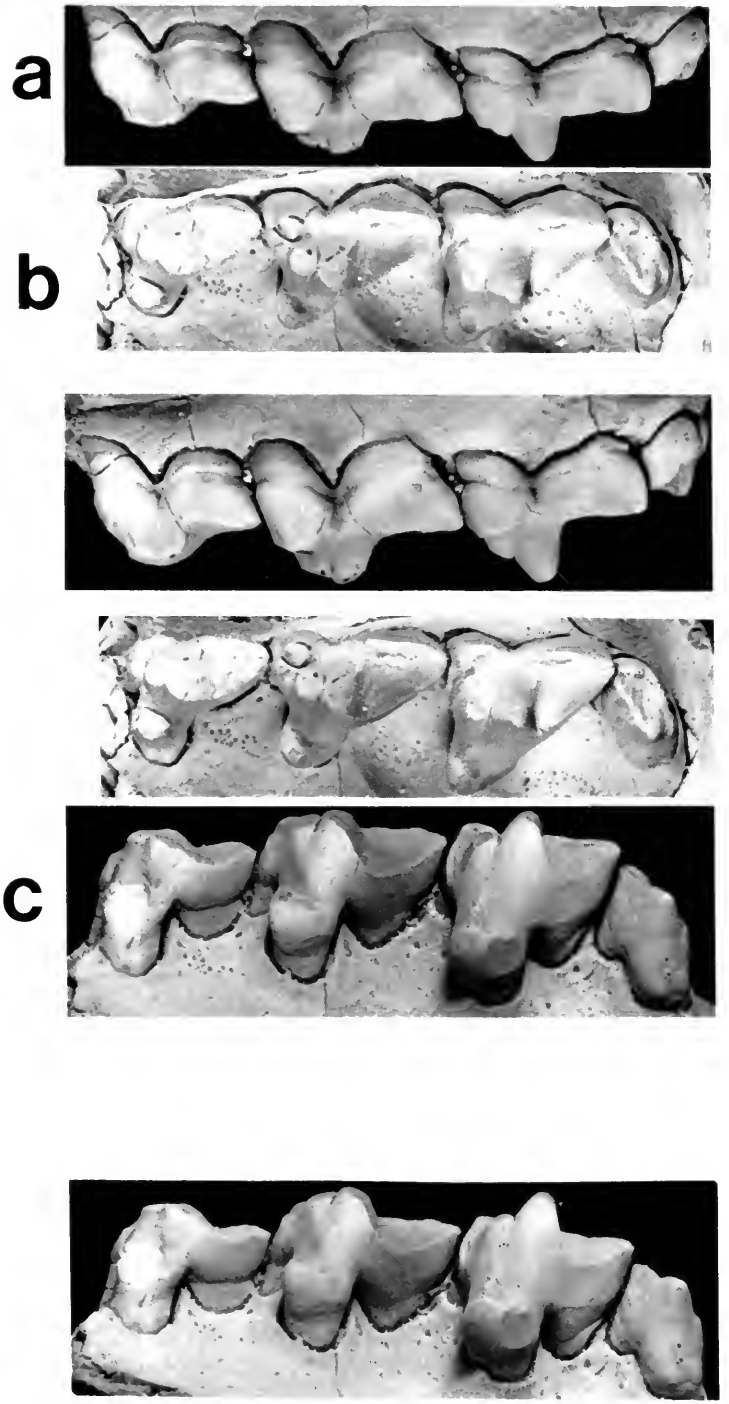

a
b
c

TABLE 2. Measurements of skull of *Prothylacynus patagonicus* (in mm.).

Measurement	MACN 5931	MACN 14453
Anterior edge of incisors to posterior edge of occipital condyles	171.0	....
Anterior edge of incisors to posterior edge of secondary palate	83.0	90.0
Interorbital breadth between postorbital processes	39.5	42.0
Maximum combined transverse breadth of occipital condyles	42.0	....
Maximum dorso-ventral depth of occipital condyles	19.5	....
Internal breadth between mastoid processes	32.5	....
Maximum width of rostrum immediately anterior to infraorbital foramen	....	34.0
Transverse breadth of palate between canines	....	19.0
Transverse breadth of palate between M^4's	....	48.0
Ventral edge of occipital condyle to dorsal edge of nuchal crest	....	39.5
Maximum transverse breadth of nuchal crest at level of occipital condyles	....	55.0

surface; a tiny, but distinct, tympanic process is present. Basioccipital and basisphenoid are relatively flat transversely; they lack a distinct medial keel, progressively increase in width posteriorly, and at their contact form a fairly prominent transverse ridge. Posterior carotid foramina and foramen lacerum posterius open into ear region between basioccipital and petrosal. Alisphenoid-squamosal suture lies along innermost edge of glenoid fossa.

Measurements of upper canines: left side of MACN 14453, height of crown = 22.0 mm.; anteroposterior diameter of base of crown = 11.0 mm.; transverse breadth of base of crown = 8.0 mm. Measurements of lower canines: anteroposterior diameter of base of crown in MACN 706 = 12.0 mm., MACN 5926 = 9.5 mm., MACN 649 = 12.2 mm.; transverse breadth of base of crown in MACN 706 = 8.0 mm., MACN 5926 = 7.8 mm., MACN 649 = 8.8 mm.

TABLE 3. Measurements of upper cheek teeth of *Prothylacynus patagonicus*.

Specimen	P^1		P^2		P^3		M^1		M^2		M^3		M^4		P^1-M^3	M^{1-3}
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	L
MACN 707	....	....	....	....	....	....	10.8	8.0	13.0	10.2	12.5	12.2	9.8	4.8	....	36.0
MACN 5931 (l)	5.7	3.3	9.1	4.7	....	....	10.5	7.8	12.6	10.1	13.1	11.0	9.5	4.6	61.5	36.4
MACN 5931 (r)	5.5	3.0	9.0	4.5	....	....	10.8	7.7	12.9	10.1	13.0	11.1	....	....	61.3	36.6
MACN 14453 (l)	....	....	8.2	4.3	8.6	4.6	9.8	6.9	11.7	9.0	12.5	11.5	10.8	5.3	59.0	33.8
MACN 14453 (r)	....	....	8.0	4.1	8.6	4.4	9.9	6.7	11.7	8.9	12.2	11.2	....	....	58.6	34.0
AMNH 9561	....	....	....	....	....	....	....	....	11.9	ca. 9.0	12.1	11.1	9.3	5.2	....	....

TABLE 4. Measurements of lower cheek teeth of *Prothylacynus patagonicus*.

Specimen	P_1		P_2		P_3		M_1		M_2		M_3		M_4		P_1-M_4	M_{1-4}
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	L
MLP 11-38 (l)	....	....	....	....	....	....	9.0	....	10.8	....	12.6	....	14.0	7.6	ca. 72.0	47.3
MACN 706	6.2	3.1	9.5	5.0	9.3	5.0	8.9	5.3	10.9	6.2	12.7	6.9	15.0	8.4	72.5	47.5
MACN 5926 (l)	....	....	....	....	....	....	9.4	5.5	11.3	6.2	12.7	7.2	15.0	8.5	....	49.5
MACN 5926 (r)	....	....	9.5	5.0	....	....	....	....	11.1	6.2	12.5	7.1	14.6	8.6	....	....
MACN 11640 (l)	....	....	....	....	....	....	....	....	9.5	5.5	11.0	6.5	13.2	7.8	....	....
MACN 11640 (r)	....	....	....	....	....	....	....	....	....	....	11.1	6.4	....	7.6	....	....

TABLE 5. Measurements of mandibular ramus of *Prothylacynus patagonicus*.

Specimen	Depth of ramus below labial side of M1	Breadth of same	Depth of ramus below labial side of M4	Breadth of same
MACN 189	....	....	28.0	10.2
MACN 706	28.0	12.5	31.0	13.3
MACN 5926 (l)	26.2	12.0	....	....
MACN 11640 (l)	....	....	28.0	11.3
MACN 11640 (r)	....	....	28.6	10.9

Comments.—All of Ameghino's figures of *Prothylacynus patagonicus* are based on the holotype, MACN 706-720. MACN 706, a nearly complete left mandibular ramus, was figured by Ameghino (1894, figs. 47, 48; 1898, fig. 56; 1904, fig. 9; 1906, fig. 185). Although he figured (1894, fig. 48; 1898, fig. 56) this specimen as a complete mandible, he does not mention that the right ramus was ever complete. The right ramus was apparently restored in these figures by making a mirror image of the complete left ramus. The left maxillary fragment of the type, MACN 707, containing M^{1-4} was figured by Ameghino in 1894 (fig. 49) and 1898 (fig. 57a).

Ameghino (1894, p. 380) distinguished "*Prothylacynus brachyrhynchus*" (type, MACN 5926) from *P. patagonicus* in being a little smaller in size and proportionately more massive in structure; in having smaller lower canines which almost contacted, leaving little room for the incisors which "must have been" rudimentary; and in the transverse placement of the P_1. The canine of MACN 5926 is certainly smaller than that in the type of *P. patagonicus*, although these differences are not excessive and they surely represent no more than individual variation. Ameghino's reference to the smaller size of "*P. brachyrhynchus*" can only be applied to the canine, as in all other features this specimen is as large as or larger than the type of *P. patagonicus* (table 4). Ameghino's comment that the incisors "ought" to be rudimentary is only an assumption, as neither the incisors nor their roots or alveoli are preserved in this specimen.

The specific name "*brachyrhynchus*" was surely applied in reference to the short massive nature of the jaw and crowding of the anterior cheek teeth. Both of these features are alluded to by Ameghino, but neither is real. The anterior edge of the mandible, including the incisor alveoli and left canine alveolus, was broken off MACN 5926 and lost. When the left canine was restored onto the specimen, it was placed in the vacuity left by this missing portion of the jaw, and now the canine lies in the area originally occupied by

the anterior root of the P_1. The canine is thus very close to the P_2, giving the jaw the "brachyrhynchus" appearance; an artificial feature and the result of erroneous restoration.

"*Agustylus carnifex*" was erected by Mercerat (1891, p. 54) on the basis of a nearly complete, but poorly preserved mandibular ramus, MLP 11-38. Ameghino (1894, p. 380) recognized this species as a junior synonym of *P. patagonicus.* Cabrera (1927, pp. 300-301, figs. 13, 14), however, redescribed and first figured MLP 11-38, recognizing it as a valid species of *Prothylacynus.* He called attention to the fact that "*P. carnifex*" was smaller than *P. patagonicus*, it had a more reduced M_4 talonid, and the symphysis was longer. He further noted that all of these features agreed with "*P. brachyrhynchus*" which he seems to have regarded as a synonym of that species, but he is not clear on this matter.

The characters used by Cabrera to support his claims are all attributable, in large part, to the poor state of preservation of MLP 11-38. The symphysis is long and low because its ventral edge has been removed by erosion, and there is matrix surrounding the symphysis, giving it a superficially elongated appearance. Similarly, the M_4 talonid, although small, is covered by matrix and is not really absent. In size, this specimen agrees well with dimensions of the type of *P. patagonicus* (table 4), although it does tend, on the whole, to be somewhat smaller. There is little doubt, however, that "*A. carnifex*" is referable to *P. patagonicus.*

The only character used by Ameghino (1894, p. 381) to distinguish "*Napodonictis thylacynoides*" from *P. patagonicus* was that in the former the M^4 had "el talón interno mucho más reducido." He later (1898, p. 189) noted that "*N. thylacynoides*" and *P. patagonicus* were very similar, but again called attention to differences in morphology of the M^4.

The M^4 of the type of *P. patagonicus* (MACN 707) is slightly longer and wider than the type (MACN 5931-5937) of "*N. thylacynoides*" (table 3). Morphologically, however, these elements are identical and I can find no trace of the unique features alluded to by Ameghino. Considering the fact that these specimens agree perfectly in all other respects, there is little problem in recognizing them as synonymous.

The only other specimen referrable to *P. patagonicus* for which there exists a prior literature reference, is a syntype of "*Borhyaena excavata.*" This "species" was erected by Ameghino (1894, p. 377) on four specimens: MACN 649, a nearly complete left lower canine;

MACN 650, part of a left mandibular ramus with two molars; MACN 651, a right lower canine; and MACN 652, part of an M_4. All are listed in Ameghino's catalogue in the MACN as belonging to "*B. excavata*," the first three are labeled "TIPO," and are specifically referred to in his original description of that "species." MACN 649, which is hereby designated as lectotype, is referrable to *P. patagonicus*. MACN 650 and 652 could not be located in the MACN collection and their precise identifications are thus not definitely known. MACN 651 is referrable to *Borhyaena tuberata* (Marshall, 1978, p. 50).

Prothylacynus patagonicus is very similar to the Colhuehuapian species *Pseudothylacynus rectus*. The principal features shared by these species include: relative proportions of jaw, canine, and cheek tooth row; P_1 notably smaller than P_{2-3} and set obliquely in jaw; P_{1-3} with a posterobasal heel which increases in relative size from P_1 to P_3; M_{1-3} with small to moderately well-developed talonid and M_4 with much smaller talonid; and with a weak anterobasal cingulum on M_{2-4}, but absent from M_1.

The principal differences between these species include: *P. patagonicus* being larger in size; cheek tooth row being more crowded and with P_1-M_4 being proportionately shorter and more robust; P_1 being relatively smaller than P_{2-3} and set more obliquely in jaw; talonids on M_{1-4} being smaller relative to trigonids and never incipiently basined but flat or slightly cuspate; M_4 talonid being very reduced but distinctly basined as in *P. rectus*; and mandibular symphysis being ankylosed and with both rami solidly fused in the adult.

Individually,these differences are not excessive and there are no characters in *P. rectus* which would exclude it as a direct ancestral form of *P. patagonicus*. In fact, most of the features by which they differ are either incipiently developed in *P. rectus*, or are developed to different degrees in both species. An ancestral-descendant relationship for these species appears probable.

Lycopsis Cabrera, 1927

Lycopsis Cabrera, 1927, p. 295.

Type.—*Lycopsis torresi* Cabrera, 1927, p. 295.

Distribution.—Santa Cruz Formation, Argentina; and "Monkey Unit" of Honda Group, Colombia.

Diagnosis.—Medium to large in size. Protocone large and deeply basined on M^{1-3}, slightly smaller on M^4. Paracone becomes smaller

from M^1 to M^3; metacone becomes relatively, and absolutely, larger than paracone from M^1 to M^3. Upper molars virtually lack stylar shelf; ectocingulum is present labial to paracone; parastyle is large; ligamentous mandibular symphysis, unfused in adult; protoconid trenchant and about twice as high as paraconid. Talonid basin large on M_{1-3}, small on M_4. P1 has slight oblique implantation labially at anterior end; P2 and 3 are aligned anteroposteriorly; P3 is well developed but not prominent.

Lycopsis torresi Cabrera, 1927. Figures 9-13; Table 6.

Lycopsis torresi Cabrera, 1927, p. 295, figs. 11, 12.
Anatherium(?) *oxyrhynchus* Ameghino, 1894, p. 384.
Anatherium oxyrhynchus Cabrera, 1927, p. 298.
Anatherium oxyrhynchum Roger, 1896, p. 17.
Cladosictis oxyrhynchus Sinclair, 1906, p. 447.
Cladosictis oxyrhyncha Simpson, 1930, p. 45.

Type.—*L. torresi*: MLP 11-113, a fragment of a left maxilla with P^2 and M^{1-4} nearly complete; a right maxillary fragment with M^{1-4} complete; part of a left mandibular ramus with P_3-M_3 complete and talonid of M_4; and greater part of right mandibular ramus with C-P_3 complete, M_{2-3} partially broken, and posterior root of M_4; all of a single associated individual.

Type.—*A. oxyrhynchum*: MACN 5930, a left mandibular ramus with alveolus of C, alveoli of P_1, posterior half of P_2, P_3 complete, roots of M_1, talonid of M_2, and greater part of M_{3-4}.

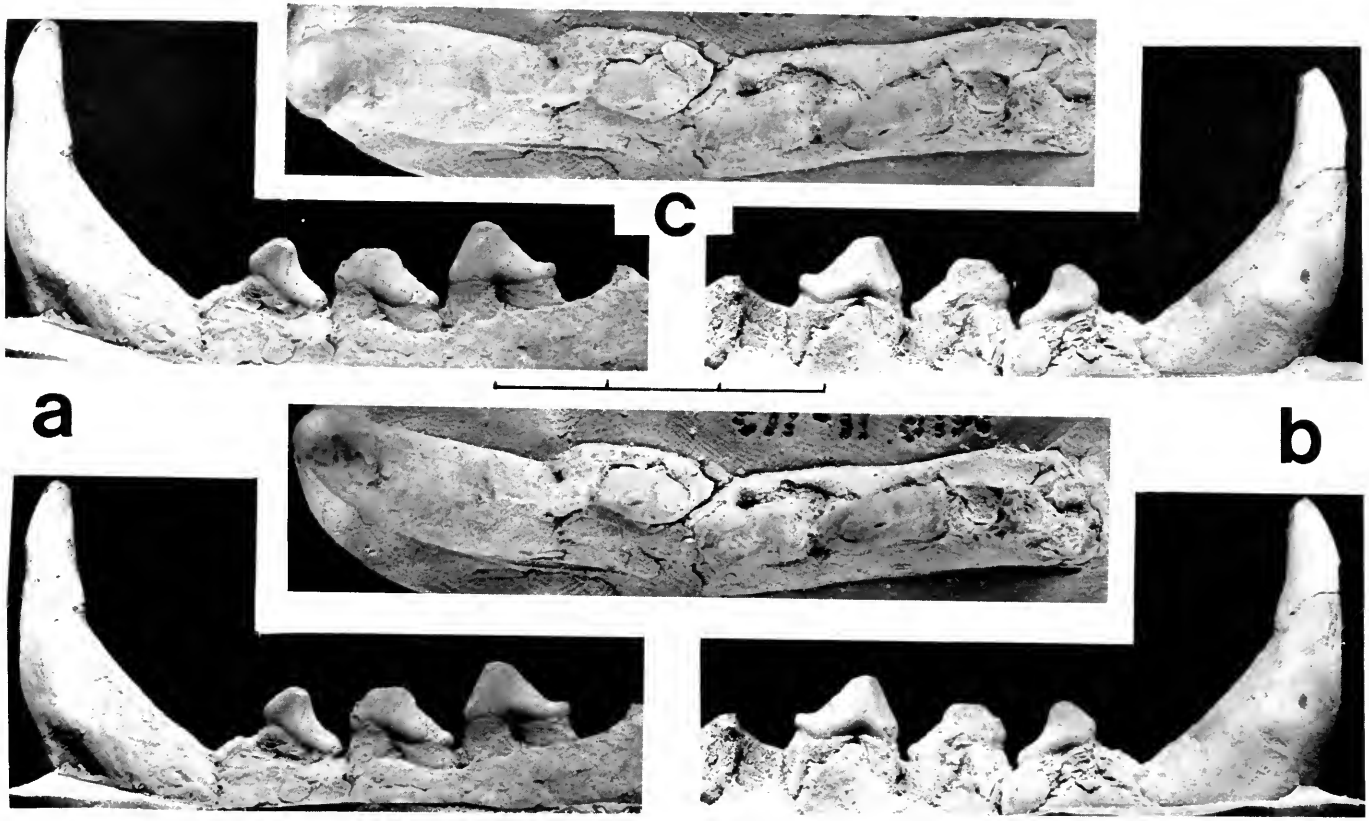
Hypodigm.—Types only.

Horizon and Locality.—Both specimens were collected from the Santa Cruz Formation, Santa Cruz Province, Argentina. MLP 11-113 was collected by C. Berry in 1895 from an unspecified site along the Río Santa Cruz. MACN 5930 was collected by C. Ameghino from *Corriquen-Kaik*.

Age.—Santacrucian.

Diagnosis.—Differs from *L. longirostrus* in being smaller in size, in M^4 being wider than M^3, in protocone on M^{1-4} and talonid basin being relatively and absolutely smaller; in P_2 and P_3 being subequal in size; and in M_{1-4} being relatively and absolutely shorter and more robust.

Description.—In length $P_1 < P_2 \leq P_3$. A distinct posterobasal heel is present on P_{1-3}. P_1 is set at 20° angle relative to rest of tooth row. Talonid is broader than trigonid on M_1, subequal on M_2, and nar-


c
a
b

rower on M_{3-4}. Hypoconid cuspate and larger than entoconid on M_{1-2}, but noncuspate and subequal to entoconid on M_{3-4}. Distinct hypoconulid visible on M_{1-3} in unworn teeth.

P^2 has well-developed posterobasal heel. Upper molars increase in length and breadth from M^1 to M^3; M^4 is wider than M^3. Para- and metaconules distinguishable on M^{2-4}. Metacone very large and connate basally with smaller paracone. Parastyle large and connected to protocone by paracingulum along anterior surface of paracone. Small stylar shelf developed on M^1 just labial to metacone, but does not connect up with parastyle. No distinct ectocingulum developed posterior to paracone-metacone junction on M^{1-3}. Ectocingulum encloses pocket between it and paracone on M^{2-3}, but not on M^1. Large ectoflex present on M^3. Paracone on M^4 is dominant cusp and is connected to parastyle by large paracrista. Cranial characters are unknown.

Comments.—Anatherium(?) *oxyrhynchus* was erected by Ameghino (1894, p. 384) on a partial left mandibular ramus with dentition. This specimen, MACN 5930, presently consists of a very fragmentary mandiblular ramus with part of the P_2, all of the P_3, talonid of the M_2, and nearly complete crowns of M_{3-4}. It is accompanied by numerous tooth fragments and parts of the symphyseal region of the ramus. Judging from Ameghino's original description, this specimen was more complete when he studied it, presenting details no longer preserved. As noted by Ameghino (1894, p. 384), "The space between the two lower canines is very reduced and the incisors are in part atrophied. The canine is strongly inclined anteriorly, the symphysis is very long and ends almost in a point. The first premolar is situated obliquely or almost transversely; the second (P_2) and third (P_3) have the posterior heel atrophied. The talonid of the M_4 is well developed. The distance from the anterior part of the mandible to the posterior border of the M_4 is 97.0 mm. P_1-M_4 measures 76.0 mm. in length. The M_4 measures 13.0 mm. in length. The surface of the symphysis measures 48.0 mm. in length and 15.0 mm. in maximum height. The mandible is 19.0 mm. in height below the P_2, and this height is conserved more or less to the last molar . . ." (translated from Spanish).

Opposite

FIG. 9. *Lycopsis torresi* Cabrera, 1927. Stereopairs of complete right C-P_3 and alveoli of M_1 of MLP 11-113 (type): **a**, lingual; **b**, labial; and **c**, occlusal views. Scale = 3 cm.

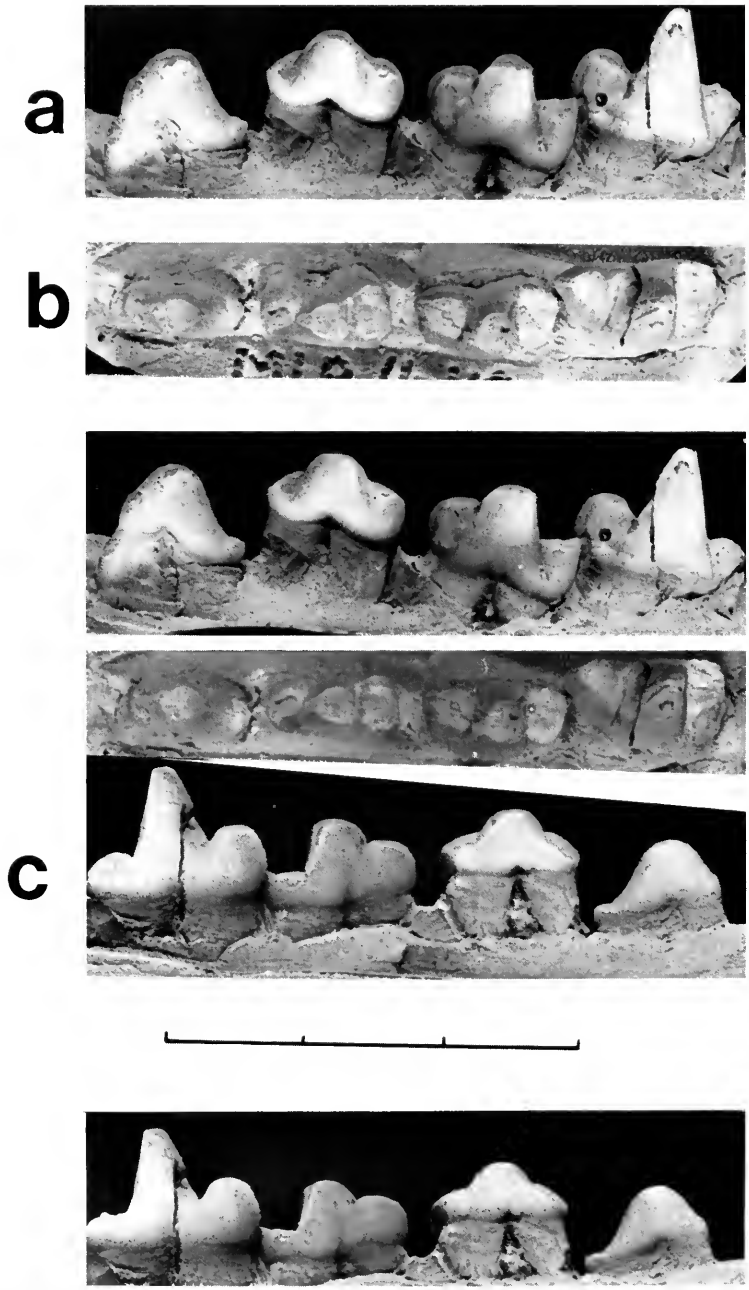


FIG. 10. *Lycopsis torresi* Cabrera, 1927. Stereopairs of left P_3-M_3 of MLP 11-113 (type): **a**, labial; **b**, occlusal; and **c**, lingual views. Scale = 3 cm.

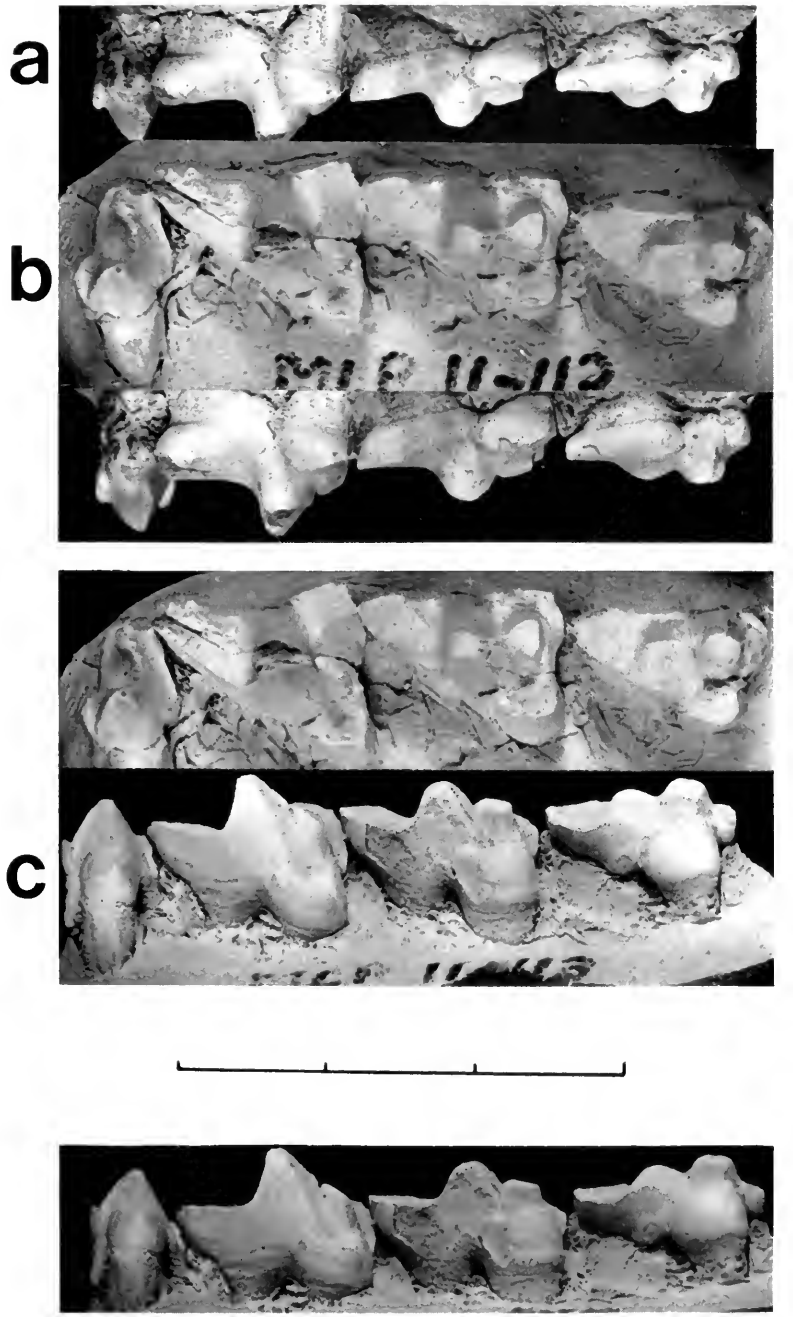


FIG. 11. *Lycopsis torresi* Cabrera, 1927. Stereopairs of right M^{1-4} of MLP 11-113 (type): **a**, labial; **b**, occlusal; and **c**, lingual views. Scale = 3 cm.

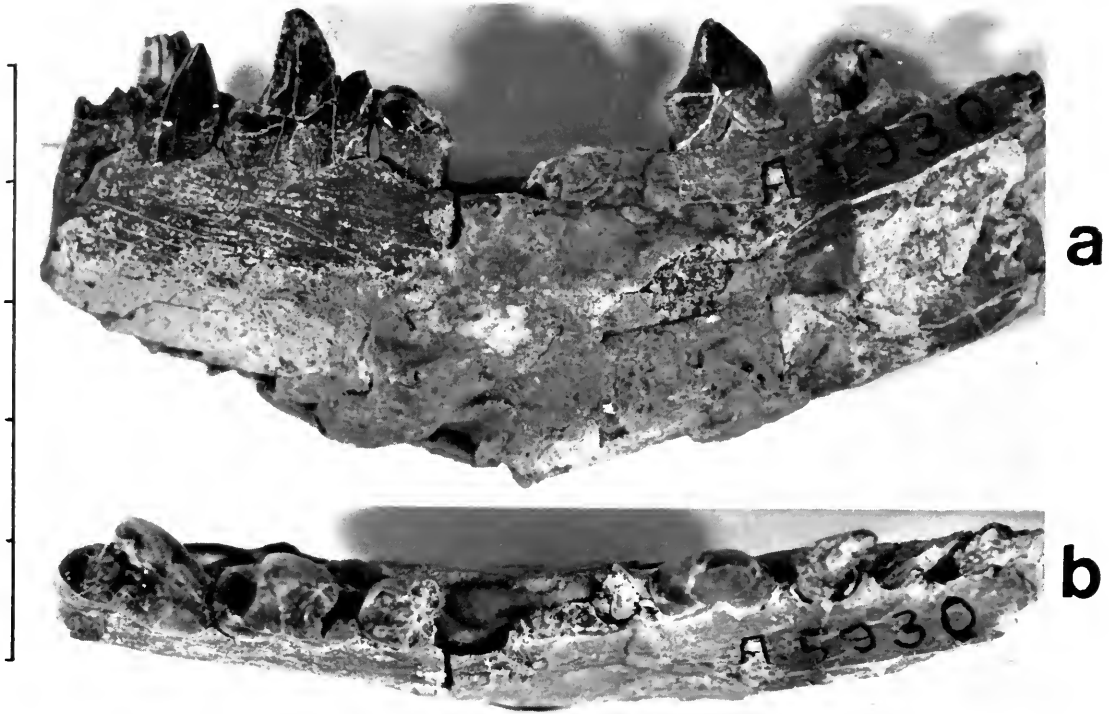


FIG. 12. *Lycopsis torresi* Cabrera, 1927. MACN 5930, a left mandibular ramus with alveolus of C, alveoli of P_1, posterior half of P_2, P_3 complete, roots of M_1, talonid of M_2, and greater part of M_{3-4}: **a**, lingual and **b**, occlusal views. Scale = 5 cm.

TABLE 6. Measurements of lower cheek teeth of *Lycopsis torresi*, *L. longirostrus*, and *Pseudolycopsis cabrerai*

Specimen	P1		P2		P3		M1		M2		M3		M4		$M^{1-3}/_{1-4}$
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L
Upper cheek teeth															
L. torresi															
MLP 11-113 (l)	....	....	10.5	4.6	....	....	....	8.0	13.2	9.4	13.5	11.2	12.6	5.3	40.4
MLP 11-113 (r)	....	....	....	....	....	....	12.5	7.9	13.1	9.3	13.5	11.5	12.4	5.5	40.7
L. longirostrus															
UCMP 38061	9.7	5.0	11.1	5.4	13.5	5.6	13.1	9.0	15.3	11.3	17.5	13.5	11.4	6.0	45.6
P. cabrerai															
MLP 57-XI-9-1 (l)	....	....	....	....	8.0	3.1	10.8	6.0	11.5	7.7	....	8.8	....	....	....
MLP 57-XI-9-1 (r)	....	....	....	....	....	....	....	....	11.4	....	12.0	8.7	....	....	....
Lower cheek teeth															
L. torresi															
MLP 11-113 (l)	....	....	....	....	9.4	4.0	10.4	5.4	11.2	6.0	12.6	6.8	....	....	ca. 49.7
MLP 11-113 (r)	7.8	4.2	9.2	4.4	9.5	4.0	....	....	11.3	5.9	....	....	....	....	....
MACN 5930	....	....	....	....	9.0	4.5	....	....	....	6.0	12.0	7.0	12.5	ca. 7.5	ca. 50.0
L. longirostrus															
UCMP 38061	9.0	5.6	12.8	5.8	12.2	5.1	13.0	5.8	13.8	6.7	15.3	6.4	17.4	ca. 7.2	58.0

In Cabrera's (1927, p. 295, figs. 11, 12) original description of *Lycopsis torresi*, he specifically compared it with "*Anatherium oxyrhynchus*." He noted, by inference, that "*A. oxyrhynchus*" had atrophied talonids on P_{2-3}, while in *L. torresi* these were better developed. The talonids in "*A. oxyrhynchus*" are indeed smaller than in the type of *L. torresi*, but these differences are minor and are of no taxonomic importance.

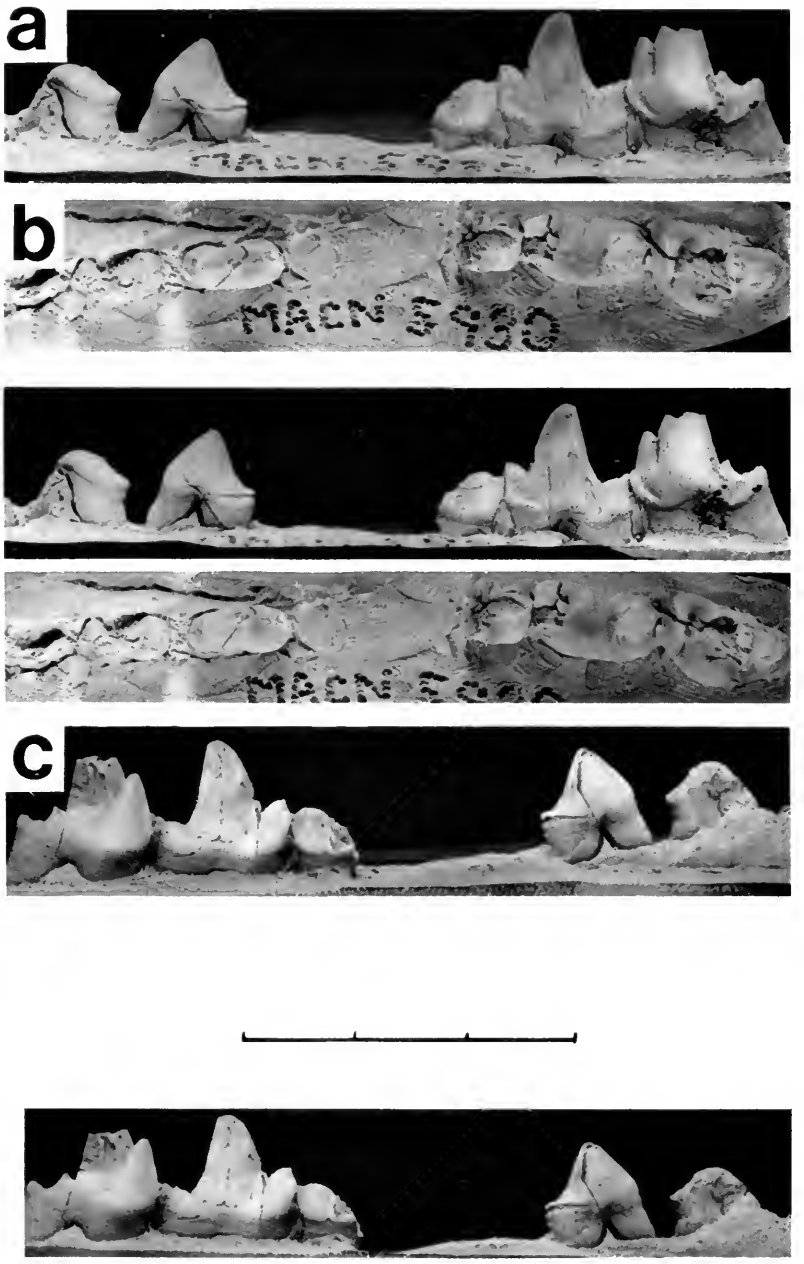
Cabrera further noted that in "*A. oxyrhynchus*" the depth of the mandibular ramus was relatively constant from P_2 to M_4, but becomes markedly deeper from P_2-M_4 in *L. torresi.* The mandibular ramus of the type of *L. torresi* has been extensively restored with wax, such that the true structure of this element below the molars is open to question. Similarly, the ramus of the type of "*A. oxyrhynchus*" is now totally destroyed below the molar series and what its condition was when studied by Ameghino is not surely known. As indicated by tooth wear, the type of "*A. oxyrhynchus*" is of a young animal, while that of *L. torresi* is of a middle-aged adult. As size of the mandibular ramus is subject to age and sex differences, it is of dubious value as a taxonomic character. In all other respects these specimens are virtually identical and they are surely synonymous.

Cabrera concluded his discussion on *L. torresi* by noting that "*A. oxyrhynchus*" possessed none of the characters peculiar to the genus "*Anatherium*," and that it may warrant being placed in a new genus. His intuition was correct. The type species of *Anatherium*, *A. defossum*, is now included within *Cladosictis* (see Marshall, 1978, p. 21), and the genus *Anatherium* is no longer valid.

Lycopsis torresi differs from *L. longirostrus*, primarily in its smaller size, in the M^4 being wider than the M^3, in the metastylar shear being proportionately less well developed, in the lower premolars and molars being proportionately shorter and more squat, and in the talonid basin being proportionately and absolutely smaller. These differences are minor and, as I proposed earlier (1977), it is probable that *L. torresi* represents an ancestral form of *L. longirostrus.*

Opposite

FIG. 13. *Lycopsis torresi* Cabrera, 1927. Stereopairs of MACN 5930, a left mandibular ramus with alveolus of C, alveoli of P_1, posterior half of P_2, P_3 complete, roots of M_1, talonid of M_2, and greater part of M_{3-4}: **a**, labial; **b**, occlusal; and **c**, lingual views. Scale = 3 cm.


a
b
MACN 5930
c

It is likewise probable that *L. torresi* evolved from a form not too different from the Colhuehuapian species *Pseudothylacynus rectus.* Both share the following features: P_1 is smaller than P_{2-3} and is set at 20° in the jaw relative to the rest of the tooth row; P_{2-3} are elongated anteroposteriorly and have a distinct posterobasal cusp (heel); talonid basin is distinct and is well developed on M_{1-3}, smaller on M_4; and the hypoconid is cuspate and is larger than the entoconid on M_{1-2}, subequal and less distinct on M_{3-4}. In addition, the overall proportions of the teeth of these species are similar. They differ in that *L. torresi* is larger in size and has relatively and absolutely larger talonid basins on M_{1-4} (especially M_4).

The overall morphology of *P. rectus* does, however, indicate closer affinities with *P. patagonicus* than with *L. torresi.* Because of this I propose that *P. rectus* be regarded as directly ancestral to *P. patagonicus* and that *L. torresi* evolved from a pre-*P. rectus* form and not directly from that species.

Lycopsis longirostrus Marshall, 1977. Table 6.

Lycopsis longirostrus Marshall, 1977, p. 634, figs. 1-4.

Type.—UCMP 38061, right half of a skull with C-M^4, right dentary with roots of C, P_1-M_4 complete, and greater part of articulated skeleton.

Hypodigm.—Type only.

Horizon and Locality.—"Monkey Unit" of Honda Group from Upper Magdalena Basin, northeast of village of Villavieja in northern part of Department of Huila, Colombia. Type locality is UCMP V-4521.

Age.—Friasian (medial Miocene).

Diagnosis.—Differs from *L. torresi* in being larger in size, in M^4 being narrower than M^3, in protocone on M^{1-4} being relatively and absolutely larger, and in P_2 being larger than P_3. In addition, a paracingulum occurs on M^{1-3}; hypoconid is larger than hypoconulid or entoconid on M_{1-2}; skull is dolichocephalic; petrosal lacks a subarcuate fossa, pars mastoidea, and tympanic process; tympanic process of alisphenoid is lacking; no evidence of an ossified auditory bulla; foramen ovale is small; foramen lacerum medium, carotid canal, and transverse canal are all very small.

Description.—A detailed description of UCMP 38061 along with illustrations of the dentition, skull and skeleton are given by Marshall (1977).

Comments.—*Lycopsis longirostrus* probably passed through a *L. torresi* grade at some time in its evolution as all of the characters in the former can be derived with but minor modification from the latter. Considering the overall morphological similarities between these species and their occurrence in consecutive land mammal faunas, an ancestral-descendant relationship is probable.

Pseudolycopsis Marshall, 1976d

Pseudolycopsis Marshall, 1976d, p. 291.

Type.—*Pseudolycopsis cabrerai* Marshall, 1976d.

Distribution.—Arroyo Chasicó Formation, Department of Villarino, southwest corner of Buenos Aires Province, Argentina.

Diagnosis.—As for type and only known species.

Pseudolycopsis cabrerai Marshall, 1976d. Figure 14, Table 6.

Pseudolycopsis cabrerai Marshall, 1976d, p. 291, fig. 1.

Type.—MLP 57-XI-9-1, a fragment of a palate with left P^3-M^3 and right M^{2-3}.

Hypodigm.—Type only.

Horizon and Locality.—Arroyo Chasicó Formation, Department of Villarino, southwest corner of Buenos Aires Province, Argentina.

Age.—Chasicoan (medial to late Miocene).

Diagnosis.—Protocone is located toward anterior edge of tooth and lies directly opposite paracone; parastyle is very large on M^1 and it has form of spur that projects anteriorly toward P^3; main cusp of M^1 parastyle is in line with para- and metacone; molars lack ecto- and paracingulum; metacrista is very long and narrow; molars are overall very narrow transversely and are elongated anteroposteriorly.

Description.—Similar in size to *Prothylacynus patagonicus.* P^3 is small, gracile, and lacks a distinct posterobasal heel; its crown is about same height as metacone of M^1. Molars increase in length and width from M^1 to M^3. Protocone is well developed and has a shallow basin on M^{1-3}; protocone decreases slightly in size from M^1 to M^3. Paracone is small and is fused basally with larger metacone; paracone becomes slightly smaller from M^1 to M^3, while metacone becomes relatively and absolutely larger in the same direction. Parastyle on M^2 and M^3 is shorter than on M^1, is cuspate, and is set

labiad of a line connecting paracone and metacone. A broad shallow ectoflex is present on M^3 opposite metacone.

Comments.—In the upper dentition of *Lycopsis torresi* the molars have a large basined protocone, a large (but not huge) parastyle, and a reduced ectocingulum which appears only on the M^1 posterior to the metacone, being absent on M^{2-3}. These same features probably occurred in the ancestor of *P. cabrerai* and only slight modification of the dentition of *L. torresi* is required to obtain the dental specializations seen in *P. cabrerai.*

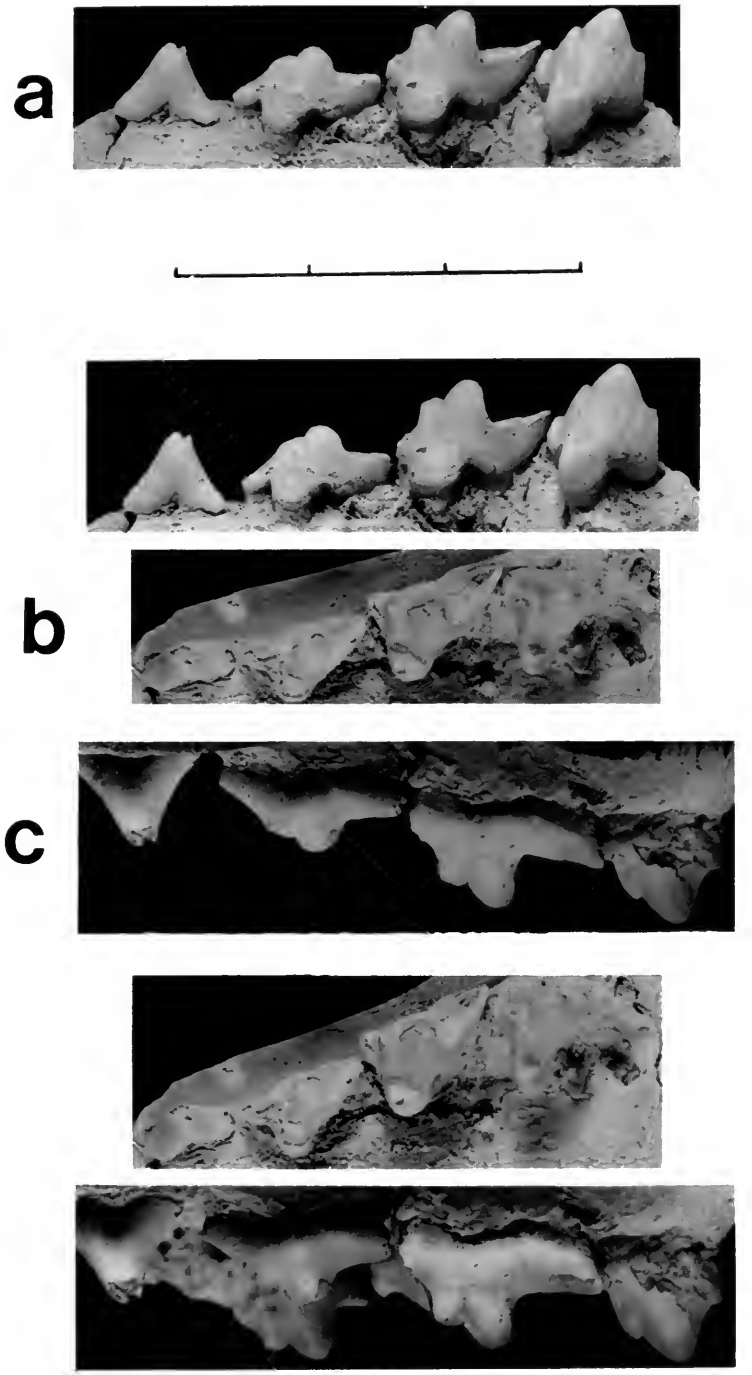
There are, however, two factors which suggest that *L. torresi* may not in fact be ancestral to *P. cabrerai.* First, *L. torresi* is larger than *P. cabrerai*, and if an ancestral-descendant relationship exists then a diminution in size would have had to occur in this lineage. Second, it appears more likely that *L. torresi* is ancestral to *L. longirostrus* (Marshall, 1977) and that within that lineage, and assuming no branchings, there was a tendency for increase in size and for greater development of the protocone and talonid basins. Notwithstanding these factors, *L. torresi* is basically very similar to *P. cabrerai* and although the former may not be ancestral to the latter, it certainly approximates what would be expected in an ancestral form of that species.

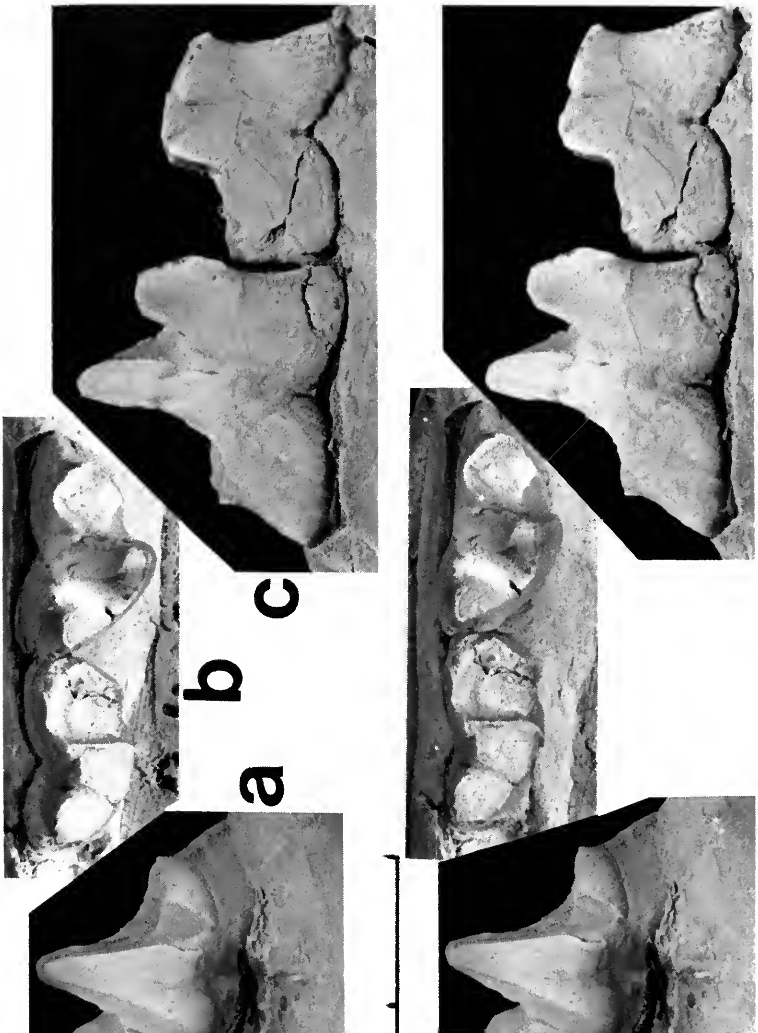
The upper molars of *Prothylacynus patagonicus* are similar in size to those of *Pseudolycopsis cabrerai*, although there are characters present in the former which suggest that it is not involved in the ancestry of the latter. These characters include: 1) the protocone, although large and well developed, is cuspate and is not basined; 2) the parastyle is very large and a large ectocingulum occurs on M^{1-3}; and 3) the P^3 is large and rather robust, although not to the degree seen in *Borhyaena*, and it has a distinct posterobasal heel. It appears that unless there occurred a secondary enlargement of the protocone and a very marked reduction in size of the parastyle, ectocingulum, and P3, then *P. patagonicus* can probably be eliminated as a potential ancestor for *P. cabrerai.*

Pseudothylacynus rectus may be involved in the ancestry of *Pseudolycopsis cabrerai*, and, for that matter, *L. torresi* and/or *Prothylacynus patagonicus* as well (see above). The upper dentition of *P.*

Opposite

FIG. 14. *Pseudolycopsis cabrerai* Marshall, 1976d. Stereopairs of left side of MLP 57-XI-9-1, a fragment of a palate with P^3-M^2 and M^3 broken: a, lingual; b, occlusal; and c, labial views. Scale = 3 cm.


a
b
c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cabrerai complements the lower dental structure of *P. rectus*; i.e., they are similar in size and they occlude rather closely. *P. cabrerai*, however, has a smaller protocone than is expected in the upper dentition of *P. rectus*. Nothing definite can be said about the relationship of these taxa, except that in their complementary morphology they are similar. Whether or not this similarity is a reflection of direct phylogenetic affinity is presently not known.

Stylocynus Mercerat, 1917

Stylocynus Mercerat, 1917, p. 20.

Sthylocynus (sic) L. Kraglievich, 1934, p. 62.

Type.—*Stylocynus paranensis* Mercerat, 1917, p. 20.

Distribution.—Formation "Entrerriense," near Paraná, Entre Ríos Province, Argentina.

Diagnosis.—As for type and only known species.

Stylocynus paranensis Mercerat, 1917. Figures 15-18; Tables 7-8.

Achlysictis lelongi Ameghino, 1891, p. 147 (*partim*, not holotype).

Stylocynus paranensis Mercerat, 1917, p. 20n; L. Kraglievich, 1917, p. 278 (as *nomen nudum*); 1934, p. 62; Cabrera, 1927, p. 278, fig. 3.

Type.—MLP 11-94, originally a nearly complete left mandibular ramus with alveoli of incisors and C, P_{1-2} present but broken, roots of P_3-M_1, base of M_2, and M_{3-4} complete. Since the specimen was described by Mercerat and figured in Cabrera, the ramus has been broken in several places and is now partially restored in plaster. Only M_{3-4} remain—P_1, P_2, and part of the M_2 have been lost.

Hypodigm.—The type and MLP 41-XII-13-1112, a fragment of a right mandibular ramus with alveoli of C, P_1-M_1 complete; MACN 5893, a fragment of a right maxilla with M^2 complete, roots of M^1, and posterior alveolus of P^3; and MACN 13203, a right maxillary fragment with P^2 and M^{1-2} present but very worn, and alveoli of P^3.

Horizon and Locality.—All specimens were collected from the "barrancas del río Paraná," "Formación Entrerriense," Entre Ríos Province, Argentina.

Age.—Montehermosan.

Opposite

FIG. 15. *Stylocynus paranensis* Mercerat, 1917. Stereopairs of M_{3-4} of MLP-11-94 (type): **a**, labial; **b**, occlusal; and **c**, lingual views. Scale = 3 cm.

Diagnosis.—Largest known species of Prothylacyninae. Mandibular ramus is exceptionally deep and narrow relative to size of teeth. An enormous mental foramen is located below P_2. Mandibular symphysis is broad, ligamentous, and rami are unfused in adult. All lower premolars are large and well developed. Small, but distinct metaconid present on M_{1-4}. Talonid extremely large and basined on M_{1-3}, slightly smaller but still large on M_4. M^{1-3}, and probably also M^4, with very large basined protocones.

Description.—Symphysis extends posteriorly to point below anterior root of P_3. Two medialmost incisors are larger than labialmost incisor. In length $P_1 < P_2 > P_3$. P_1 is set at 15° angle relative to rest of tooth row. A distinct posterobasal heel is present on P_{2-3}, but only a hint of this structure occurs on P_1. Small diastems separate P_{1-3} from each other as well as from adjacent teeth. Lower molars increase in length and width from M_1 to M_4. Distinct anterobasal cingulum is present on M_{1-4}. Talonid is wider than trigonid on M_{1-3}, but is smaller on M_4. Hypoconid is markedly larger than entoconid on M_1 (and probably M_2), subequal on M_{3-4}. Infraorbital foramen opens immediately above P^3. P^{2-3} are aligned in same anteroposterior axis. Metacone is larger than paracone on M^1, becoming progressively and absolutely larger on M^2. Paracone and metacone are connected basally by low, broad ridge. Small parastyle is present on M^2, and weak labial shelf extends posteriorly from it to point opposite middle of metacone. Metastylar region is well developed, but is not prominent.

Comments.—On the type (MLP 11-94), prominent rugosities, probably representing muscle scars, occur along the labial surface of the mandibular ramus and are especially prominent along the upper surface between M_1 and M_4. These scars probably indicate the presence of a large superficial masseter muscle, and together with the dental specializations (e.g., large protocones and talonids) suggest a predominately omnivorous diet.

The name *Stylocynus paranensis* was applied by Mercerat (1917, p. 20, footnote 1) to a left mandibular ramus with partial dentition, collected from "los depósitos sedimentarios terciarios del Paraná." The description given by Mercerat is complete, is accompanied by measurements of the specimen, and the species is compared with other Borhyaenidae, especially with *Prothylacynus patagonicus.* This comparison was well chosen as *P. patagonicus* was, at that time, the only species of borhyaenid sharing numerous characters with *S. paranensis.* Nevertheless, L. Kraglievich (1917, p. 278)

FIG. 16. *Stylocynus paranensis* Mercerat, 1917. MLP 41-XII-13-1112, a fragment of a right mandibular ramus with alveoli of C, P_1-M_1 complete: **a**, labial and **b**, occlusal views. Scale = 5 cm.

regarded *S. paranensis* as a *nomen nudum*, without giving sound justification for such action. Cabrera (1927, p. 278, fig. 3) later redescribed and figured the type, noting (p. 280) that *contra* L. Kraglievich, the species is perfectly valid.

Stylocynus paranensis is one of the most specialized borhyaenids known. The protocone on M^{1-3} and corresponding talonid basins on M_{1-3} (and to a lesser extent on M_4) are relatively and absolutely larger than in any other known species. The small, but distinct metaconid on M_{1-4}, when considered with the large talonid, presents a pair of characters unknown in other members of the family, but resembles the Friasian didelphid *Hondadelphys fieldsi* (Marshall, 1976c). The enormous size of the anterior mental foramen below the P_2 further represents a diagnostic feature found only in this species among Prothylacyninae.

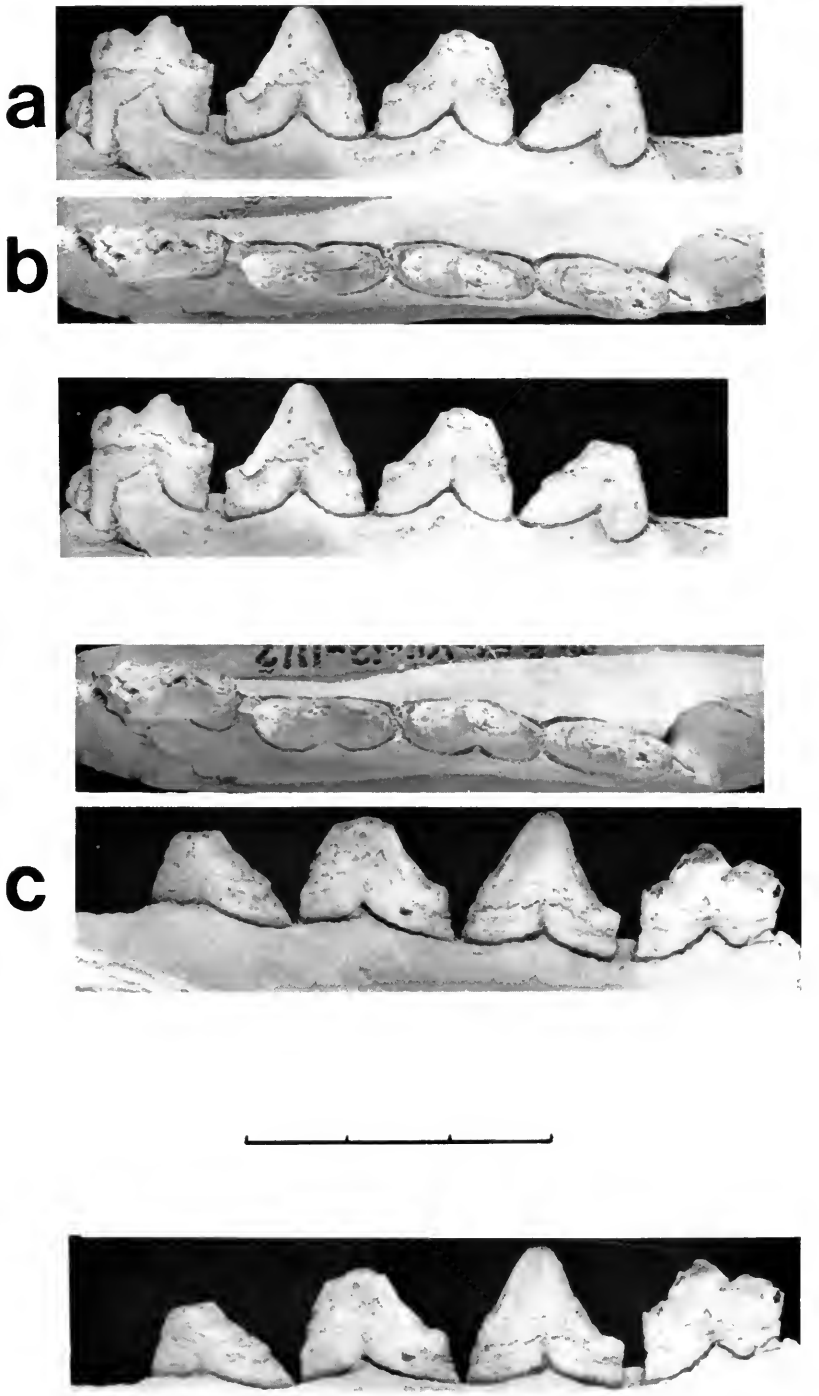
In Ameghino's (1891a) original description of *Achlysictis lelongi*, a species now referred to the saber-tooth family Thylacosmilidae (Marshall, 1976a), he referred a "penultimate" upper molar to that species. This specimen, MACN 5893, is referable to *S. paranensis*. Although Ameghino (1891a, p. 147) mentioned MACN 5893 first in his description of *A. lelongi*, he distinctly indicated in his catalogue that the mandibular ramus fragment, MACN 5892, which he illustrated (1891a, fig. 52), was the "TIPO."

Of all known Prothylacyninae, *S. paranensis* shows special affinity only with *Lycopsis longirostrus*. The upper molars of these species have large protocones, very large metacones which are connate basally with much reduced paracones, and distinct parastyles. Differences are that in *S. paranensis* the protocone is proportionately and absolutely larger, the parastyle is more reduced, and the metacrista is proportionately shorter and more robust.

Noteworthy similarities in their lower dentitions include: size (*S. paranensis* is slightly larger in some dimensions, and *L. longirostrus* in others), canines are moderately developed, premolars are anteroposteriorly elongated and are set in a relatively straight line in the jaw, P_2 is larger than P_3, in presence of a distinct posterobasal heel on P_{2-3}, in M_{1-3} having a very large and deeply basined talonid, in M_4

Opposite

FIG. 17. *Stylocynus paranensis* Mercerat, 1917. Stereopairs of MLP 41-XII-13-1112, a fragment of a right mandibular ramus with alveoli of C, P_1-M_1 complete: **a**, labial; **b**, occlusal; and **c**, lingual views. Scale = 3 cm.


a
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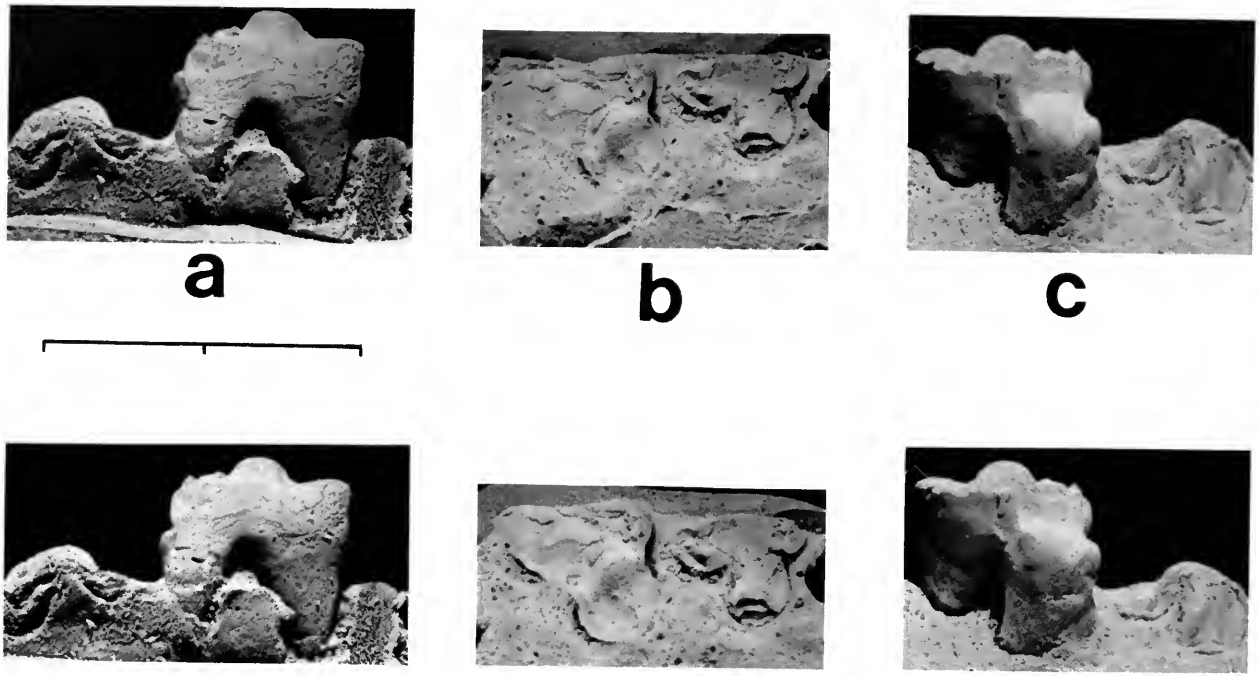

FIG. 18. *Stylocynus paranensis* Mercerat, 1917. Stereopairs of MACN 5893, a fragment of a right maxilla with M^2 complete, roots of M^1, and posterior alveolus of P^3: **a**, labial, **b**, occlusal; and **c**, lingual views. Scale = 2 cm.

TABLE 7. Measurements of cheek teeth of *Stylocynus paranensis*.

Specimen	P1		P2		P3		M1		M2		M3		M4		M_{1-4}	M_{1-3}	P_1-M_1
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	L	L
Upper cheek teeth																	
MACN 5893	....	....	....	....	....	....	....	....	11.6	9.6	....	....	....	....	....	....	....
MACN 13203	....	....	ca. 10.2	ca. 14.0	....	....	....	....	....	....	....	....	....	....	....	....	....
Lower cheek teeth																	
MLP 11-94	....	....	....	....	....	....	....	....	....	....	14.0	7.2	15.0	8.0	ca. 56.0	ca. 40.0	....
MLP 41-XII-13-1112	12.3	5.2	14.4	5.0	14.0	5.0	13.7	6.1	....	....	....	....	....	....	....	....	62.4

having a distinct talonid basin which is smaller than that on M_{1-3}, in talonids being markedly wider than trigonids on M_{1-2}, and in the hypoconid being much larger than the entoconid on M_{1-2} but more subequal on M_{3-4}. Furthermore, the mandibular symphysis is ligamentous in both species and the rami are unfused in adults.

The lower jaw and dentition of *S. paranensis* differs from *L. longirostrus* in the ramus being proportionately deeper and the ventral border markedly convex, in the presence of a very large anterior mental foramen below the P_2, in the proportionately larger size of P_{1-3} relative to M_{1-4}, in the proportionately and absolutely larger talonid basin on M_{1-4}, in the overall greater robustness of the entire lower dentition and jaw, and, lastly and most importantly, in the presence of a small but distinct metaconid on M_{1-4}.

All in all, these taxa are very similar and of the many points just considered only the presence of a small metaconid in *S. paranensis* could possibly exclude it as a direct descendent of *L. longirostrus* which lacks a metaconid. The presence of a metaconid in *S. paranensis* dictates the reappearance of a feature lost (or, better, suppressed)

TABLE 8. Measurements of mandibular ramus of *Stylocynus paranensis*.

Specimen	Depth of ramus below labial side of P3	Breadth of same	Depth of ramus below labial side of M4	Breadth of same
MLP 11-94	27.0	11.0	37.0	14.6
MLP 41-XII-13-1112	29.0	11.0	....	....

in *L. longirostrus* if such a relationship exists. Kurtén (1963) has demonstrated the re-establishment of M_2, a molar thought to be lost in all Miocene felids, in the dentitions of a part of the population of the modern northern European lynx, *Felis lynx*. Absence of a metaconid in *L. longirostrus* would thus not necessarily bar this species from the ancestry of *S. paranensis*. Keeping in mind the study of Kurtén, the fact that the metaconid in *S. paranensis* is quite small, and the close agreement of these species in almost every other comparable character, it seems plausible to regard the metaconid as being secondarily regained. Assuming this to be correct, then an ancestral-descendant relationship for these species is a distinct possibility.

SUMMARY OF PHYLOGENETIC RELATIONSHIPS OF PROTHYLACYNINAE

Members of the Prothylacyninae are known from beds of Colhuehuapian (late Oligocene) through Montehermosan (Pliocene) in age. In beds of pre-Huayquerian age they are the only medium-to-large terrestrial mammalian omnivore-carnivores on the South American continent.

The six species of Prothylacyninae share a suite of characters not found jointly in other borhyaenids. These include: a medium-to-large size; a typically moderately well-developed canine; P_{1-3} aligned in relatively straight line with P_1 being set at slight angle relative to rest of tooth row, less so in later forms; P3 only moderately well developed and not proodont as is typical in other borhyaenids; M^{1-3} usually with well-developed protocones; talonid moderate to well-developed on M_{1-3}; metaconid absent except in *Stylocynus*; P_{1-3} typically (except in *Prothylacynus*) elongated anteroposteriorly and with distinct posterobasal heel which is usually best developed on P_{2-3}; anterobasal cingulum usually present on M_{1-4}, but weakly developed or absent on M_1 in *Prothylacynus* and *Pseudothylacynus*.

The oldest known species of Prothylacyninae is *Pseudothylacynus rectus*. *P. rectus* makes an ideal structural ancestor for *Prothylacynus patagonicus*, and *Lycopsis torresi* may likewise have evolved from a *P. rectus*-like form.

Evolution of the *Prothylacynus patagonicus* lineage involved changes toward "brachycephaly" and carnivorous dental specializations. The primary changes from *P. rectus* to *P. patagonicus* include: increase in size; crowding of cheek tooth row such that P1 comes to lie more obliquely in jaw and premolars and molars become relatively shorter and absolutely more robust; reduction in size of protocone in upper molars and talonid in lower molars; and mandibular symphysis becoming shortened, ankylosed, and the rami tightly fused in the adult. *P. patagonicus* is the least specialized of known Prothylacyninae for an omnivorous diet, and shares many features with smaller members of the more carnivorous Borhyaeninae, such as *Acrocyon sectorius* (Marshall, 1978).

In contrast, evolution of *Lycopsis torresi* from a *P. rectus*-like form involved specializatons toward "dolichocephaly" and omnivory. The primary changes include: increase in size; elongation of the tooth row as reflected in cheek teeth becoming absolutely and relatively longer anteroposteriorly; increase in size of protocone on

TABLE 9. Summary of some diagnostic characters of species of Prothylacyninae.

Character	*Pseudothylacynus rectus*	*Prothylacynus patagonicus*	*Lycopsis torresi*	*Lycopsis longirostrus*	*Pseudolycopsis cabrerai*	*Stylocynus paranensis*
1. Size	medium	medium-large	medium-large	large	medium	large
2. Skull	mesatocephalic	brachycephalic	dolichocephalic	dolichocephalic	....	dolichocephalic
3. Mandibular symphysis	ankylosed but unfused	ankylosed and fused	ligamentous	ligamentous	....	ligamentous
4. Metaconid	absent	absent	absent	absent	absent	present
5. Protocone	....	small and cuspate	large and basined	large and basined	small and basined	enormous and basined
6. Talonid	moderate in size, basined lingually, cuspate labially	small and unbasined	large and basined	large and basined	....	enormous and basined
7. Angle of orientation of P_1 in jaw relative to rest of tooth row	25°	30°	20°	20°	....	15°
8. Foramen ovale	....	large	....	small	....	....
9. Size of P_1 relative to P_{2-3}	small	small	small	medium	....	large
10. Length of P_{1-3}	$P_1 < P_2 < P_3$	$P_1 < P_2 > P_3$	$P_1 < P_2 \leq P_3$	$P_1 < P_2 > P_3$	....	$P_1 < P_2 > P_3$
11. Width of P_{1-3}	$P_1 < P_2 < P_3$	$P_1 < P_2 \approx P_3$	$P_1 < P_2 > P_3$	$P_1 < P_2 > P_3$	....	$P_1 > P_2 \approx P_3$

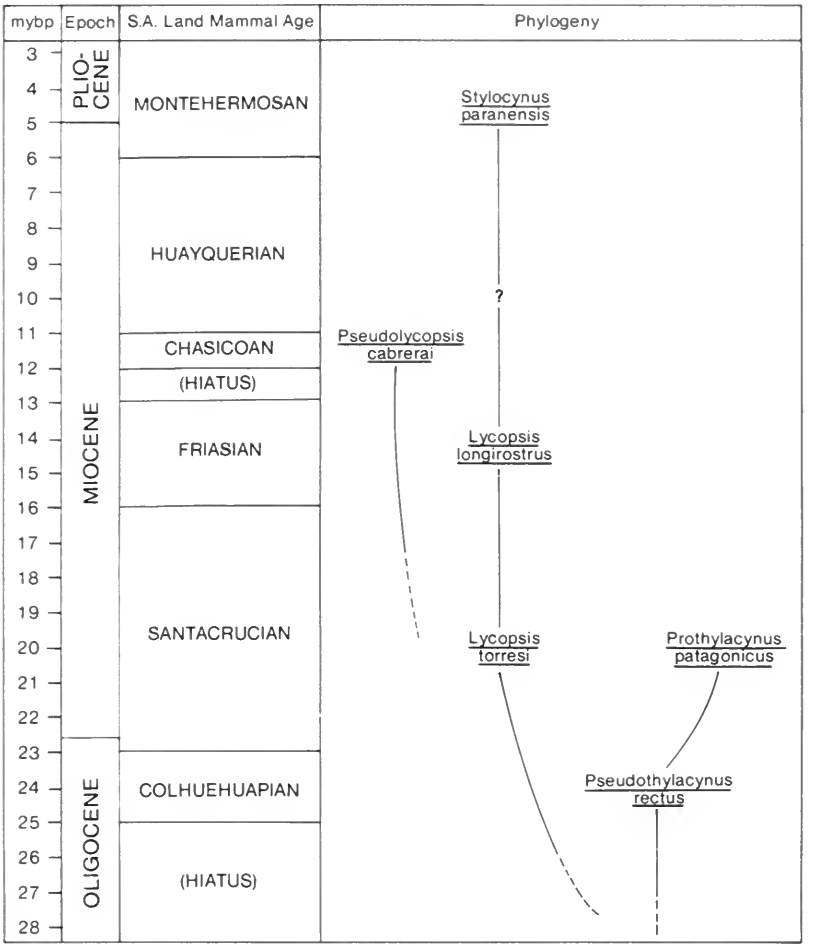

FIG. 19. Proposed phylogeny of the Prothylacyninae.

upper molars and talonid becoming larger and basined on lower molars; and in the mandibular symphysis becoming completely ligamentous and more elongated, and the rami unfused in the adult.

Changes in the *L. torresi-L. longirostrus* lineage involved continuation of the trend toward "dolichocephaly" and omnivory—i.e., further increase in size; greater elongation of cheek tooth row; cheek teeth become proportionately more elongate anteroposteriorly and small diastems develop between premolars and adjacent teeth; increase in size of protocone and talonid; and ligamentous mandibular symphysis becomes more elongate.

These trends were continued in the evolution of *Stylocynus paranensis*, and the trend toward size increase of the protocone and talonid reached its greatest development in this species. *S. paranensis* is large and was apparently bear-like in its feeding habits. This species presents some phylogenetic problems, since in size and structure it is remarkably similar to *L. longirostrus* except that it has a small metaconid on M_{2-4}, a feature lacking in *L. longirostrus*. Presence of a metaconid in *S. paranensis* may represent the reappearance of a "lost" character, in which case that species could have evolved from a form like *L. longirostrus*. Alternatively, *S. paranensis* may represent the last member of an evolutionary line distinct from *Lycopsis*, the mid-Tertiary record for which is either not known or not recognized.

There is no known species of Santacrucian borhyaenid which can confidently be regarded as ancestral to *Pseudolycopsis cabrerai*, although *L. torresi* approaches closest in molar morphology to what would be expected in an ancestral form. *Prothylacynus patagonicus* is clearly too specialized to be ancestral to *P. cabrerai*. *Pseudothylacynus rectus* from the Colhuehuapian may be ancestral to *P. cabrerai*, although the latter is known only from upper dentitions and the former only from lowers. Consequently, direct comparison of these taxa is not possible at this time.

Diagnostic characters for species of Prothylacyninae are compared in Table 9. The probable phylogenetic relationships of these taxa are shown diagramatically in Figure 19.

ACKNOWLEDGEMENTS

This research was supported, in part, by two grants (1329, 1698) from the National Geographic Society, Washington, D.C. A large part of this study was carried out in the Vertebrate Paleontology Section of the MACN, and I thank Guillermo del Corro, Chief of Section, and José Gallardo, Director, for making collections and working space available to me at that institution. Rosendo Pascual, MLP, allowed study of collections under his care and facilitated research in many ways. For loan of specimens and/or access to relevant museum records I extend my sincere thanks to Robert Hoffstetter, Institut de Paléontologie, MNHN; Roger Hamilton, BM(NH); M. C. McKenna and R. H. Tedford, AMNH; W. A. Clemens, UCMP; and Donald Baird, PU.

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