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CONTENTS

LIST OF ILLUSTRATIONS

LIST OF TABLES

ABSTRACT

Members of the extinct "dog-like" marsupial subfamily HATHLYACYNINAE (Borhyaenidae, Borhyaenoidea) are known from beds of Late Paleocene (Riochican) through Pliocene (Montehermosan) age in Argentina and beds of early Oligocene (Deseadan) age in Bolivia. Twelve genera and 18 species are recognized: *Patene simpsoni* Paula Couto, 1952; *Patene coluapiensis* Simpson, 1935; *Procladosictis anomala* Ameghino, 1902; *Pseudonotictis pusillus* (Ameghino, 1891) gen. nov.; *Notictis ortizi* Ameghino, 1889; *Perathereutes pungens* Ameghino, 1891; *Borhyaenidium musteloides* Pascual & Bocchino, 1963; *Borhyaenidium riggsi* sp. nov.; *Sipalocyon externa* (Ameghino, 1902); *Sipalocyon gracilis* Ameghino, 1887; *Sipalocyon obusta* (Ameghino, 1891); *Notocynus hermosicus* Mercerat, 1891; *Notogale mitis* (Ameghino, 1897); *Cladosictis centralis* Ameghino, 1902; *Cladosictis patagonica* Ameghino, 1887; *Chasicostylus castroi* Reig, 1957; *Anatherium herrerae* sp. nov.; and *Anatherium defossus* Ameghino, 1887. In addition, *Procladosictis erecta* Ameghino, 1902; *Pseudocladosictis determinabile* Ameghino, 1902; and *Notogale tenuis* (Ameghino, 1897) are regarded as *nomina vana*.

The species and genera are distinguished largely on the basis of absolute and relative size differences in the dentition. Such characters as presence or absence of a metaconid; relative size of protocone, talonid, and stylar shelf; spacing differences between C, P_1, and P_2; and orientation of P_1 in the jaw relative to other cheek teeth also proved useful in distinguishing these taxa.

With regard to dental structure and incisor number, hathlyacynes are the most generalized of known borhyaenids, and early members (i.e., *Patene*) closely approximate the expected condition of their presumed didelphoid ancestors. The general evolutionary trend within the Hathlyacyninae involved increase in carnassial specializations resulting in loss of metaconid and reduction in size of protocone, stylar shelf, and talonid. The group has been extremely conservative during its evolutionary history, and structurally the taxa are monotonously alike. Nevertheless, if sheer numbers of individuals and taxa are a gauge, then the Hathlyacyninae was the most successful of the borhyaenid subfamilies.

INTRODUCTION

This paper presents a detailed systematic revision of an extinct subfamily of South American "dog-like" marsupials, the Hathlyacyninae. The taxonomic history of the Hathlyacyninae is reviewed, the possible phylogenetic relationships of the included taxa are discussed, and the group's taxonomy at the generic and specific levels is stabilized. This study represents an attempt to bring together in one place an updated and expanded treatment of these animals. Sys-

tematic revisions of other extinct carnivorous marsupial groups in South America are presented elsewhere [Thylacosmilidae (Marshall, 1976b); Borhyaenidae in general and Borhyaeninae in particular (Marshall, 1978); Prothylacyninae (Marshall, 1979)].

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, including two new species, but is essentially based on a reappraisal of previously known specimens and literature.

The fossil localities mentioned below (figs. 1, 2) are shown on maps and are discussed in detail in Marshall (1976c) and in Marshall, Hoffstetter, & Pascual (in press). The chronology and usage of South American Land Mammal Ages follows Marshall, Hoffstetter, & Pascual (in press), which is based largely on the radioisotope time scale in Marshall, Pascual, et al. (1977) and Marshall, Butler, et al. (1979). All measurements are in millimeters (mm) unless indicated otherwise. The serial designation for cheek tooth number employed in this study is based on the dental formula $P^{1\text{-}2\text{-}3}_{1\text{-}2\text{-}3}$, $M^{1\text{-}2\text{-}3\text{-}4}_{1\text{-}2\text{-}3\text{-}4}$.

ABBREVIATIONS

Abbreviations used in text, figure captions, and tables of measurements are: C, canine; ca., approximate measurement; CV, coefficient of variation; I, incisor; L, length; M, molar; N, number; OR, observed range of sample; P, premolar; s, standard deviation of sample; x, mean; W, width.

The following abbreviations are used for specimens from institutional collections: AC, Amherst College, Amherst, Mass.; AMNH, American Museum of Natural History, New York; BM(NH), British Museum (Natural History), London; CMNH, Carnegie Museum of Natural History, Pittsburgh; DGM, Divasão de Geologia e Mineralogia do Departamento Nacional da Produção Mineral, Rio de Janeiro, Brazil; FMNH, Field Museum of Natural History, Chicago; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMP, Museo Municipal de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia," Mar del Plata, Argentina; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MNRJ, Museu Nacional e Universidade Federal do Rio de Janeiro, Brazil; PU, Princeton University, Princeton, N.J.; UCMP, University of California Museum of Paleontology, Berkeley, Calif.; USNM, United States National Museum, Washington, D.C.

ACKNOWLEDGMENTS

I am indebted to the following individuals for allowing me to study specimens at their respective institutions: D. Baird (PU), R. H. Tedford (AMNH), R. Pascual (MLP), J. Bonaparte (MACN), F. L. de Souza Cunha (MNRJ), L. Price (DGM), A. J. Sutcliff [BM(NH)], R. Hoffstetter (MNHN), M. Coombs (AC), and M. Dawson (CMNH).

For many helpful comments on various phases of this study and/or for reading the manuscript, I thank M. C. McKenna, R. Pascual, R. H. Tedford, and W. D. Turnbull. The figures of specimens (except figs. 49, 51-55) were drawn by Marlene Hill Werner from original specimens and/or epoxy casts. The latter were

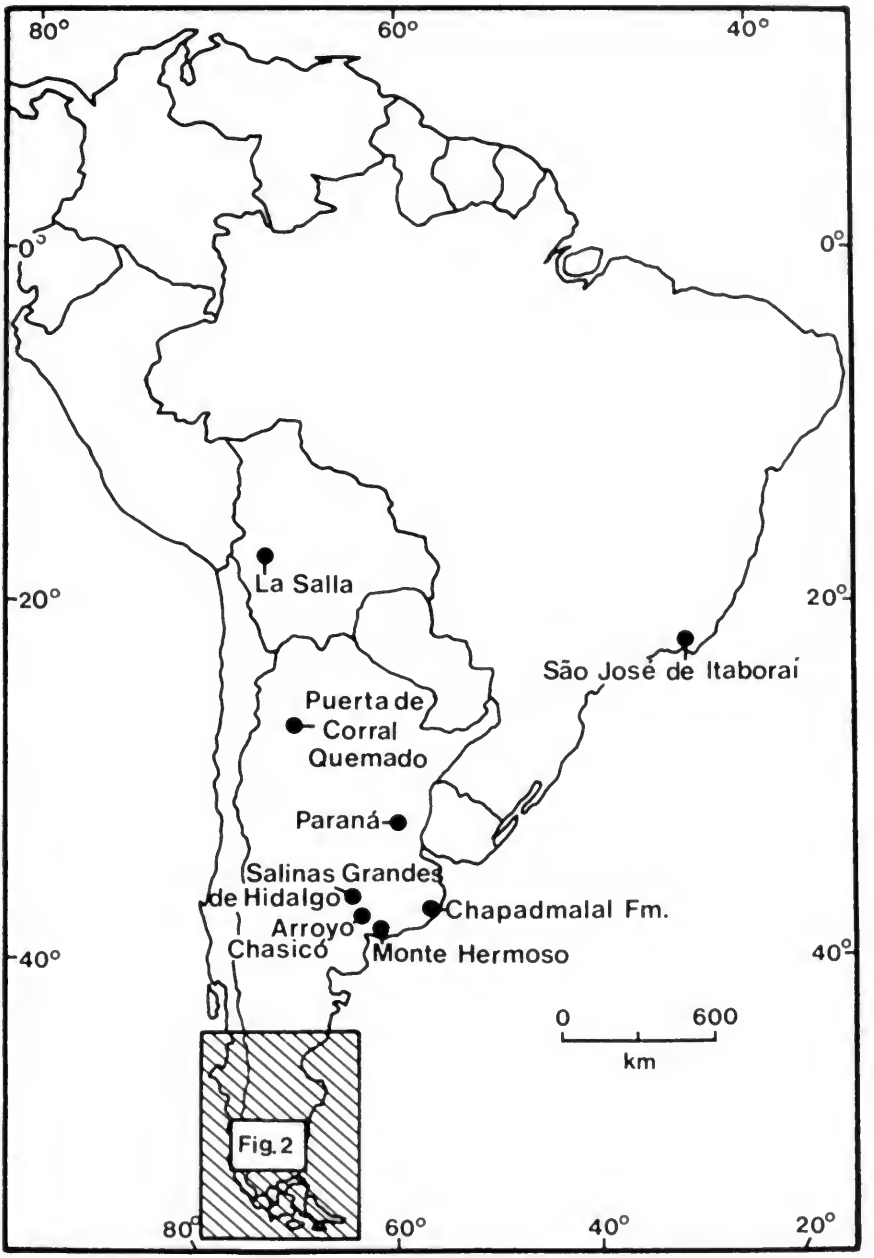

FIG. 1. Map of South America showing some vertebrate fossil localities (circles) discussed in text.

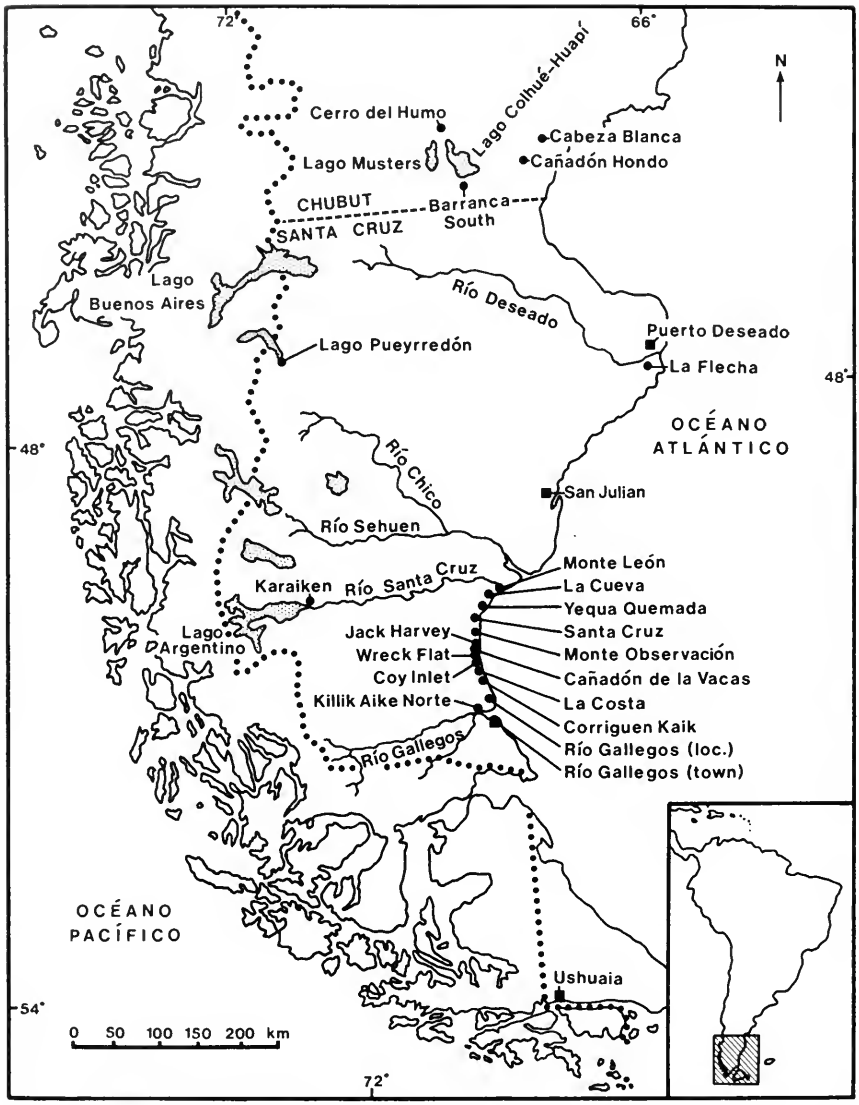

FIG. 2. Map of southern tip of South America showing vertebrate fossil localities (circles) discussed in text.

made by Mrs. Barbara Waters at UCMP. The stereo photographs were made by Ron Testa from epoxy casts.

Initial stages of this study were facilitated by support from UCMP for travel and graduate study and by grants no. 1329, 1698, 1943 from the National Geographic Society, Washington, D.C.; its completion was made possible by National Science Foundation grant DEB-7901976.

SYSTEMATICS

Superfamily BORHYAENOIDEA (Ameghino, 1894, p. 371) Simpson, 1930, p. 9.

Diagnosis.—Dental formula $I\frac{3-4}{3}$, $C\frac{1}{1}$, $P\frac{3-4}{3}$, $M\frac{4}{4}$; 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, p. 371

Diagnosis.—Dental formula $I\frac{3-4}{2-3}$, $C\frac{1}{1}$, $P\frac{3}{3}$, $M\frac{4}{4}$; small to large size; skull dolichocephalic to brachycephalic, rostrum robust and well developed; upper and lower C *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 $M\frac{1}{1}$ to $M\frac{3}{4}$; protocone large to very reduced; paracone often reduced; paracone and metacone approximated on $M^{1\text{-}3}$; 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 HATHLYACYNINAE (Ameghino, 1894, p. 382) Kirsch, 1977, p. 112

[Including Acyonidae,[1] Ameghino, 1889, p. 894; 1891a, p. 147n; Hathlyacynidae Ameghino, 1894, p. 382; Amphiproviverridae Ameghino, 1894, p. 333n (formally proposed on p. 389); Cladictidae Winge, 1923, p. 77; Cladosictidae Ameghino, 1935, p. 131; Cladosictinae Cabrera, 1927, p. 273]

[1]The family-group name Acyonidae was formally proposed by Ameghino (1891a, p. 147n) to accommodate *Acyon* and *Sipalocyon*. The name first appears in a list of families in Ameghino (1889, p. 894). Trouessart (1898, p. 1215) later recognized this taxon as a

Diagnosis.—$I\frac{4}{3}$, $C\frac{1}{1}$, $P\frac{3}{3}$, $M\frac{4}{4}$ (when known); small to medium-sized borhyaenids; mandibular rami long, shallow, and generally gracile; symphysis ligamentous and rami never fused in adult; symphysis typically extends posteriorly to point below P_3; I_{1-3} subequal in size; C weakly or moderately developed; $P\frac{1}{1}$ much smaller than $P\frac{2}{2}$ or $P\frac{3}{3}$; $P\frac{2}{2}$ and $P\frac{3}{3}$ either subequal in size or latter is larger; P_{1-3} usually have small but distinct posterobasal cusps; molars increase in size from M_1 to M_4; metaconid present only in earliest forms (*Patene*); M_{1-3} have large, basined talonid (M_4 with reduced talonid that may or may not be basined); small but distinct anterobasal cingulum on M_{2-4}, weak or absent on M_1; I^{1-4} of subequal size; M^{1-4} with well-developed protocone; paracone well developed and distinct on M^{1-3}, but smaller and fused basally with larger metacone; weak but distinct parastyle on M^{1-3}, increasing in size from M^1 to M^3; distinct paracingulum connects parastyle with protocone; metacrista moderately well developed; M^3 usually with distinct ectoflex, small ectoflex sometimes present on M^2; skull dolichocephalic; large ossified auditory bulla (alisphenoid forms anterior two-thirds, pars mastoidea of periotic forms posterior one-third—Patterson, 1965); ectotympanic has large incisura tympanica dorsally; epitympanic recess rather large and circular; paroccipital process heavy, squat, and blunt; pars petrosa of periotic rather sharply pointed anteriorly; foramen ovale, foramen lacerum posterium, and posterior carotid foramen all large; foramen lacerum medium absent; terminal phalanges uncleft, laterally compressed, and pointed.

Known range.—Riochican through Montehermosan.

Patene Simpson, 1935

Patene Simpson, 1935, p. 3.
Ischyrodidelphis Paula Couto, 1952b, p. 9.

Type of Patene.—*Patene coluapiensis* Simpson, 1935, p. 3.

Type of Ischyrodidelphis.—*Ischyrodidelphis castellanosi* Paula Couto, 1952b, p. 11.

Distribution.—Riochican of Brazil and Casamayoran of Argentina.

Diagnosis.—Borhyaenids of small size; M^{1-4} with large, well-developed protocone and basined talon; paracone slightly smaller than and well separated from metacone on M^{1-3} (both cusps are more external on M^1 and medial on M^3); metastylar spur weakly developed; M^{1-3} with distinct but vestigial protoconules

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subfamily, Acyoninae, and included it with the Borhyaenidae. The last instance in which the family-group name Acyonidae is employed as a valid name appears in Trouessart (1904, p. 176), who recognized it as distinct from the family-group name Borhyaenidae, and in Palmer (1904, p. 877), who included it as a synonym of the family-group name Borhyaenidae. Palmer (1904, p. 877n) noted that "Acyonidae has priority of five years merely by publication in a nominal list, but as Borhyaenidae has come into more general use it is here adopted provisionally."

The family-group name Acyonidae has remained unused as a senior synonym in all zoological literature for the last 70 years. During this time, the family-group name Borhyaenidae has always been used, and Acyonidae has been ignored by everyone working on members of this family. In addition, *Acyon* Ameghino, 1887, is a junior synonym of *Cladosictis* Ameghino, 1887 (Cabrera, 1927, p. 288; this study). A proposal has been submitted to the Commission requesting use of its plenary powers to suppress the family-group name Acyonidae Ameghino, 1889, for the purposes of the Law of Priority, but not for those of the Law of Homonymy, and to place this family-group name on the Official Index of Rejected and Invalid Family-Group Names in Zoology (Marshall, Clemens, et al., 1977, 1978).

and metaconules; shallow but distinct ectoflex present on M^3; M^4 with strong parastylar spur, paracone median, metacone represented by basal cuspule; stylar shelf well developed on M^{1-3}; parastyle small but distinct on M^{1-2}, weakly developed on M^3; P_3^3 proodont with distinct posterobasal cuspule; trigonids prominent and much higher than talonids; metaconid well developed on M_{2-4}, smaller on M_1; talonids well developed and basined on M_{1-4} and narrower than trigonids; M_{1-4} with well-developed anterobasal cingular shelf; no evidence of diastems between C, P_1, and/or P_2.

Patene simpsoni Paula Couto, 1952a. Figures 3–8; Table 1.

Patene simpsoni Paula Couto, 1952a, p. 23, fig. 8A, B; 1961, p. 329, figs. 8–10; 1970, p. 33.

Ischyrodidelphis castellanosi Paula Couto, 1952b, p. 11; 1962, p. 140, fig. 1.

Type of Patene simpsoni.—MNRJ 1331-V, a right maxillary with P^3-M^4 (figured by Paula Couto, 1961, figs. 8-9).

Type of Ischyrodidelphis castellanosi.—MNRJ 1351-V, a partial right mandibular ramus with roots of P_2, P_3-M_2, and trigonid of M_3 present, and alveoli of M_3 talonid and M_4 (figured by Paula Couto, 1962, fig. 1A-B).

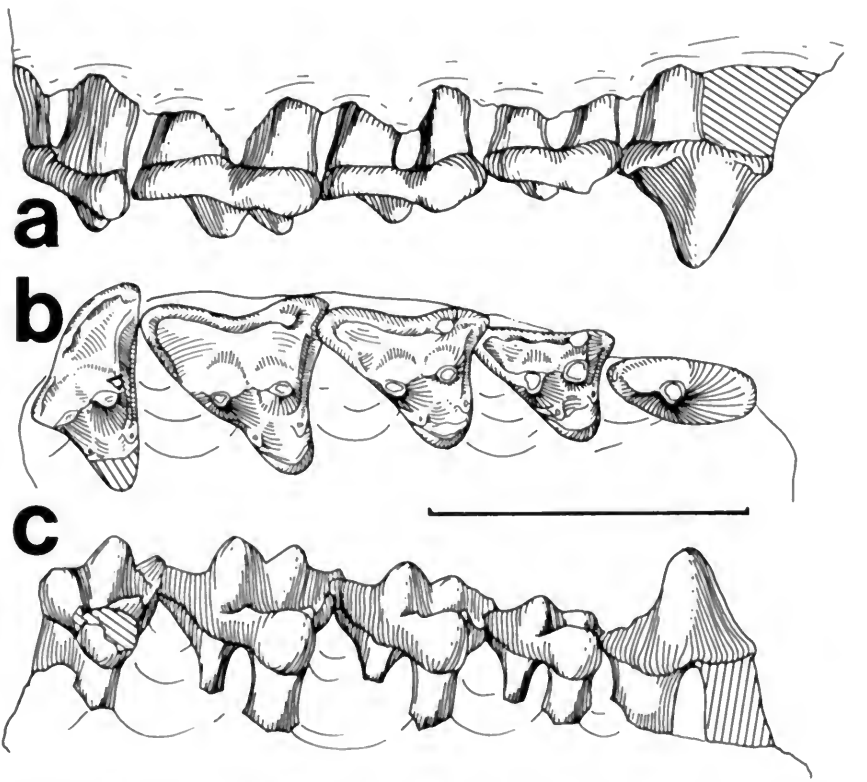


FIG. 3. *Patene simpsoni* Paula Couto, 1952a (Riochican). MNRJ 1331-V (type), a right maxillary with P^3-M^4 complete: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 10 mm.

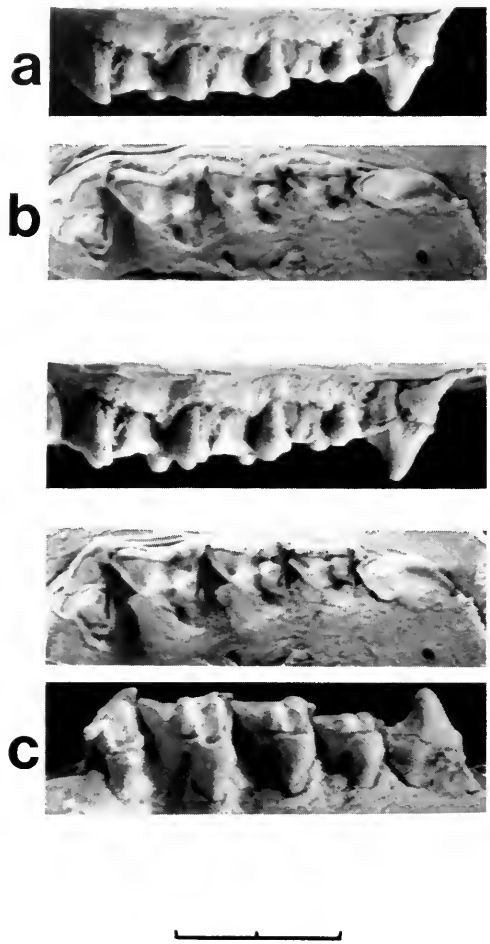


FIG. 4. *Patene simpsoni* Paula Couto, 1952a (Riochican). Stereopairs of MNRJ 1331-V (type), a right maxillary with P^3-M^4 complete: **a,** labial; **b,** occlusal; **c,** lingual views. Scale = 10 mm.

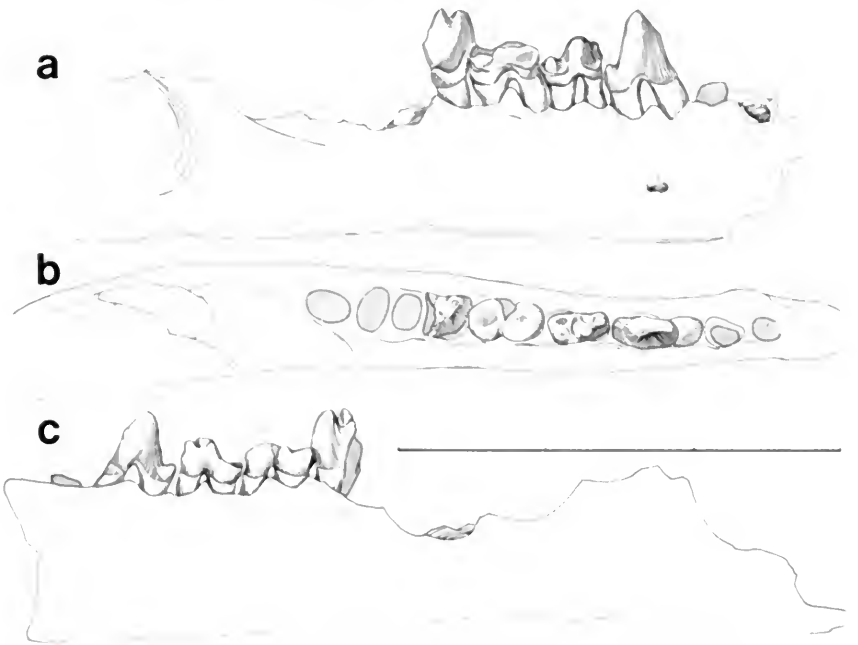


FIG. 5. *Patene simpsoni* Paula Couto, 1952a (Riochican). MNRJ 1351-V (type of *Ischyrodidelphis castellanosi* Paula Couto, 1952b), a partial right mandibular ramus with roots of P_2, P_3-M_2 and trigonid of M_3 present, and alveoli of M_3 talonid and M_4: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 30 mm.

Hypodigm.—The two types and DGM 324-M, a fragment of a right mandibular ramus with alveoli of P_2 and roots of P_3, anterior root of M_1, talonid and anterior root of M_2, M_3 virtually complete, and roots of M_4 (the M_3 is figured by Paula Couto, 1952a, fig. 8A, B; 1961, fig. 10); DGM 331-M, part of a left maxilla with alveoli of M^{1-3} and incomplete alveoli of P^3 and M^4; DGM 654-M, an isolated right M_3; DGM 655-M, an isolated right M_3; DGM 656-M, an isolated right M_3; DGM 797-M, an isolated right M^3; DGM 798-M, an isolated left M_3; MNRJ 1332-V, an isolated right M^4; MNRJ 1333-V (now AMNH 49804), an isolated left M^1; MNRJ 1334-V (now AMNH 49805), an isolated right M^2; MNRJ 1335-V, an incomplete isolated M^1 or M^2; MNRJ 1336-V, an isolated left lower trigonid; MNRJ 1337-V, an isolated left lower M_4 trigonid; MNRJ 1338-V, an isolated left lower trigonid; MNRJ 1339-V, an isolated left lower trigonid; MNRJ 1340-V, an isolated left lower trigonid; MNRJ 1341-V, an isolated left M_3 trigonid; MNRJ 1342-V, an isolated left lower trigonid; MNRJ 1343-V, an isolated left lower trigonid; MNRJ 1352-V, an isolated right M_2; MNRJ 1353-V, an isolated right M_2 (figured by Paula Couto, 1962, fig. 1C-E); MNRJ 1354-V, an isolated left M_3; MNRJ 1425-V, an isolated right P_3; MNRJ 1428-V, an isolated right lower molar trigonid; (DGM 324-M, MNRJ 1332-V, and MNRJ 1335-V are paratypes of *P. simpsoni;* and MNRJ 1352-V, 1353-V, 1354-V, and 1425-V are paratypes of *I. castellanosi*).

Horizon and locality.—All specimens were collected from fissure deposits in the Itaboraí Formation, São Jose de Itaboraí, Brazil.

Age.—Riochican.

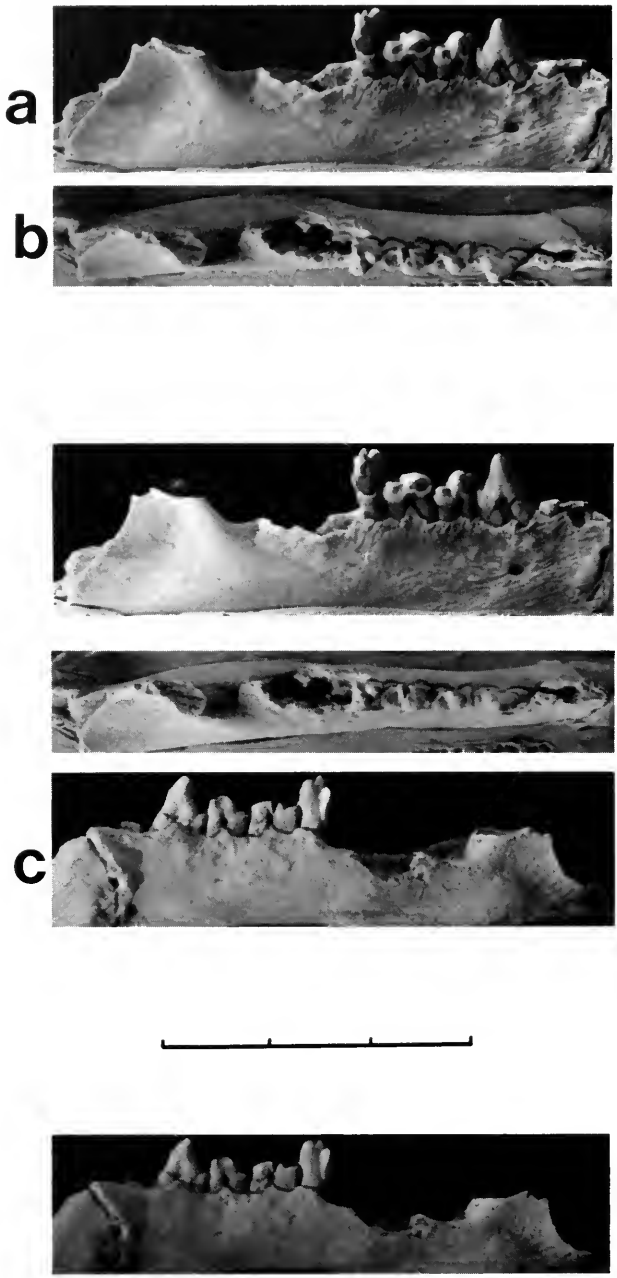


FIG. 6. *Patene simpsoni* Paula Couto, 1952a (Riochican). Stereopairs of MNRJ 1351-V (type of *Ischyrodidelphis castellanosi* Paula Couto, 1952b), a partial right mandibular ramus with roots of P_2, P_3-M_2 and trigonid of M_3 present, and alveoli of M_3 talonid and M_4: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 30 mm.

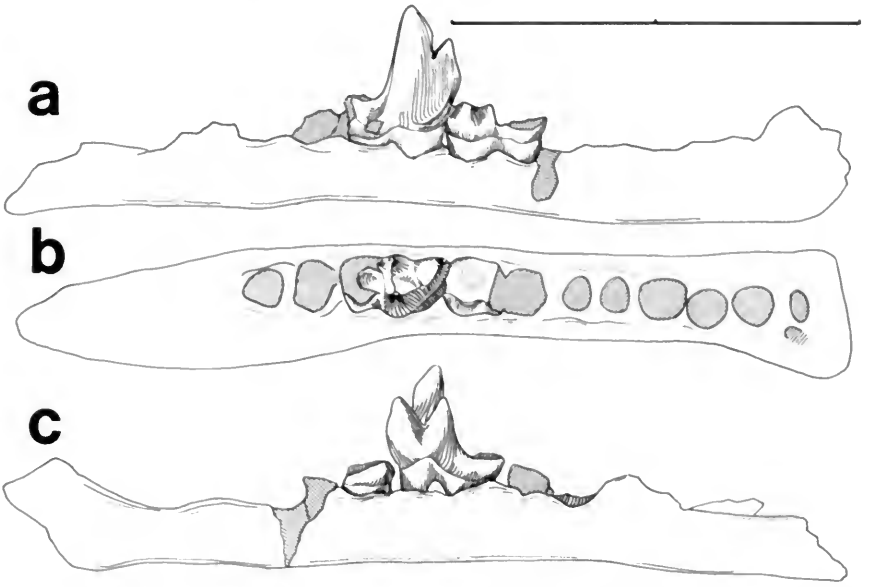


FIG. 7. *Patene simpsoni* Paula Couto, 1952a (Riochican). DGM 324-M, a fragment of a right mandibular ramus with alveoli of P_2 and roots of P_3, anterior root of M_1, talonid and anterior root of M_2, M_3 virtually complete, and roots of M_4: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 20 mm.

Diagnosis.—Differs from *Patene coluapiensis* in being about one-fourth to one-third smaller in linear tooth dimensions and in having relatively larger protocones and wider stylar shelf on M^{1-3}, a larger metacone on M^4, and a slightly shallower ectoflex on M^3.

Comments.—Paula Couto (1952b, p. 11) erected *Ischyrodidelphis castellanosi* on a partial lower dentition and several isolated cheek teeth. He assigned this species to the subfamily Didelphinae and concluded (1952b, p. 9) that "its closest affinities seem to be with the largest Recent species of the genus *Didelphis*."

I have compared all specimens assigned by Paula Couto to *I. castellanosi* with the lower dentitions of *Patene simpsoni* and found them to represent the same species. I therefore formally recognize *I. castellanosi* as a junior synonym of *P. simpsoni*. The recognition that these species are synonymous readily explains why Paula Couto did not assign upper cheek teeth to *I. castellanosi;* they were all assigned to *P. simpsoni*. In the lower dentition, he assigned complete cheek teeth from M_2 forward to *I. castellanosi*, whereas he assigned complete M_3s and M_4s to *P. simpsoni*.

Patene simpsoni is the most generalized of known borhyaenoids. Indeed, if more specialized borhyaenoids like cf. *Nemolestes* sp. were not contemporaneous with it (see Marshall, 1978, p. 27), *P. simpsoni* would be an ideal prototype for the superfamily. *Patene simpsoni* is, nonetheless, structurally the most generalized and temporally the oldest of known Hathlyacyninae and may represent the basal stock for the subfamily.

TABLE 1. Measurements of cheek teeth of *Patene simpsoni* and *P. coluapiensis*.

Specimen	P3		M1		M2		M3		M4		M1-3
	L	W	L	W	L	W	L	W	L	W	L
UPPER CHEEK TEETH											
P. simpsoni											
MNRJ 1331-V	4.8	2.5	4.3	3.8	5.2	4.7	5.8	5.9	3.5	6.7	15.2
MNRJ 1332-V	...	...	...	...	...	...	...	...	3.3	5.6	...
MNRJ 1333-V (AMNH 49804)	...	...	4.2	3.9	...	...	...	...	...	...	...
MNRJ 1334-V (AMNH 49805)	...	...	...	...	5.0	4.5	...	...	...	...	...
P. coluapiensis											
AMNH 28448	...	...	6.3	4.8	7.1	6.0	7.7	7.0	2.9	7.8	21.4
LOWER CHEEK TEETH											
P. simpsoni											
DGM 324-M	...	...	...	...	...	...	5.6	2.9	...	...	...
DGM 654-M	...	...	...	...	...	...	5.8	3.1	...	...	...
DGM 655-M	...	...	...	...	...	...	6.0	3.0	...	...	...
DGM 656-M	...	...	...	...	...	...	5.8	3.0	...	...	...
DGM 798-M	...	...	...	...	...	...	5.7	3.1	...	...	...
MNRJ 1337-V	...	...	...	...	...	...	...	...	...	3.7	...
MNRJ 1341-V	...	...	...	...	...	...	...	2.9	...	...	...
MNRJ 1351-V	4.8	2.0	4.2	2.1	4.7	2.6	...	3.0	...	...	...

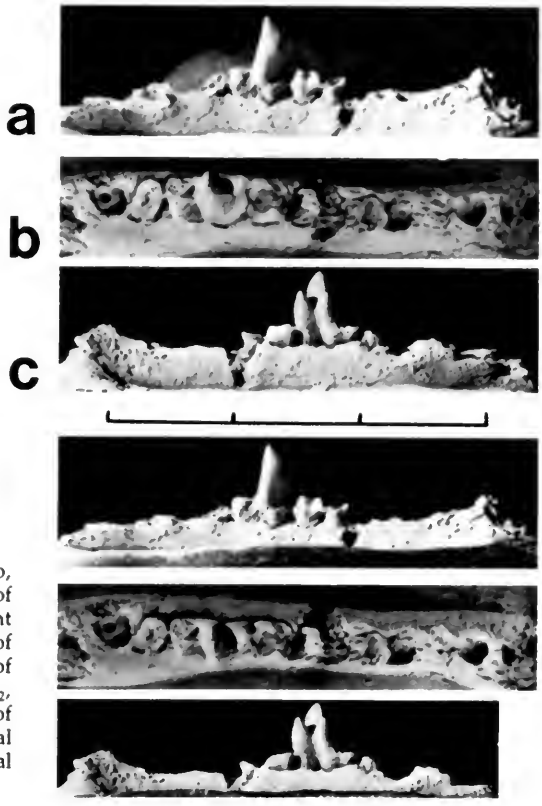


FIG. 8. *Patene simpsoni* Paula Couto, 1952a (Riochican). Stereopairs of DGM 324-M, a fragment of a right mandibular ramus with alveoli of P_2 and roots of P_3, anterior root of M_1, talonid and anterior root of M_2, M_3 virtually complete, and roots of M_4: **a**, labial; **b**, occlusal; **c**, lingual views. Scale for labial and lingual views = 30 mm.

Patene coluapiensis Simpson, 1935. Figures 9, 10; Table 1.

Patene coluapiensis Simpson, 1935, p. 3; 1948, pp. 44–45, fig. 5.

Type.—AMNH 28448, a right maxillary with M^{1-4} (figured by Simpson, 1948, fig. 5).

Hypodigm.—Type only

Horizon and locality.—From Casamayor beds south of Lago Colhué-Huapí, Chubut Province, Argentina; it is from the lowest known fossil horizon of this age.

Age.—Casamayoran.

Diagnosis.—Differs from *P. simpsoni* in being about one-fourth to one-third larger in linear tooth dimensions and in having relatively smaller protocones and a slightly narrower stylar shelf on M^{1-3}, a more reduced metacone on M^4, and a slightly deeper ectoflex on M^3.

Comments.—*Patene coluapiensis* is very similar to the Riochican *P. simpsoni*, and except for the features noted in the diagnosis above, these species are inseparable. *Patene coluapiensis* is known only from the Casamayoran of Argentina, and *P. simpsoni*, from the Riochican of Brazil. Considering their structural similarity and their occurrence in successive aged beds, they may be regarded as a single evolutionary lineage. I therefore recognize *P. coluapiensis* as a slightly larger, more specialized descendant of *P. simpsoni*.

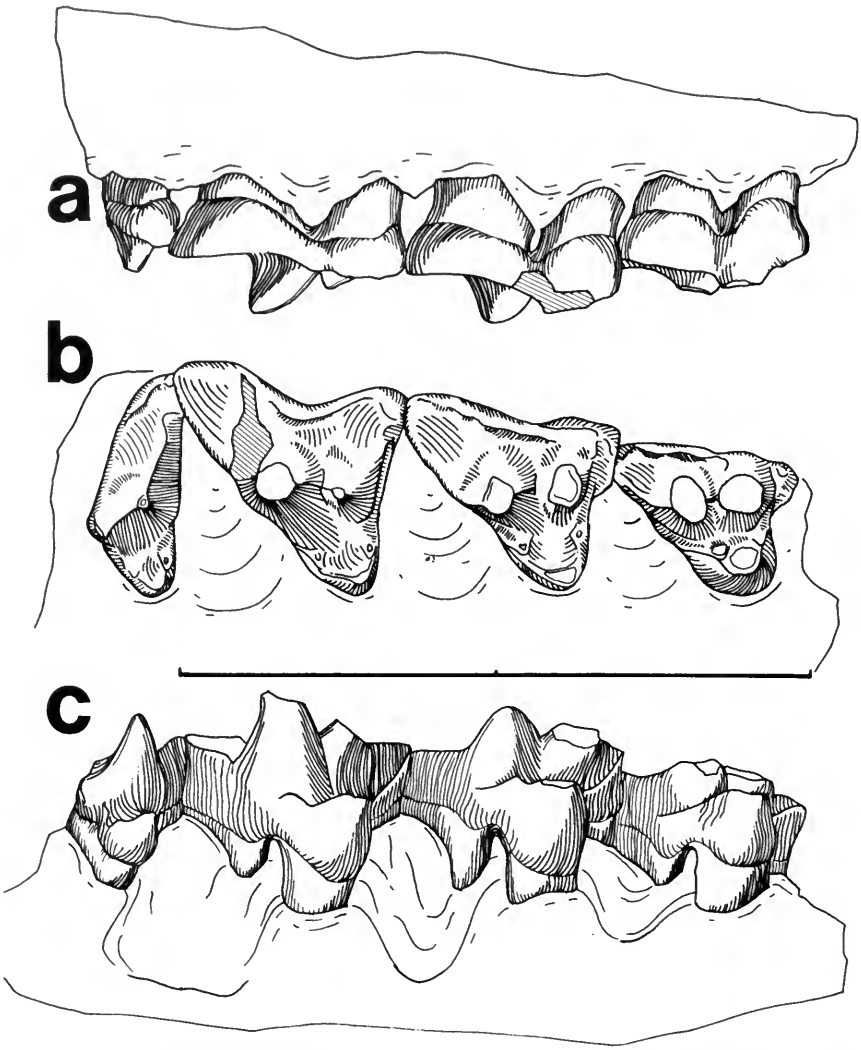


FIG. 9. *Patene coluapiensis* Simpson, 1935 (Casamayoran). AMNH 28448 (type), a right maxillary with M^{1-4}: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 20 mm.

Simpson (1948, p. 45) noted that an isolated broken upper molar (AMNH 28532) from the Rio Chico beds at Cañadón Hondo was similar to *P. coluapiensis* and accordingly he referred it to *Patene* sp. This assignment is, however, very tentative, and it could just as convincingly be argued that this specimen was referable to other Casamayoran genera such as *Nemolestes* or *Argyrolestes*, both poorly known members of the subfamily Borhyaeninae (see Marshall, 1978, pp. 26-27). My preference is to regard AMNH 28532 as Borhyaenidae, genus and species indeterminate.

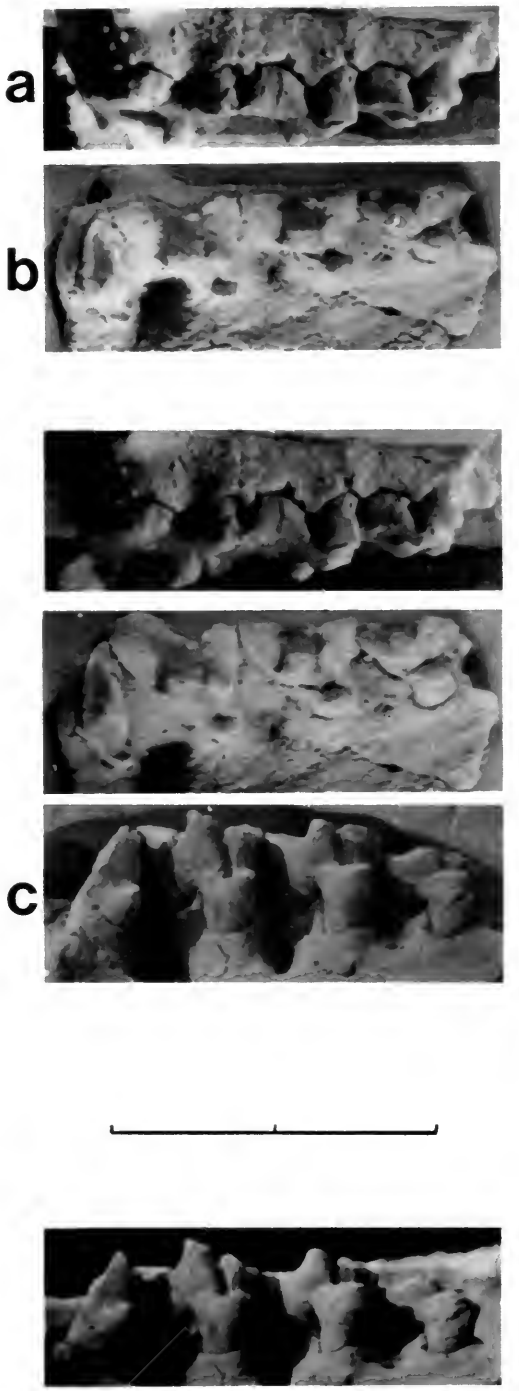


FIG. 10. *Patene coluapiensis* Simpson, 1935 (Casamayoran). Stereopairs of AMNH 28448 (type), a right maxillary with M^{1-4}: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 20 mm.

Procladosictis Ameghino, 1902b

Procladosictis Ameghino, 1902b, p. 46; 1906, p. 354; Schlosser, 1923, p. 440; Scott, 1937, p. 704.

Type.—*Procladosictis anomala* Ameghino, 1902b, p. 46.

Distribution.—Mustersan beds, Patagonia, southern Argentina.

Diagnosis.—As for type and only known species.

Procladosictis anomala Ameghino, 1902b. Figures 11, 12.

Procladosictis anomala Ameghino, 1902a, p. 320 (*nomen nudum*); 1902b, p. 46; 1906, p. 354, fig. 191; Simpson, 1948, p. 45, pl. 2, fig. 7.

Type.—MACN 10327, a fragment of a right maxillary with P^3-M^3 complete (figured by Ameghino, 1906, fig. 191; Simpson, 1948, fig. 7).

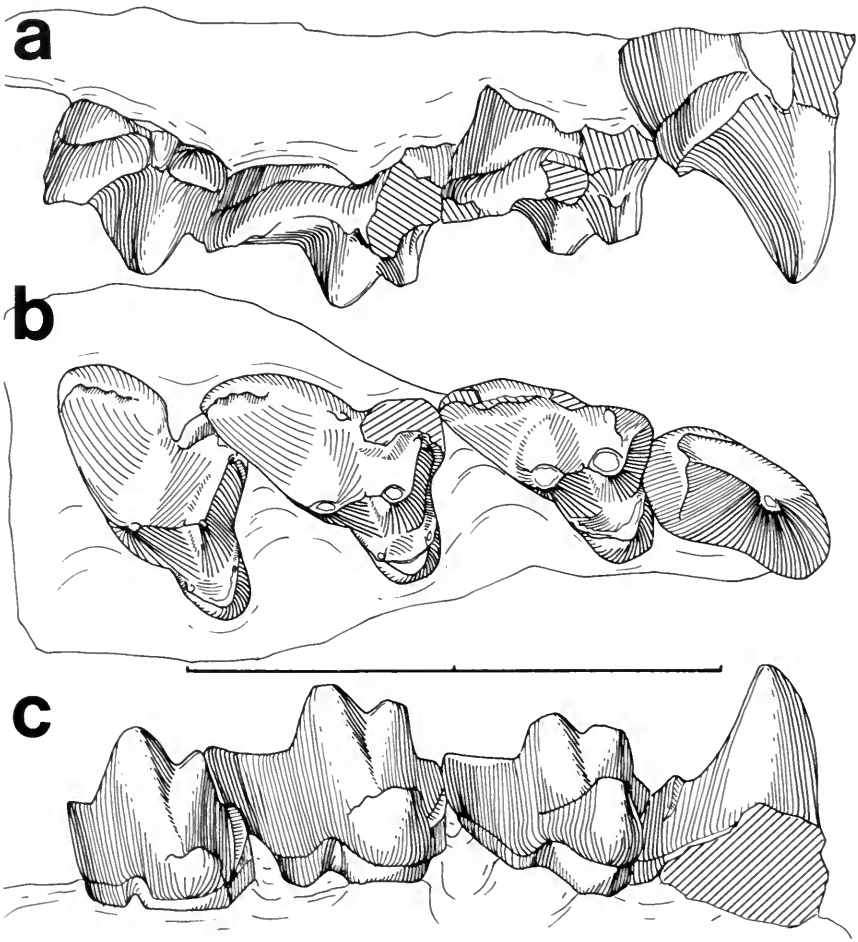


FIG. 11. *Procladosictis anomala* Ameghino, 1902b (Mustersan). MACN 10327 (type), a fragment of a right maxillary with P^3-M^3 complete: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 20 mm.

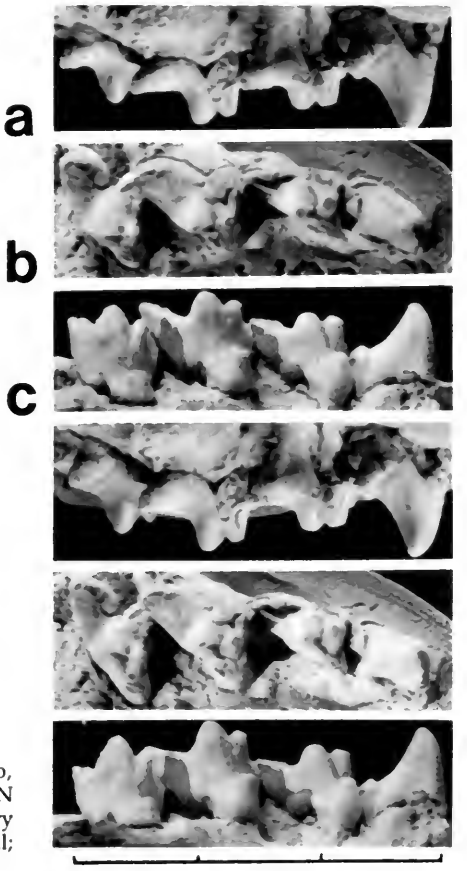


FIG. 12. *Procladosictis anomala* Ameghino, 1902b (Mustersan). Stereopairs of MACN 10327 (type), a fragment of a right maxillary with P^3-M^3 complete: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 30 mm.

Hypodigm.—Type only.

Horizon and locality.—"Couches á *Astraponotus*," Chubut Province, Patagonia, southern Argentina. No other data.

Age.—Mustersan.

Diagnosis.—Small borhyaenid; crown of P^3 higher than M^1, and with a distinct posterobasal heel; protocone distinct but low on M^{1-3}, and becoming smaller from M^1 to M^3 (very weak on M^3); talon cuspate; paracone and metacone confluent basally; metacone slightly larger than paracone on M^1, paracone smaller on M^2 and very reduced on M^3; metacone in turn becomes progressively larger from M^1 to M^3; paracone and metacone median on M^1, progressively more internal on M^{2-3}; outer margin nearly straight on M^{1-2}, and bilobed with deep ectoflex on M^3; twin styles, anterior larger and external to paracone and metacone on M^2, small on M^1, absent on M^3; distinct paracingulum on M^2, weak on M^1 and M^3 (modified from Simpson, 1948, p. 45).

Measurements.—L P^3 = 9.0 mm, W P^3 = 4.5 mm; L M^1 = 9.0 mm, W M^1 = 6.5 mm; L M^2 = 9.5 mm, W M^2 = 8.0 mm; L M^3 = 7.5 mm, W M^3 = 10.0 mm.

Comments.—The P^3 was restored onto the anterior edge of the M^1 with wax. The oblique position that this tooth now occupies, as noted by Simpson (1948,

p. 45), is thus a factor of restoration and is not a diagnostic character of the species or genus. The anterolabial corner of the M^2 is broken off and with it parts of the two stylar cusps.

The P^3-M^2 of *Procladosictis anomala* are generalized in structure and resemble not only species of *Patene* from the Riochican and Casamayoran but also later taxa of similar size such as *Sipalocyon* and *Cladosictis* from the Colhuehuapian and Santacrucian. The M^3 of *P. anomala* has a very deep ectoflex, a feature not found in other Borhyaenidae. This feature makes *P. anomala* very distinct, and represents a specialization that excludes it as an ancestor for any known later taxa. Based on present evidence, *P. anomala* is regarded as a dead-end offshoot of an early Tertiary hathlyacynine radiation. It apparently represents a slightly larger specialized descendant of a population of *Patene coluapiensis*.

Simpson (1948, p. 45) recorded that a lower isolated left molar (AMNH 29433), possibly an M_3 from Mustersan beds at Cerro del Humo, may belong to *Procladosictis*. The tooth measures L = 9.8 mm, W of trigonid = 4.9 mm, W talonid = 4.9 mm. The tooth has a minute metaconid and a narrow-basined talonid with hypoconulid poorly distinguished from entoconid.

Procladosictis erecta Ameghino, 1902b

Procladosictis erecta Ameghino, 1902a, p. 316 (*nomen nudum*); 1902b, p. 47.
"Procladosictis" erecta Simpson, 1948, p. 45 (as *nomen vanum*).

Type.—MACN 10328, a lower premolar.
Hypodigm.—Type only.
Horizon and *locality*.—"Partie superieure des couches á *Notostylops*," north of Lago Colhué-Huapí, Chubut Province, Argentina (for discussion on this locality see Simpson, 1967, p. 64).
Age.—Casamayoran.
Diagnosis.—Indeterminate.
Comments.—"There is no real reason for referring this [species] to *Procladosictis*, a genus based on upper teeth from a different horizon. Nor does there seem to be any way in which this supposed species can now be defined or distinguished. The type is a lower premolar, 9.3 mm long and 4.0 mm wide, with central cusps and sloping, noncuspidate heel. It may be kept on record, since a neotype might show the species to be distinctive, but its present value and significance are nil" (Simpson, 1948, pp. 45–46).

Pseudocladosictis Ameghino, 1902b

Pseudocladosictis Ameghino, 1902b, p. 47.

Type.—*Pseudocladosictis determinabile* Ameghino, 1902b, p. 47.
Distribution.—Casamayor beds, Patagonia.
Diagnosis.—As for type and only known species.

Pseudocladosictis determinabile Ameghino, 1902b

Procladosictis determinabile Ameghino, 1902a, p. 316 (*nomen nudum*).
Pseudocladosictis determinabile Ameghino, 1902b, p. 47; Simpson, 1948, p. 46 (as *nomen vanum*).

Type.—MACN 10325, an isolated premolar, considered a lower by Ameghino, but an upper by Simpson.

Hypodigm.—Type only.

Horizon and locality.—"Couches á *Notostylops*" (upper part, *fide* Ameghino) from Great Barranca south of Lago Colhué-Huapí, Chubut Province, Argentina.

Age.—Casamayoran.

Diagnosis.—Indeterminate.

Comments.—"The type measures 8.8 by 6.1 mm and has a central cusp and small, partly transverse, cuspidate heel. Like *Procladosictis erecta*, the species [*determinabile*] is essentially no more than preëmptive, based on no good evidence but securing the species to its author in case later work shows it to be valid" (Simpson, 1948, p. 46).

Pseudonotictis gen. nov.

Etymology.—*Pseudo-* (Gr., false or lie), name given in reference to morphological similarity to Huayquerian genus *Notictis*.

Type.—*Pseudonotictis pusillus* (Ameghino, 1891c, p. 315).

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

Diagnosis.—As for type and only known species.

Pseudonotictis pusillus (Ameghino, 1891c). Figures 13–16; Tables 2, 3.

Sipalocyon pusillus Ameghino, 1891c, p. 315; 1894, p. 393; 1935, p. 111, fig. 12 (caption only); Cabrera, 1927, p. 293.
Hathliacynus kobyi Mercerat, 1891a, p. 53.
Perathereutes kobyi Cabrera, 1927, p. 293, figs. 9, 10.

Type of Pseudonotictis pusillus.—MACN 666, a fragment of a right mandibular ramus with alveoli of I_{1-3}, C, and P_{1-2}; anterior root of P_3; posterior half of P_3; anterior half of M_1; posterior root of M_1 and anterior alveolus of M_2.

Type of Hathliacynus kobyi.—MLP 11-26, a left mandibular ramus with root of C, P_1 and P_3-M_4 complete, anterior half and posterior root of P_2 present; fragment of a right mandibular ramus with P_{1-3} complete; fragment of a right maxillary with alveoli of P^3-M^1, and a complete M^2; and various cranial fragments; a right humerus (figured by Cabrera, 1927, fig. 10); right radius; part of a right ulna; and two metapodials; all of a single associated individual. [Cabrera (1927, fig. 9) figured as *Perathereutes kobyi* an edentulous right maxillary and a left mandibular ramus in which the M_3 was missing the posterior half of the trigonid and all of the talonid. These elements are part of the type of *Hathliacynus kobyi* (MLP 11-26). In 1975, I found several isolated teeth and tooth fragments associated with these elements. An isolated right M^2 fit perfectly into the alveolar counterpart of the maxillary fragment, and the missing portion of the lower left M_3 was also present. Figures 13–16 presented here show these elements with the teeth restored.]

Hypodigm.—The two types and MLP 11-40, a fragment of a right mandibular ramus with M_1.

Horizon and locality.—All specimens are from the Santa Cruz Formation, Santa Cruz Province, Argentina. MACN 666 is from Monte Observación and was collected by Carlos Ameghino in 1890-91. MLP 11-26 and 11-40 are from Monte León (no other data).

Age.—Santacrucian.

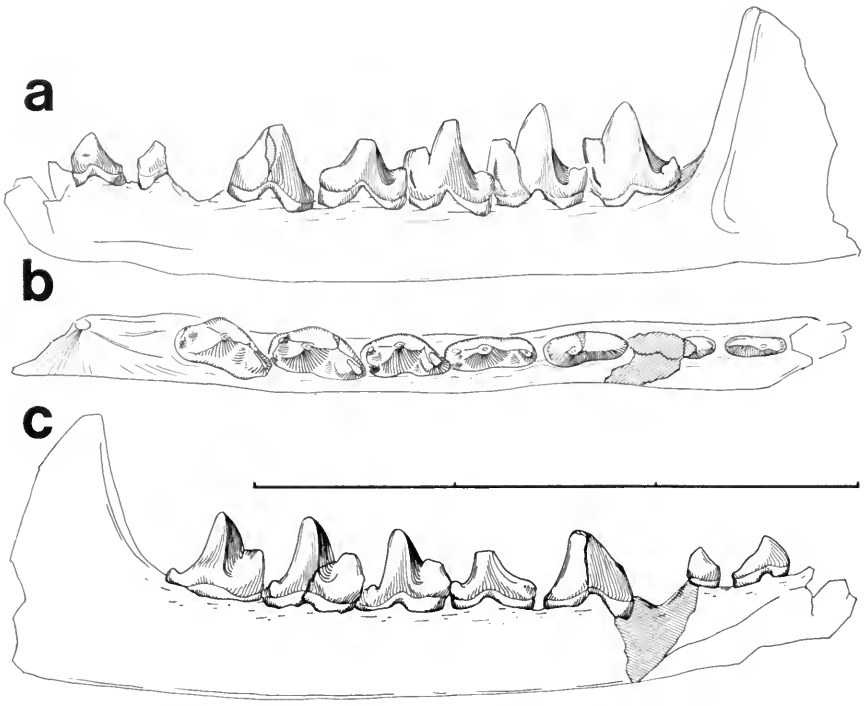


FIG. 13. *Pseudonotictis pusillus* (Ameghino, 1891c) (Santacrucian). MLP 11-26 (type of *Hathliacynus kobyi* Mercerat, 1891a), a left mandibular ramus with root of C, P_1 and P_3-M_4 complete, and anterior half and posterior root of P_2 present: **a,** labial; **b,** occlusal; **c,** lingual views. Scale = 30 mm.

Diagnosis.—Smallest known species of Santacrucian borhyaenid; C weakly developed; large, elongated mental foramen below P_{1-2} contact and below M_1; P_1 very reduced compared with P_{2-3}; M_{1-3} talonids well developed and basined, but proportionately smaller than in contemporary species of *Sipalocyon;* M_4 talonid very reduced but basined; P_{1-3} aligned in same anteroposterior axis; P_1 separated from C and P_2 by small diastems; posterobasal heel not distinct on P_{1-3}; M^2 with distinct protocone, talon not basined; paracone well developed and distinct, but smaller and fused basally with large metacone; a small but distinct ectocingulum and parastyle present on M^2, a very shallow ectoflex occurs labial to metacone; differs from *Notictis ortizi* in having proportionately smaller talonids, in an absolutely longer premolar region and a larger P_1.

Comments.—*Sipalocyon pusillus* was erected by Ameghino in 1891 (1891c, p. 315). That same year Mercerat (1891a, p. 53) described *Hathliacynus kobyi.* Three years later Ameghino (1894, p. 393) formally recognized *H. kobyi* as a junior synonym of *S. pusillus* and placed them in the Sparassodonta, family Amphiproviverridae. Cabrera (1927, p. 393, figs. 9, 10), however, recognized *H. kobyi* as a species of *Perathereutes* and regarded *S. pusillus* as valid.

In the present study I recognize the type species of *Sipalocyon, S. gracilis,* as valid, and the type species of *Hathliacynus, H. lustratus,* as a junior synonym of *Cladosictis patagonica. Perathereutes pungens* is also here recognized as valid.

TABLE 2. Measurements of cheek teeth of *Pseudonotictis pusillus* and *Notictis ortizi*.

Specimen	P1		P2		P3		M1		M2		M3		M4		P_{1-3}	P_1-M_4	M_{1-4}
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	L	L
UPPER CHEEK TEETH																	
P. pusillus																	
MLP 11-26	...	...	...	...	...	...	...	...	5.0	3.4	...	...	...	...	...	...	...
LOWER CHEEK TEETH																	
P. pusillus																	
MACN 666	...	...	...	...	...	1.6	...	1.7	...	...	...	...	...	...	13.3	...	...
MLP 11-26(l)	2.6	1.1	...	...	4.3	1.6	4.3	1.7	4.5	2.1	4.9	2.4	5.0	2.5	12.6	30.7	18.2
MLP 11-26(r)	2.5	1.2	4.0	1.3	4.3	1.7	...	...	...	...	...	...	...	...	12.6	...	...
N. ortizi																	
MACN 3996	...	...	...	...	...	...	4.5	1.7	4.8	2.2	5.0	2.4	...	...	ca. 8.5	27.0	ca. 19.0

TABLE 3. Measurements of mandibular rami of *Pseudonotictis pusillus* and *Notictis ortizi*.

Specimen	Depth of ramus below labial side of M1	Breadth of same	Depth of ramus below labial side of M4	Breadth of same
P. pusillus				
MACN 666	8.0	3.5	...	...
MLP 11-26	7.7	3.4	8.0	3.7
N. ortizi				
MACN 3996	7.3	3.3	7.5	3.9

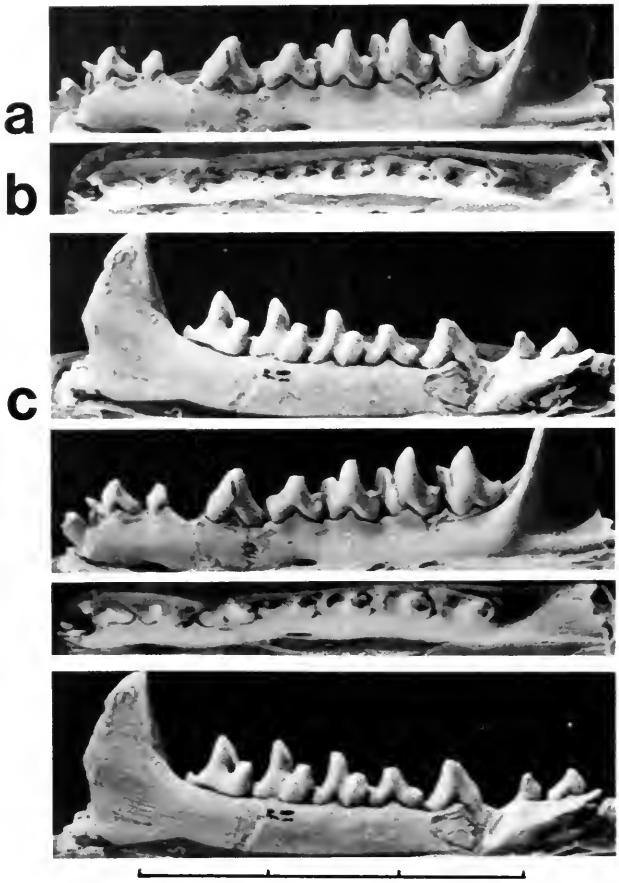


FIG. 14. *Pseudonotictis pusillus* (Ameghino, 1891c) (Santacrucian). Stereopairs of MLP 11-26 (type of *Hathliacynus kobyi* Mercerat, 1891a), a left mandibular ramus with root of C, P_1 and P_3-M_4 complete, and anterior half and posterior root of P_2 present: a, labial; b, occlusal; c, lingual views. Scale = 30 mm.

If the species *pusillus* is to be included in any presently recognized genus following arrangements of previous workers, it would have to be placed either in *Cladosictis,* from which it is certainly distinct and does not belong, or in *Sipalocyon* as originally proposed by Ameghino. There are sufficient differences, however, between *pusillus* and species of *Sipalocyon* to warrant generic separation. For this reason I have proposed the new generic name *Pseudonotictis.*

Pseudonotictis pusillus differs from species of *Sipalocyon* in being smaller in size, in having a proportionately smaller P_1, in lacking a distinct (or less prominent) posterobasal heel on P_{1-3}, in having a relatively and absolutely smaller protocone on upper molars, and in having a more weakly developed canine.

Pseudonotictis pusillus is similar in size to the Riochican species *Patene simpsoni.* These species differ in *P. pusillus* having a more specialized dentition in the

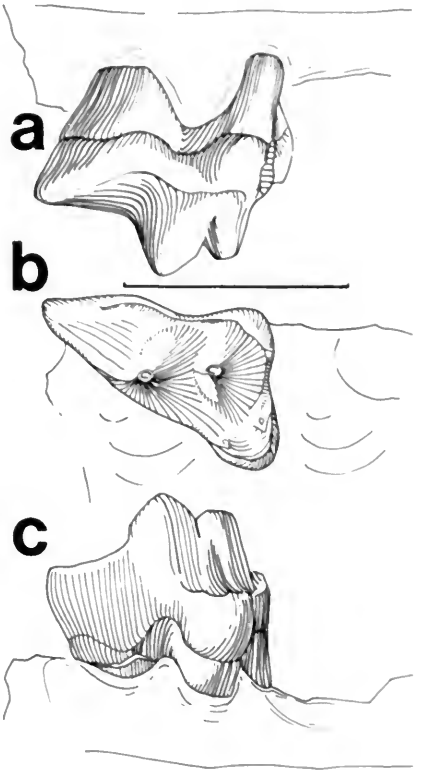


FIG. 15. *Pseudonotictis pusillus* (Ameghino, 1891c) (Santacrucian). MLP 11-26 (type of *Hathliacynus kobyi* Mercerat, 1891a), a fragment of a right maxillary with alveoli of P^3-M^1, and a complete M^2: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 5 mm.

direction of carnassialization than does *P. simpsoni*. The primary changes involved in such a lineage include reduction in size of the protocone, stylar shelf, talonid, and metacone (latter becoming fused basally with paracone); virtual loss of posterobasal cuspule on P_3; loss of metaconid; elongation and tricuspid structure of M_1; and an increase in size and importance of postvallum-prevallid shear. Considering the time involved, Riochican to Santacrucian, these changes are minor, and I thus choose to regard *P. simpsoni* as the Riochican structural ancestor of *P. pusillus*.

Pseudonotictis pusillus is in turn very similar to *Notictis ortizi* from the Huayquerian. Both species are of similar size, both have virtually identical molar morphology, both have weakly developed canines, and the size, shape, and location of the mental foramina are similar. The premolars in *N. ortizi* are absolutely and relatively smaller than in *P. pusillus*, and the premolar region of the jaw is more shortened and the teeth crowded, such that the P_1 is set obliquely in the jaw. These differences are related to shortening of the premolar region of the jaw and are thus the expression of a single basic change. Even taken as a whole, the differences between these species are not great and represent only slight modification or specialization of features seen in *P. pusillus*. An ancestral-descendant relationship for these taxa seems probable.

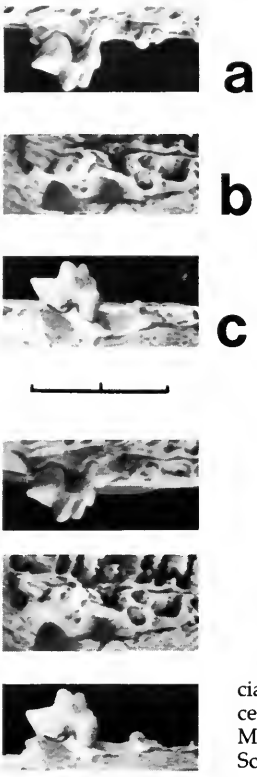


FIG. 16. *Pseudonotictis pusillus* (Ameghino, 1891c) (Santacrucian). Stereopairs of MLP 11-26 (type of *Hathliacynus kobyi* Mercerat, 1891a), a fragment of a right maxillary with alveoli of P^3-M^1, and a complete M^2: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 10 mm.

Notictis Ameghino, 1889

Notictis Ameghino, 1889, p. 911; Kraglievich, 1934, p. 62; Reig, 1952, p. 3.

Type.—*Notictis ortizi* Ameghino, 1889, p. 912.

Distribution.—"Mesopotamian beds" along río Paraná, Entre Ríos Province, Argentina.

Diagnosis.—As for type and only known species.

Notictis ortizi Ameghino, 1889. Figures 17, 18; Tables 2, 3.

Notictis ortizi Ameghino, 1889, p. 912, pl. 72, fig. 14, pl. 81, fig. 7; 1891b, p. 262; Kraglievich, 1934, pp. 62–63; Simpson, 1945, p. 42n (as *nomen vanum*); Reig, 1952, p. 3, fig. 1; Ringuelet, 1953, p. 267.

Didelphys curvidens Burmeister, 1891, p. 379, pl. 7, fig. 1.

Type.—MACN 3996, a left mandibular ramus with alveoli of C and P_1-M_1 complete, M_{2-4} present but broken (figured by Ameghino, 1889, pl. 72, fig. 14; Burmeister, 1891, pl. 7, fig. 1; Reig, 1952, fig. 1).

Hypodigm.—Type only.

Horizon and locality.—"Piso mesopotámico de la formación patagónica," "barrancas de los alrededores de la ciudad del Paraná," along the río Paraná, Entre Ríos Province, Argentina.

Age.—Huayquerian.

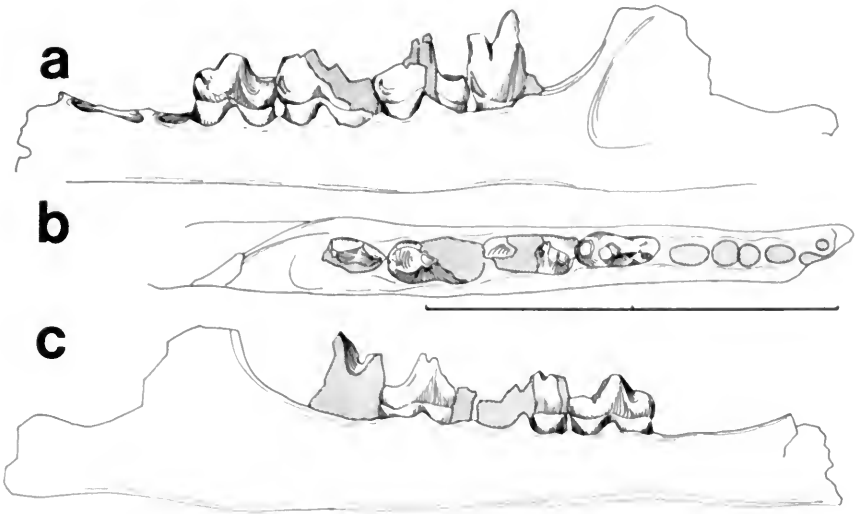


FIG. 17. *Notictis ortizi* Ameghino, 1889 (Huayquerian). MACN 3996 (type), a left mandibular ramus with alveoli of C, P_1-M_1 complete, and M_{2-4} present but broken: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 20 mm.

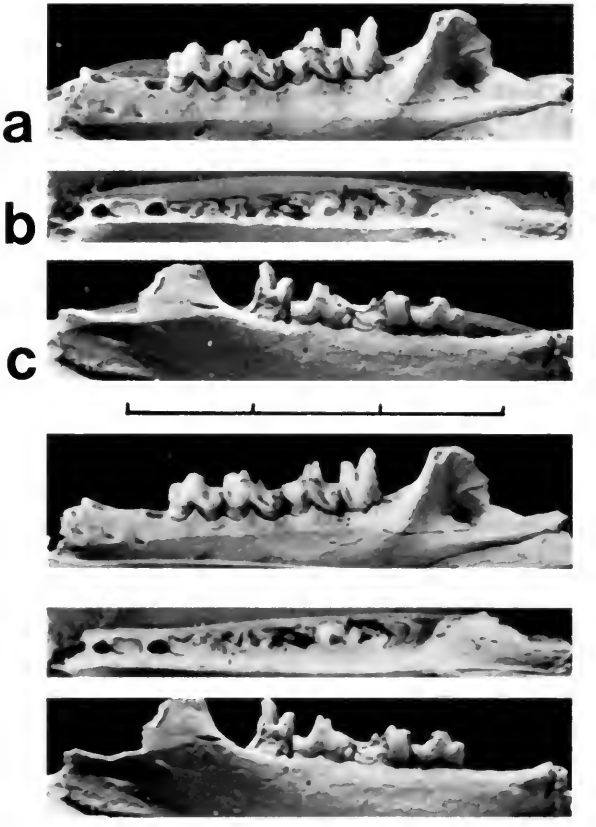


FIG. 18. *Notictis ortizi* Ameghino, 1889 (Huayquerian). Stereopairs of MACN 3996 (type), a left mandibular ramus with alveoli of C, P_1-M_1 complete, and M_{2-4} present but broken: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 30 mm.

Diagnosis.—Very small size, smallest known species of Huayquerian borhyaenid; C weakly developed; P_1 tiny and set obliquely in jaw; P_{2-3} larger and crowded, but roots aligned in same anteroposterior axis; P_1 separated from P_2 by small diastema; P_2 and P_3 crowded such that posterior alveolus of former and anterior alveolus of latter are confluent; M_{1-3} have small, but basined talonids, well-developed anterobasal cingula, and lingual side of talonid basin slightly higher than labial side; differs from *Pseudonotictis pusillus* in having relatively larger talonids, in an absolutely shorter premolar region, and smaller P_1.

Comments.—The type of *Notictis ortizi* has been redescribed and its taxonomic history discussed by Reig (1952). As demonstrated by Ameghino (1891b, p. 262) and Kraglievich (1934, pp. 62-63), *Didelphys curvidens* Burmeister (1891, p. 379) and *N. ortizi* Ameghino (1889, p. 912) were founded on the same specimen, MACN 3996. A second specimen, MACN 565 (cast) originally referred to *N. ortizi* and figured by Ameghino (1889, pl. 81, fig. 7) and later discussed by Reig (1952, p. 3), is almost certainly a didelphoid.

Notictis ortizi very probably evolved from the Santacrucian species *Pseudonotictis pusillus*. The probable phylogenetic relationships of these species are discussed in the comments section on *P. pusillus*.

Perathereutes Ameghino, 1891c

Perathereutes Ameghino, 1891c, p. 313.

Type.—*Perathereutes pungens* Ameghino, 1891c, p. 313.

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

Diagnosis.—As for type and only known species.

Perathereutes pungens Ameghino, 1891c. Figures 19–21; Table 4.

Perathereutes pungens Ameghino, 1891c, p. 313; 1894, p. 392, fig. 54; 1898, pp. 191, 193, fig. 58d; 1935, p. 108, fig. 23 (caption only).
Epanorthus aratae Ameghino, 1889, pl. 1, figs. 10–10b (*partim*).
Abderites altiramis Ameghino, 1894, p. 340; 1898, p. 186.

Type of Perathereutes pungens.—MACN 684, a left mandibular ramus with alveolus of C, roots of P_{1-3}, M_{1-4} complete but worn (figured by Ameghino, 1894, fig. 54; 1898, fig. 58d).

Type of Abderites altiramis.—MACN 8250, a fragment of a right mandibular ramus with talonid of M_3, anterior alveolus and posterior root of M_4 (figured by Ameghino, 1889, pl. 1, figs. 10–10d as *Epanorthus aratae*).

Hypodigm.—Types only.

Horizon and locality.—Both types are from the Santa Cruz Formation, Santa Cruz Province, southern Argentina. MACN 684 is from Monte Observación and was collected by C. Ameghino in 1890–91. MACN 8250 is from La Cueva and was collected by C. Ameghino in 1892–93.

Age.—Santacrucian.

Diagnosis.—Intermediate in size between *Pseudonotictis pusillus* and *Sipalocyon gracilis;* P_1 small and set at slight oblique angle in jaw and separated from C and P_2 by small but distinct diastems; talonid well developed and basined on M_{1-4}, but relatively smaller than in *Sipalocyon;* mandibular ramus exceptionally shallow in depth relative to its length; symphysis extends posteriorly to point below P_{2-3} contact; C moderately developed as in *Sipalocyon;* entoconid higher than hypoconid on M_{3-4}, lower on M_4.

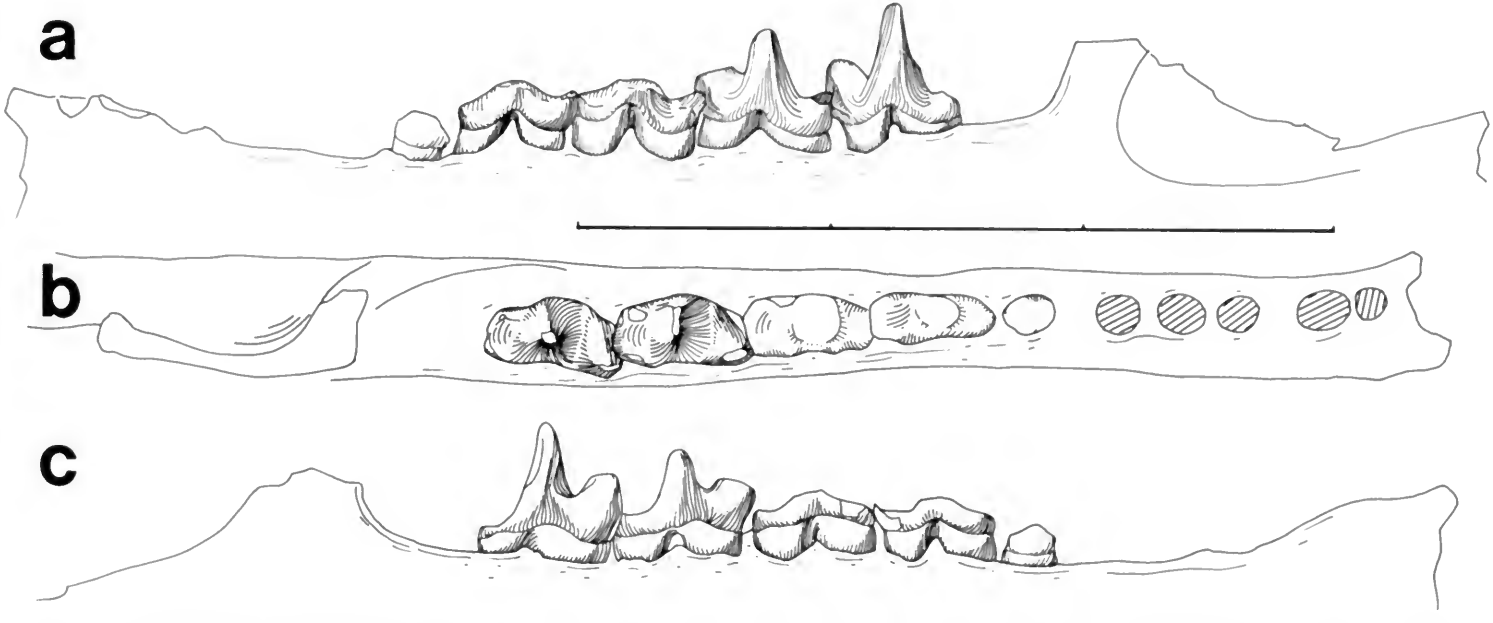


FIG. 19. *Perathereutes pungens* Ameghino, 1891c (Santacrucian). MACN 684 (type), a left mandibular ramus with alveoli of C, roots of P_{1-3}, and M_{1-4} complete but worn: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 30 mm.

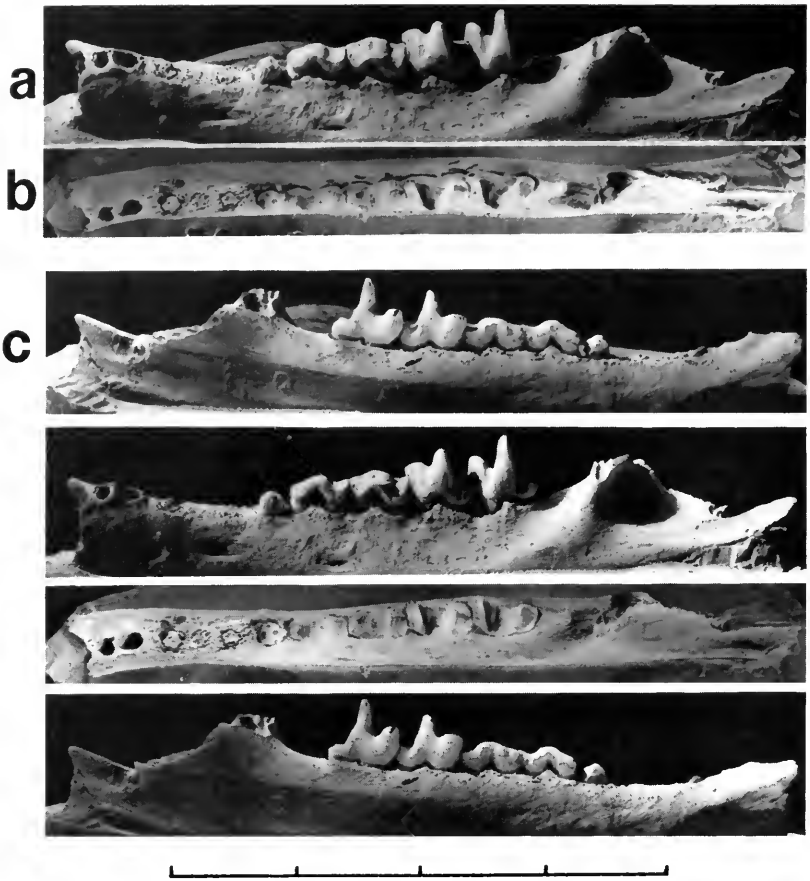


FIG. 20. *Perathereutes pungens* Ameghino, 1891c (Santacrucian). Stereopairs of MACN 684 (type), a left mandibular ramus with alveoli of C, roots of P_{1-3}, and M_{1-4} complete but worn: **a,** labial; **b,** occlusal; **c,** lingual views. Scale = 40 mm.

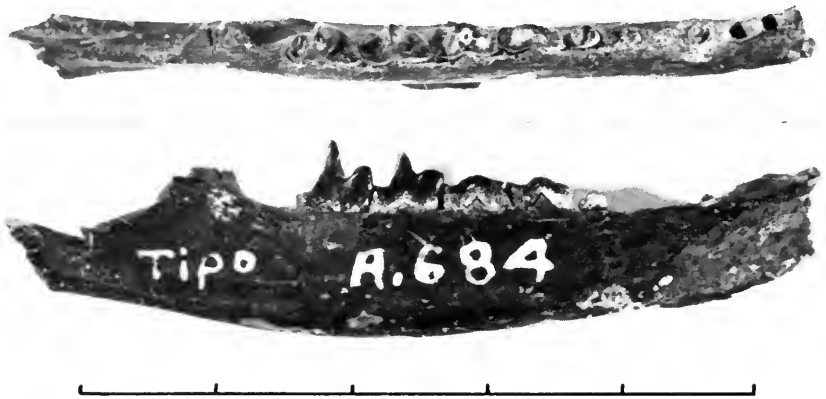


FIG. 21. *Perathereutes pungens* Ameghino, 1891c (Santacrucian). MACN 684 (type), a left mandibular ramus with alveoli of C, roots of P_{1-3}, and M_{1-4} complete but worn: **top,** occlusal; **bottom,** lingual views. Scale = 50 mm.

TABLE 4. Measurements of lower cheek teeth and mandibular rami of *Perathereutes pungens*.

Specimen	M_1		M_2		M_3		M_4		M_{1-4}	P_1-M_4	Depth of ramus below labial side of M4	Breadth of same
	L	W	L	W	L	W	L	W	L	L		
MACN 684	4.6	2.0	4.8	2.4	5.3	2.8	5.6	2.8	20.0	36.0	9.6	4.3
MACN 8250	...	...	...	...	...	2.6	ca. 5.4	...	...	...	8.8	4.2

Description.—Three mental foramina occur on type: largest below diastema between P_1 and P_2, a slightly smaller one below P_{2-3} contact, and one of similar size to latter below M_{1-2} contact. The region of the mandibular ramus near the P_2 and anterior root of the P_3 is covered with secondary bone growth, indicating that this area was either diseased or injured during the life of the animal.

Comments.—*Abderites altiramis* was erected by Ameghino (1894, p. 304) on a fragment of a right mandibular ramus (MACN 8250) that preserves the anterior alveolus and talonid of M_3 and roots of M_4. Ameghino characterized this species as being almost twice as large as *Abderites crassiramis*. MACN 8250 is not, however, an abderitine, but a small borhyaenid. Size of the M_{3-4} roots and structure of the M_3 talonid agree almost perfectly with the type of *Perathereutes pungens* (MACN 684). The ramus of *A. altiramis* is slightly shallower and more gracile than in *P. pungens*, but these differences are minor, and *A. altiramis* is regarded a junior synonym of *P. pungens*. MACN 8250 was figured by Ameghino (1889, pl. 1, figs. 10–10b) as *Epanorthus aratae*. Ameghino (1891c, p. 313) originally placed *P. pungens* in the family Thylacynidae, but later (1894, p. 392) included it in his group Sparassodonta, family Amphiproviverridae.

Perathereutes pungens is similar to *Sipalocyon gracilis*, although there are important differences; *P. pungens* differs from specimens of the latter (i.e., MACN 5938) in being smaller in size, in having P_1 set at a sharper oblique angle in jaw and being separated from C and P_2 by distinct diastems, and in a proportionately smaller talonid basin, especially on M_4. Although isolated teeth and partial jaw fragments of these species may be difficult to separate, more complete material as described here shows these forms to be distinct and the taxa valid.

The most likely ancestor for *P. pungens* is the Riochican species *Patene simpsoni*. These taxa are similar in size and structure, but differ in *P. pungens* having P_1 set obliquely in jaw and being separated from C and P_2 by distinct diastems, in lacking a metaconid, in a slightly more reduced talonid on M_{1-4}, and in a more elongated and tricuspid M_1.

Perathereutes pungens is in turn similar to *Borhyaenidium musteloides* from beds of Huayquerian age and most probably represents an ancestor of that species. Both species have P_1 set at a slight oblique angle in the jaw, the P_1 is separated from the C and P_2 by distinct diastems, and talonids (especially on M_4) are more reduced than in species of *Sipalocyon*. *Borhyaenidium musteloides* differs from *P. pungens* primarily in being slightly larger in size and in the talonid basin being proportionately and absolutely more reduced.

The fact that talonid reduction is already begun in *P. pungens* makes this species a more likely ancestor for *B. musteloides* than does *S. gracilis*. For *S. gracilis* to have been ancestral to *B. musteloides*, it would have had to have undergone talonid reduction and hence passed through a stage similar to that seen in *P. pungens*. The *S. gracilis* lineage, however, with the larger talonid basins appears to have continued into the Montehermosan as evidenced by *Notocynus hermosicus*. The lineages that terminated in the reduced talonid form of *B. musteloides* in the Huayquerian and the large talonid form of *N. hermosicus* in the Montehermosan were thus already distinct in the Santacrucian.

Borhyaenidium Pascual & Bocchino, 1963

Borhyaenidium Pascual & Bocchino, 1963, p. 101.

Type.—*Borhyaenidium musteloides* Pascual & Bocchino, 1963, p. 101.

Distribution.—Known from beds of Huayquerian and Montehermosan age in Argentina.

Diagnosis.—Similar in size to *Sipalocyon* and *Notocynus;* a large mental foramen occurs below posterior root of P_1; P_1 separated from C and P_2 by small diastems; talonid distinct, not basined, and relatively smaller than in *Sipalocyon* and *Notocynus;* trigonid relatively narrower and more elongated than in *Notocynus, Sipalocyon,* and *Perathereutes,* and paraconid lies more directly anteriad of protoconid; protocone distinct but smaller than in *Sipalocyon, Pseudonotictis,* and *Cladosictis,* and set more anteriad relative to para- and metacone as in *Chasicostylus castroi;* paracone small and fused basally to larger metacone and becoming smaller from M^1 to M^3, whereas metacone becomes larger in same direction; para- and metacone set more labiad on M^1 and more mediad on M^3; parastyle large and elongated anteriorly on M^1 and in same axis as para- and metacone; parastyle on M^2 shorter and set on anterolabial corner of tooth labiad to para-metacone axis; parastyle on M^3 smaller and set completely on labial side of tooth; M^3 with small but distinct ectoflex opposite metacone; metacrista well developed and its shear surface continues along inner surface of protocone.

Borhyaenidium musteloides Pascual & Bocchino, 1963. Figures 22–25; Tables 5, 6.

Borhyaenidium musteloides Pascual & Bocchino, 1963, p. 101, pls. 1, 2.

Type.—MLP 57-X-10-153, poorly preserved partial skull with left M^{1-3} and right M^{2-3}; a nearly complete left mandibular ramus with C, roots of P_1, P_{2-3} complete, posterior half of M_1, M_2 complete, and M_{3-4} missing tip of protoconid; a fragment of a right mandibular ramus with complete P_3-M_1 and broken M_{2-4}; proximal and distal ends of a humerus; proximal end of an ulna; and assorted postcranial fragments, all of a single associated individual (figured by Pascual & Bocchino, 1963, pls. 1, 2).

Hypodigm.—Type only.

Horizon and locality.—Type from Epecuén Formation, Salinas Grandes de Hidalgo, La Pampa Province, Argentina.

Age.—Huayquerian.

Diagnosis.—Differs from *Borhyaenidium riggsi* in having, in most cases, slightly smaller linear tooth dimensions (see table 5); a slightly smaller talonid on M_4; and a slightly smaller paracone (especially on M^3).

Comments.—It is probable that *Perathereutes pungens* is the Santacrucian ancestor of *Borhyaenidium musteloides. Perathereutes pungens* is slightly smaller than *B. musteloides,* and its talonids are slightly larger and more distinctly basined. However, these taxa are similar in having P_1 separated from C and P_2 by small but distinct diastems. In *Pseudonotictis pusillus* the talonids are proportionately smaller relative to trigonids than occurs in species of *Sipalocyon* and *Cladosictis.* We thus see in *P. pusillus* the incipient talonid reduction that is continued in this lineage and that appears to a more extreme degree in *B. musteloides.*

Borhyaenidium musteloides has a dental structure very similar to that of *Chasicostylus castroi.* Both species have the upper molars greatly elongated anteroposteriorly, the parastyle on M^1 is very large and projects anteriorly in the same axis as para- and metacone, whereas on M^2 the parastyle is shorter and is set at the anterolabial corner of the tooth labiad to the para-metacone axis; protocone is reduced and is set anteriad of para- and metacone, and shear along metacrista

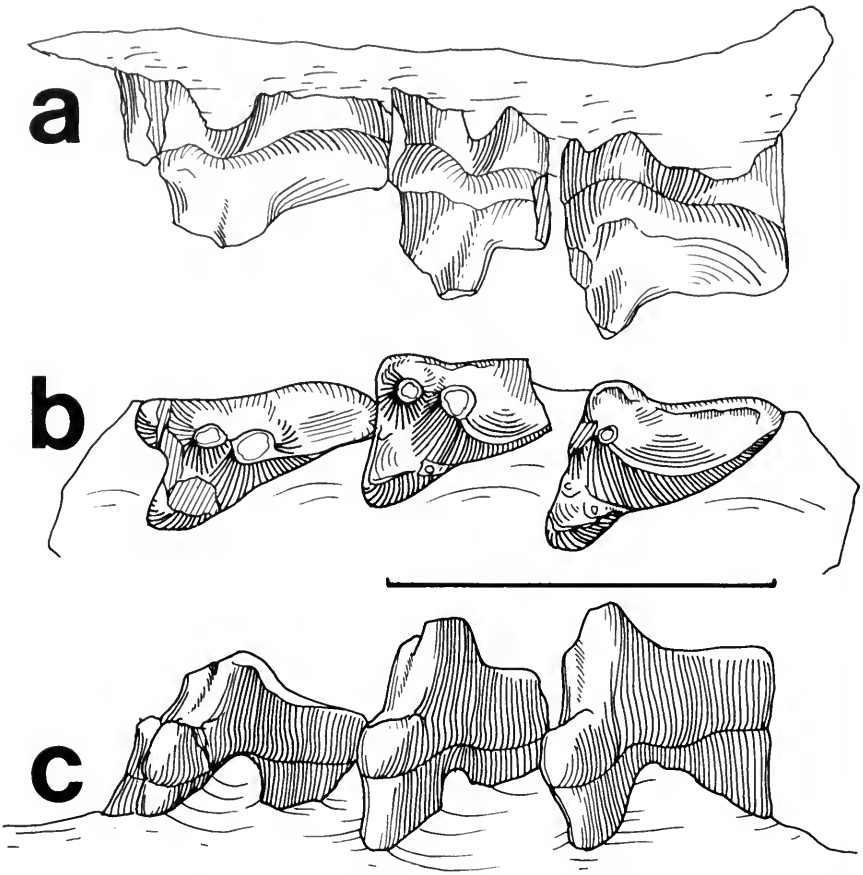


FIG. 22. *Borhyaenidium musteloides* Pascual & Bocchino, 1963 (Huayquerian). MLP 57-X-10-153 (type), a left maxillary with M^{1-3}: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 10 mm.

is increased by elongation of that area and by its extension anteriorly along inner surface of protocone; lower molars are also elongated anteroposteriorly, especially the protoconid and paraconid, and the talonid is more reduced than occurs in species of *Sipalocyon*, *Cladosictis*, and *Notocynus*. These features are thus very distinct, and they do not occur jointly in other borhyaenid species of similar size.

Chasicostylus castroi differs from *B. musteloides* in being larger in size, in having a relatively larger protocone and talonid basin, and in having the protocone not set as far anteriad relative to the para- and metacones. Apart from these few differences, these taxa are structurally very similar.

The dental specializations seen in *C. castroi* have been carried further in *B. musteloides*, in which the protocone is more reduced and is set more anteriad of the para- and metacone, resulting in elongation of the metacrista shear by making it more continuous and unobstructed. *Borhyaenidium musteloides* thus has slightly more advanced carnassial specializations than does *C. castroi*.

TABLE 5. Measurements of cheek teeth of *Borhyaenidium musteloides*, *B. riggsi* sp. nov., and *Notocynus hermosicus*.

Specimen	P1		P2		P3		M1		M2		M3		M4		P1-3	M1-3 / M1-4	P1-4
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	L	L
UPPER CHEEK TEETH																	
Borhyaenidium musteloides																	
MLP 57-X-10-153(l)	...	...	...	...	...	...	6.0	3.4	...	3.9	5.1	4.4	...	...	...	ca. 15.5	...
MLP 57-X-10-153(r)	...	...	...	...	...	...	...	...	6.0	4.0	5.0	4.4	...	...	...	...	...
Borhyaenidium riggsi sp. nov.																	
FMNH P14409	...	...	...	...	...	...	6.0	3.7	6.0	4.4	6.0	5.1	...	...	...	18.2	...
LOWER CHEEK TEETH																	
Borhyaenidium musteloides																	
MLP 57-X-10-153(l)	...	...	5.3	1.7	5.6	2.3	...	2.4	5.4	2.8	5.6	3.0	6.0	3.3	19.1	ca. 22.5	42.0
MLP 57-X-10-153(r)	...	...	...	...	5.5	...	5.2	2.5	5.4	2.8	...	...	6.1	3.2	...	22.4	...
Borhyaenidium riggsi sp. nov.																	
FMNH P14409(l)	ca. 4.8	...	ca. 6.1	...	...	...	5.6	2.1	ca. 5.9	2.8	6.4	3.0	6.7	3.3	ca. 20.0	24.2	...
Notocynus hermosicus																	
MLP 11-91	...	...	5.0	2.0	...	...	5.6	...	...	...	6.2	3.4	...	...	16.5	...	...

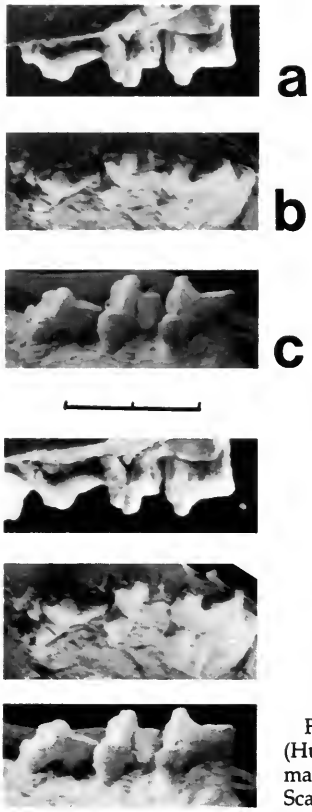


FIG. 23. *Borhyaenidium musteloides* Pascual & Bocchino, 1963 (Huayquerian). Stereopairs of MLP 57-X-10-153 (type), a left maxillary with M^{1-3}: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 10 mm.

TABLE 6. Measurements of mandibular rami of *Borhyaenidium musteloides*, *B. riggsi* sp. nov., and *Notocynus hermosicus*.

Specimen	Depth of ramus below labial side of M_1	Breadth of same	Depth of ramus below labial side of M_4	Breadth of same
Borhyaenidium musteloides				
MLP 57-X-10-153(l)	11.0	4.3	11.8	4.9
MLP 57-X-10-153(r)	11.0	4.4	11.7	5.0
Borhyaenidium riggsi sp. nov.				
FMNH P14409(l)	11.0	4.2	10.2	5.4
FMNH P14409(r)	10.9	3.8	9.9	5.2
Notocynus hermosicus				
MLP 11-91	10.7	4.2	...	...

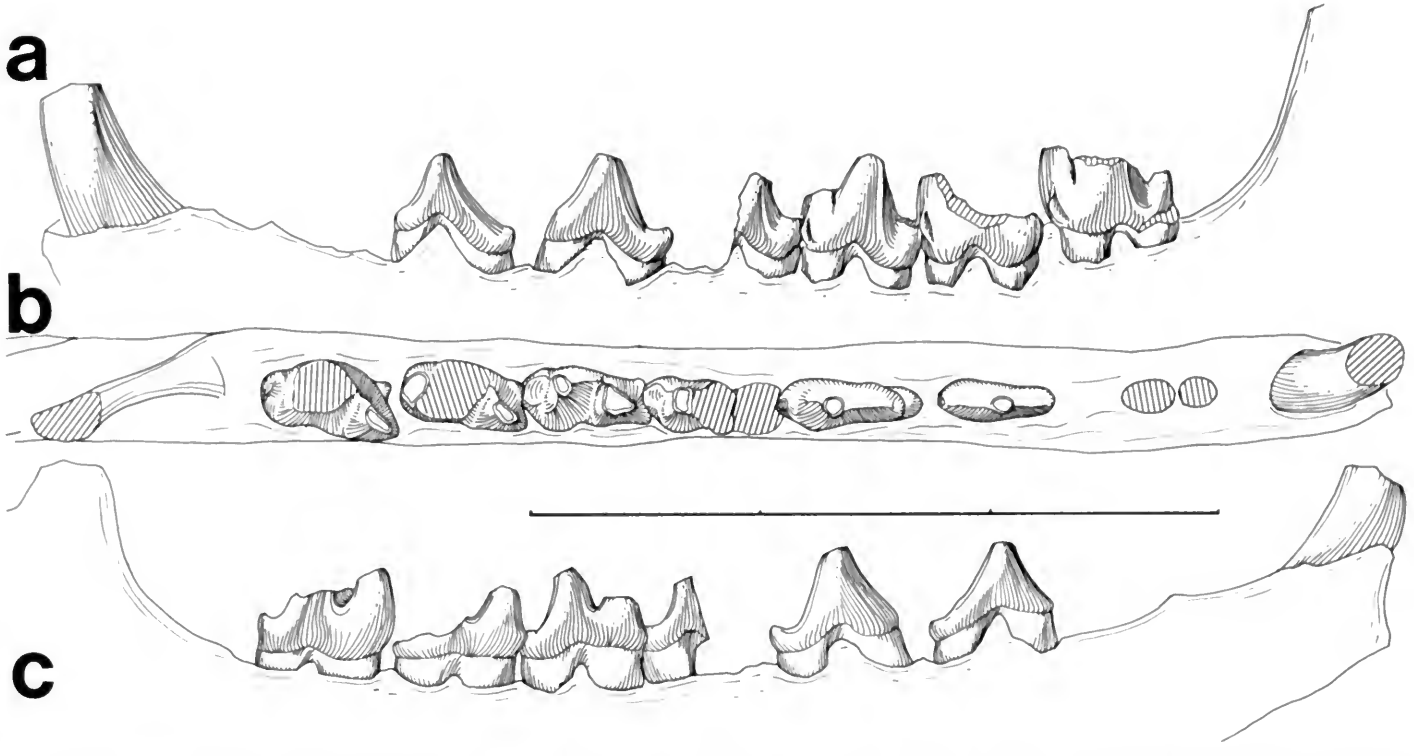


FIG. 24. *Borhyaenidium musteloides* Pascual & Bocchino, 1963 (Huayquerian). MLP 57-X-10-153 (type), a nearly complete left mandibular ramus with C, roots of P_1, P_{2-3} complete, posterior half of M_1, M_2 complete, and M_{3-4} missing tip of protoconid: **a,** labial; **b,** occlusal; **c,** lingual views. Scale = 30 mm.

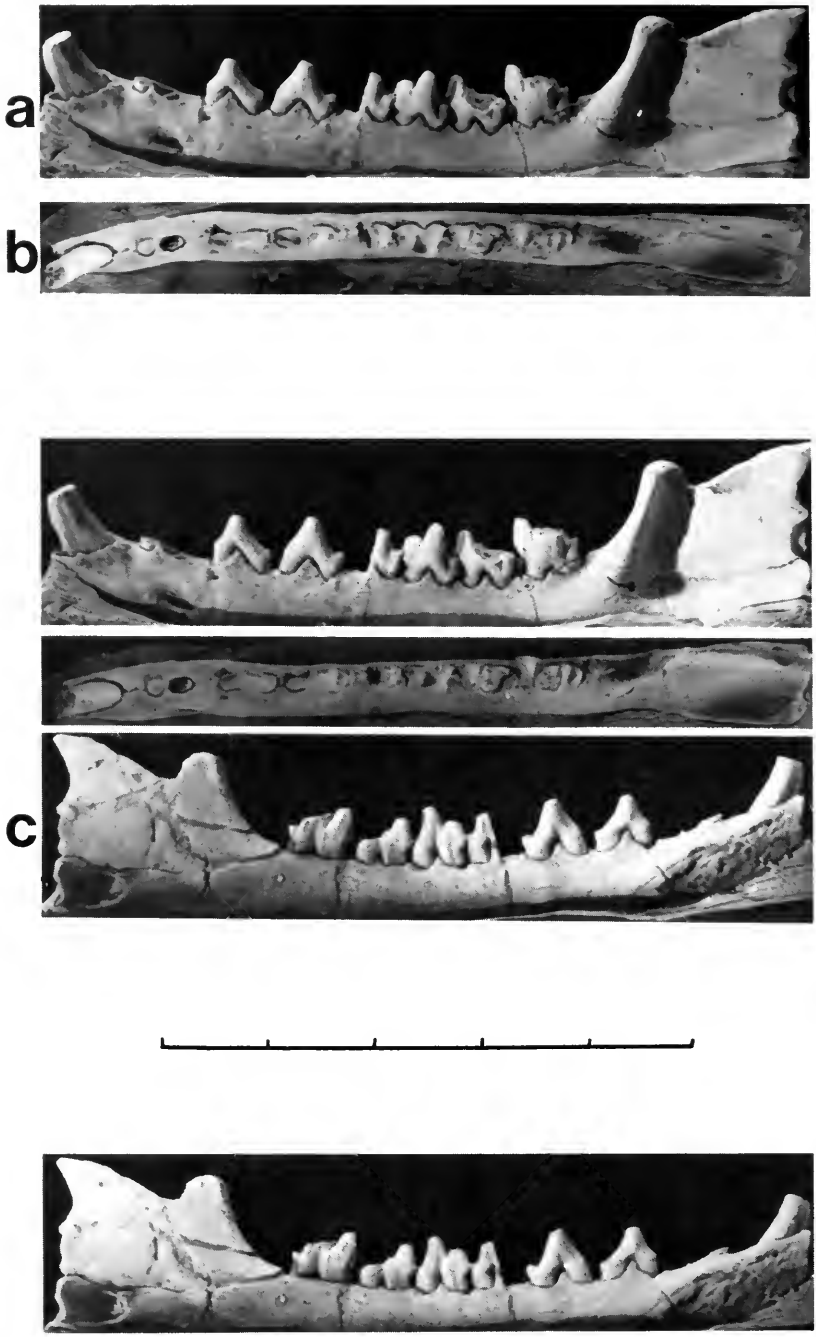


FIG. 25. *Borhyaenidium musteloides* Pascual & Bocchino, 1963 (Huayquerian). Stereopairs of MLP 57-X-10-153 (type), a nearly complete left mandibular ramus with C, roots of P_1, P_{2-3} complete, posterior half of M_1, M_2 complete, and M_{3-4} missing tip of protoconid: **a,** labial; **b,** occlusal; **c,** lingual views. Scale = 50 mm.

Borhyaenidium riggsi sp. nov. Figures 26–29; Tables 5, 6.

Notocynus hermosicus Riggs & Patterson, 1939, p. 149.

Etymology.—*riggsi* named in honor of Elmer S. Riggs, leader of the 1926–1927 Second Marshall Field Paleontological Expedition to Catamarca Province, Argentina.

Type.—FMNH P14409, two fragments of left maxillary, one with C and anterior root of P^1 and the other with M^{1-3}; a left mandibular ramus with root of C, roots of P_{1-3}, M_1 almost complete but missing anterior edge, M_2 missing talonid, and M_{3-4} complete; and a broken right mandibular ramus with roots of C-M_4; all of a single, associated individual.

FIG. 26. *Borhyaenidium riggsi* sp. nov. (Montehermosan). FMNH P14409 (type), a left mandibular ramus with root of C, roots of P_{1-3}, M_1 almost complete but missing anterior edge, M_2 missing talonid, and M_{3-4} nearly complete: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 30 mm.

Hypodigm.—Type only.

Horizon and locality.—Type collected by R. D. Thorne from unit 32 of Corral Quemado Formation at Puerta de Corral Quemado, Departamento de Belén, Catamarca Province, Northwest Argentina.

Age.—Montehermosan.

Diagnosis.—Differs from *B. musteloides* in having, in most cases, slightly larger linear tooth dimensions (see table 5); a slightly larger talonid on M_4; and a slightly larger paracone (especially on M^3).

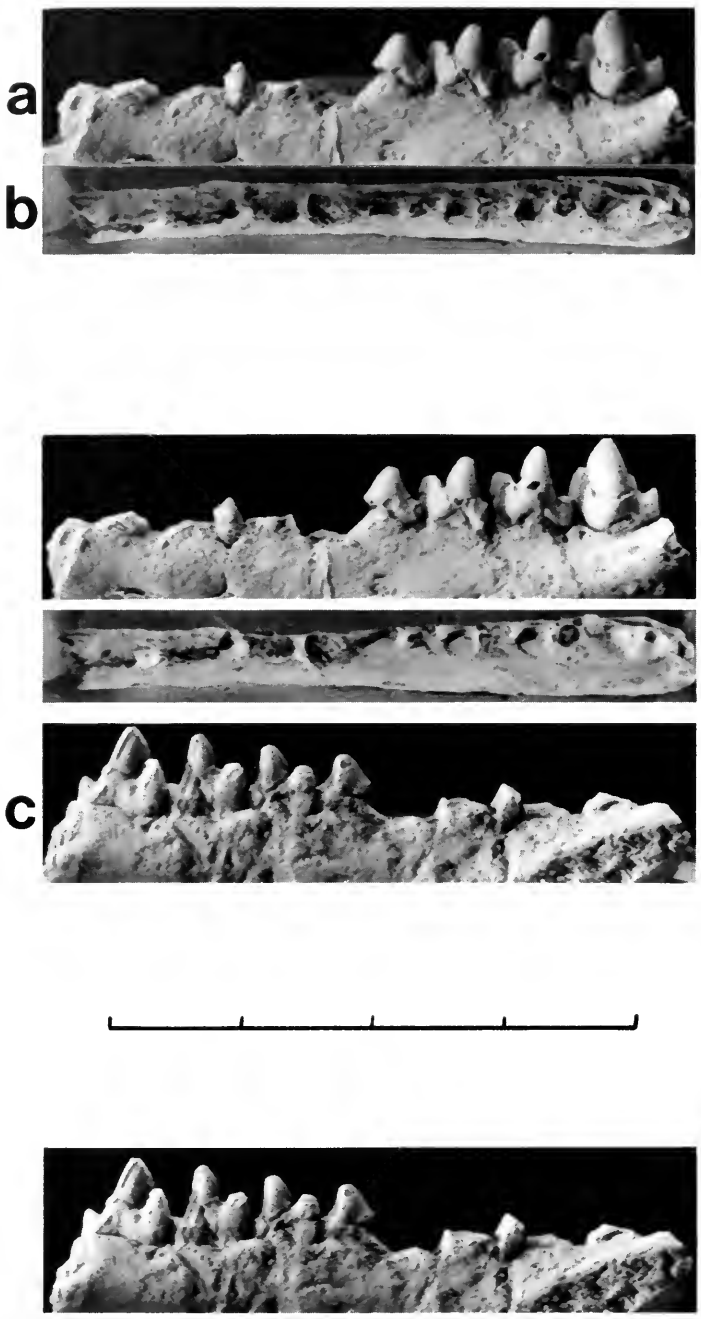


FIG. 27. *Borhyaenidium riggsi* sp. nov. (Montehermosan). Stereopairs of FMNH P14409 (type), a left mandibular ramus with root of C, roots of P_{1-3}, M_1 almost complete but missing anterior edge, M_2 missing talonid, and M_{3-4} nearly complete: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 40 mm.

Comments.—The type of *B. riggsi* is the specimen referred by Riggs & Patterson (1939, p. 149) to *Notocynus hermosicus*. This assignment was made largely on the basis of the similarity in size of these animals and their occurrence in beds of similar age. However, these specimens differ in *N. hermosicus* having a more crowded premolar series with no diastems separating P_1 from C or from P_2, and in the M_3 talonid being relatively larger and distinctly basined.

Borhyaenidium riggsi is tentatively recognized as a species distinct from *B. musteloides*. The three characters I have used to distinguish these species may yet be shown to represent only individual variation within members of a single species. Both species are known only by their types, which come from beds of different ages as demonstrated by study of the associated faunas. These specimens are clearly similar, and the species may be regarded as representing a single evolutionary lineage. I therefore recognize *B. musteloides* as the Huayquerian ancestor of *B. riggsi*.

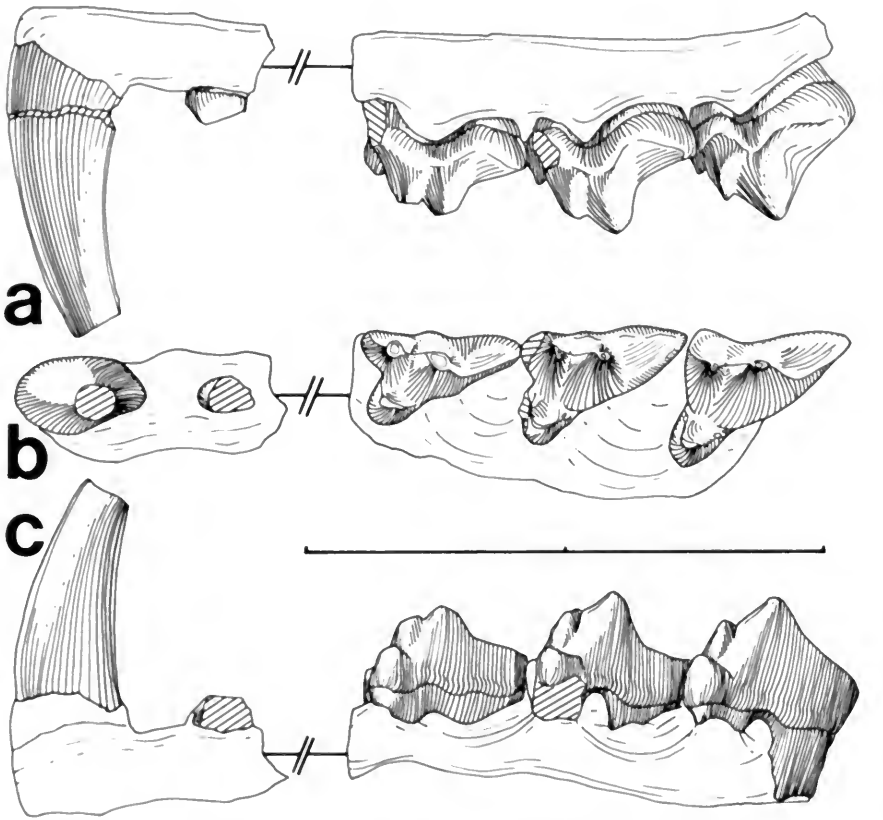


FIG. 28. *Borhyaenidium riggsi* sp. nov. (Montehermosan). FMNH P14409 (type), two fragments of a left maxillary, one with C and anterior root of P^1 and other with M^{1-3}: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 20 mm.

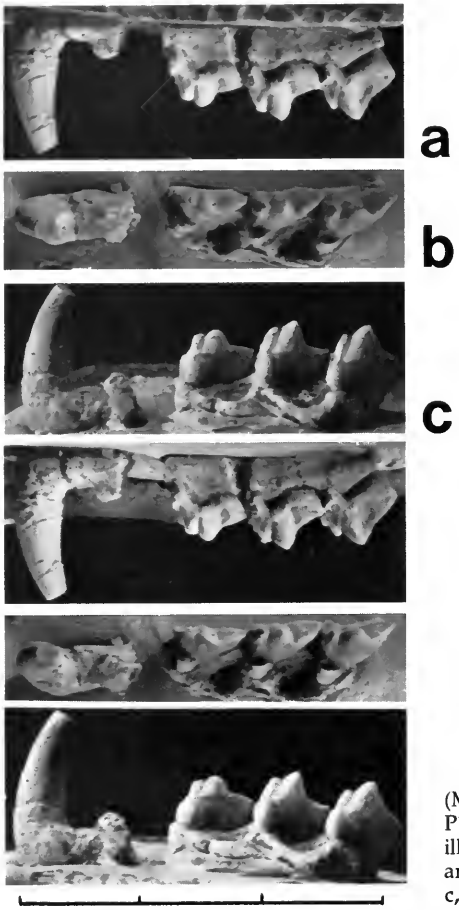


FIG. 29. *Borhyaenidium riggsi* sp. nov. (Montehermosan). Stereopairs of FMNH P14409 (type), two fragments of a left maxillary, one with C and anterior root of P^1 and other with M^{1-3}: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 30 mm.

Sipalocyon Ameghino, 1887

Sipalocyon Ameghino, 1887, p. 8; 1889, p. 292.
Amphithereutes Ameghino, 1935, p. 108.
Thylacodictis Mercerat, 1891a, p. 54.
Protoproviverra Ameghino, 1891c, p. 312, *nec* Lemoine, 1891, p. 379 (Creodonta).
Amphiproviverra Ameghino, 1891e, p. 397n, to replace *Protoproviverra*, which was preoccupied.

Type of Sipalocyon.—*Sipalocyon gracilis* Ameghino, 1887, p. 8.

Type of Amphithereutes.—*Amphithereutes amputans* (Ameghino, 1891c, p. 313).

Type of Thylacodictis.—*Thylacodictis exilis* Mercerat, 1891a, p. 54.

Type of Protoproviverra.—*Protoproviverra manzaniana* Ameghino, 1891c, p. 312.

Type of Amphiproviverra.—*Amphiproviverra manzaniana* (Ameghino, 1891c, p. 312).

Distribution.—Colhuehuapian and Santacrucian, Patagonia, southern Argentina.

Diagnosis.—Small to medium-sized borhyaenids; mandibular rami gracile and shallow in depth; lower premolars increase in size from P_1 to P_3; all have distinct posterobasal cusps or heels that increase in size from P_1 to P_3; P_1 either separated from P_2 and C by tiny diastems or all abut (character variable), when tightly packed anterior roots tend to lie slightly labiad of posterior roots; lower molars increase slightly in size from M_1 to M_4, all have a very large and deeply basined talonid, and distinct anterobasal cingula; protoconid usually twice as large as paraconid; lingual side of talonid basin higher than labial side in unworn teeth; I^{1-4} subequal in size but with slight decrease from I^1 to I^4; upper premolars increase in size from P^1 to P^3; P^1 usually separated from C and P^2 by small diastema; P^2 may or may not be separated from P^3 by small diastema; P^{1-3} aligned in same anteroposterior axis; M^{1-4} with large protocone and deeply basined trigonid; distinct para- and metaconules; paracone and metacone fused basally; paracone becomes smaller relative to metacone from M^1 to M^3; metacone becomes relatively

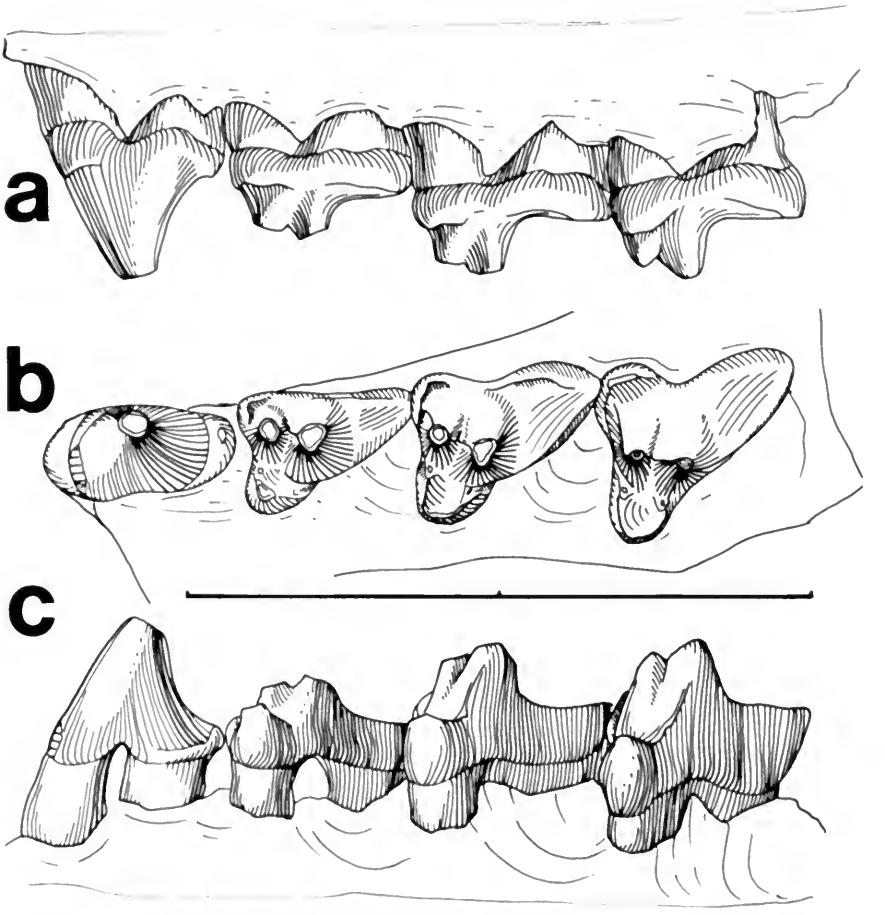


FIG. 30. *Sipalocyon externa* (Ameghino, 1902c) (Colhuehuapian). MACN 52-383 (type), left P^3-M^3: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 20 mm.

and absolutely larger from M^1 to M^3; M^4 with large protocone and paracone, metacone absent; weak but distinct parastyle on M^{1-3} which becomes larger from M^1 to M^3; parastyle on M^4 connected with paracone by parastylar ridge; M^3 has shallow but distinct ectoflex; infraorbital canal large and opens over anterior root of P^3; supraorbital processes weakly developed.

Sipalocyon externa (Ameghino, 1902c). Figures 30, 31; Table 7.

Cladosictis externa Ameghino, 1902c, p. 129.

Type.—MACN 52-383, a partial cranium (poorly preserved) with left P^3-M^3, and roots of right P^1, P^2-M^2, and complete M^4.

Hypodigm.—Type only.

Horizon and locality.—Colhué-Huapí Formation, Chubut Province, Argentina; specimen labeled "la barranca al sur del Lago Colhué-Huapí"; collected by C. Ameghino.

Age.—Colhuehuapian.

Diagnosis.—Slightly smaller than specimens of *Sipalocyon gracilis.*

Comments.—*Sipalocyon externa* is slightly smaller and relatively more gracile than specimens of *S. gracilis* from the Santacrucian. Morphologically, these species are very similar. Compared with some specimens of *S. gracilis* (e.g., MACN

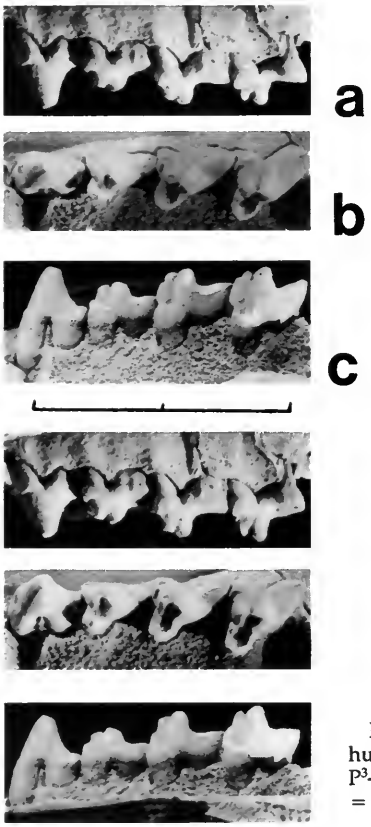


FIG. 31. *Sipalocyon externa* (Ameghino, 1902c) (Colhuehuapian). Stereopairs of MACN 52-383 (type), left P^3-M^3: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 20 mm.

TABLE 7. Measurements of upper dentition of *Sipalocyon externa*.

Specimen	P^2		P^3		M^1		M^2		M^3		M^4		M^{1-3}
	L	W	L	W	L	W	L	W	L	W	L	W	L
MACN 52-383(l)	...	...	6.0	3.0	6.0	4.0	6.3	5.2	6.5	6.0	...	...	18.4
MACN 52-383(r)	5.2	2.1	6.0	3.1	5.9	4.0	6.2	5.1	...	...	6.3	3.0	...

5959), *S. externa* has a slightly smaller protocone, a proportionately shorter metacrista, and a more distinct ectoflex on the M^3 and a proportionately larger one on the M^2. There is sufficient variation, however, in the large comparative sample of *S. gracilis* from the Santacrucian to include a significant part of these differences and to cast doubt on the validity of these features as diagnostic characters. The slightly smaller size of MACN 52-383 appears to be the only nondisputable character that can be used to separate it from specimens of *S. gracilis*. In view of their close similarity in size and morphology, *S. externa* is regarded as the Colhuehuapian ancestor of *S. gracilis*.

Sipalocyon gracilis Ameghino, 1887. Figures 32–43; Tables 8–13.

Sipalocyon gracilis Ameghino, 1887, p. 8; 1889, p. 292; 1891c, p. 315; 1891d, p. 354; 1894, pp. 393, 394, fig. 55; 1898, pp. 191, 193, fig. 58e; 1935, p. 110, fig. 25 (caption only).
Protoproviverra manzaniana Ameghino, 1891c, p. 312.
Amphiproviverra manzaniana Ameghino, 1894, p. 389, fig. 52; 1898, p. 193, figs. 58a, b; 1906, fig. 188; 1935, p. 107, figs. 4, 27 (captions only); Sinclair, 1906, p. 400 (with numerous plates and figures); Schlosser, 1925, p. 35, fig. 56; Scott, 1937, fig. 415.
Thylacodictis manzaniana Cabrera, 1927, p. 304, fig. 17B.
Perathereutes amputans Ameghino, 1891c, p. 313; 1894, p. 393.
Amphithereutes amputans Ameghino, 1935, p. 108, fig. 33 (caption only).
Perathereutes obtusus Ameghino, 1891c, p. 313; 1894, p. 392; 1935, p. 108, fig. 7 (caption only).
Thylacodictis obusta Cabrera, 1927, p. 302, figs. 15, 17c.
Hathliacynus lynchi Mercerat, 1891a, p. 53; Ameghino, 1894, p. 387 (as junior synonym of *Cladosictis patagonica*).
Thylacodictis exilis Mercerat, 1891a, p. 54; Ameghino, 1891d, p. 354 (as junior synonym of *S. gracilis*); Cabrera, 1927, p. 303, figs. 16, 17.
Amphiproviverra minuta Ameghino, 1894, p. 390; 1935, p. 107, fig. 6 (caption only); Sinclair, 1906, p. 404, pl. 59, figs. 3, 3a, pl. 60, figs. 3, 3a.
Sipalocyon curtus Ameghino, 1894, p. 394; 1935, p. 111, fig. 28 (caption only).
Sipalocyon mixtus Ameghino, 1894, p. 394; 1935, p. 111, fig. 11 (caption only).
Amphiproviverra crassa Ameghino, 1894, p. 391.
Thylacodictis crassa Simpson, 1930, p. 50.
Sipalocyon altiramis Ameghino, 1894, p. 395.
Sipalocyon longus Ameghino, 1894, p. 395.

Type of Sipalocyon gracilis.—MACN 647, a fragment of a right mandibular ramus with alveoli of I_{1-3}, root of C, alveoli of P_1, P_2-M_2 complete (figured by Ameghino, 1894, fig. 55; 1898, fig. 58e).

Type of Thylacodictis exilis.—MLP 11-12, a fragment of a right mandibular ramus with alveolus of C, roots of P_{1-3}, M_1 complete, and anterior half of M_2.

Type of Amphiproviverra minuta.—MACN 685, part of an isolated left M^2 with proto-, para-, and metacones, but lacking metastylar region (protocone was at one time broken off and has since been glued back on the specimen).

Type of Protoproviverra manzaniana.—MACN 691–703, a left and right mandibular ramus with complete dentition (691), a left maxillary and premaxillary with dentition (692), and associated fragmentary postcranial remains (693–703) (figured by Ameghino, 1894, fig. 52; 1898, figs. 58a, b; 1906, fig. 188; listed as "tipo" in Ameghino's catalogue and fits original description perfectly).

Type of Perathereutes amputans.—MACN 682, a fragment of a right mandibular ramus with alveoli of C-P_2, roots of P_3, M_{1-2} complete but worn, anterior half and posterior root of M_3 (listed as "tipo" in Ameghino's catalogue and matches original description perfectly).

FIG. 32. *Sipalocyon gracilis* Ameghino, 1887 (Santacrucian). MACN 647 (type), a fragment of a right mandibular ramus with alveoli of I_{1-3}, root of C, alveoli of P_1, P_2-M_2 complete: **top,** occlusal; **bottom,** labial views. Scale = 30 mm.

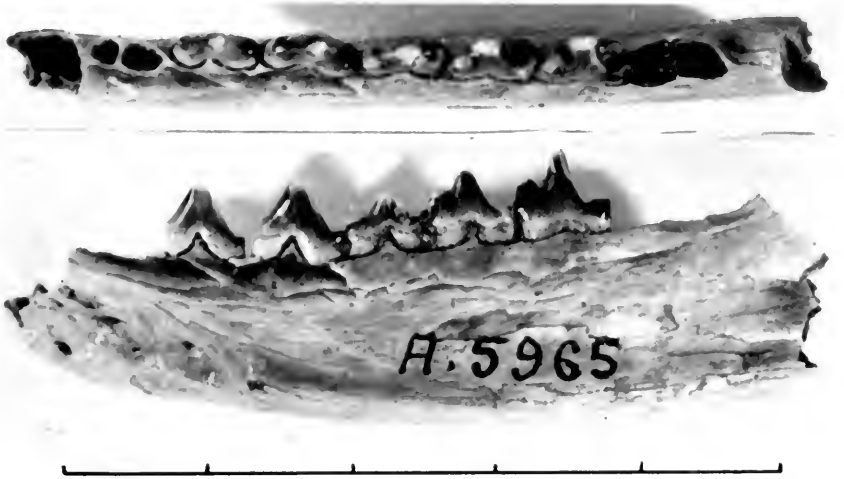


FIG. 33. *Sipalocyon gracilis* Ameghino, 1887 (Santacrucian). MACN 5965 (type of *Sipalocyon longus*), a right mandibular ramus with alveolus of C, roots of P_1 and M_4, and P_2-M_3 complete: **top,** occlusal; **bottom,** lingual views. Scale = 50 mm.

FIG. 34. *Sipalocyon gracilis* Ameghino, 1887 (Santacrucian). MACN 5963 (type of *Sipalocyon mixtus*), a fragment of a right mandibular ramus with roots of C, P_1, P_3 and M_2, and with P_2, M_1, and M_3 complete: **top,** occlusal: **bottom,** labial views. Scale = 30 mm.

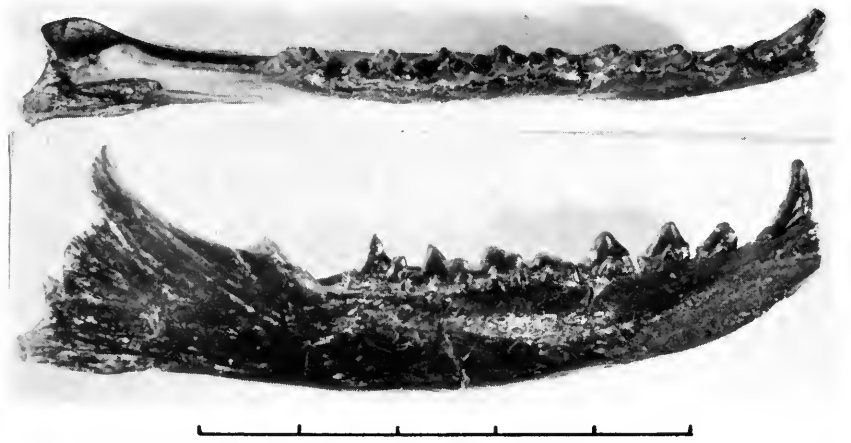


FIG. 35. *Sipalocyon gracilis* Ameghino, 1887 (Santacrucian). MACN 5938, a nearly complete left mandibular ramus with dentition: **top,** occlusal; **bottom,** lingual views. Scale = 50 mm.

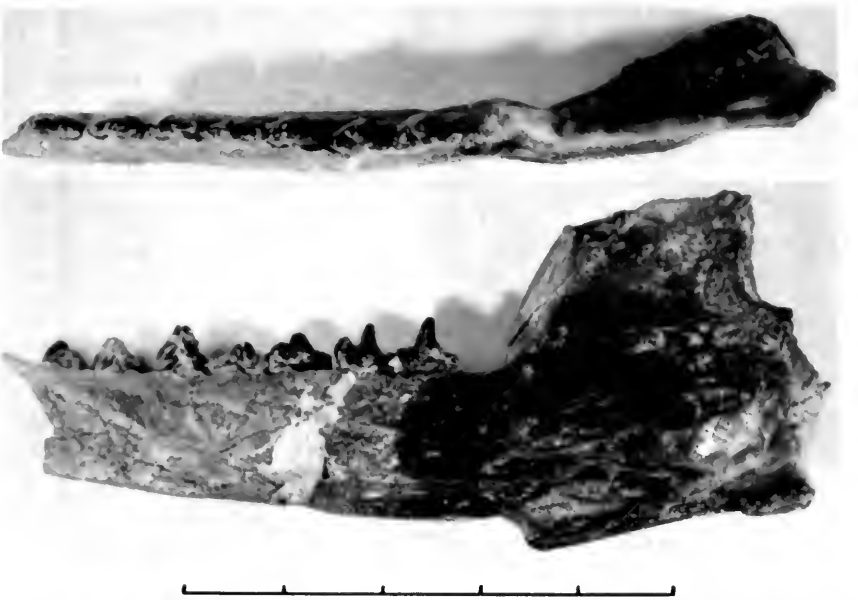


FIG. 36. *Sipalocyon gracilis* Ameghino, 1887 (Santacrucian). MACN 5964 (type of *Sipalocyon altiramis*), greater part of a right mandibular ramus with P_1-M_4 complete: **top,** occlusal; **bottom,** lingual views. Scale = 50 mm.

Type of Perathereutes obtusus.—MACN 683, a fragment of a right mandibular ramus with root of C, alveoli of P_1, roots of P_{2-3}, M_1 complete, and anterior half of M_2 (listed as "tipo" in Ameghino's catalogue and matches original description perfectly).

Type of Sipalocyon altiramis.—MACN 5964, a right mandibular ramus with P_1-M_4 complete (not listed as type in Ameghino's catalogue or on specimen, but original description fits perfectly).

Type of Sipalocyon curtus.—MACN 5960–62; 5960, a fragment of a right mandibular ramus with C, posterior half of P_1, P_2 complete, and anterior root of P_3; 5961, assorted tooth fragments (both upper and lower); and 5962, a caudal vertebra (all of a single individual).

Type of Sipalocyon longus.—MACN 5965, a right mandibular ramus with alveolus of C, roots of P_1 and M_4, and P_2-M_3 complete (not listed as type in Ameghino's catalogue or on specimen, but it is only specimen listed by this name in his catalogue, and original description fits perfectly).

Type of Sipalocyon mixtus.—MACN 5963, a fragment of a right mandibular ramus with roots of C, P_1, P_3, and M_2, and with P_2, M_1, and M_3 complete.

Syntypes of Amphiproviverra crassa.—MACN 5957, a left mandibular ramus with roots of P_1, P_{2-3} complete, M_{1-3} broken, M_4 complete; and MACN 5958, a left maxillary fragment with P^1-M^4 complete. (These specimens have slightly different preservation, and the teeth in MACN 5958 are more deeply worn than in MACN 5957, indicating that they are of different individuals, but are certainly of the same species. They are not listed as types in the catalogue or on the specimens, but they are the only specimens listed under the name *A. crassa* in Ameghino's catalogue, and they fit the original description of this species perfectly.)

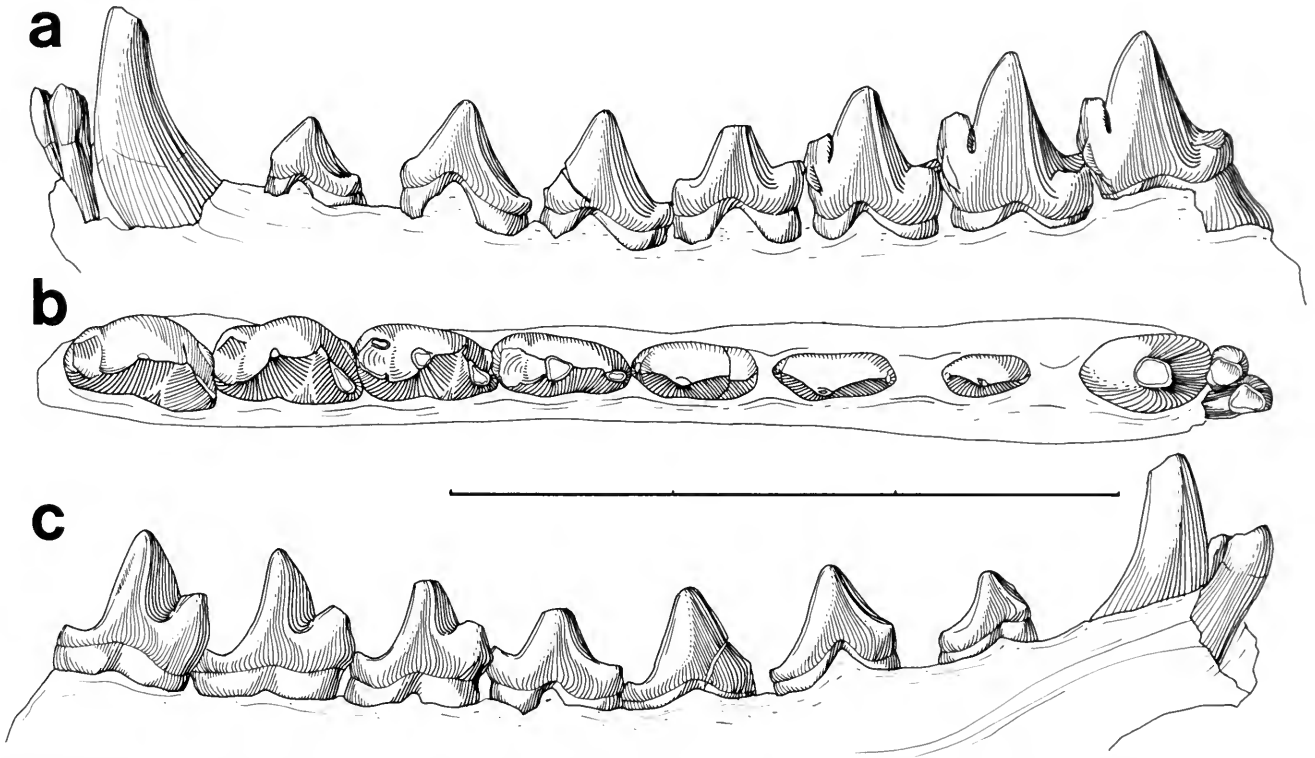


FIG. 37. *Sipalocyon gracilis* Ameghino, 1887 (Santacrucian). MACN 691 (type of *Protoproviverra manzaniana*), a nearly complete left mandibular ramus with complete dentition: **a,** labial; **b,** occlusal; **c,** lingual views. Scale = 30 mm.

TABLE 8. Measurements of mandibular rami of *Sipalocyon gracilis*.

Specimen	Depth of ramus below labial side of M_1	Breadth of same	Depth of ramus below labial side of M_4	Breadth of same
MACN 647	10.5	4.6	...	...
MACN 668	10.7	5.0	...	...
MACN 682	12.3	5.3	...	...
MACN 691(l)	...	5.1	...	5.3
MACN 691(r)	12.6	5.3	13.2	5.7
MACN 5938	10.5	5.0	11.8	5.2
MACN 5940	10.7	5.0	11.6	5.3
MACN 5953	...	...	13.7	6.3
MACN 5963	13.7	5.1	...	...
MACN 5964	13.6	5.6	14.6	5.5
MACN 5965	12.8	4.9	13.3	5.2
MACN 9353	11.5	5.0	...	...
MLP 11-12	11.2	5.1	...	...
MLP 11-41	12.6	5.2	...	...

TABLE 9. Statistics for some dimensions of mandibular rami of *Sipalocyon gracilis*.

Dimension	N	OR	x	s	CV
Depth of ramus below labial side of M_1	12	10.5–13.7	11.89	1.19	10.01
Breadth of ramus below M_1	13	4.6–5.6	5.09	0.24	4.72
Depth of ramus below labial side of M_4	6	11.6–14.6	13.03	1.15	8.83
Breadth of ramus below M_4	7	5.2–6.3	5.50	0.40	7.27

Lectotype of Hathliacynus lynchi.—MLP 11-7, a fragment of a left mandibular ramus with M_{1-4} complete.

Type of Thylacodictis exilis.—MLP 11-12, a fragment of a right mandibular ramus with alveoli of C-P_1, roots of P_{2-3}, M_1 complete, anterior half of M_1 complete.

Hypodigm.—The 13 types and MACN 648, a fragment of a right mandibular ramus with alveoli of P_{1-2}, and P_3 complete; MACN 667, a fragment of a right mandibular ramus with C-P_2 complete, and alveoli of P_3; MACN 668, a fragment of a left mandibular ramus with posterior root of P_2, roots of P_3, and M_{1-3} complete; MACN 688, a right maxillary fragment with root of C, P^1 complete, and alveoli of P^{2-3} (listed as *Amphiproviverra manzaniana* in Ameghino's catalogue); MACN 704, a left maxillary fragment with M^{2-3} (listed as *A. manzaniana* in Ameghino's catalogue); MACN 5938–5949, associated left and right mandibular rami almost complete, a maxillary fragment with left M^{2-4}, right M^{3-4}, crowns of both upper C's, and various postcranial elements, all of a single individual; MACN 5952, greater part of a cranium with most of dentition; MACN 5953, a fragment of a left mandibular ramus with M_{3-4} (same individual as MACN 5952); MACN 5959, rostral portion of a skull with most of dentition of left side and alveoli of I^{1-4}, root of C, and P^1 complete on right side; MACN 6286, a fragment of a left mandibular ramus with posterior alveolus of P_1 and P_{2-3} (listed as *Anodonictis obliterata* in Ameghino's catalogue); MACN 9352, a left maxillary fragment with alveolus of C, P^{1-2} complete, P^3-M^2 broken, alveoli of M^{3-4} (listed as *A. manzaniana* in Ameghino's catalogue); MACN 9353, a fragment of a left mandibular ramus

TABLE 10. Measurements of upper cheek teeth of *Sipalocyon gracilis*.

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 685	...	...	...	...	...	...	...	...	...	4.8	...	...	...	...	...	...
MACN 688	3.8	1.6	...	...	...	...	...	...	...	...	...	...	...	...	...	...
MACN 692	4.0	1.6	5.0	1.8	5.7	2.8	6.8	4.4	7.0	5.0	6.5	6.6	7.3	2.8	41.0	20.5
MACN 704	...	...	...	...	...	...	...	...	7.3	6.0	6.7	6.7	...	...	...	...
MACN 5939(l)	...	...	...	...	...	...	...	...	6.5	4.5	6.2	...	6.0	2.4	...	...
MACN 5939(r)	...	...	...	...	...	...	...	...	...	...	...	5.7	6.0	2.4	...	...
MACN 5952(l)	3.8	1.4	...	...	...	...	6.4	3.7	6.6	...	6.5	5.8	6.0	2.6	36.2	19.4
MACN 5952(r)	3.8	1.4	4.9	1.7	5.6	2.5	6.3	3.8	6.5	4.8	6.5	6.0	6.0	2.6	36.9	19.5
MACN 5958	4.2	1.7	5.2	1.9	6.1	2.9	7.2	4.5	7.4	5.4	7.5	6.7	7.0	2.7	42.6	22.0
MACN 5959(l)	3.9	1.5	5.0	1.8	5.4	2.5	6.4	3.8	6.6	4.8	6.6	5.9	6.1	2.5	37.0	19.8
MACN 5959(r)	3.9	1.5	...	...	...	...	...	...	...	...	...	...	...	...	...	...
MACN 9352	4.4	1.7	5.1	1.8	6.2	3.2	...	4.4	...	...	...	...	...	...	ca. 43.3	ca. 21.6
FMNH P13777(l)	...	...	5.2	2.0	...	...	ca. 7.5	...	7.5	...	7.5	7.8	...	...	...	22.6
FMNH P13777(r)	...	...	...	...	...	...	...	...	7.6	...	7.5	7.9	...	...	...	...
PU 15148	3.9	1.8	...	...	6.4	3.1	7.5	4.5	7.6	6.0	7.2	7.8	7.5	2.9	...	22.0
PU 15373(l)	3.8	1.5	5.0	1.8	5.4	2.5	6.4	3.8	6.3	4.8	6.0	5.7	5.5	2.4	35.4	18.5
PU 15373(r)	3.9	1.5	5.2	2.0	5.2	2.5	6.3	3.8	6.3	4.9	6.2	5.7	5.5	2.4	35.6	18.7
AMNH 9254(l)	4.1	1.6	5.0	2.0	5.6	2.5	6.6	4.2	6.8	5.4	6.3	6.0	6.0	2.5	36.5	19.5
AMNH 9254(r)	4.0	1.7	5.0	1.9	5.7	2.6	6.7	4.2	6.7	5.5	6.4	6.1	6.1	2.4	36.5	19.3

TABLE 11. Statistics for some upper cheek tooth dimensions of *Sipalocyon gracilis*.

Dimensions		N	OR	x	s	CV
P^1	L	13	3.8–4.4	3.96	0.18	4.55
	W	13	1.4–1.8	1.58	0.12	7.59
P^2	L	10	4.9–5.2	5.06	0.11	2.17
	W	10	1.7–2.0	1.87	0.11	5.88
P^3	L	10	5.2–6.4	5.73	0.39	6.81
	W	10	2.5–3.2	2.71	0.27	9.96
M^1	L	11	6.3–7.5	6.74	0.46	6.82
	W	11	3.7–4.5	4.10	0.32	7.80
M^2	L	14	6.3–7.6	6.91	0.48	6.95
	W	12	4.5–6.0	5.16	0.49	9.50
M^3	L	14	6.0–7.5	6.69	0.52	7.77
	W	14	5.7–7.9	6.46	0.82	12.69
M^4	L	12	5.5–7.5	6.25	0.65	10.40
	W	12	2.4–2.9	2.55	0.17	6.67
P^1-M^3	L	10	36.2–43.3	38.10	2.99	7.85
M^{1-3}	L	12	18.5–22.6	20.28	1.41	6.95

with posterior root of P_2, P_3-M_1 complete, roots of M_{2-3}; MACN 9354, a fragment of a right mandibular ramus with P_1 complete, roots of P_2, P_3-M_1 complete; MACN 9355, maxillary fragment with a molar; MACN 9356, maxillary fragment with a molar; MACN 9357, an isolated C; MACN 9358, distal end of a humerus (MACN 9353–9358 are of a single individual); MACN 9389, a fragment of a left mandibular ramus with roots of P_{1-2}, and P_3-M_2 complete, M_3 missing tips of protocone and paracone; MACN 9390, an isolated left M^1; MACN 9391, an isolated right M^3; MACN 9392, an isolated vertebra and assorted tooth fragments (MACN 9389–92 are of the same individual, labeled *Sipalocyon altiramis* in Ameghino's catalogue); MLP 11-22, a fragment of a left mandibular ramus with roots of P_{1-2}, P_3-M_2 complete, anterior root of M_3; MLP 11-25, a fragment of a right mandibular ramus with alveoli of P_1, roots of P_2, P_3 complete, alveoli of M_1, and M_{2-4} complete; MLP 11-39, a fragment of a left mandibular ramus of a juvenile with M_1, and associated fragment of a right mandibular ramus with P_2 erupting (anterior edge is up, but posterior edge is not), alveoli of DP_3, M_1 complete, and alveoli of M_2 (both specimens of same individual) (no trace of P_3 because this portion of the ramus is broken away) (see Marshall, 1976a, 1978); MLP 11-41, a fragment of a left mandibular ramus with root of C, P_1 complete, roots of P_2, P_3 complete, and alveoli of M_1; MLP 11-76, a fragment of a left mandibular ramus with M_2; MLP 11-77, a fragment of a right mandibular ramus with M_3; MLP 11-105, an isolated C, and a right M_{1-2}, supposedly of same individual; FMNH P13777 [= P13275], greater part of skull (partially restored with plaster) with posterior half of left C, P^1, P^3, M^{1-2} and M^4 broken, and P^2 and M^3 complete, and roots of right P^1-M^4 (all broken), and three vertebrae in matrix; AMNH 9238, a fragment of a left mandibular ramus with M_{1-2} complete and M_3 broken; AMNH 9254, a nearly complete skull and partial mandibular ramus; PU 15029, an incomplete skull and mandible; PU 15148, a fragment of a right maxillary with alveoli of C, P^1 complete, roots of P^2, and P^3-M^4 complete; PU 15154, a crushed skull, atlas, third cervical, and portions of right fore- and left hindlimbs; PU 15312, fragments of lower jaws and upper teeth (exchanged to AC in 1922); PU 15373, an incomplete skull and mandible, fragments of a left ulna, phalanges, distal end of a metapodial, and part of a patella.

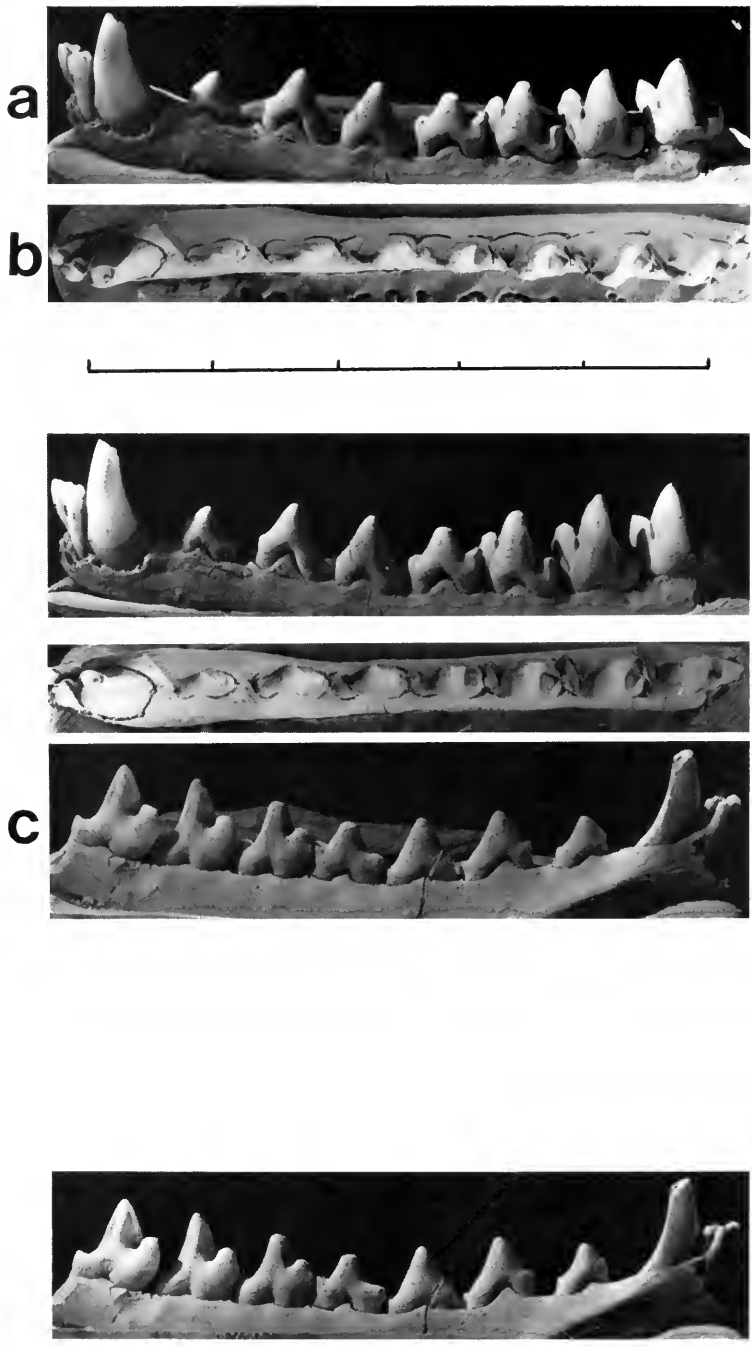


FIG. 38. *Sipalocyon gracilis* Ameghino, 1887 (Santacrucian). Stereopairs of MACN 691 (type of *Protoproviverra manzaniana*), a nearly complete left mandibular ramus with complete dentition: **a,** labial; **b,** occlusal; **c,** lingual views. Scale = 50 mm.

TABLE 12. Measurements of lower cheek teeth of *Sipalocyon gracilis*.

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
MACN 647	...	...	5.0	2.0	5.3	2.3	5.5	2.3	6.1	2.9	...	...	...	...	...	...
MACN 648	...	...	...	...	5.9	2.5	...	...	...	...	...	...	...	...	...	...
MACN 667	4.2	1.8	5.5	2.1	...	...	...	...	...	...	...	...	...	...	...	...
MACN 668	...	...	...	...	...	...	5.7	2.3	6.3	3.0	6.6	3.2	...	...	...	...
MACN 682	...	...	...	...	...	...	6.1	2.7	6.4	3.4	...	...	...	...	...	...
MACN 683	...	...	...	...	...	...	6.0	2.5	...	...	...	...	...	...	...	...
MACN 691(l)	4.2	2.0	5.8	2.2	6.0	2.5	6.0	2.9	6.5	3.4	6.9	4.0	7.0	4.0	44.2	25.9
MACN 691(r)	4.3	2.0	5.8	2.2	5.9	2.4	6.0	2.8	6.4	3.4	6.8	4.0	7.0	4.0	44.9	26.0
MACN 5938	4.1	1.8	5.0	2.0	5.5	2.3	5.4	2.2	6.0	3.0	6.3	3.3	6.4	3.2	38.8	22.7
MACN 5940	4.0	1.8	...	2.0	5.5	2.2	5.5	2.2	6.0	3.0	...	3.2	6.4	3.2	38.9	22.8
MACN 5953	...	...	...	...	...	...	...	...	...	...	6.4	3.4	6.5	3.6	...	...
MACN 5957	...	...	5.8	2.1	6.7	2.5	...	...	6.6	3.3	...	...	7.2	4.1	...	ca. 26.0
MACN 5960	...	...	6.0	2.2	...	...	...	...	...	...	...	...	...	...	...	...
MACN 5963	...	...	5.5	2.0	...	...	6.1	2.5	...	...	6.9	3.6	...	...	...	...
MACN 5964	4.4	1.7	5.1	1.9	5.9	2.4	5.9	2.4	6.0	3.0	6.2	3.4	6.4	3.3	42.4	24.9
MACN 5965	...	...	5.2	2.0	5.8	2.5	5.6	2.6	6.0	3.0	6.3	3.6	...	...	43.0	25.0
MACN 9353	...	...	...	...	5.8	2.4	6.1	2.8	...	...	...	...	...	...	...	...
MACN 9354	4.2	1.8	...	...	5.7	2.3	6.1	2.8	6.5	3.5	6.9	3.7	...	...	...	...
MACN 9389	...	...	...	...	6.2	2.3	5.8	2.5	6.4	3.2	6.8	3.6	...	...	...	...
MLP 11-7	...	...	...	...	...	...	5.7	2.3	6.0	3.1	6.5	3.4	6.5	3.5	...	24.4
MLP 11-12	...	...	...	...	...	...	5.7	2.3	...	...	...	...	...	...	...	...
MLP 11-22	...	...	...	...	5.7	2.2	5.8	2.3	6.1	3.0	...	...	...	...	...	...
MLP 11-25	...	...	...	...	5.6	2.2	...	...	6.0	2.9	6.2	3.3	6.3	3.4	ca. 42.5	ca. 23.6
MLP 11-39(l)	...	...	...	...	...	...	5.9	2.5	...	...	...	...	...	...	...	...
MLP 11-39(r)	...	...	...	...	...	...	5.9	2.5	...	...	...	...	...	...	...	...
MLP 11-41	...	...	...	...	6.0	2.3	...	...	...	...	...	...	...	...	...	...
MLP 11-76	...	...	...	...	...	...	...	...	6.5	3.4	...	...	...	...	...	...
MLP 11-77	...	...	...	...	...	...	...	...	...	...	6.4	3.7	...	...	...	...
MLP 11-105	...	...	...	...	...	...	6.2	2.8	6.3	3.2	...	...	...	...	...	...
AMNH 9238	...	...	...	...	...	...	5.5	2.3	6.0	3.0	6.5	ca. 3.3	...	...	...	...
PU 15373(l)	4.2	1.6	5.2	1.9	5.5	2.3	5.8	2.6	6.2	3.2	6.4	3.4	6.4	3.3	38.8	23.1
PU 15373(r)	4.2	1.6	5.2	2.0	5.6	2.2	5.7	2.7	6.3	3.1	6.2	3.4	6.3	3.3	39.2	22.9

TABLE 13. Statistics for some lower cheek tooth dimensions of *Sipalocyon gracilis*.

Dimension		N	OR	x	s	CV
P_1	L	9	4.0–4.4	4.20	0.11	2.62
	W	9	1.6–2.0	1.79	0.15	8.38
P_2	L	12	5.0–6.0	5.43	0.35	6.45
	W	13	1.9–2.2	2.05	0.11	5.37
P_3	L	17	5.3–6.7	5.80	0.33	5.69
	W	17	2.2–2.5	2.34	0.11	4.70
M_1	L	23	5.4–6.2	5.83	0.23	3.95
	W	23	2.2–2.9	2.51	0.22	8.76
M_2	L	20	6.0–6.6	6.23	0.21	3.37
	W	20	2.9–3.5	3.15	0.19	6.03
M_3	L	16	6.2–6.9	6.52	0.26	3.99
	W	17	3.2–4.0	3.50	0.24	6.86
M_4	L	11	6.3–7.2	6.58	0.32	4.86
	W	11	3.2–4.1	3.54	0.34	9.60
P_1-M_4	L	9	38.8–44.9	41.41	2.49	6.01
M_{1-4}	L	11	22.7–26.0	24.30	1.34	5.51

Horizon and locality.—All specimens are from the Santa Cruz Formation, Santa Cruz Province, Argentina. The specific localities of collection are as follows: *Río Santa Cruz* MLP 11-7, 11-25; *Monte Observación* MACN 647, 667, 668, 683, 685, 688, 704 (collected by C. Ameghino 1890–91), MACN 682, 6286 (collected by C. Ameghino 1891–92); *Monte León* MLP 11-12, 11-22, 11-39; *La Cueva* MACN 5938–5949, 5959, 5963, 5964, 5965, 9353, 9354 (collected by C. Ameghino 1892–93); *Corriquen Kaik* MACN 5952, 5953, 5957, 5958, 9352 (collected by C. Ameghino 1892–93); *Shehuén* (=*Sehuen*) MACN 648, 691–703 (collected by C. Ameghino 1890–91); *Yequa Quemada* MACN 5960, 9389–91 (collected by C. Ameghino 1892–93); *Killik Aike Norte* (=*Felton's Estancia*) PU 15373 (collected by J. B. Hatcher), AMNH 9254 (collected by B. Brown); *La Costa, 7 miles south of Puerto Coyle* FMNH P13777 (collected by F. G. Sternberg 1923); *Cañadón de las Vacas*

FIG. 39. *Sipalocyon gracilis* Ameghino, 1887 (Santacrucian). MACN 691 (type of *Protoproviverra manzaniana*), a nearly complete right mandibular ramus with complete dentition: **top**, occlusal; **bottom**, labial views. Scale = 50 mm.

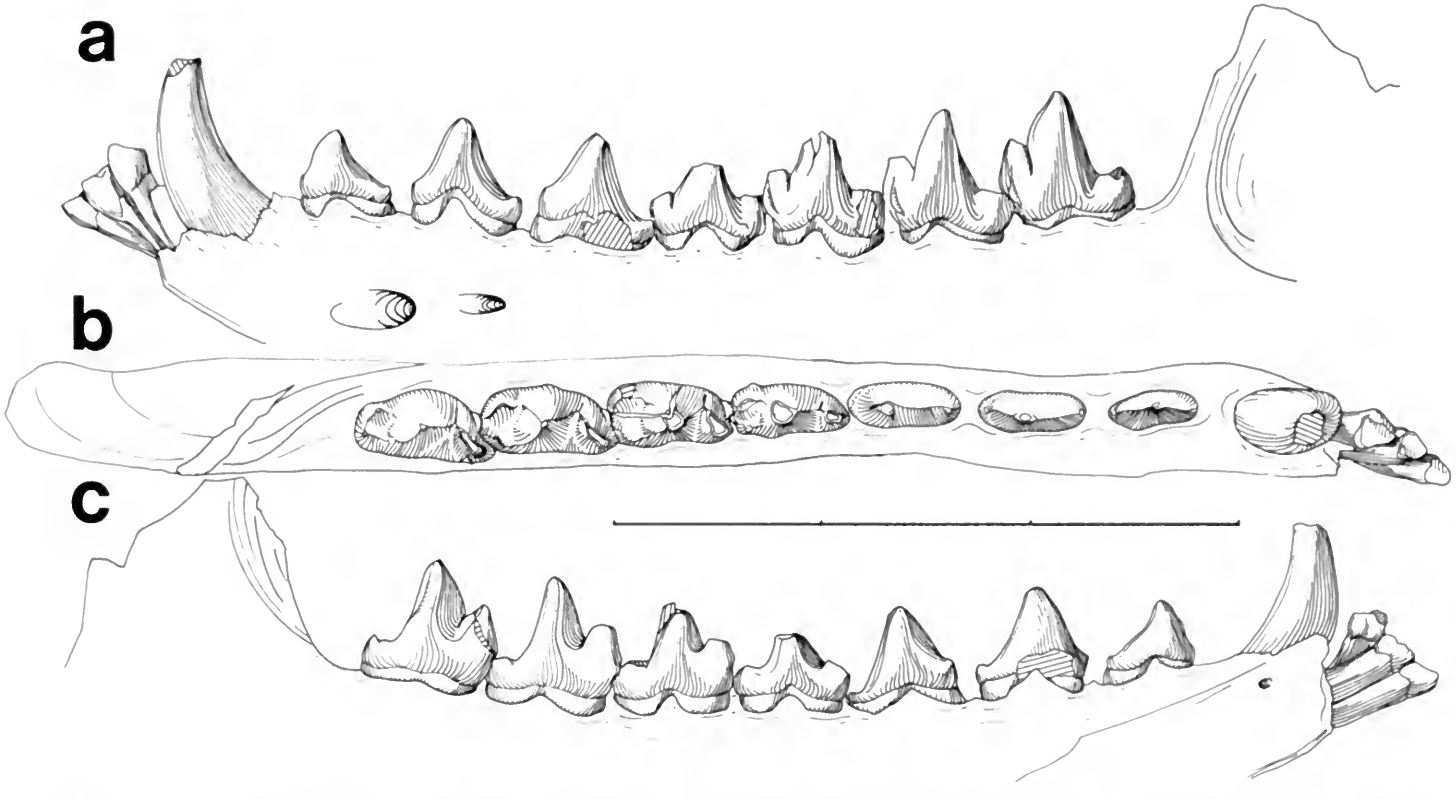


FIG. 40. *Sipalocyon gracilis* Ameghino, 1887 (Santacrucian). PU 15373, a nearly complete left mandibular ramus with most of dentition: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 30 mm.

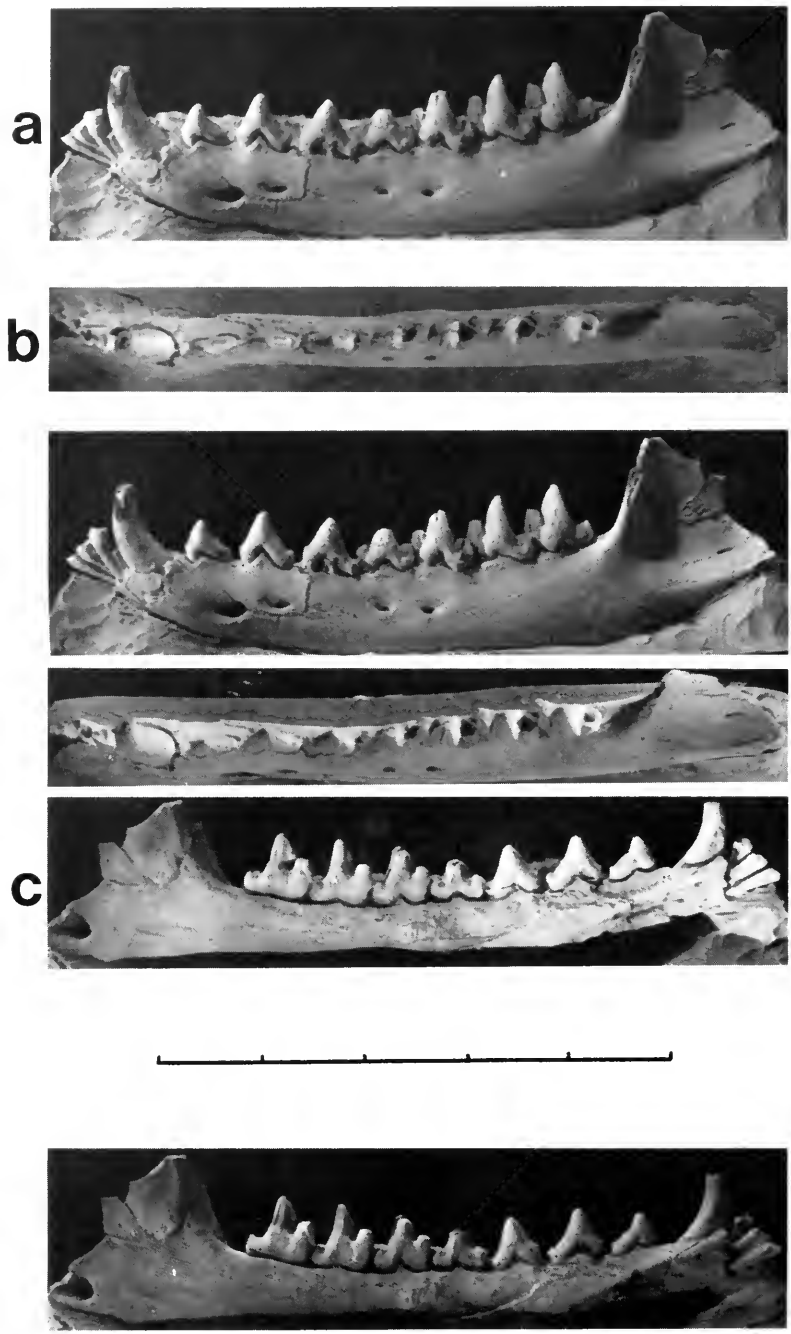


FIG. 41. *Sipalocyon gracilis* Ameghino, 1887 (Santacrucian). Stereopairs of PU 15373, a nearly complete left mandibular ramus with most of dentition: **a,** labial; **b,** occlusal; **c,** lingual views. Scale = 50 mm.

AMNH 9238 (collected by B. Brown 1899); *10 miles south of Coy Inlet* PU 15029 (collected by J. B. Hatcher 1896), 15148, 15154, 15312 (collected by O. A. Peterson 1896); *No data* MLP 11-41, 11-76, 11-77, 11-105.

Age.—Santacrucian.

Diagnosis.—Slightly larger than *Sipalocyon externa* in linear tooth dimensions; differs from *S. obusta* in having a deeper and more robust mandibular ramus and a larger talonid on M_4.

Description.—In the type of *Sipalocyon gracilis*, MACN 647, a very large mental foramen occurs below the P_{1-2} contact (its size is accentuated by the pathological disorder discussed below), and four smaller foramina occur more posteriorly—one below the middle of P_2, one below P_{2-3} contact, one below the middle of P_3, and the largest of the four is below M_1. The teeth are relatively unworn, indicating that this was a young animal. The P_{1-3} are separated from each other by tiny diastems, and the alveolus of the anterior root of P_1 lies slightly labiad of the posterior alveolus. The P_{2-3} have small but distinct posterobasal cusps. A small but distinct entoconid and hypoconulid are easily distinguished on the talonid of M_2, and together these cusps are about equal in size to the hypoconid.

Periosteal proliferations.—Several specimens of *S. gracilis* (including MACN 647, 682, 683, 5960, 6286) have a pathological disorder in the anterior part of the mandibular ramus. This infection is expressed as irregular rugosities around the mental foramina below the premolars and canine, often extending onto the symphyseal surface.

In MACN 647, the type of *S. gracilis*, the bone in the symphyseal region and around the large mental foramen below the P_{1-2} contact is swollen and is covered by numerous rugosities. The infection has resulted in a significant increase in size of this foramen.

In MACN 682, the type of *Amphithereutes amputans*, a small rugosity occurs on the ventral border of the ramus below the P_3-M_1 contact. In the type of *Perathereutes obtusus*, MACN 683, the symphyseal region and area below the premolars on the labial side is swollen and covered with rugosities. The anterior root of the P_1 is all but obliterated and is filled with secondary bone growth. This condition accentuated the size of the diastema between the C and P_1, a feature noted by Ameghino in the original description of this species.

In MACN 5960 the incisor region is greatly distorted by the infection and is an amorphous mass of secondary bone growth. The mental foramen below the P_{1-2} contact is extremely large and is surrounded and filled by rugosities. The ventral border of the ramus and the inner side of the symphysis are also affected, and rugosities extend to a point below the anterior root of the P_3. The C is very blunt, suggesting that infection caused malocclusion.

The most extreme case of the infection occurs in MACN 6286. The entire canine alveolus and anterior root of the P_1 are filled with cancellous bone, and it appears that these teeth were either lost during the life of the animal or were never present. The ventral border of the symphysis is also very swollen, and the mental foramen below the P_{1-2} contact is enormous (4 × 2 mm), and the border is very swollen.

Comments.—MACN 648 is listed as *Sipalocyon gracilis* in Ameghino's catalogue and on the specimen. There is, however, no direct reference to this specimen in Ameghino's description of this species, and it therefore does not appear to represent a syntype. MACN 648 is slightly larger than the type, MACN 647, and

the posterobasal heel on the P_3 is better developed. The P_1 is separated from P_2 by a small (1.5 mm) diastema.

MACN 667 is listed as the "tipo" of *Sipalocyon mixtus* in Ameghino's catalogue. However, he neither gave measurements for nor made special reference to this specimen in the original description of this species. The specimen used by Ameghino in the original description of *S. mixtus* is clearly MACN 5963, and this is the type. MACN 5963 is listed as *S. mixtus* in Ameghino's catalogue, but is not listed as the "tipo" either in the catalogue or on the specimen. The incisor alveoli of this specimen are broken away, and these teeth are not "rudimentary" as believed by Ameghino.

In Ameghino's catalogue MACN 668 is listed as the "tipo" of *Sipalocyon curtus*. However, the specimen referred to in Ameghino's original description of this species is MACN 5960 (–62), which is identified by that name in his catalogue but is not listed as the type.

Ameghino (e.g., 1894, fig. 52) figured, as *Amphiproviverra manzaniana*, a nearly complete palate with complete dentition. This figure is based on the left maxillary and premaxillary with complete dentition of the type of *A. manzaniana*, MACN 692. There is no trace of the right side nor did Ameghino note its presence in his catalogue. The only part of the upper right dentition preserved with the type is an isolated C. Ameghino apparently restored the right side in his figure by making a mirror image of the left.

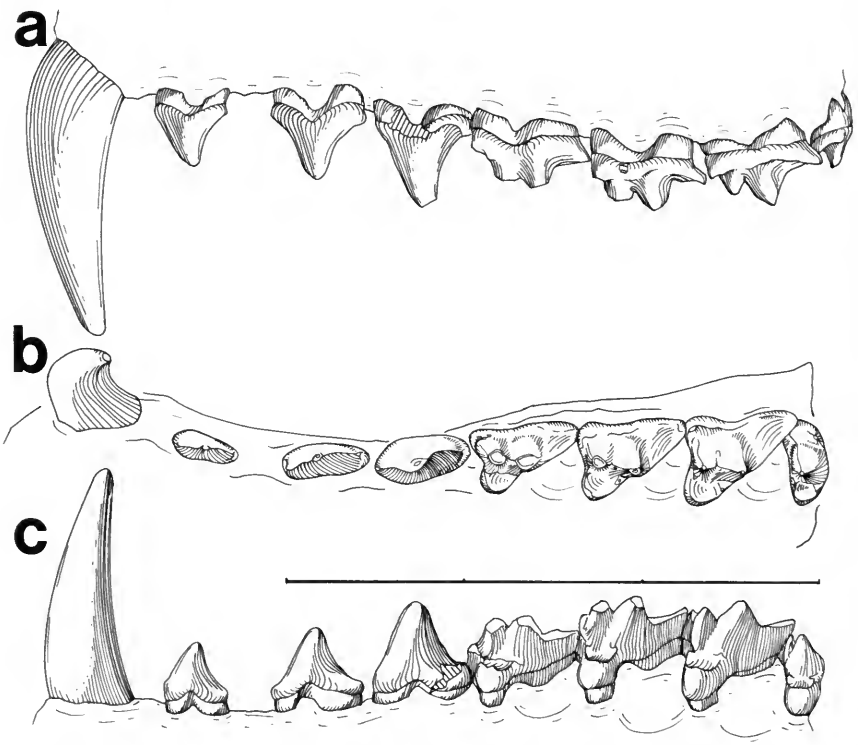


FIG. 42. *Sipalocyon gracilis* Ameghino, 1887 (Santacrucian). PU 15373, left C-M^4 of an incomplete skull: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 30 mm.

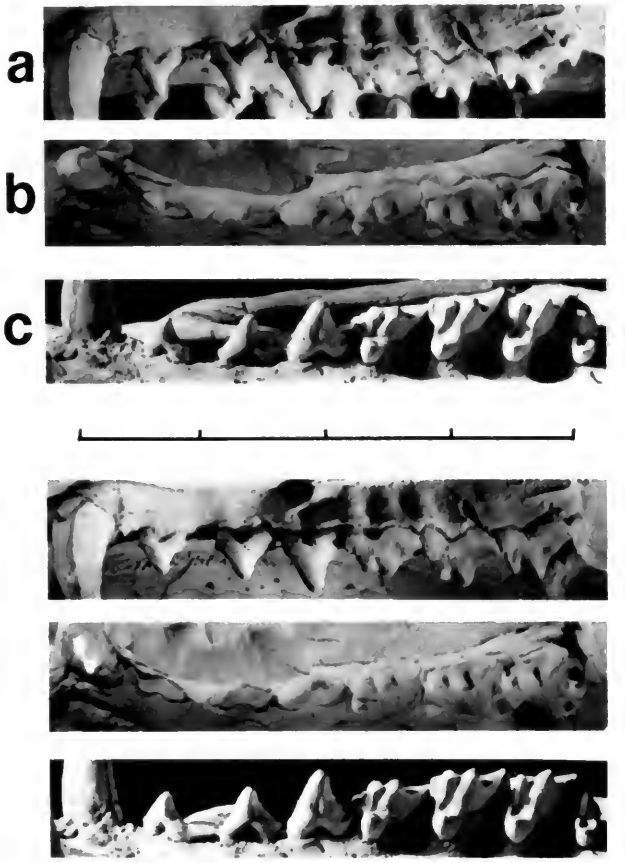


FIG. 43. *Sipalocyon gracilis* Ameghino, 1887 (Santacrucian). Stereopairs of PU 15373, left C-M^4 of an incomplete skull: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 40 mm.

Sipalocyon gracilis is, as noted above, very similar to the Colhuehuapian species *S. externa* and may be regarded as the direct descendant of that species. The primary changes in this lineage include a slight increase in size, shallowing of the ectoflex, and increase in size of the metacrista on M^3.

Sipalocyon gracilis is structurally very similar to the contemporaneous species *Perathereutes pungens*. Both have the P_1 set at a slight (10°) angle relative to the rest of the tooth row, P_1 is separated from C and P_2 by small but distinct diastems, and talonids on M_{1-4} are well developed and basined. These species differ in *P. pungens* being smaller in size, in having relatively larger talonids on M_{1-4}, and in M_1 being relatively longer and narrower, and the paraconid being subequal to the talonid in size (latter is larger in *S. gracilis*). Overall, these differences are minimal, and *Perathereutes* and *Sipalocyon* appear to be more closely related than either is to any other contemporaneous genus. These genera shared a common ancestor (possibly in the Deseadan) that was not shared with any other known genus of Hathlyacyninae.

Sipalocyon obusta (Ameghino, 1891c). Figures 44–46; Table 14.

Protoproviverra obusta Ameghino, 1891c, p. 313.
Amphiproviverra obusta Ameghino, 1894, p. 389.
Thylacodictis robusta (sic) Simpson, 1930, p. 51

Type.—MACN 686, a fragment of a left mandibular ramus with base of P_3, M_{1-2} complete, roots of M_3, M_4 complete; and MACN 687, a fragment of a right mandibular ramus (both specimens are of same individual).

Hypodigm.—Type only.

Horizon and locality.—Collected by C. Ameghino in 1890–91 from the Santa Cruz Formation at Monte Observación, Santa Cruz Province, Argentina.

Age.—Santacrucian.

Diagnosis.—Similar in size to *S. gracilis*, but with a very shallow and gracile mandibular ramus and a very reduced talonid on M_4.

Comments.—This species is tentatively recognized as valid. In size and structure of the P_3-M_3 and trigonid portion of the M_4, *S. obusta* is virtually identical to specimens of *S. gracilis*. However, it differs from specimens of *S. gracilis* in the M_4 having a very reduced talonid and in the very shallow and gracile structure of the mandibular ramus. These features may be a reflection of the young age of this specimen because the posterior molars show no indication of occlusal wear and there are growth lines on the ramus in the area of the M_4, suggesting that this element has not yet completed growth. This specimen might thus represent a variant individual of *S. gracilis*, although it is very unique and there

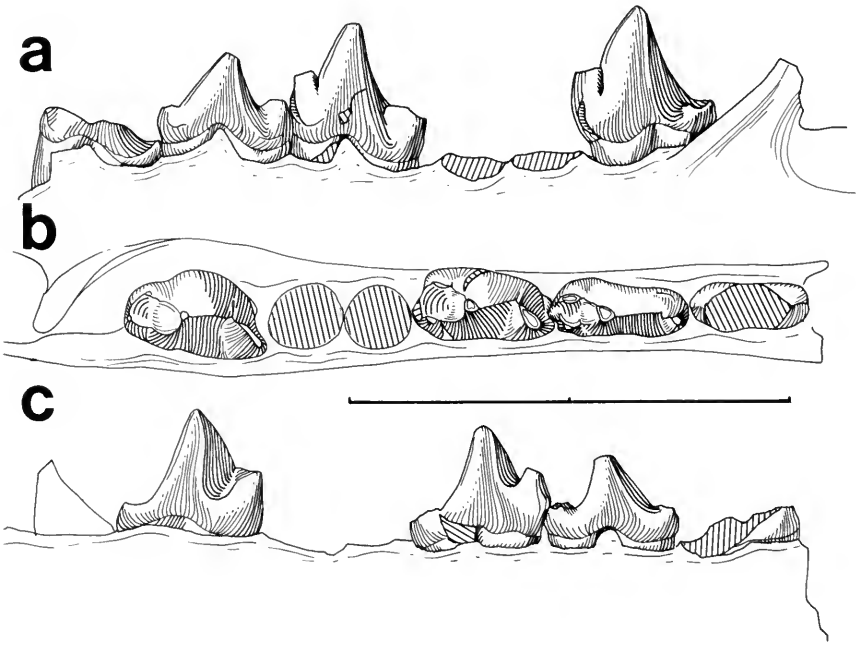


FIG. 44. *Sipalocyon obusta* (Ameghino, 1891c) (Santacrucian). MACN 686 (type), a fragment of a left mandibular ramus with base of P_3, M_{1-2} complete, roots of M_3, and M_4 complete: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 20 mm.

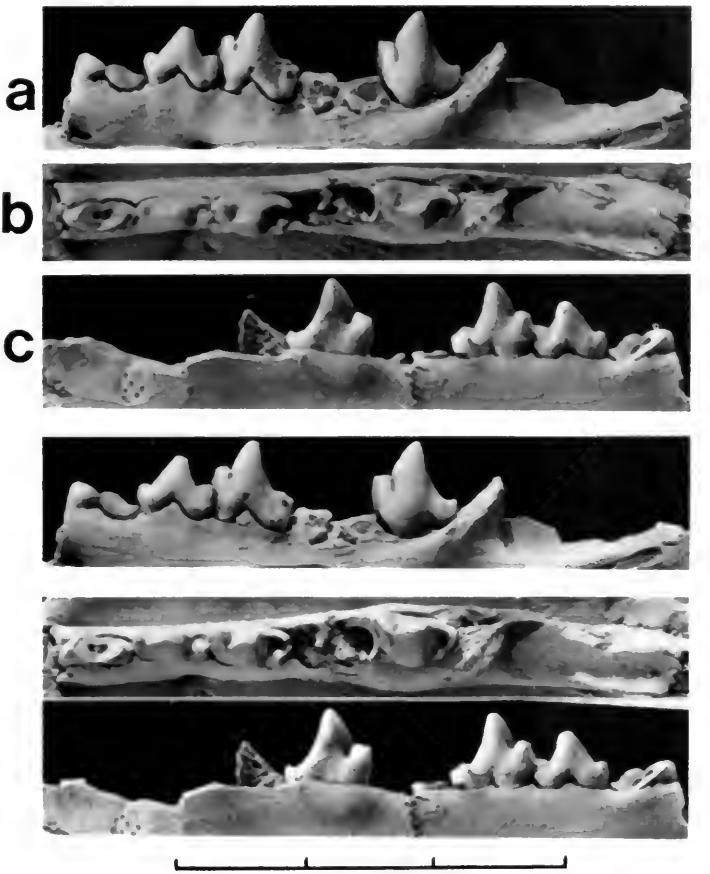


FIG. 45. *Sipalocyon obusta* (Ameghino, 1891c) (Santacrucian). Stereopairs of MACN 686 (type), a fragment of a left mandibular ramus with base of P_3, M_{1-2} complete, roots of M_3, and M_4 complete: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 30 mm.

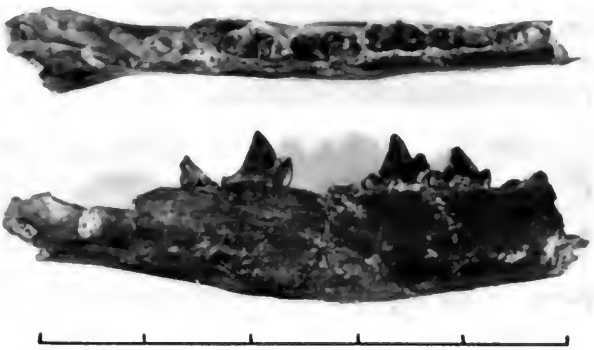


FIG. 46. *Sipalocyon obusta* (Ameghino, 1891c) (Santacrucian). MACN 686 (type), a fragment of a left mandibular ramus with base of P_3, M_{1-2} complete, roots of M_3, and M_4 complete: **top**, occlusal; **bottom**, lingual views. Scale = 50 mm.

TABLE 14. Measurements of cheek teeth and mandibular rami of *Sipalocyon obusta*.

Specimen	M_1		M_2		M_4		M_{1-4}	Depth of ramus below labial side of M1	Breadth of same	Depth of ramus below labial side of M4	Breadth of same
	L	W	L	W	L	W	L				
MACN 686	6.0	2.5	6.3	3.2	6.5	3.7	24.7	9.8	4.0	9.4	5.4
MACN 687	...	...	...	...	6.6	3.8	...	...	...	9.2	5.6

is nothing else quite like it in the Ameghino collection. *Sipalocyon obusta* thus apparently represents a species distinct from that of *S. gracilis*, and they may both have evolved from a Colhuehuapian ancestor like *S. externa*.

Ameghino (1891c, p. 313) orginally placed this species in the Dasyura, family Thylacinidae, but later (1894, p. 389) put it in his group Sparassodonta, family Amphiproviverridae.

Notocynus Mercerat, 1891b

Notocynus Mercerat, 1891b, p. 81.

Type.—*Notocynus hermosicus* Mercerat, 1891b, p. 81.
Distribution.—Montehermosan, Buenos Aires Province, Argentina.
Diagnosis.—As for type and only known species.

Notocynus hermosicus Mercerat, 1891b. Figures 47, 48; Tables 5, 6.

Notocynus hermosicus Mercerat, 1891b, p. 81; Ameghino, 1891f, p. 438; Rovereto, 1914, p. 159; Cabrera, 1927, p. 305, fig. 18; Ringuelet, 1966, p. 55, pl. 11, figs. D, E.
Notocynus hermosieus (sic) Mercerat, 1898, p. 58.
Didelphys triforata Ameghino, 1891f, p. 438 *(partim)*.

Type.—MLP 11-91, a fragment of a left mandibular ramus with roots of C and P_1, base of P_2, roots of P_3-M_2 (M_1 crown was lost since the specimen was figured by Cabrera, 1927, fig. 18), M_3 present but missing tips of protoconid and paraconid, and anterior root of M_4 present.

Hypodigm.—Type only.

Horizon and locality.—Monte Hermoso, type locality of Montehermosan, Buenos Aires Province, Argentina.

Age.—Montehermosan.

Diagnosis.—Small borhyaenid, similar to *Sipalocyon gracilis* in size and structure; C weakly developed; tooth row tight, no diastems separating antemolar cheek teeth; P_{1-3} aligned in same anteroposterior axis; P_2 with small but distinct posterobasal heel; M_{1-3} with large-basined talonid; small anterobasal cingular cusp present on M_{2-3}, but not on M_1; a large mental foramen opens below anterior root of P_2, and another tiny one opens below posterior root of P_2.

Comments.—*Notocynus hermosicus* was erected by Mercerat (1891b, p. 81) on a partial left mandibular ramus collected from Monte Hermoso, type locality of the Montehermosan. Ameghino (1891f, p. 438) critically and unjustly attacked Mercerat, noting in his opinion that *N. hermosicus* was a synonym of *Didelphys triforata*. The latter, from the same locality as *N. hermosicus*, was earlier named and figured by Ameghino (1889, p. 280, pl. 22, figs. 37-38). Mercerat later (1898, p. 58) pointed out that Trouessart (1898, p. 1232) accepted *N. hermosicus* as valid, an opinion *contra* to that of Ameghino. Ameghino refused, however, to recognize this species, and in his classic work of 1898 *Sinopsis geológico-paleontológica* he did not even mention the name *N. hermosicus*. Cabrera (1927, p. 305, fig. 18) later redescribed and figured the type specimen (MLP 11-91) and rightly concluded that *N. hermosicus* was indeed valid.

Two additional specimens from different horizons and localities than the type have been referred in literature to *N. hermosicus*. Riggs & Patterson (1939, p. 149) noted that:

> a portion of maxillary with M^{1-3} and the mandibular rami of the small borhyaeninae may be referred with confidence to *N. hermosicus* Mercerat, hitherto known only from the Monte Hermoso beds. . . .

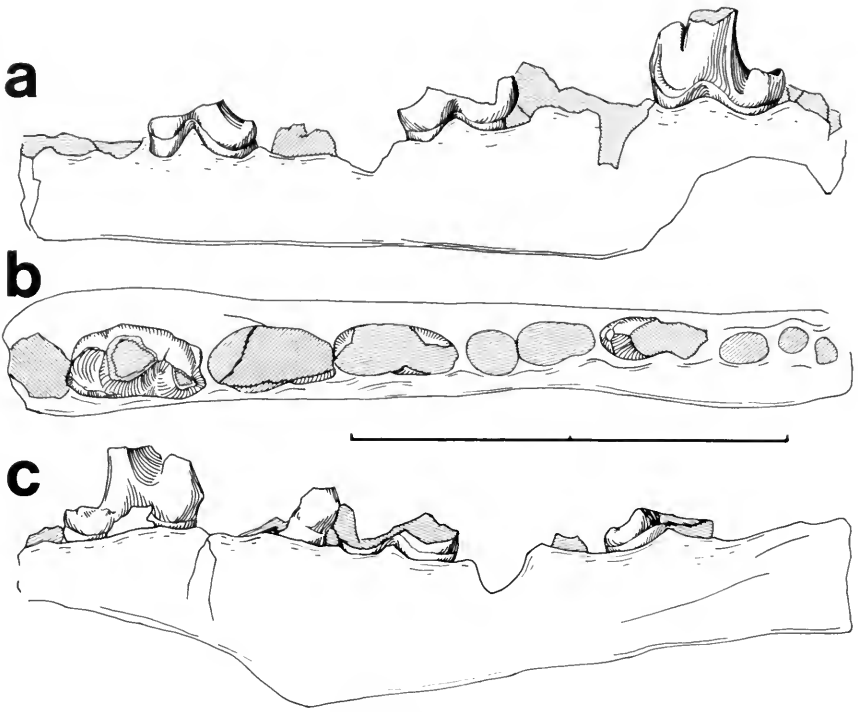


FIG. 47. *Notocynus hermosicus* Mercerat, 1891b (Montehermosan). MLP 11-91 (type), a fragment of a left mandibular ramus with roots of C and P_1, base of P_2, roots of P_3-M_2, M_3 present but missing tips of protoconid and paraconid, and anterior root of M_4 present: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 20 mm.

This specimen (FMNH P14409) from beds of Montehermosan age in the province of Catamarca is here (p. 37) named a new species of *Borhyaenidium*.

Reig (1958a, p. 249) tentatively included cf. *Notocynus hermosicus* in a list of taxa from the Chapadmalal Formation. He later (1958b, p. 280) mentioned that this tentative identification was applied to a cranial fragment (MMP S-240) of a large marsupial that was distinct from other species in the fauna. He pointed out that this specimen was larger than *Sparassocynus* and did not have an epitympanic sinus, but there was evidence of a large alisphenoid bulla. Reig believed this specimen to be of a borhyaenid, and on the basis of its size had earlier (1958a, p. 249) assigned it provisionally to *Notocynus*. I have not seen this specimen, and its true identity is not known.

Notocynus hermosicus is very similar to *Sipalocyon gracilis* (i.e., MACN 5938) from the Santacrucian. In both species there is a small but distinct heel on P_2, the M_3 has a very large and deeply basined talonid, there is a small anterobasal cingulum, and the size and proportions of the teeth and mandibular ramus are virtually identical. These species differ in *N. hermosicus* having the P_1 aligned in the same anteroposterior axis as the rest of the cheek teeth and not being set obliquely as in *S. gracilis*, and in the P_1 in *N. hermosicus* not being separated from

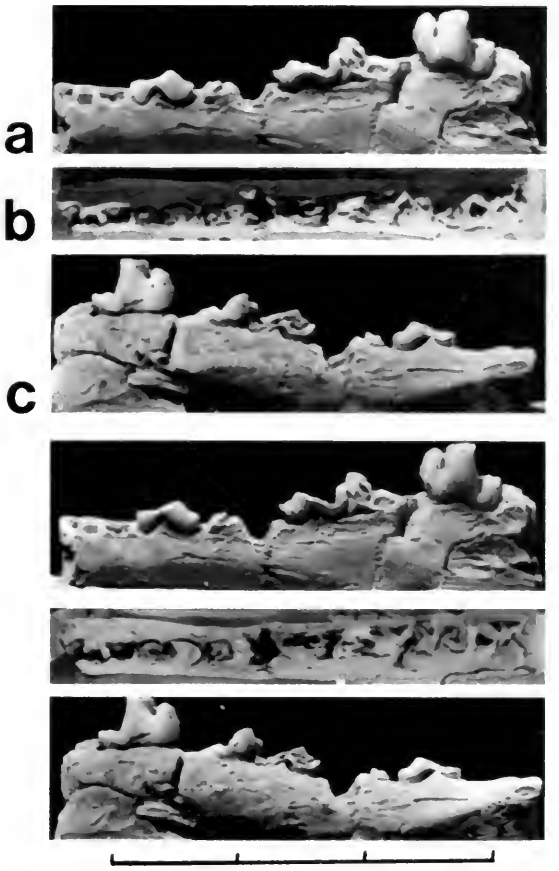


FIG. 48. *Notocynus hermosicus* Mercerat, 1891b (Montehermosan). Stereopairs of MLP 11-91 (type), a fragment of a left mandibular ramus with roots of C and P_1, base of P_2, roots of P_3-M_2, M_3 present but missing tips of protoconid and paraconid,and anterior root of M_4 present: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 30 mm.

the C and P_2 by diastems. These differences are minor, and I regard *S. gracilis* as the Santacrucian ancestor of *N. hermosicus*.

Notogale Loomis, 1914

Notogale Loomis, 1914, p. 216.

Type.—?*Pharsophorus mitis* Ameghino, 1897, p. 504.
Distribution.—Deseadan of Patagonia, and Bolivia.
Diagnosis.—As for type and only known species.

Notogale mitis (Ameghino, 1897). Figures 49–55; Table 15.

?*Pharsophorus mitis* Ameghino, 1897, p. 504.
Notogale mitis Loomis, 1914, p. 216, figs. 142, 143; Patterson & Marshall, 1978, figs. 2-7.

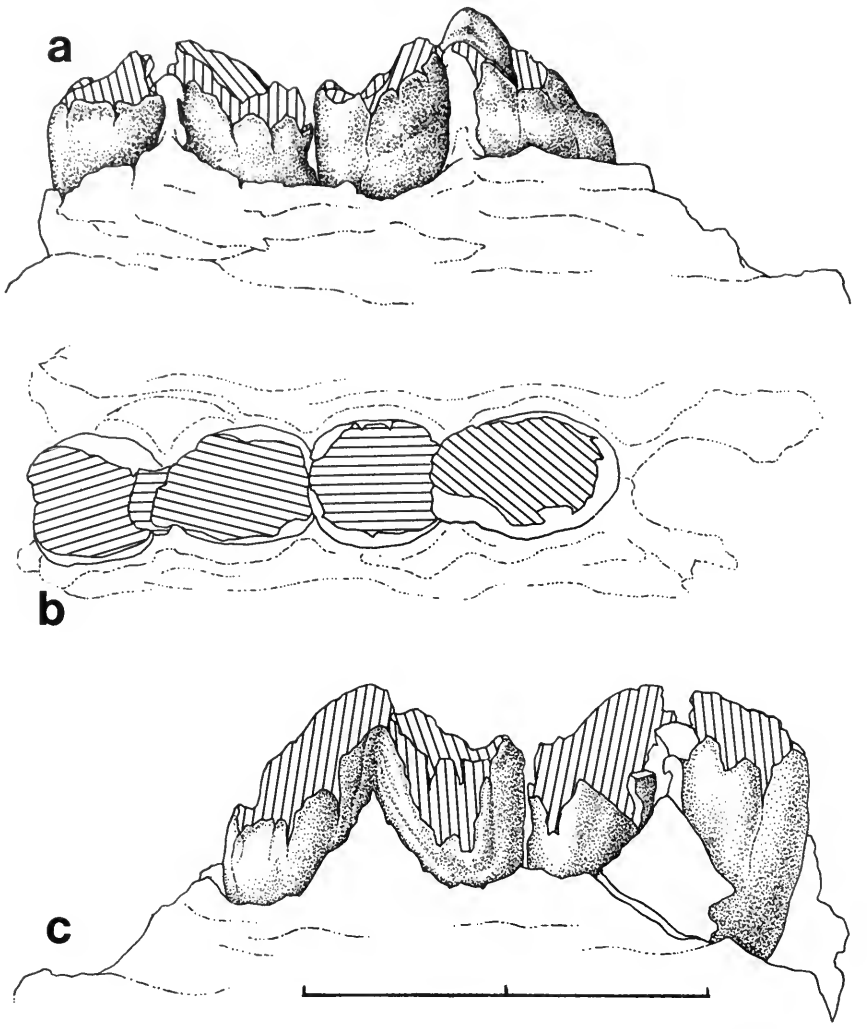


FIG. 49. *Notogale mitis* (Ameghino, 1897) (Deseadan). MACN 52-368 (type), a fragment of a right mandibular ramus with basal portions of M_{2-3}: a, labial; b, occlusal; c, lingual views. Scale = 10 mm.

Type.—MACN 52-368, a fragment of a mandibular ramus with basal portions of M_{2-3} (figured by Patterson & Marshall, 1978, fig. 2).

Hypodigm.—The type and AC 3060, a fragment of a left mandibular ramus with P_3 and M_4 present (figured by Loomis, 1914, fig. 143; Patterson & Marshall, 1978, fig. 3); AC 3117, a left maxillary fragment originally with part of M^2, M^3 incomplete, and M^4 (M^4 now missing) (figured by Loomis, 1914, fig. 142; Patterson & Marshall, 1978, fig. 6); PU 21867, a fragment of a right mandibular ramus with talonid of M_3, M_4 complete (figured by Patterson & Marshall, 1978, fig. 4); PU 21868, a fragment of a right mandibular ramus with M_3 (missing tip

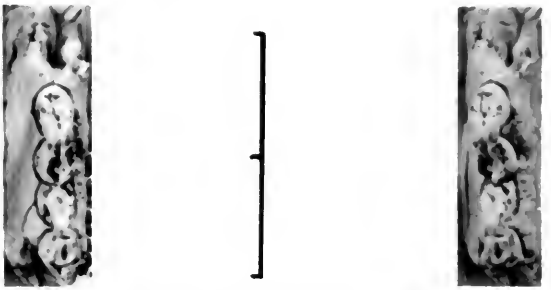


FIG. 50. *Notogale mitis* (Ameghino, 1897) (Deseadan). Stereopairs of MACN 52-368 (type), a fragment of a right mandibular ramus with basal portions of M_{2-3}: occlusal view. Scale = 20 mm.

of protoconid) (figured by Patterson & Marshall, 1978, fig. 5c, d); PU 21869, a fragment of a right mandibular ramus with roots of C, P_{1-2}, and anterior root of P_3; PU 21871, a fragment of a rostrum with roots (or alveoli) of left I^{1-4}, and base of right C, alveolus of left C, and roots of right P^1; PU 21872, a fragment of a left mandibular ramus with P_2 (figured by Patterson & Marshall, 1978, fig. 5a, b); PU 21874, a fragment of a left mandibular ramus with base of C and alveoli of I_{1-3}; PU 21875, a fragment of a right maxillary with M^2 (figured by Patterson & Marshall, 1978, fig. 7, as an M^1); PU 21876, a fragment of a left maxillary with M^1; PU 21877, greater part of crown of C lacking enamel; PU 21993, a fragment of a right mandibular ramus with bases of M_{3-4}; and PU 21996, a fragment of a right mandibular ramus with M_2 (broken).

Horizon and localities.—The type is probably, and the AC specimens are certainly, from Cabeza Blanca, Chubut Province, Argentina. PU 21996 is from Branisa Loc. V-5, Salla-Luribay Basin; the other PU specimens are from the general locality of Salla, Bolivia.

Age.—Deseadan.

Diagnosis.—Similar in size and structure to species of *Cladosictis* from beds of Colhuehuapian and Santacrucian age of Argentina; upper and lower P1 separated from C and P2 by small but distinct diastemas; P1-3 oriented along same axis as molar series, P_1 not set obliquely in jaw; P_2 longer and narrower than P_3; P_3 with large, distinct posterobasal cuspule, a feature only faintly developed on P_2; protocone of M^1 large, paracone about three-fourths size of metacone; paracone and metacone approximated, united basally; parastyle small but distinct; stylar shelf virtually absent; protocone of M^3 large; shallow ectoflex present; metastylar shear better developed than in M^1; lower molars with small but distinct anterobasal cingulum; talonids of M_{3-4} distinct, narrower than trigonids; talonids of M_3 with distinct hypoconid, entoconid, and hypoconulid; talonid of M_4 essentially unicusped with enlarged hypoconulid dominant; minute entoconid and hypoconid visible in unworn teeth (e.g., PU 21867).

Comments.—In the type (MACN 52-368) (figs. 49, 50), both teeth have lost all traces of enamel, their bases are fractured, and only a small portion of the mandibular ramus surrounding them is preserved. Their position in the series is not quite certain. Large alveoli can be seen anterior and posterior to them, and their size and relative proportions indicate that they are certainly molars.

TABLE 15. Measurements of cheek teeth of *Notogale mitis* (after Patterson & Marshall, 1978, table 2).

Specimen		P1		P2		P3		M1		M2		M3		M4	
		L	W	L	W	L	W	L	W	L	W	L	W	L	W
UPPER CHEEK TEETH															
AC	3117	...	...	...	...	...	...	...	...	...	...	8.0	7.0	2.0*	6.0*
PU	21871	ca. 6.4	ca. 2.5	...	...	...	...	...	...	...	...	...	...	...	...
PU	21875	...	...	...	...	...	...	...	...	6.5	5.5	...	...	...	...
PU	21876	...	...	...	...	...	...	ca. 6.9	5.5	...	...	...	...	...	...
LOWER CHEEK TEETH															
MACN	52-368	...	...	...	...	...	...	...	...	ca. 6.5	ca. 3.3	ca. 7.5	ca. 3.3	...	...
AC	3060	...	...	...	...	...	6.0	2.3	...	...	...	...	...	7.7	4.2
PU	21867	...	...	...	...	...	...	...	...	...	...	...	...	7.8	5.0
PU	21868	...	...	...	...	...	...	...	...	...	...	7.2	4.0	...	...
PU	21993	...	...	...	...	...	...	...	...	...	...	7.1	ca. 4.2	...	...
PU	21872	...	...	7.0	2.4	...	...	...	...	...	...	...	...	...	...
PU	21996	...	...	...	...	...	...	...	...	...	3.8	...	...	...	...
PU	21869	ca. 6.0	...	ca. 7.3	...	...	...	...	...	...	...	...	...	...	...

*After Loomis (1914, p. 217).

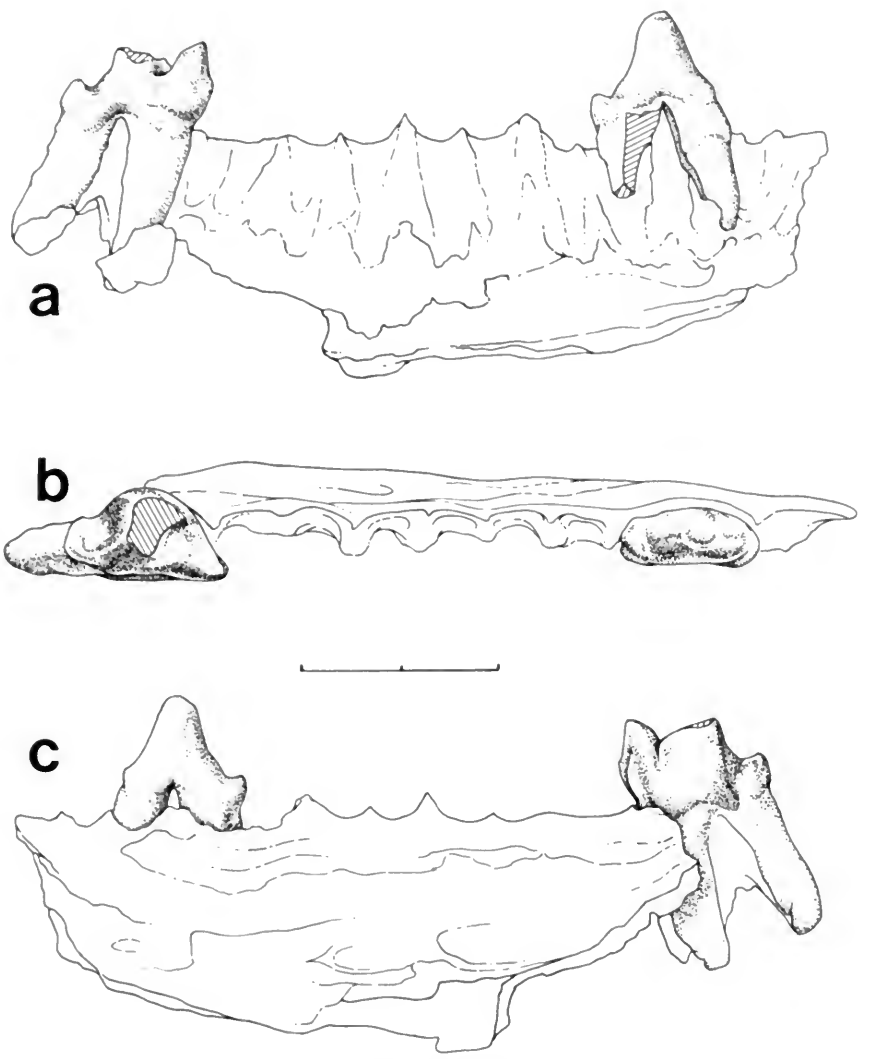


FIG. 51. *Notogale mitis* (Ameghino, 1897) (Deseadan). AC 3060, a fragment of a left mandibular ramus with P_3 and M_4 present: **a**, lingual; **b**, occlusal; **c**, labial views. Scale = 10 mm.

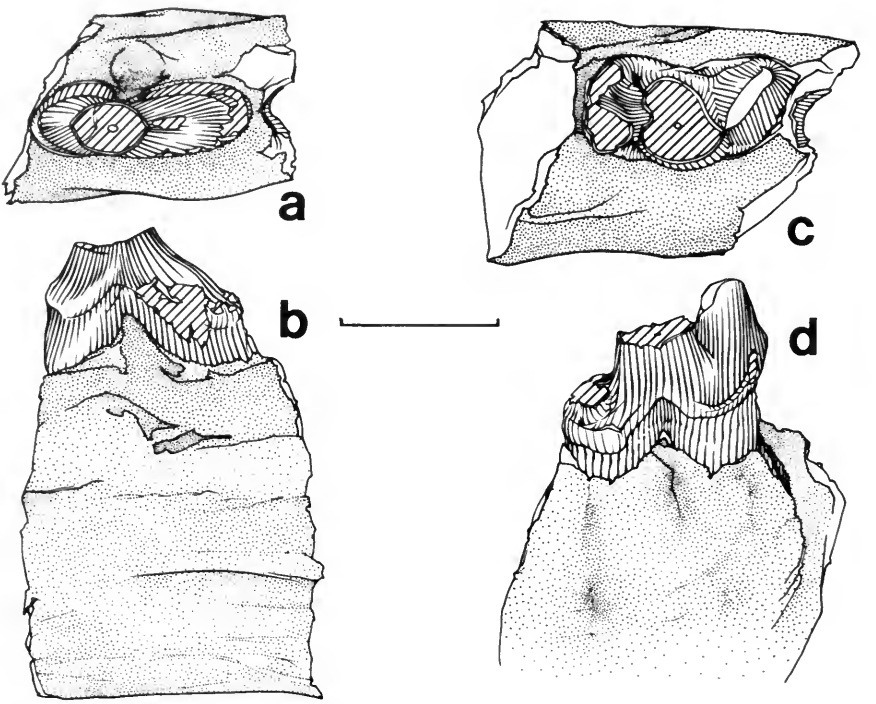


FIG. 52. *Notogale mitis* (Ameghino, 1897) (Deseadan). PU 21872, a fragment of a left mandibular ramus with P_2: **a**, occlusal; **b**, labial views. PU 21868, a fragment of a right mandibular ramus with M_3 (missing tip of protoconid): **c**, occlusal; **d**, labial views. Scale = 50 mm.

It is assumed that the larger tooth is more posterior in the series, and these teeth are identified as $M_{2\text{-}3}$ although they could possibly, but less probably, represent $M_{1\text{-}2}$. The proportions and size of the roots of the type match the alveoli of AC 3060, figured by Loomis (1914, p. 217, fig. 143). The P_2 has been lost since the specimen was figured by him. The two remaining teeth are P_3 and M_4; the latter is clearly not M_3 as thought by Loomis, who further complicated matters by labeling it M_2. The M_4 was probably isolated from the rest of the jaw when the specimen was collected and was restored into the M_3 position. Patterson & Marshall (1978, fig. 3) restored M_4 in its correct position (fig. 51).

In the same box with the type of *Notogale mitis* (MACN 52-368) is an isolated right P^1 of a borhyaenid. This tooth measures 7.3 mm in length and 4.5 mm in width. It is similar in size and structure to specimens of *Borhyaena tuberata* from the Santa Cruz Formation. Its preservation suggests, however, that it is from Cabeza Blanca and is thus of Deseadan age. Ameghino makes no mention of this tooth, and how it came to be associated with the type of *N. mitis* is not known. This P^1 is clearly not referable to *N. mitis*, but may prove referable to a species of *Pharsophorus*, perhaps *P. lacerans*.

Notogale mitis is the most abundant species of Borhyaenidae in the Salla fauna. It is small with a rather generalized dentition, suggesting that it may have been

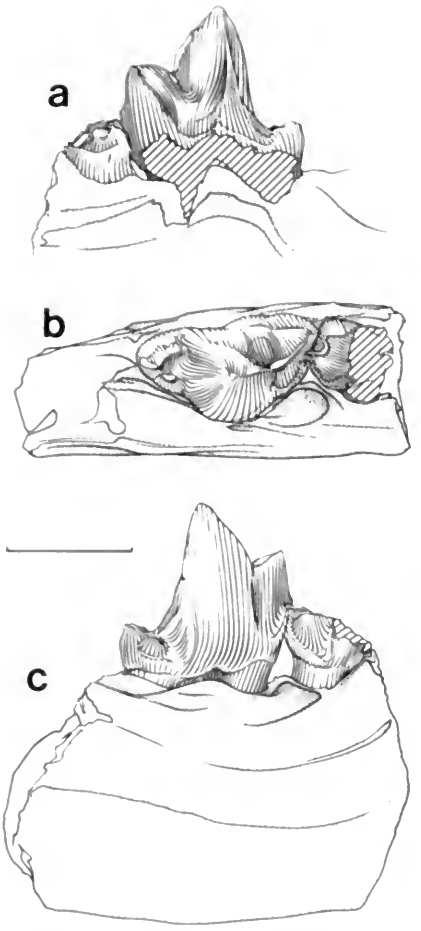


FIG. 53. *Notogale mitis* (Ameghino, 1897) (Deseadan). PU 21867, a fragment of a right mandibular ramus with talonid of M_3, and M_4 complete: **a**, lingual; **b**, occlusal; **c**, labial views. Scale = 50 mm.

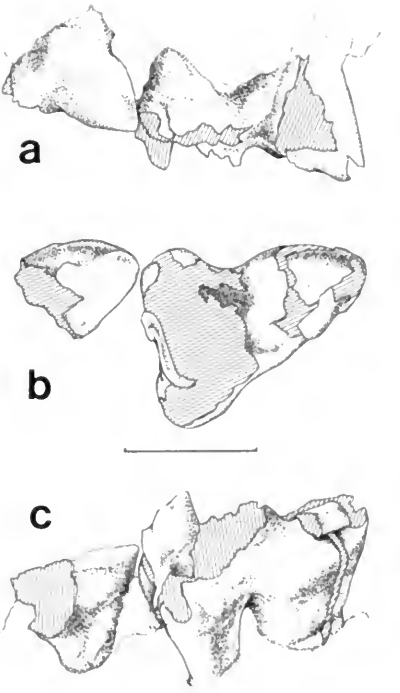


FIG. 54. *Notogale mitis* (Ameghino, 1897) (Deseadan). AC 3117, a left maxillary fragment with posterior edge of M^2 and M^3 very broken: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 50 mm.

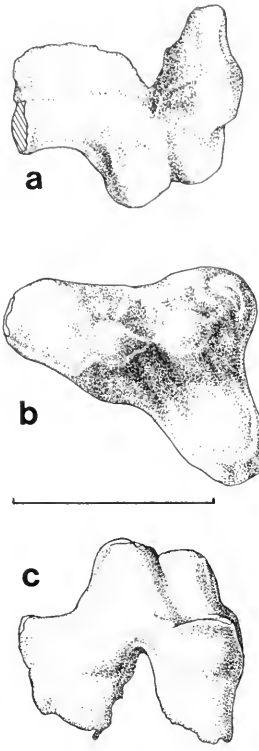


FIG. 55. *Notogale mitis* (Ameghino, 1897) (Deseadan). PU 21875, a fragment of a right maxillary with M^2: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 50 mm.

a fox-like carnivore. *Notogale mitis* is similar in size to some large species of Pliocene-Pleistocene Didelphidae, and it is conceivable that the unconfirmed reports of didelphids in the Salla fauna of Bolivia (Hoffstetter, 1968, 1976) and in the type Deseadan fauna at La Flecha (Tournouër, 1903, p. 469) were based on fragmentary remains of this species. *Notogale mitis* is similar in size and structure to species of *Cladosictis* from beds of Colhuehuapian and Santacrucian age and may be regarded as ancestral to that genus.

Notogale tenuis (Ameghino, 1897)

?*Pharsophorus tenuis* Ameghino, 1897, p. 504.
Notogale tenuis Loomis, 1914, p. 217; Patterson & Marshall, 1978, p. 54 (as *nomen vanum*).

Type.—MACN 52-387, an isolated upper? premolar.

Hypodigm.—Type only.

Locality.—No specific locality data, but probably from Cabeza Blanca, Chubut Province, Argentina.

Age.—Deseadan.

Comments.—Ameghino (1897, p. 504) believed this tooth to be a third lower premolar. It is, however, probably an upper, but which one is not certain. The crown is low, and dentine is exposed on the lingual? surface. The tooth measures 3.4 mm long, 2.6 mm wide. Its features suggest possible affinity with other marsupial groups, notably the Caenolestidae and more specifically the Palae-

othentinae. In any case, this tooth is clearly not of a borhyaenid, and the taxon is a *nomen vanum*.

Cladosictis Ameghino, 1887

Cladosictis Ameghino, 1887, p. 7; 1889, p. 286.
Clasodictis (sic) Roger, 1896, p. 13.
Cladictis (sic) Winge, 1923, p. 67.
Hathliacynus Ameghino, 1887, p. 7.
Agustylus Ameghino, 1887, p. 7.
Ictioborus Ameghino, 1891c, p. 315.

Type of Cladosictis.—*Cladosictis patagonica* Ameghino, 1887, p. 7.
Type of Hathliacynus.—*Hathliacynus lustratus* Ameghino, 1887, p. 7.
Type of Agustylus.—*Agustylus cynoides* Ameghino, 1887, p. 7.
Type of Ictioborus.—*Ictioborus fenestratus* Ameghino, 1891c, p. 315.

Diagnosis.—Medium-sized borhyaenids; teeth aligned in a straight line in tooth row, P1 not set at angle relative to main horizontal axis of jaw; P1 separated from C and from P2 by small but distinct diastems; talonid very reduced and with shallow basin on $M_{1\text{-}4}$ (M_4 sometimes only cuspate); P3 large and proodont; trigon on $M^{1\text{-}3}$ with shallow basin in unworn teeth; trigon on M^4 very reduced and typically cuspate; stylar shelf greatly reduced; small but distinct parastyle present on $M^{1\text{-}4}$.

Cladosictis centralis Ameghino, 1902c. Figures 56–59, Table 16.

Cladosictis centralis Ameghino, 1902c, p. 128.

Type.—MACN 11639, anterior half of an edentulous cranium with roots of right C-M^4 and roots of left C-M^1.

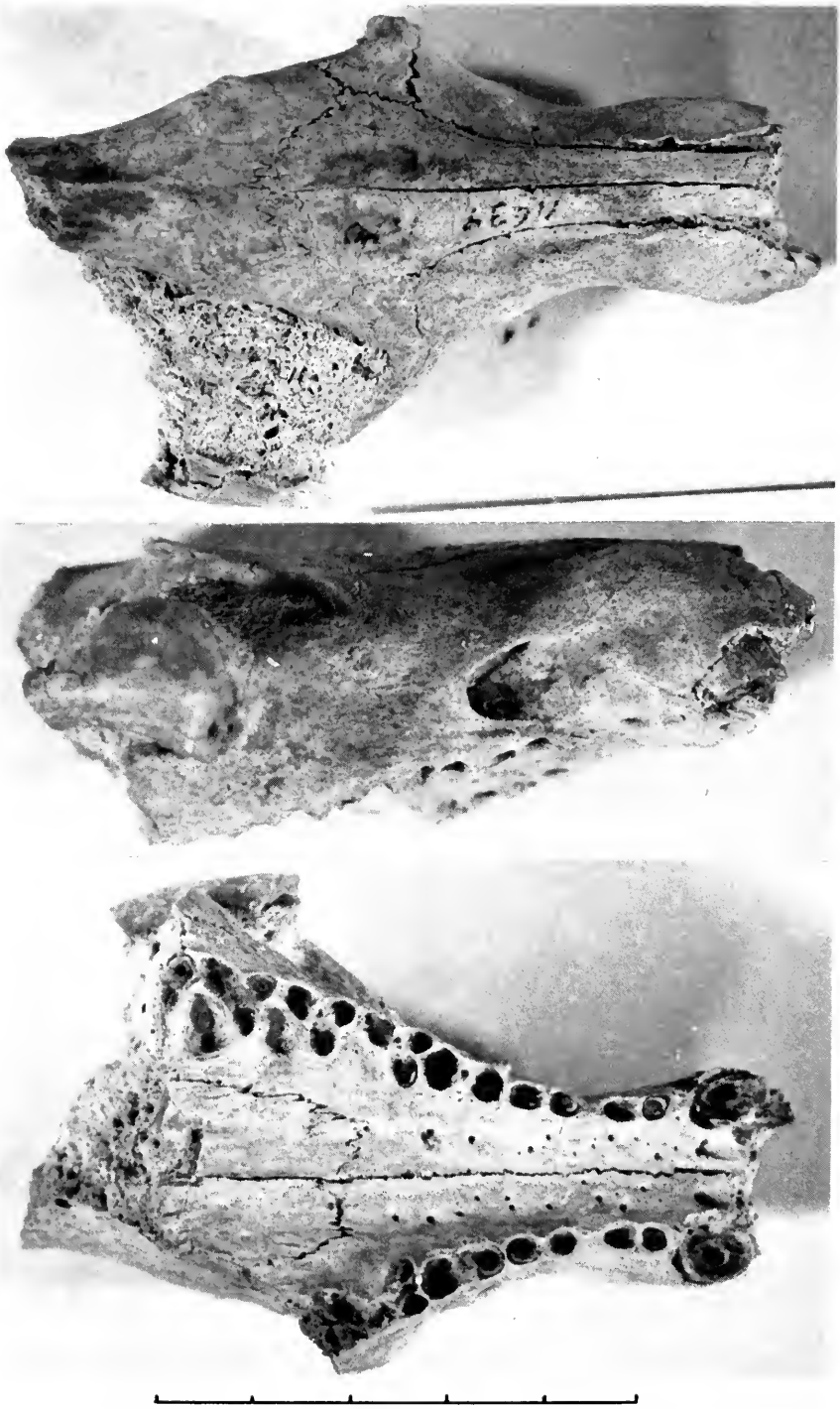
Hypodigm.—Type and MNHN col. 4, a left mandibular ramus with alveolus of C, roots of P_1 and P_2-M_4 complete; and a right mandibular ramus with C-M_4 complete (only tip of P_3 is missing), both of same individual.

Horizon and locality.—Both specimens are from the Colhué-Huapí Formation at the Barranca south of Lago Colhué-Huapí, Chubut Province, Argentina; the type was collected by C. Ameghino and the MNHN specimen by A. Tournouër.

Age.—Colhuehuapian.

Diagnosis.—Smallest and most generalized species of genus; talonid of M_4 distinctly basined.

Description.—Rostral region of skull is long and narrow, minimal breadth between $P^{1\text{-}2}$ contact is 18.0 mm; sagittal crest was probably large and well developed, judging from its anteriormost edge, which is preserved; supraorbital processes are large, are formed by frontals, and measure 21.7 mm between them; nasals are narrow anteriorly, becoming very broad posteriorly in region of nasolacrimal and nasofrontal contacts; nasofrontal contact is broad (breadth = 19.5 mm), and nasals form V at this contact; lacrimal bone extends onto rostral region, but lacrimal duct lies completely within orbit; a small rugosity is developed on lacrimals along edge bordering orbit, and distance between these rugosities is 31.0 mm; nasolacrimal contact is very broad and measures 7.0 mm on left side and 6.5 mm on right; a large infraorbital canal opens in maxillary just above middle of P^3 and has a maximum dorsoventral diameter of 7.0 mm on left side and 7.3 mm on right side; maxillaries are swollen anteriorly by roots of canines; maxillary part of palate is perforated only by small nutrient foramina



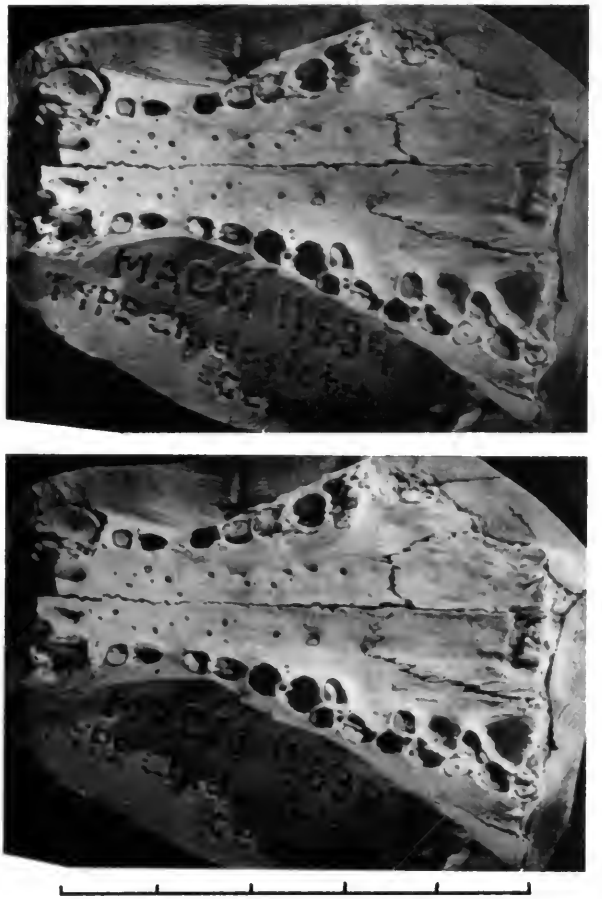


FIG. 57. *Cladosictis centralis* Ameghino, 1902c (Colhuehuapian). Stereopairs of MACN 11639 (type), anterior half of an edentulous cranium with roots of right C-M^4 and roots of left C-M^1: palatal view. Scale = 50 mm.

along its entire length, and two well-developed nutrient foramina occur at anterior edge and just medial to posterior edge of Cs; palatine bones lack nutrient foramina and are solid throughout their length; palatines extend anteriorly to a point between M^2s and obtain a combined maximum breadth anteriorly of 11.5 mm and a breadth of 17.5 mm between middle of M^3s; C root of right side measures L = 9.0 mm, W = 5.5 mm; breadth of palate between Cs = 10.5 mm.

Opposite:

FIG. 56. *Cladosictis centralis* Ameghino, 1902c (Colhuehuapian). MACN 11639 (type), anterior half of an edentulous cranium with roots of right C-M^4 and roots of left C-M^1: **top**, dorsal; **middle**, left lateral; **bottom**, palatal views. Scale = 50 mm.

TABLE 16. Measurements of lower cheek teeth of *Cladosictis centralis*.

	P1		P2		P3		M1		M2		M3		M4		P1-M4	M1-4
Specimen	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**L**
MNHN col. 4 (l)	...	...	6.5	2.3	6.5	2.8	6.6	2.9	6.8	3.6	7.5	4.3	7.8	4.4	ca. 52.4	29.1
MNHN col. 4 (r)	4.6	1.9	6.6	2.4	6.5	2.9	6.7	2.8	6.9	3.6	7.7	4.3	7.8	4.5	51.3	29.3

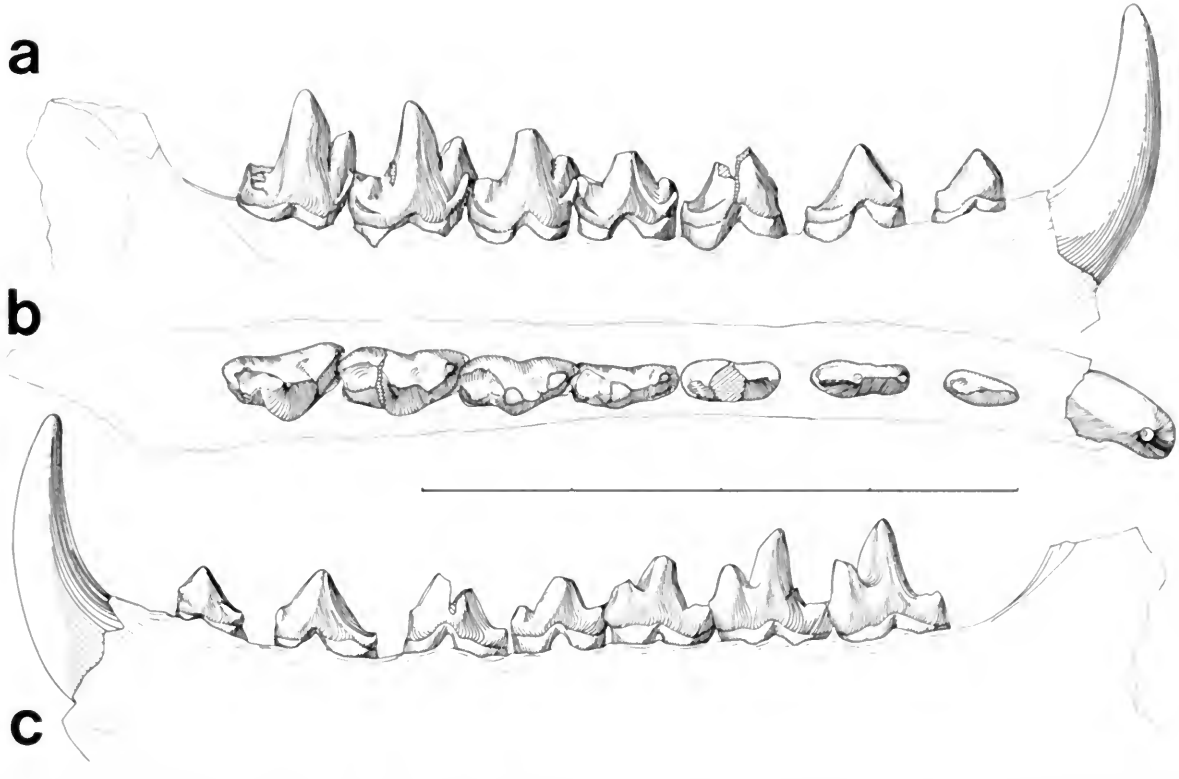
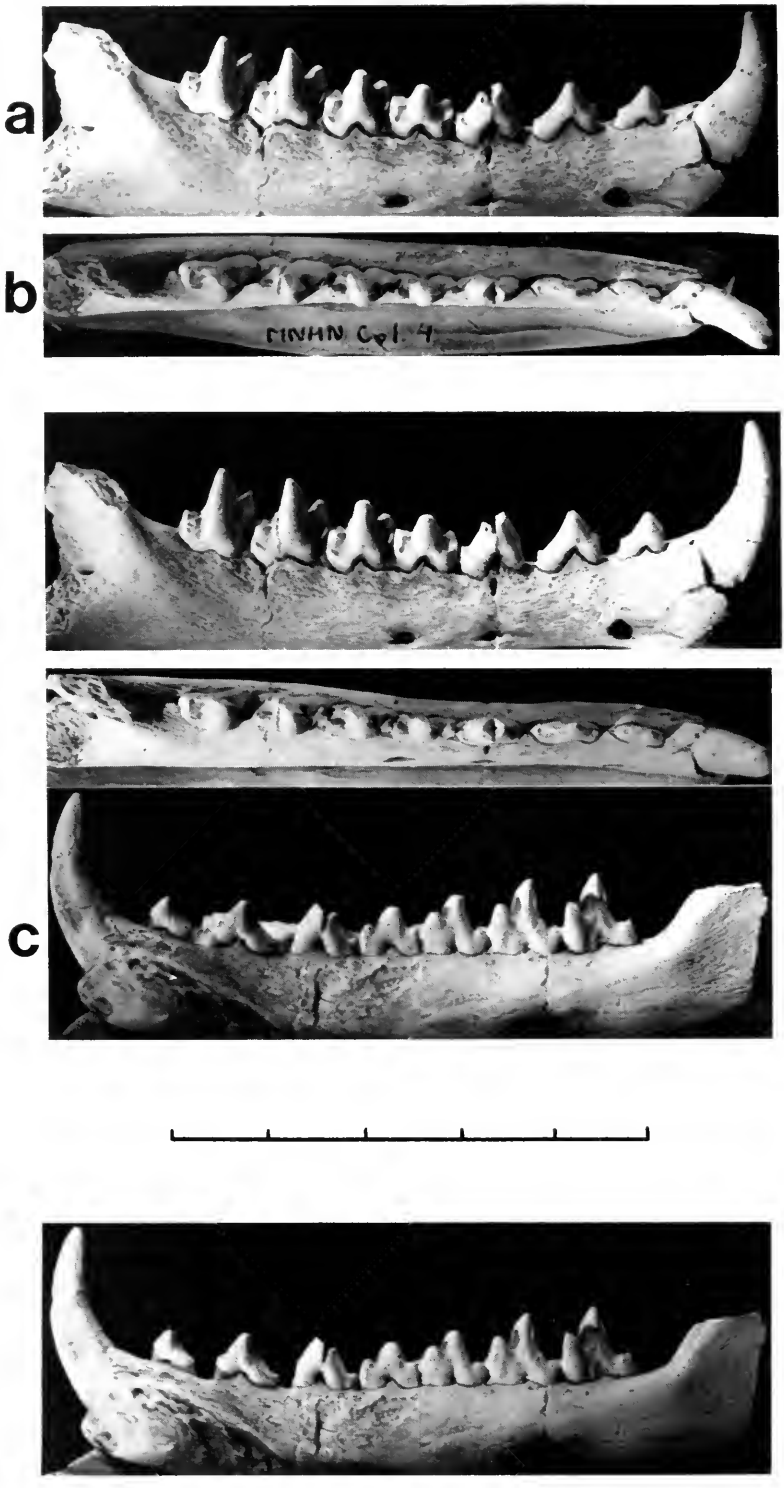


FIG. 58. *Cladosictis centralis* Ameghino, 1902c (Colhuehuapian). MNHN col. 4, a right mandibular ramus with C-M_4 complete: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 40 mm.


a
b
MNHN Col. 4
c

Premolars increase in size from P^1 to P^3; P^1 is separated from C and P^2 by a small diastema (ca. 2.0 mm); posterior root of P^3 is very large; some measurements of alveoli on right side are: P^1 L = 6.4 mm, W = 2.8 mm; P^2 L = 7.0 mm, W = 2.9 mm; P^3 L = 8.0 mm, W = 4.7 mm; P^{1-3} L = 23.7 mm; maximum breadth of palate between P^1s = 10.3 mm; maximum breadth of palate between posterior roots of P^3s = 16.3 mm.

Molars increase slightly in size from M^1 to M^3; orientation of medial and posterior roots indicates that a significant metastylar shear was developed; M^4 is two rooted; some measurements of alveoli on right side include: M^1 L = 7.7 mm, W = 5.9 mm; M^2 L = 8.1 mm, W = 6.3 mm; M^3 L = 8.4 mm, W = 6.8 mm; M^{1-3} L = 23.0 mm; P^1-M^3 L = 46.0 mm.

Comments.—The type of *Cladosictis centralis*, MACN 11639, is slightly smaller and more gracile than all specimens of *C. patagonica* with which it was compared. I here regard *C. centralis* as the slightly smaller but direct ancestor of the Santacrucian species *C. patagonica*. In turn, *C. centralis* probably evolved from the Deseadan species *Notogale mitis*.

Cladosictis patagonica Ameghino, 1887. Figures 60–67; Tables 17–22.

Cladosictis patagonica Ameghino, 1887, p. 7; 1889, p. 286; 1894, p. 387; 1905, p. 8, fig. 7; Cabrera, 1927, p. 280, figs. 4, 5.

Hathliacynus lustratus Ameghino, 1887, p. 7; 1889, p. 286; 1894, p. 383; 1935, p. 106, fig. 3 (caption); Mercerat, 1891a, p. 53.

Cladosictis lustratus Sinclair, 1905, pl. I; 1906, p. 386, pl. 59, fig. 7; Schlosser, 1925, fig. 55; Piveteau, 1961, fig. 26.

Cladosictis lustrata Cabrera, 1927, p. 385, fig. 5.

Cladosictis lateralis Ameghino, 1894, p. 388.

Proviverra trouessartii Ameghino, 1891a, p. 149, fig. 54; 1891d, p. 354.

Cladosictis trouessarti Ameghino, 1894, p. 387, figs. 50, 51; 1898, p. 192, fig. 57c–d; 1904, p. 38, fig. 24; 1906, figs. 189, 190.

Protoproviverra ensidens Ameghino, 1891c, p. 313.

Amphiproviverra ensidens Ameghino, 1894, p. 389; 1935, p. 107, fig. 5 (caption only).

Thylacodictis ensidens Cabrera, 1927, p. 300, fig. 17.

Cladosictis petersoni Sinclair, 1906, p. 391, with 14 figures.

Hathliacynus fischeri Mercerat, 1891a, p. 52; Ameghino, 1894, p. 383 (as a junior synonym of *H. lustratus*).

Ictioborus fenestratus Ameghino, 1891c, p. 315; 1894, p. 396, fig. 56; 1898, pp. 191, 193, fig. 58f; 1935, p. 111, fig. 13 (caption only).

Amphithereutes obscurus Ameghino, 1894 *fide* Roger, 1896 (*nomen nudum*); Ameghino, 1935, p. 108, fig. 8 (caption only).

Agustylus minus Ameghino, 1935, p. 109, fig. 22 (caption only) (*nomen nudum*).

Acrocyon sectorius Ameghino, 1889, p. 289n, pl. 1, fig. 19 (*partim*).

Agustylus cynoides Ameghino, 1887, p. 7; 1889, p. 287; 1891c, p. 315; 1894, p. 391, fig. 53; 1898, pp. 191, 193, fig. 58c; 1935, p. 109, fig. 38; Mercerat, 1891a, p. 54; Cabrera, 1927, p. 290, fig. 7.

Agustylus primaevus Mercerat, 1891a, p. 54; Cabrera, 1927, p. 291, fig. 8.

Hathliacynus cultridens Mercerat, 1891a, p. 53; Cabrera, 1927, p. 280, 291 (as partial synonym of *Cladosictis patagonica* and *Agustylus primaevus*, respectively).

Hathlyacynus cultridens Ameghino, 1894, p. 387 (as junior synonym of *Cladosictis trouessarti*).

Opposite:

FIG. 59. *Cladosictis centralis* Ameghino, 1902c (Colhuehuapian). Stereopairs of MNHN col. 4, a right mandibular ramus with C-M_4 complete: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 50 mm.

Cladosictis dissimilis Mercerat, 1891a, p. 51; Ameghino, 1891d, p. 354 and 1894, p. 387 (as junior synonym of *Proviverra troussartii*).

Hathliacynus rollieri Mercerat, 1891a, p. 53; Ameghino, 1894, p. 391 (as junior synonym of *Agustylus cynoides*).

Type of Hathliacynus patagonica.—MLP 11-103, a fragment of a left maxillary with M^{3-4}.

Type of Hathliacynus fischeri.—MLP 11-19, rostrum of skull and attached mandible with nearly complete dentition.

Type of Cladosictis lateralis.—MACN 5950, a rostral portion of skull with roots of left I^1-P^2, and right I^1-P^3, and with left P^3-M^4 and right M^{1-4} complete (this specimen is not listed as "tipo" in Ameghino's catalogue or on the specimen, but the original description fits it perfectly—MACN 5951, the distal end of a humerus, is listed as belonging to the same individual, but Ameghino makes no mention of it in his original description of this species).

Lectotype of Hathliacynus lustratus.—MLP 11-17, a right maxillary fragment with M^{1-2} (originally with a P^3, but this has since been lost, see Cabrera, 1927, p. 285). (Mercerat referred to both upper and lower dentitions in the original description of this species. The upper dentition is surely MLP 11-17 and is here recognized as the lectotype. The lower dentition is probably MLP 11-11 because it is listed as cotype of this species in the MLP catalogue, and it agrees perfectly with the original description.)

Type of Proviverra trouessartii.—MACN 2079, greater part of left side of skull with partial dentition but missing basicranium, right zygomatic arch, right maxillary, and all of right dentition [listed as type in catalogue and on specimen; figured by Ameghino (1894, figs. 50, 51; 1898, figs. 57c, d; 1904, fig. 24; 1906, figs. 189, 190)].

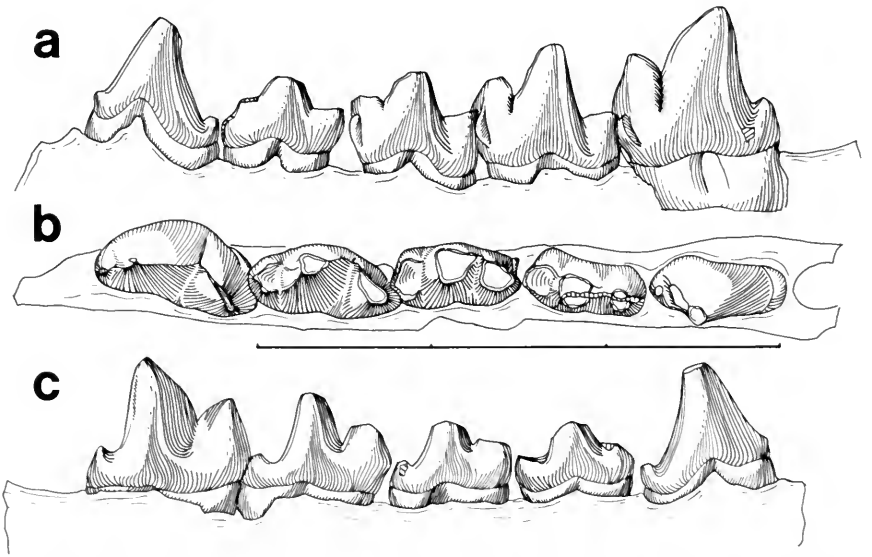


FIG. 60. *Cladosictis patagonica* Ameghino, 1887 (Santacrucian). MACN 674, a fragment of a left mandibular ramus with P_3-M_4: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 30 mm.

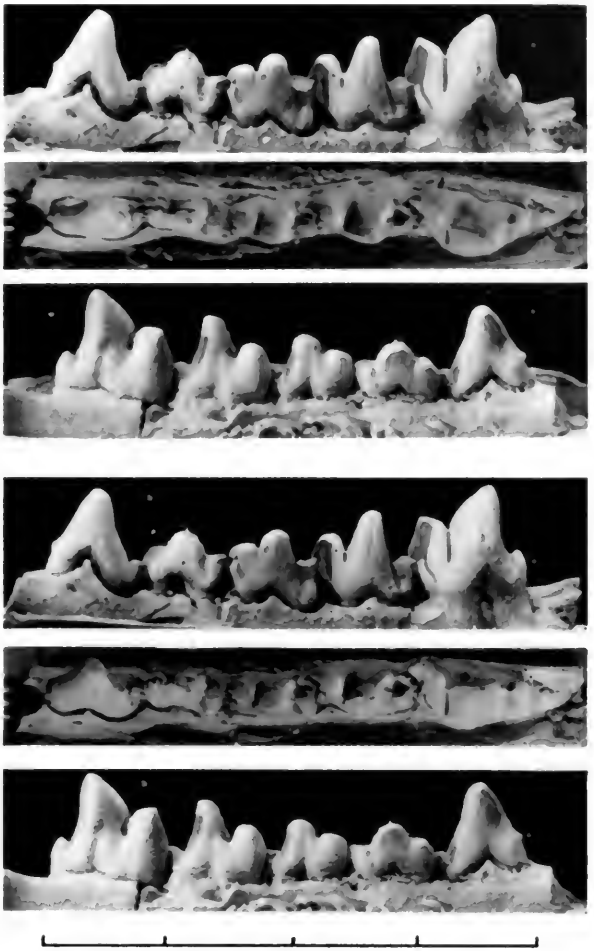


FIG. 61. *Cladosictis patagonica* Ameghino, 1887 (Santacrucian). Stereopairs of MACN 674, a fragment of a left mandibular ramus with P_3-M_4: a, labial; b, occlusal; c, lingual views. Scale = 40 mm.

TABLE 17. Measurements of mandibular rami of *Cladosictis patagonica*.

Specimen	Depth of ramus below labial side of M_1	Breadth of same	Depth of ramus below labial side of M_4	Breadth of same
MACN 664	14.5	5.2	...	...
MACN 681	14.5	6.0	...	...
MACN 6288(l)	20.2	7.7	...	...
MACN 6288(r)	21.0	8.3	...	...
MACN 9360	14.0	5.9	14.0	7.2
MACN 9386	...	...	15.0	7.0
MACN 11-2	17.5	7.0	...	...
MACN 11-10	14.5	5.8	...	...

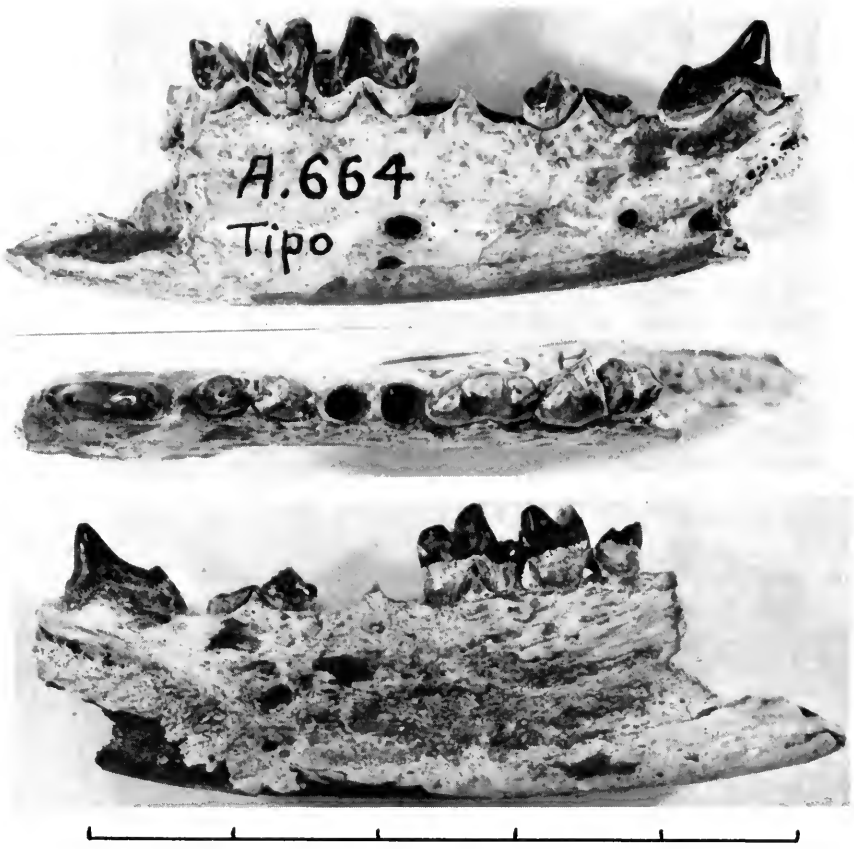


FIG. 62. *Cladosictis patagonica* Ameghino, 1887 (Santacrucian). MACN 664 (type of *Ictioborus fenestratus*), a fragment of a right mandibular ramus with posterior alveolus of P_1, P_2 complete, base of P_3, alveoli of M_1, M_2 complete, and M_3 missing protoconid: **top,** labial; **middle,** occlusal; **bottom,** lingual views. Scale = 50 mm.

TABLE 18. Statistics for some dimensions of mandibular rami of *Cladosictis patagonica*.

Dimension	N	OR	x	s	CV
Depth of ramus below labial side of M_1	7	14.0–21.0	16.60	2.98	17.95
Breadth of ramus below M_1	7	5.2–8.3	6.56	1.13	17.23
Depth of ramus below labial side of M_4	2	14.0–15.0	14.50	0.71	4.90
Breadth of ramus below M_4	2	7.0–7.2	7.10	0.14	1.97

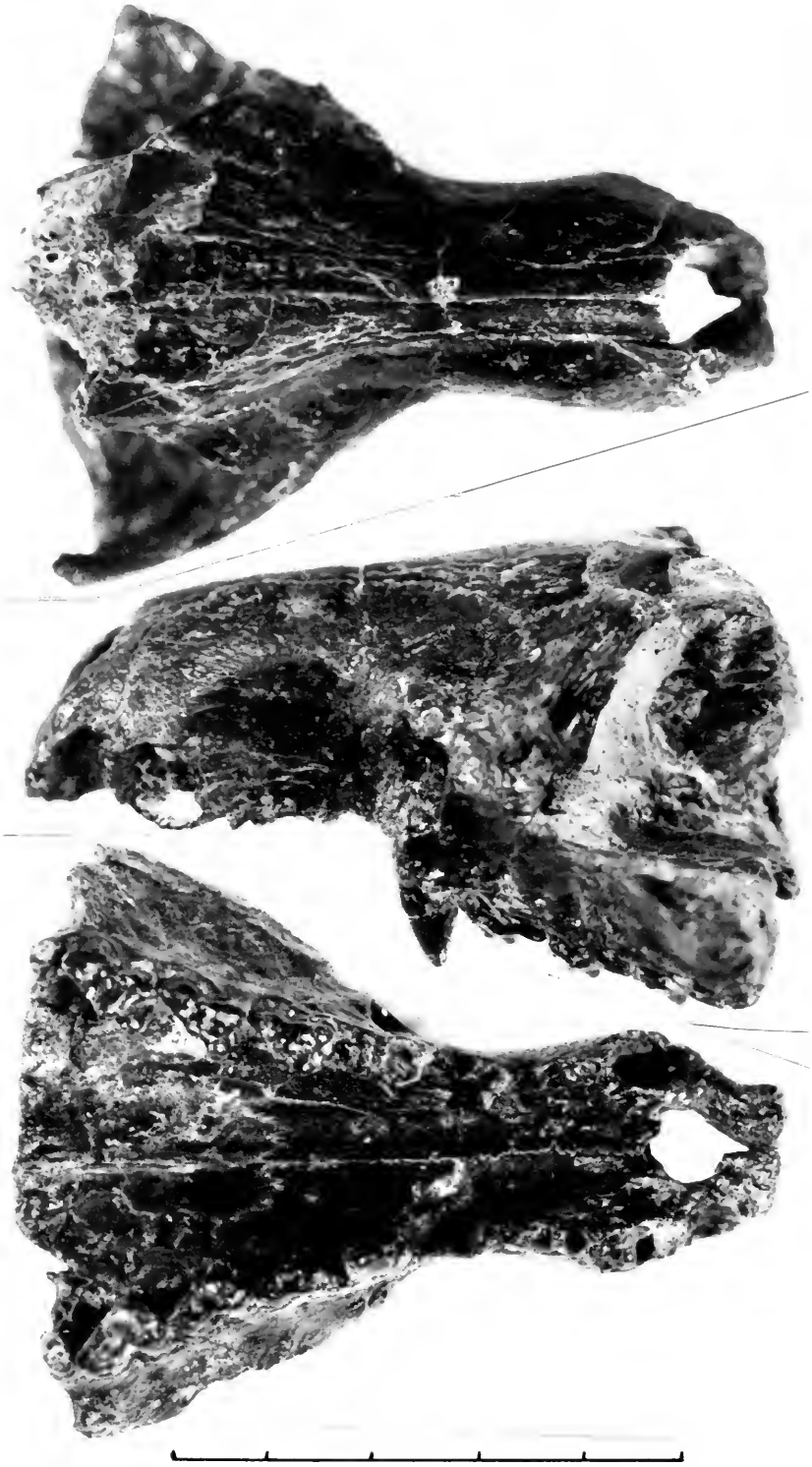
FIG. 63. *Cladosictis patagonica* Ameghino, 1887 (Santacrucian). MACN 2079 (type of *Proviverra trouessartii*), greater part of left side of skull with partial dentition but missing basicranium, right zygomatic arch, right maxillary, and all of right dentition: **top,** dorsal; **middle,** left lateral; **bottom,** palatal views. Scale = 50 mm.

Type of Cladosictis petersoni.—PU 15702, rostral part of skull and associated partial skeleton.

Type of Protoproviverra ensidens.—MACN 689, a fragment of a right mandibular ramus with posterior half of P_1 and P_2, P_3 complete, and anterior root of M_1 (listed as "tipo" in Ameghino's catalogue and on specimen).

Type of Agustylus minus.—MACN 671, a fragment of a left mandibular ramus with M_{2-4} broken; and MACN 672, a fragment of a right mandibular ramus with roots of M_1, M_{2-3} complete, M_4 broken; both specimens of same individual (listed as "tipo" both in Ameghino's catalogue and on specimen—the specific name *minus* is crossed out, and *cynoides* is written above it).

Type of Amphithereutes obscurus.—MACN 681, a fragment of a left mandibular ramus with roots of C-M_1 [listed as type in Ameghino's catalogue and on spec-



imen, and it is only specimen listed by this name in the Ameghino collection. This name is, however, crossed out, and "Sparassodont (Amphiproviverridae)" is substituted above it].

Type of Ictioborus fenestratus.—MACN 664, a fragment of a right mandibular ramus with posterior alveolus of P_1, P_2 complete, base of P_3, alveoli of M_1, M_2 complete, M_3 missing protoconid [listed as "tipo" in Ameghino's catalogue and on specimen, and original description fits perfectly—figured by Ameghino (1894, fig. 56; 1898, fig. 58f)].

Lectotype of Agustylus cynoides.—MLP 11-78, a fragment of a left mandibular ramus with P_2 missing anterior edge and anterior root of P_3 (P_3 broken since figured by Cabrera, 1927, fig. 7). (Ameghino originally described two specimens, both partial rami with a P_3. MLP 11-78 is regarded as the lectotype, and the other specimen, a cotype, is almost certainly MLP 11-100.)

Type of Agustylus primaevus.—MLP 11-4, greater part of a right mandibular ramus with C missing tip of crown, P_1 complete, P_2 missing posterior edge, P_3-M_1 complete, alveoli of M_2, and M_{3-4} complete (figured by Cabrera, 1927, fig. 8B).

Lectotype of Hathliacynus cultridens.—MLP 11-2, fragment of a left mandibular ramus with alveoli of I_{1-3}, base of C, P_{1-2} complete, alveoli of P_3-M_1 (made lectotype by Cabrera, 1927, p. 282).

Type of Cladosictis dissimilis.—MLP 11-86, a fragment of a right maxillary with alveoli of M^1, and M^{2-4} complete.

Type of Hathliacynus rollieri.—MLP 11-10, a fragment of a left mandibular ramus with posterior root of P_3, and M_{1-4} present (M_{2-4} missing tips of protoconids).

Hypodigm.—The 15 types and MACN 85, a left maxillary fragment with P^3-M^1 complete; MACN 86, a right maxillary fragment with posterior half of P^3, and M^{1-3} complete; MACN 639, an isolated C; MACN 640, an isolated C; MACN 641, a right maxillary fragment with M^1 (latter three specimens are listed as probably belonging to *Cladosictis trouessarti*); MACN 665, a fragment of a left mandibular ramus with roots of P_{1-3} [listed in Ameghino's catalogue as probably belonging to *Ictioborus fenestratus;* figured by Ameghino (1889, pl. 1, fig. 19) as *Acrocyon sectorius*]; MACN 673, fragment of a right mandibular ramus with C-M_4 (partially broken); MACN 674, a fragment of a left mandibular ramus with P_3-M_4 (same individual as 673) [this specimen originally had the C and P_2 as shown in Ameghino (1894, fig. 53; 1898, fig. 58c)]; MACN 675a, a fragment of a right mandibular ramus with M_{1-2}, and left M_{1-3} (both specimens are of same individual and are listed as *Agustylus cynoides* in Ameghino's catalogue); MACN 690, a right maxillary fragment with P^3 (same individual as 689 and possible cotype of *Amphiproviverra ensidens*, but there is no direct mention of this specimen in the original description of that species); MACN 705, a left maxillary fragment with P^3-M^2 complete, an upper isolated P^2?, and two fragments of an upper C; MACN 2080 (possibly same individual as 2079 and possible cotype of *Proviverra trouessartii*), a fragment of a left mandibular ramus with roots of M_{2-4}; MACN 5927, nearly complete cranium with teeth (listed as *Hathliacynus lustratus* in Ame-

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Opposite:

FIG. 64. *Cladosictis patagonica* Ameghino, 1887 (Santacrucian). MACN 5950 (type of *Cladosictis lateralis*), a rostral portion of skull with roots of left I^1-P^2 and right I^1-P^3, and with left P^3-M^4 and right M^{1-4} complete: **top,** dorsal; **middle,** left lateral; **bottom,** palatal views. Scale = 50 mm.

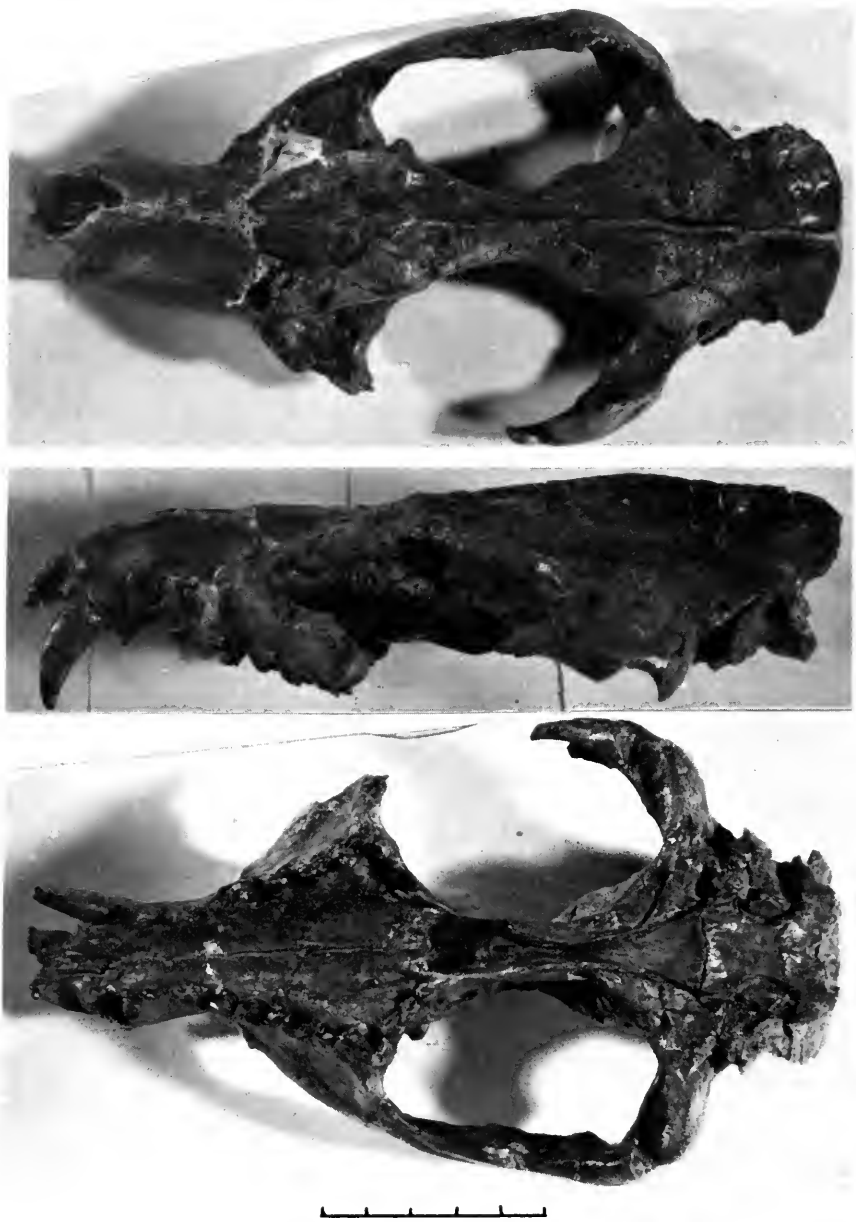

FIG. 65. *Cladosictis patagonica* Ameghino, 1887 (Santacrucian). MACN 5927, nearly complete skull with most of dentition: **top,** dorsal; **middle,** left lateral; **bottom,** palatal views. Scale = 50 mm.

ghino's catalogue—it is the most complete skull of this species in the Ameghino collection); MACN 5928, a right mandibular ramus with I_{1-3}, C, P_1 complete, posterior root of P_2, P_3-M_2 complete, and roots of M_{3-4}; MACN 5929, vertebrae and other bones (same individual as MACN 5927 and 5928—I could not locate MACN 5928 in the Ameghino collection); MACN 5951, distal end of humerus (supposedly same individual as 5950); MACN 6280, a left maxillary fragment with C-M^4 complete, and associated postcranial elements (6281–6285)—fragment of cranium with nuchal and sagittal crest (6281), vertebrae (6282, 6283), proximal end of right femur (6284), most of right fibula (6285)—listed as *Cladosictis trouessarti* and supposedly of a single individual; MACN 6288–6298 (listed as *Anatherium defossus* in Ameghino's catalogue), both mandibular rami with teeth [6288—figured by Ameghino (1898, fig. 57b). Ameghino noted in his catalogue that this specimen had all the teeth preserved, and in his illustration all are indeed present. Now the specimen is missing the medial portion of the coronoid process on the right side (more than is shown in the illustration), the tip of the P_2 and all of M_{2-3} are also missing. The jaw has also been broken below the M_4 and M_1, respectively. The rest of the dentition is present as figured by Ameghino], a left maxillary fragment with roots of P^3, M^{1-2} complete and alveoli of M^3 (6289), isolated teeth (6290–92), and various postcranial fragments (6293–98); MACN 9350, a left maxillary fragment with roots of P^1, P^2-M^4 complete, but very worn; MACN 9351, a fragment of a left mandibular ramus with roots of M_1, M_{2-3} complete, but very worn (same individual as 9350; both listed as *Cladosictis lateralis* in Ameghino's catalogue); MACN 9359, a fragment of a right mandibular ramus with P_{1-2} complete (listed as *Amphiproviverra ensidens* in Ameghino's catalogue); MACN 9360, a fragment of a right mandibular ramus with M_{1-4} complete; MACN 9361, a fragment of a left maxillary with M^{2-3}; MACN 9386, a fragment of a right mandibular ramus with M_{3-4} complete (listed as *Agustylus cynoides* in Ameghino's catalogue); MACN 9387, a fragment of a right mandibular ramus with M_{3-4}; MACN 9388, a fragment of a left mandibular ramus with M_3 (MACN 9387–88 are listed as *Agustylus cynoides* in Ameghino's catalogue); MLP 11-8, a fragment of a right mandibular ramus with anterior alveoli and posterior half of M_1, M_{2-3} complete, and anterior alveolus of M_4 (original cotype of *Hathliacynus cultridens*); MLP 11-9, a fragment of a left mandibular ramus with M_4; MLP 11-11, a fragment of a right mandibular ramus with alveoli of I_{1-3}, base of C, roots of P_{1-2} (probable cotype of C. *lustratus*); MLP 11-13, greater part of a left mandibular ramus with P_1-M_4 complete; MLP 11-15, a fragment of a right mandibular ramus with M_3; MLP 11-63, a fragment of a left mandibular ramus with M_{1-4} complete (labeled *Thylacodictis ensidens*); MLP 11-68, a fragment of a left mandibular ramus with root of C, P_1 complete, roots of P_{2-3}; MLP 11-87, a fragment of a left maxillary with M^2 broken, and M^3 complete; MLP 11-100, a fragment of a right mandibular ramus with P_2 (probable cotype of *Agustylus cynoides;* this is the specimen that could not be located by Cabrera, 1927, p. 291); MLP 11-120, a fragment of a left mandibular ramus with alveoli of P_1-M_1, and M_2 complete; PU 15015 (now UCMP 26617), a right mandibular ramus with C-M_4; PU 15046, a skull, mandible, and partial skeleton; PU 15097, a left mandibular ramus with C, alveoli of P_{1-2} (which were erupted, but are missing from specimen), DP_3-M_2 erupted, and M_3 erupting (an incompletely developed and unerupted P_3 is also preserved and is visible below anterior root of DP_3); PU 15170, skull, mandible, and partial skeleton; PU 15704 (now CMNH 2893), a right mandibular ramus

TABLE 19. Measurements of upper cheek teeth of *Cladosictis patagonica*.

Specimen	P^1		P^2		P^3		M^1		M^2		M^3		M^4		P^{1-3}	M^{1-3}
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	L
MACN 85	...	...	...	...	7.0	3.1	6.9	5.0	...	...	...	...	...	...	...	...
MACN 86	...	...	...	...	...	...	8.0	5.1	8.7	5.8	8.8	7.0	...	...	...	25.0
MACN 641	...	...	...	...	...	...	7.5	5.0	...	...	...	...	...	...	...	...
MACN 690	...	...	...	...	7.4	3.4	...	...	...	...	...	...	...	...	...	...
MACN 705	...	...	...	...	7.3	3.7	7.8	5.2	8.6	5.7	...	...	...	...	...	...
MACN 2079	...	...	6.5	2.5	...	...	7.0	5.3	...	...	...	...	5.7	2.5	ca. 47.0	23.0
MACN 5927(l)	4.6	2.1	...	...	...	...	7.0	5.3	8.0	6.0	9.0	6.6	5.7	2.8	54.4	24.3
MACN 5927(r)	...	...	...	...	...	...	7.2	5.2	8.1	5.8	8.8	6.5	5.5	2.8	54.2	24.4
MACN 5950(l)	...	...	...	...	...	3.2	7.4	5.0	7.8	5.5	8.3	6.2	4.8	2.9	ca. 46.5	ca. 23.4
MACN 5950(r)	...	...	...	...	...	...	7.3	5.0	7.8	5.5	8.3	6.3	...	...	ca. 46.8	23.4
MACN 6280	4.6	2.0	6.2	2.5	6.9	3.4	7.2	5.3	7.9	5.7	8.6	6.5	6.5	2.7	46.4	23.0
MACN 6289	...	...	...	...	...	...	7.3	5.3	8.2	5.8	...	...	...	...	...	...
MACN 9350	...	...	6.4	2.2	6.8	3.0	6.9	4.7	7.4	5.4	8.0	6.1	4.7	2.5	ca. 46.3	22.2
MACN 9361	...	...	...	...	...	...	...	...	8.5	5.7	9.3	6.9	...	...	...	...
MLP 11-87	...	...	...	...	...	...	...	...	...	...	9.0	7.3	...	...	...	...
MLP 11-86	...	...	...	...	...	...	...	...	7.8	5.7	8.7	7.2	6.4	3.1	...	...
MLP 11-103	...	...	...	...	...	...	...	...	...	...	8.7	6.2	4.9	2.2	...	...
MLP 11-17	...	...	...	...	...	...	7.5	5.1	8.2	5.8	...	...	...	...	...	...
AMNH 9134	6.0	...	6.9	2.7	7.4	3.4	8.0	...	8.5	...	8.5	...	5.9	2.7	...	24.8

TABLE 20. Statistics for some upper cheek tooth dimensions of *Cladosictis patagonica*.

Dimension		N	OR	x	s	CV
P^1	L	3	4.6–6.0	5.07	0.81	15.98
	W	2	2.0–2.1	2.05	0.07	3.41
P^2	L	4	6.2–6.9	6.50	0.29	4.46
	W	4	2.2–2.7	2.48	0.21	8.47
P^3	L	6	6.8–7.4	7.13	0.27	3.79
	W	7	3.0–3.7	3.31	0.23	6.95
M^1	L	14	6.9–8.0	7.36	0.37	5.03
	W	13	4.7–5.3	5.12	0.18	3.52
M^2	L	13	7.4–8.7	8.12	0.38	4.68
	W	12	5.4–6.0	5.70	0.17	2.98
M^3	L	12	8.0–9.3	8.67	0.36	4.15
	W	11	6.1–7.3	6.62	0.42	6.34
M^4	L	9	4.7–6.5	5.57	0.66	11.85
	W	9	2.2–3.1	2.69	0.26	9.67
P^1-M^3	L	7	46.3–54.4	48.80	3.77	7.73
M^{1-3}	L	9	22.2–25.0	23.72	0.95	4.01

with P_{2-3} and M_{2-4} complete, and M_1 broken; PU 15556, part of a humerus; PU 15705, fragments of skull and skeleton (collected as float); PU 15831, very fragmentary skull and postcranial remains; PU 15837, very fragmentary skull and postcranial remains; FMNH 13255, a nearly complete skull with dentition; AMNH 9134, a fragment of a left maxillary with C-M^4, a fragment of a left mandibular ramus with P_3 broken, M_{1-2} complete, and M_{3-4} broken, partial skull with occipital region, and assorted vertebrae and bone fragments; AMNH 9548, a fragment of a right mandibular ramus with P_2-M_1 complete and M_{2-4} broken, and a fragment of left mandibular ramus with P_{1-2} and M_{1-3} complete, and P_3 and M_4 broken; AMNH 9574 (now USNM 5936), a right mandibular ramus with P_1, P_2 broken, and P_3-M_3, and a left mandibular ramus with alveoli of C and M_{2-3}, and P_{1-3}, M_1, and M_4 present.

Horizon and locality.—All specimens are from the Santa Cruz Formation, Santa Cruz Province, Argentina, and their localities of collection are as follows: *Barrancas del río Santa Cruz* MLP 11-78, 11-103 (collected by C. Ameghino, 1887), 11-103; *Santa Cruz* MACN 85, 86, 665 (collected by C. Ameghino, 1887), MLP 11-2, 11-8, 11-9, 11-10, 11-11, 11-15, 11-17, 11-120; *Karaiken* MACN 2079, 2080 (collected by C. Ameghino, 1889–1890); *Monte Observación* MACN 639, 640, 641, 664, 671, 672, 673, 674, 675, 689, 690 (collected by C. Ameghino, 1890–91), MACN 9350, 9351 (collected by C. Ameghino, 1891–92); *Río Gallegos* MACN 705 (collected by C. Ameghino, 1890–91); *Sehuen* MACN 681 (collected by C. Ameghino, 1890–91); *La Cueva* MACN 9359, 9360, 9361, 9387, 9388 (collected by C. Ameghino, 1892–93); *Corriquen-Kaik* MACN 5927, 5928, 5950, 5951, 6280–6285 (collected by C. Ameghino, 1892–93); *Jack-Harvey* MACN 6288–6298, 9386 (collected by C. Ameghino, 1892–93); *Monte Leon*(?) MLP 11-4, 11-19, 11-86; *no locality data* MLP 11-13, 11-63, 11-68, 11-87, 11-100; *10 miles south of Coy Inlet* PU 15702 (collected by O. A. Peterson, 1899), PU 15015, 15170 (collected by O. A. Peterson, 1896), PU 15046, 15097 (collected by J. B. Hatcher, 1896); *Coy Inlet* PU 15704 (collected by O. A. Peterson, 1899); *Lake Pueyrredon* PU 15556, 15705, 15831, 15837 (collected by J. B. Hatcher, 1899); *Wreck Flat* or *Smith's Rock Flat, 10 miles north of Coy Inlet* FMNH P13255; *Cañadón de las Vacas, 35 miles south of Santa Cruz* AMNH 9134, 9548, 9574 (collected by B. Brown, 1899).

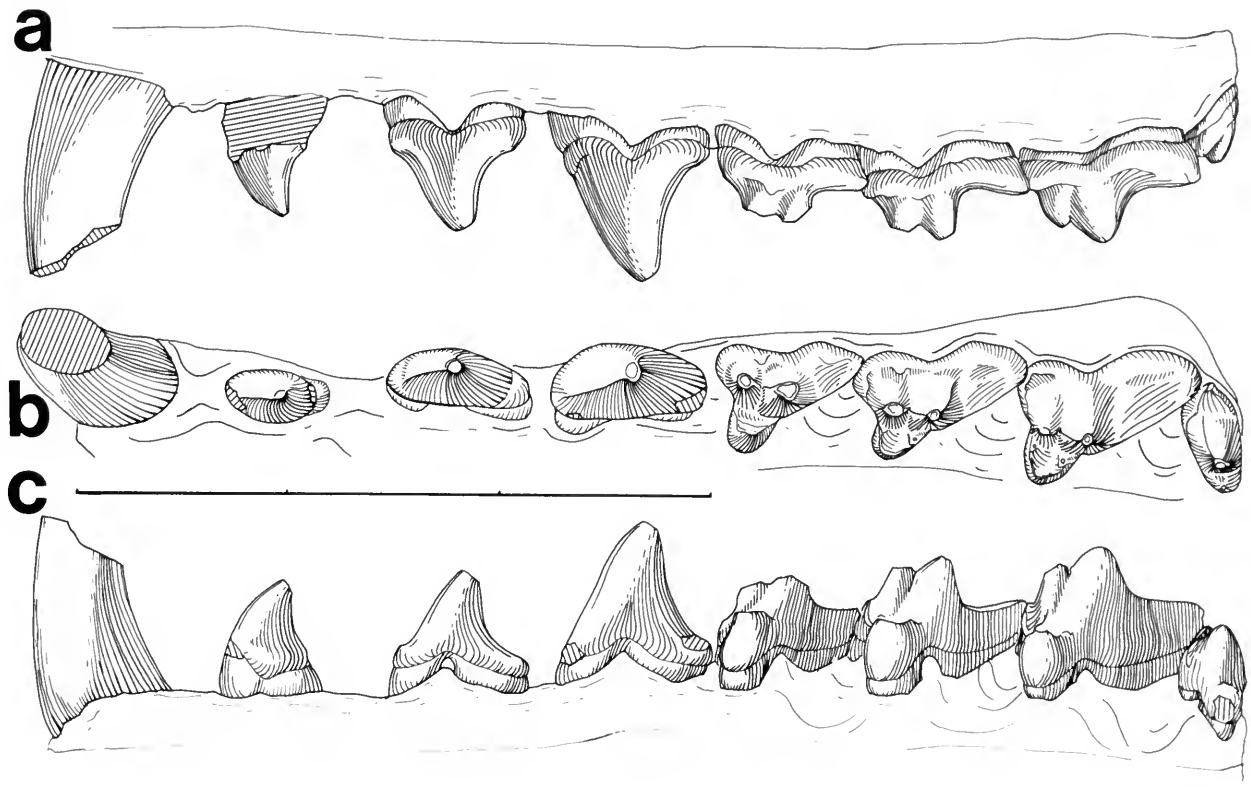

FIG. 66. *Cladosictis patagonica* Ameghino, 1887 (Santacrucian). MACN 6280, a left maxillary fragment with C-M_4 complete: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 30 mm.

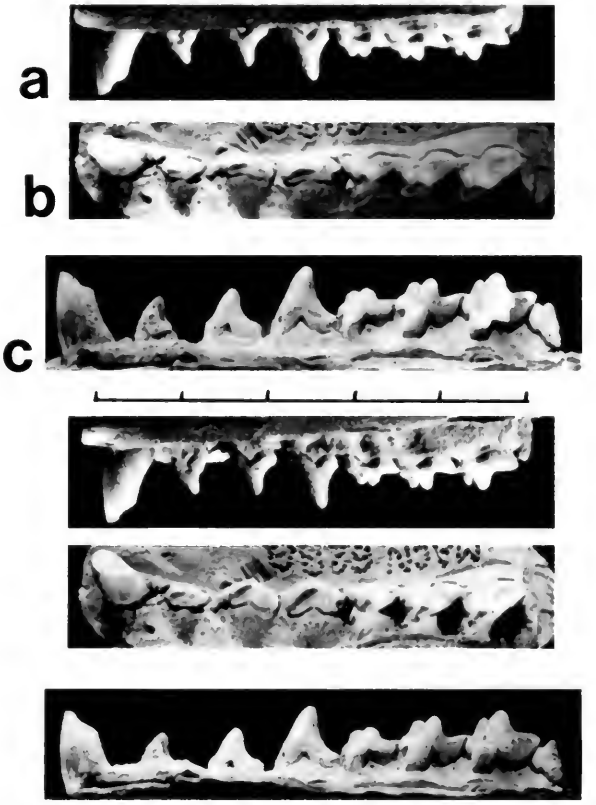

FIG. 67. *Cladosictis patagonica* Ameghino, 1887 (Santacrucian). Stereopairs of MACN 6280, a left maxillary fragment with C-M^4 complete: **a**, labial; **b**, occlusal; **c**, lingual views. Scale for lingual view = 50 mm.

Age.—Santacrucian.

Diagnosis.—Slightly larger than *Cladosictis centralis;* talonid of M_4 cuspate.

Comments.—The type of *Proviverra trouessartii* (MACN 2079) consists of the greater part of a left side of a skull with partial dentition, but missing the basicranium, right zygomatic arch, right maxillary, and all of right dentition. This specimen is figured by Ameghino (1894, fig. 50; 1898, fig. 57c; 1904, fig. 24; 1906, fig. 190) in dorsal view in which the left side and posteriormost edge is restored. The canine and incisors were also restored because none are now present on the specimen. The zygomatic arch region is very narrow in the figure, reflecting the fact that the left arch, although almost complete, is crushed in this specimen but in life was certainly much broader. Ameghino restored the skull with the arches crushed, and the specimen and figure are identical in this respect. The palate and dentition of MACN 2079 are figured by Ameghino (1894, fig. 51; 1898, fig. 57d; 1906, fig. 189). Only parts of the left dentition are preserved, and these are precisely illustrated in the figures. Except for the roots of P^{1-2}, all of the right dentition is missing. Ameghino restored the right side by making a mirror image of the left, a point which is readily apparent by comparing teeth on each side, which are broken in exactly the same way.

TABLE 21. Measurements of lower cheek teeth of *Cladosictis patagonica*.

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
MACN 664	...	...	7.3	2.7	7.7	ca. 2.8	...	...	7.0	3.6	8.0	4.1	...	...	...	...
MACN 672	...	...	...	...	...	...	...	...	6.4	3.2	7.0	3.5	...	...	...	...
MACN 674	...	...	...	...	7.3	3.2	6.7	3.2	7.0	3.6	8.0	4.0	9.0	4.7	...	31.2
MACN 675(l)	...	...	...	...	...	...	6.7	2.9	7.0	3.5	7.7	4.0	...	...	...	...
MACN 675(r)	...	...	...	...	...	...	6.6	2.9	7.0	3.4	...	...	...	...	...	...
MACN 673	5.3	2.6	7.6	3.0	7.2	3.1	6.8	3.1	6.9	3.6	...	...	...	...	...	...
MACN 689	...	...	...	...	7.4	3.3	...	...	...	...	...	...	...	...	...	...
MACN 5928	5.5	2.4	...	...	7.8	3.3	6.8	3.1	7.0	3.4	...	...	...	...	ca. 57.2	ca. 30.5
MACN 6288(1)	5.5	2.5	7.7	3.1	7.5	3.4	7.0	3.3	7.2	3.9	...	...	...	...	ca. 60.0	ca. 33.0
MACN 6288(4)	5.5	2.4	7.5	3.0	7.4	3.5	7.0	3.3	...	...	...	...	9.3	5.1	ca. 62.5	...
MACN 9351	...	...	...	...	...	...	...	...	7.0	3.5	7.2	4.0	...	...	...	...
MACN 9359	5.1	2.5	7.4	2.8	...	...	...	...	...	...	...	...	...	...	...	...
MACN 9360	...	...	...	...	...	...	6.2	3.0	6.6	3.4	7.5	3.9	8.6	4.8	...	29.5
MACN 9386	...	...	...	...	...	...	...	...	...	...	7.2	3.8	8.2	4.7	...	...
MACN 9387	...	...	...	...	...	...	...	...	...	...	7.6	4.2	8.7	5.1	...	...
MACN 9388	...	...	...	...	...	...	...	...	...	...	8.0	4.2	...	...	...	...
MLP 11-63	...	...	...	...	...	...	6.5	3.1	7.0	3.8	7.5	4.0	9.0	4.8	...	30.0
MLP 11-78	...	...	...	...	...	3.4	...	...	...	...	...	...	...	...	...	...

TABLE 21. *Continued.*

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 11-68	5.2	2.2	...	...	...	...	...	...	...	...	...	...	...	...	...	...
MLP 11-13	5.3	2.3	7.3	2.7	7.3	3.2	6.7	3.1	7.2	3.5	8.0	4.0	9.6	4.7	57.0	31.2
MLP 11-4	5.3	2.5	...	...	7.4	3.3	6.4	3.2	...	...	7.8	4.1	8.5	5.1	...	...
MLP 11-2	5.3	2.5	7.0	2.9	...	...	...	...	...	...	...	...	...	...	...	...
MLP 11-8	...	...	...	...	...	...	...	3.1	7.0	3.4	7.8	4.0	...	...	...	...
MLP 11-9	...	...	...	...	...	...	...	...	...	...	...	...	8.4	4.4	...	...
MLP 11-15	...	...	...	...	...	...	...	...	...	...	8.0	4.0	...	...	...	...
MLP 11-120	...	...	...	...	...	...	...	...	7.2	3.7	...	...	...	...	...	...
MLP 11-10	...	...	...	...	...	...	6.9	2.6	7.2	3.3	8.0	3.8	9.6	5.0	...	31.8
MLP 11-100	...	...	8.0	2.9	...	...	...	...	...	...	...	...	...	...	...	...
PU 15704 (=CMNH 2893)	...	...	6.7	2.9	7.3	3.4	...	...	7.3	3.5	8.5	4.2	9.4	4.8	...	...
AMNH 9574(l) (=USNM 5936)	5.2	2.5	...	3.0	7.4	3.1	6.7	3.0	...	...	...	...	8.8	4.4	...	...
AMNH 9574(r) (=USNM 5936)	5.4	2.5	7.2	2.9	7.0	3.2	6.4	3.0	6.8	3.3	7.9	3.8	...	...	...	...
AMNH 9548(l)	5.9	2.5	6.9	2.9	7.5	ca. 3.1	6.7	3.0	6.9	3.5	7.9	4.0	9.0	...	...	29.9
AMNH 9548(r)	...	...	7.0	2.8	7.3	3.1	6.7	3.0	7.0	3.4	7.9	...	9.0	...	...	30.0

TABLE 22. Statistics for some lower cheek tooth dimensions of *Cladosictis patagonica*.

Dimension		N	OR	x	s	CV
P_1	L	12	5.1–5.9	5.38	0.21	3.90
	W	12	2.2–2.6	2.45	0.11	4.49
P_2	L	12	6.7–8.0	7.30	0.37	5.07
	W	13	2.7–3.1	2.89	0.12	4.15
P_3	L	14	7.0–7.8	7.39	0.20	2.71
	W	15	2.8–3.5	3.23	0.18	5.57
M_1	L	16	6.2–7.0	6.68	0.22	3.29
	W	17	2.6–3.3	3.05	0.17	5.57
M_2	L	19	6.4–7.3	6.98	0.21	3.01
	W	19	3.2–3.9	3.50	0.17	4.86
M_3	L	19	7.0–8.5	7.76	0.36	4.64
	W	18	3.5–4.2	3.98	0.17	4.27
M_4	L	14	8.2–9.6	8.94	0.43	4.81
	W	12	4.4–5.1	4.80	0.24	5.00
P_1-M_4	L	4	57.0–62.5	59.18	2.61	4.41
M_{1-4}	L	9	29.5–33.0	30.79	1.12	3.64

MACN 2080 is listed as "tipo" of *C. trouessarti* in Ameghino's catalogue and on the specimen. In the catalogue it is indicated that this specimen and MACN 2079 are of the same individual. However, there is no specific reference to MACN 2080, a partial left mandibular ramus, in Ameghino's original description of this species, and it cannot therefore be regarded as an official cotype.

Ameghino (1891c, p. 315) diagnosed *Ictioborus fenestratus* as having two lower incisors, a single-rooted rudimentary P_1, P_2 being double rooted and very large, P_3 somewhat smaller, M_{1-4} similar to species of *Sipalocyon* "pero con una pequeño callo basal estiliforme sobre la cara anteroexterna del lóbulo anterior de cada muela." In the type (MACN 664) as shown in Ameghino (1894, fig. 56; 1898, fig. 58f), the anterior edge of the mandibular ramus, including the anterior root of the P_1 and the incisors, is missing. This feature of preservation led Ameghino to believe that the incisors were reduced to two in number (although there is no evidence even for this), and he misinterpreted the posterior alveolus of P_1 as a single-rooted P_1. The other features he mentions do not serve to separate this species from any of the other specimens here assigned to *Cladosictis patagonica*.

Ameghino (1889, p. 289, pl. 1, fig. 19) figured a fragment of a left mandibular ramus with roots of P_{1-3} and referred it to *Acrocyon sectorius*. Mercerat (1891a, p. 55) noted that this specimen did not appear to be referable to either this genus or species. Cabrera (1927, p. 313) later commented that this specimen was apparently lost, because he could not locate it in the MLP collection. He also called attention to the fact that this specimen did not appear to be referable to *A. sectorius*. During the winter of 1974, I found this specimen in the Ameghino collection in the MACN (No. 665) where it was apparently taken by Ameghino. It is clearly referable to *Cladosictis patagonica* and not to *A. sectorius*, which is a small Santacrucian member of the subfamily Borhyaeninae (Marshall, 1978, pp. 61–63).

Two specimens in the MACN are listed in Ameghino's catalogue as being collected by Carlos Ameghino in 1890–91, but are indicated to be types of species that were erected in 1887. The specimens in question are MACN 673–674, listed as type of *Agustylus cynoides*, and MACN 705, listed as type of *Hathliacynus*

lustratus. These specimens are clearly not the types that are in the MLP. An explanation for this situation exists and is discussed by Marshall (1980, p. 36n).

A fragment of a right mandibular ramus (MACN 13205) with a broken but relatively complete M_4 was collected from late Tertiary beds along the Río Paraná near Paraná, Entre Ríos Province, Argentina. It was collected from "Paraná Entre Ríos, Formación Entrerriana" by Alberto Lelong and acquired by the MACN in 1941. The M_4 measures L = 9.0 mm, W = 5.0 mm, and it is identical in size and structure to specimens of *C. patagonica*.

The "Formacion Entrerriana" is late Miocene in age (Pascual & Odreman Rivas, 1973, chart opposite p. 318). Pascual & Odreman Rivas (1971, p. 404) note that the predominant faunal elements from these beds indicate a Huayquerian age, although there are also taxa of Santacrucian and Chasicoan age (e.g., *Protypotherium* sp., *Borhyaena tuberata*). These authors interpret the presence of these forms in Huayquerian age beds as being deposited from reworking of beds of Santacrucian and/or Chasicoan age. Such is apparently the case with MACN 13205.

Cladosictis patagonica is here regarded as the Santacrucian descendant of the Colhuehuapian species *C. centralis* and as the Santacrucian ancestor of the Chasicoan species *Chasicostylus castroi*.

Chasicostylus Reig, 1957

Chasicostylus Reig, 1957, p. 29.

Type.—*Chasicostylus castroi* Reig, 1957, p. 29.

Distribution.—Arroyo Chasicó Formation, Buenos Aires Province, Argentina.

Diagnosis.—As for type and only known species.

Chasicostylus castroi Reig, 1957. Figures 68–71; Table 23.

Chasicostylus castroi Reig, 1957, p. 29, figs. 1–3; Ringuelet, 1966, p. 55, pl. 11, figs. A–C.

Type.—MLP 57-XI-9-2, a fragment of a left maxillary with M^{1-2}, a fragment of right mandibular ramus with posterior half of M_1 and M_{2-3} complete, and an isolated left M_1, all of a single associated individual.

Hypodigm.—The type and possibly MLP 55-IV-28-59, a fragment of a right mandibular ramus with base of C and alveoli of P_{1-3}.

Horizon and locality.—Both specimens are from the Arroyo Chasicó Formation, Arroyo Chasicó, Buenos Aires Province, Argentina.

Age.—Chasicoan.

Diagnosis.—Medium-sized borhyaenid, slightly larger than *Cladosictis patagonica;* lower molars increase slightly in size from M_1 to M_3, all are very narrow transversely (especially trigonid) and have a small but distinctly basined talonid; small anterobasal cingular cusp present on M_{2-3}, absent on M_1; upper molars with small but distinct protocone, paracone fused basally with larger metacone; parastyle very large on M^1 and extends anteriorly toward P^3; parastyle-paracone-metacone on M^1 lie in same axis; parastyle on M^2 shorter and situated labiad of paracone-metacone axis; paracone and metacone lie on labial side of crown on M^1, more medially on M^2; no trace of ectocingulum or ectoflex on M^1 or M^2; metacrista very well developed.

Comments.—*Chasicostylus castroi* is similar to, and is probably descendant from the Santacrucian species *Cladosictis patagonica*. In fact, all of the specializations that make *C. castroi* so unique, as noted by Reig (1957), are incipiently developed

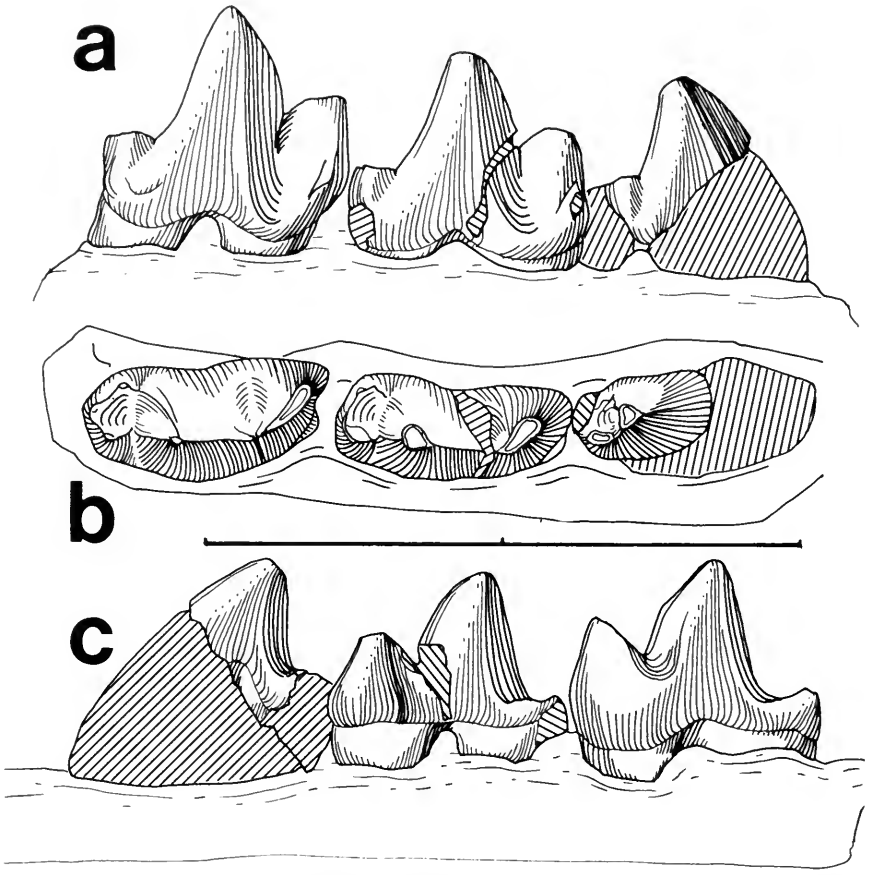

FIG. 68. *Chasicostylus castroi* Reig, 1957 (Chasicoan). MLP 57-XI-9-2 (type), a fragment of a right mandibular ramus with posterior half of M_1 and M_{2-3} complete: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 20 mm.

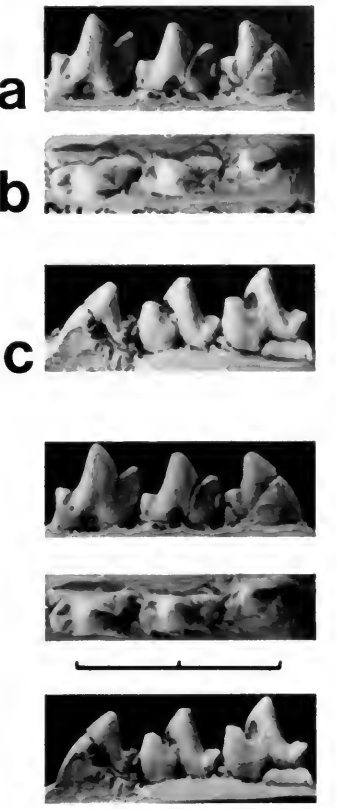

FIG. 69. *Chasicostylus castroi* Reig, 1957 (Chasicoan). Stereopairs of MLP 57-XI-9-2 (type), a fragment of a right mandibular ramus with posterior half of M_1 and M_{2-3} complete: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 20 mm.

TABLE 23. Measurements of cheek teeth of *Chasicostylus castroi*.

	M1		M2		M3	
Specimen	**L**	**W**	**L**	**W**	**L**	**W**
MLP 57-XI-9-2						
Upper dentition	8.6	4.4	8.9	4.8	...	...
Lower dentition(l)	7.5	2.7	...	...	...	...
Lower dentition(r)	...	2.8	8.2	3.6	8.4	3.8

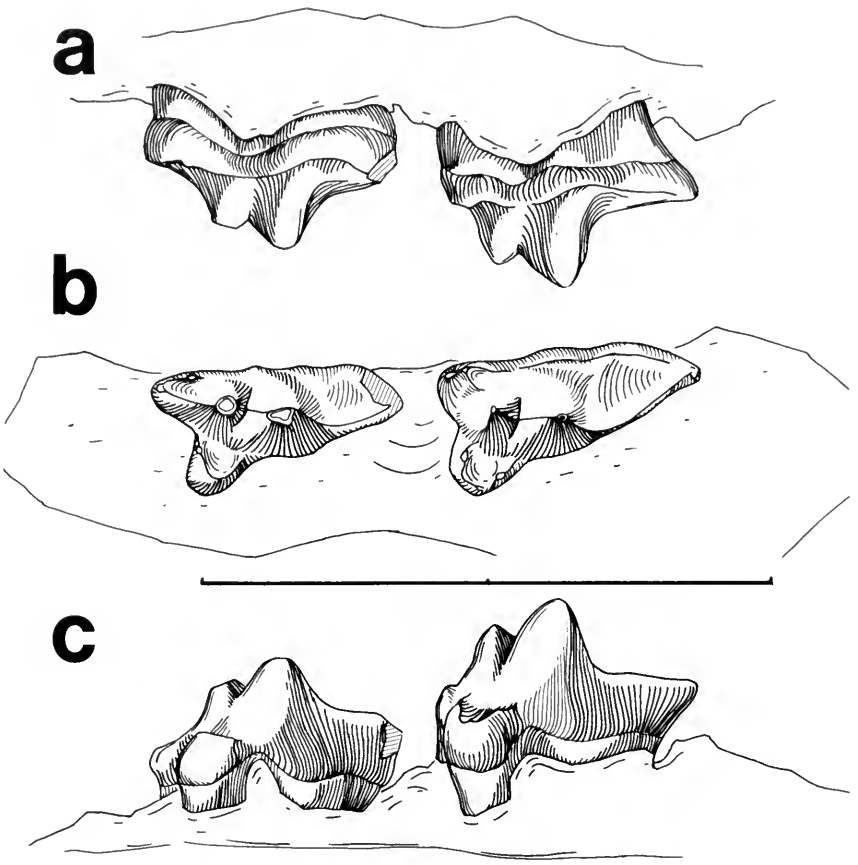

FIG. 70. *Chasicostylus castroi* Reig, 1957 (Chasicoan). MLP 57-XI-9-2 (type), a fragment of a left maxillary with M^{1-2}: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 20 mm.

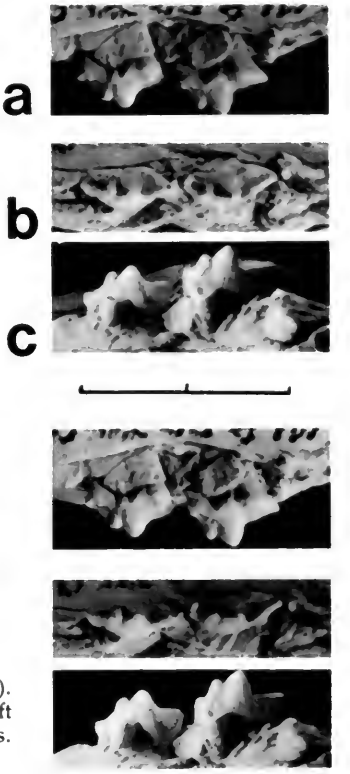

FIG. 71. *Chasicostylus castroi* Reig, 1957 (Chasicoan). Stereopairs of MLP 57-XI-9-2 (type), a fragment of a left maxillary with M^{1-2}: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 20 mm.

in *Cladosictis patagonica*, and are simply carried to an extreme in *C. castroi*. The primary differences between these species include: *C. castroi* being slightly larger in size, in having the upper and lower molars proportionately more elongated anteroposteriorly, in the upper molars having a larger parastyle that extends more anteriorly, in having the protocone set more anteriad relative to the para- and metacone, and in having a more elongated metacrista that is partially a function of the anterior displacement of the protocone. These differences show *C. castroi* to have better developed shearing specializations than occur in *Cladosictis patagonica*.

Anatherium Ameghino, 1887

Anatherium Ameghino, 1887, p. 8.
Acyon Ameghino, 1887, p. 8.

Type of Anatherium.—*Anatherium defossus* Ameghino, 1887, p. 8.

Type of Acyon.—*Acyon tricuspidatus* Ameghino, 1887, p. 8.

Distribution.—Colhuehuapian and Santacrucian of Patagonia, southern Argentina.

Diagnosis.—Largest known genus of Hathlyacyninae; P_1 separated from C and from P_2 by large diastems: P_{1-3} set in straight line in jaw; talonids of M_{1-3} very reduced and not basined; M_4 talonid cuspate; anterobasal cingulum well developed on M_{2-4}; posterobasal cuspule weakly developed on P_{2-3}.

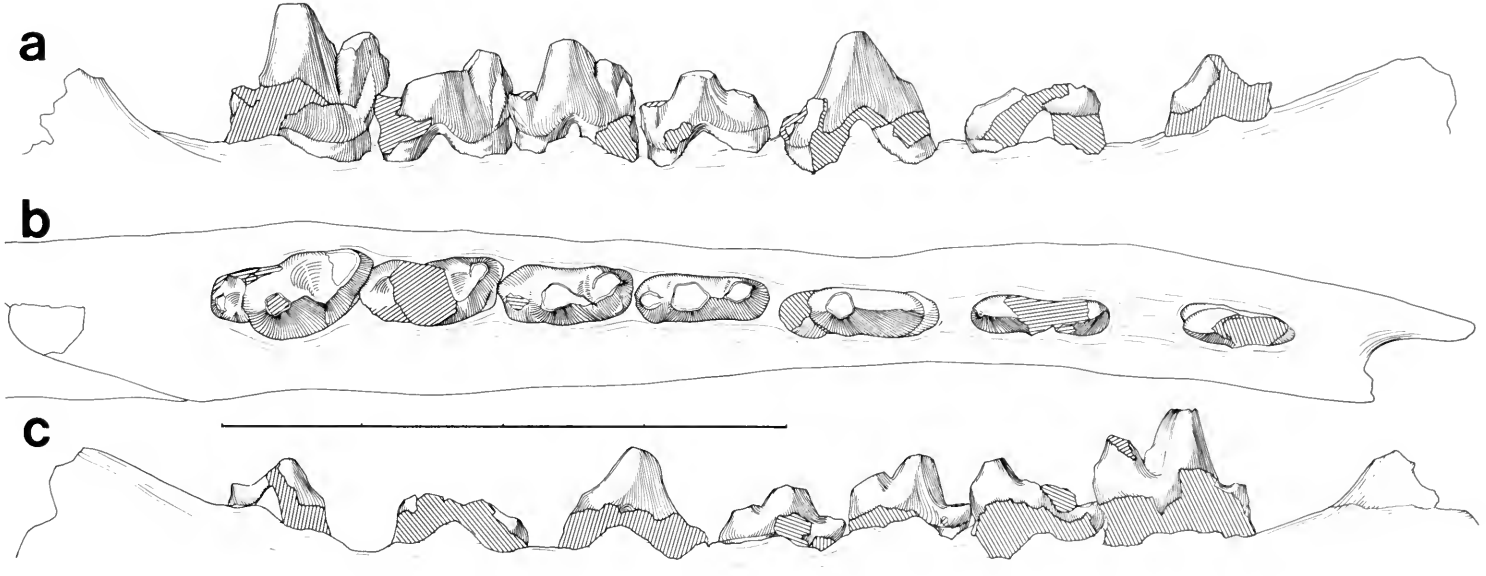

FIG. 72. *Anatherium herrerae* sp. nov. (Colhuehuapian). FMNH P13521 (type), a greater part of a right mandibular ramus with base of C, and with P_1-M_4 (tips of P_{1-2} and protoconid of M_3 are missing): **a,** labial; **b,** occlusal; **c,** lingual views. Scale = 40 mm.

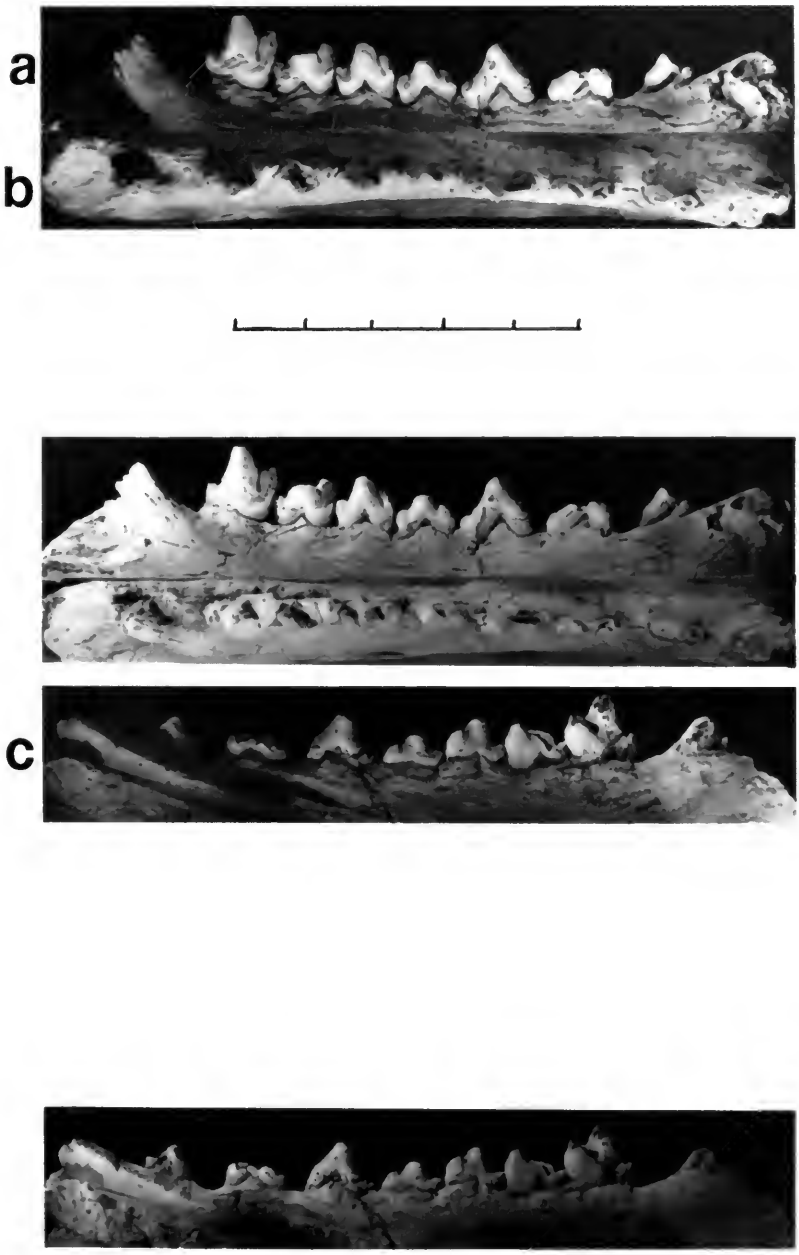

FIG. 73. *Anatherium herrerae* sp. nov. (Colhuehuapian). Stereopairs of FMNH P13521 (type), greater part of a right mandibular ramus with base of C, and with P_1-M_4 (tips of P_{1-2} and protoconid of M_3 are missing): **a**, labial; **b**, occlusal; **c**, lingual views. Scale for labial view = 50 mm.

TABLE 24. Measurements of lower cheek teeth of *Anatherium defossus* and *A. herrerae* sp. nov.

Specimen	P1		P2		P3		M1		M2		M3		M4		P1-3	M1-4	P1-M4
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	L	L
A. defossus																	
MACN 9	...	...	...	...	...	...	...	...	...	...	8.8	4.1	10.1	5.5	...	ca. 34.0	...
MACN 669	...	...	7.8	2.8	...	...	...	...	...	...	...	...	...	...	...	...	...
MACN 5988	...	...	...	...	...	...	...	...	8.0	3.8	...	...	...	...	...	...	...
MACN 11-64	...	...	...	...	...	2.9	...	2.9	8.0	3.9	8.7	4.3	...	...	...	ca. 36.5	...
A. herrerae sp. nov.																	
FMNH P13521(l)	6.0	2.3	9.5	2.8	9.5	3.4	8.4	3.4	...	3.8	9.4	4.6	10.4	5.7	34.0	37.1	71.8
FMNH P13521(r)	...	2.4	9.3	2.7	10.0	3.3	8.9	3.4	8.9	4.0	9.4	4.5	10.5	5.7	34.1	37.5	72.1

Anatherium herrerae, sp. nov. Figures 72, 73; Tables 24, 25.

Cladosictis sp. Sinclair, 1930, p. 39, pl. 8, fig. 4, 4a.

Etymology.—herrerae named in honor of Señorita Hebe E. Herrera (Museo de La Plata, La Plata and Universidad de la Patagonia, Comodoro Rivadavia) in recognition of her ongoing studies of the marsupial fauna from, and geology of, the Barranca south of Lago Colhué-Huapí from whence this specimen was collected.

Type.—FMNH P13521, associated left and right mandibular rami with bases of Cs, and P_1-M_4 (tips of right P_{1-2} and protoconids of right M_3 and left M_{3-4} missing).

Hypodigm.—Type only.

Horizon and locality.—Colhué-Huapí Formation at Barranca south of Lago Colhué-Huapí, Chubut Province, Argentina; collected by C. H. Riggs (son of E. S. Riggs) on Nov. 26, 1923.

Age.—Colhuehuapian.

Diagnosis.—Largest known species of genus; diastems separating P_1 from C and P_2 larger than in *Anatherium defossus*.

TABLE 25. Measurements of mandibular rami of *Anatherium defossus* and *A. herrerae* sp. nov.

Specimen	Depth of ramus below labial side of M_1	Breadth of same	Depth of ramus below labial side of M_4	Breadth of same
A. defossus				
MACN 9	17.4	7.6	19.8	8.1
MACN 5988	20.5	8.5	...	...
MACN 11-64	18.7	7.3	...	...
A. herrerae sp. nov.				
FMNH P13521(l)	21.0	9.3	...	...
FMNH P13521(r)	21.5	10.0	22.4	10.8

Comments.—Anatherium herrerae is the largest species of Hathlyacyninae known. Apart from its slightly larger size and greater size of the diastems separating P_1 from C and P_2, *A. herrerae* is identical in dental morphology to the Santacrucian species *A. defossus*. I therefore recognize *A. herrerae* as the slightly larger Colhuehuapian ancestor of *A. defossus*.

Anatherium defossus Ameghino, 1887. Figures 74–78; Tables 24, 25.

Anatherium defossus Ameghino, 1887, p. 8; 1889, p. 289; 1891c, p. 315; 1891d, p. 354; 1894, p. 384; 1898, p. 192, fig. 57b; 1935, p. 110, fig. 10 (caption only).
Anatherium defassus (sic) Palmer, 1904, p. 101.
Hathliacynus defossus Mercerat, 1891a, p. 53.
Acyon tricuspidatus Ameghino, 1887, p. 8; 1889, p. 290; 1894, p. 397; 1935, p. 110; Roger, 1896, p. 18.
Acyon tricuspidactus (sic) Mercerat, 1891a, p. 55.
Hathliacynus tricuspidatus Mercerat, 1891a, p. 52.
Cladosictis tricuspidata Cabrera, 1927, p. 288, fig. 6.
Acyon? bardus Ameghino, 1889, pp. 292, 293, pl. 1, fig. 18.
Agustylus bardus Ameghino, 1894, p. 392; 1935, p. 109, fig. 9 (caption only).
Ictioborus destructor Ameghino, 1894, p. 396.

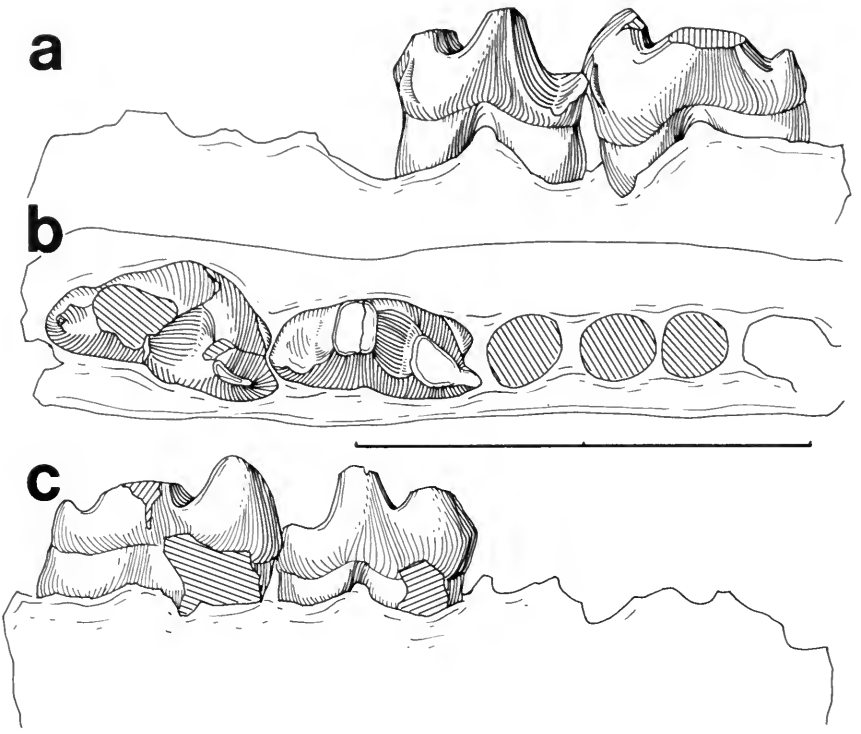

FIG. 74. *Anatherium defossus* Ameghino, 1887 (Santacrucian). MACN 9 (type of *Acyon? bardus*), a fragment of a left mandibular ramus with roots of M_{1-2}, M_3 complete, M_4 missing tip of protoconid (crowns of M_{3-4} are heavily worn): **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 20 mm.

Type of Anatherium defossus.—MACN 669, a fragment of a right mandibular ramus with roots of I_{1-3}, base of C, base of P_1, and P_2 complete (listed as "tipo" in Ameghino's catalogue, and original description fits perfectly).

Type of Acyon tricuspidatus.—MLP 11-64, a right mandibular ramus in two parts, anterior with root of C, alveoli of P_{1-2}; and posterior with P_3-M_4 all present but partially broken (figured by Cabrera, 1927, fig. 6).

Type of Acyon? bardus.—MACN 9, a fragment of a left mandibular ramus with roots of M_{1-2}, M_3 complete, M_4 missing tip of protoconid—crowns of M_{3-4} are heavily worn (listed as "tipo" in Ameghino's catalogue and on specimen—figured by Ameghino, 1889, pl. 1, fig. 18).

Type of Ictioborus destructor.—MACN 5988, a fragment of a right mandibular ramus with posterior root of P_1, roots of P_{2-3}, M_{1-2} complete but very, very worn (this specimen is not listed as type in Ameghino's catalogue, but it is listed as "tipo" on a card with the specimen, and the original description of the species matches this specimen perfectly).

Hypodigm.—The four types and MACN 646, a fragment of a left mandibular ramus with posterior half of P_3, and roots of M_{1-2}, base of M_3 and anterior alveolus of M_4 (listed as *Agustylus bardus* in Ameghino's catalogue).

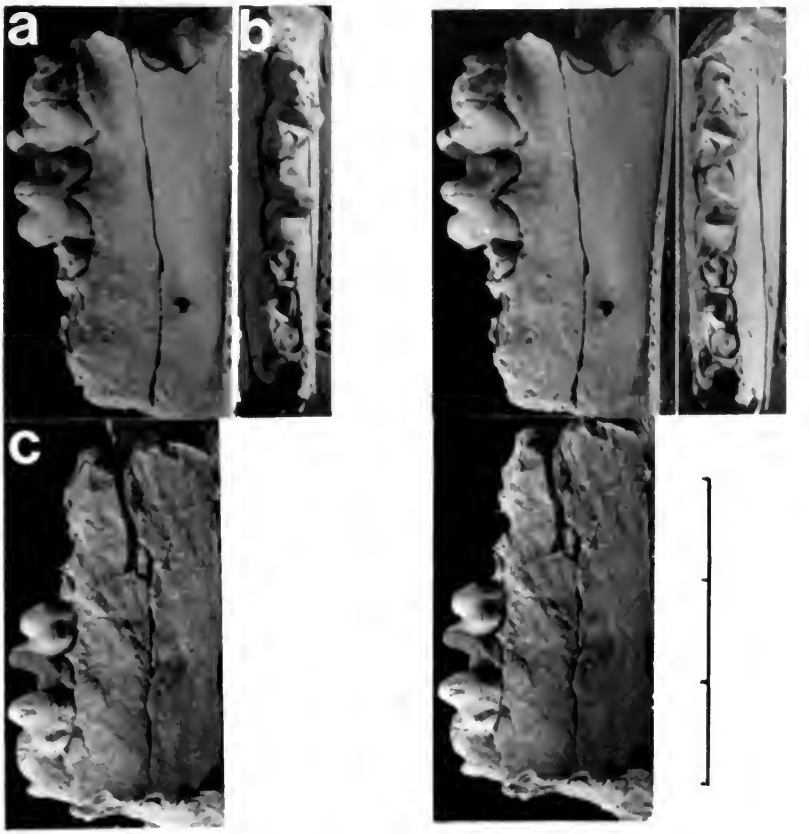

FIG. 75. *Anatherium defossus* Ameghino, 1887 (Santacrucian). Stereopairs of MACN 9 (type of *Acyon? bardus* Ameghino, 1889), a fragment of a left mandibular ramus with roots of M_{1-2}, M_3 complete, M_4 missing tip of protoconid—crowns of M_{3-4} are heavily worn: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 30 mm.

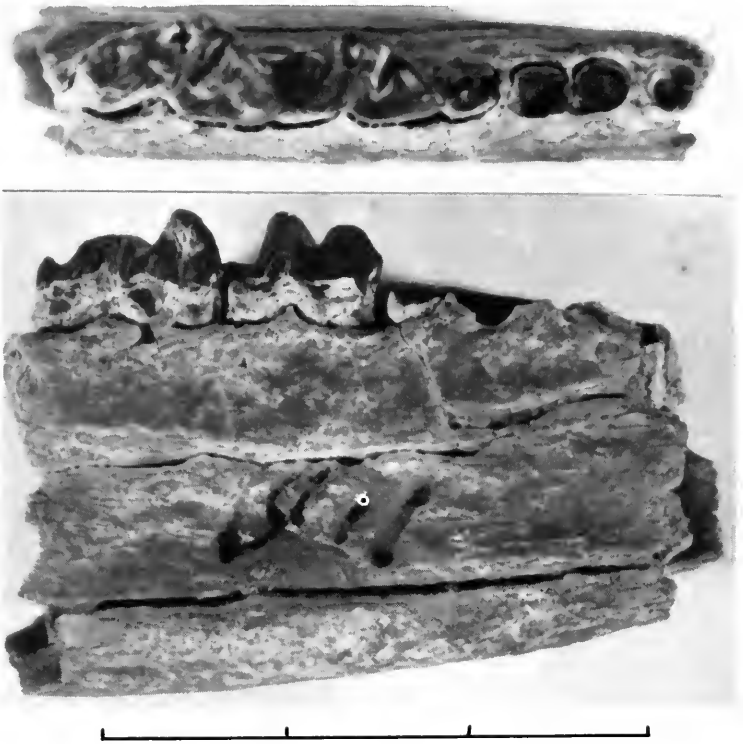

FIG. 76. *Anatherium defossus* Ameghino, 1887 (Santacrucian). MACN 9 (type of *Acyon? bardus*), a fragment of a left mandibular ramus with roots of M_{1-2}, M_3 complete, M_4 missing tip of protoconid—crowns of M_{3-4} are heavily worn: **top**, occlusal; **bottom**, lingual views. Scale = 30 mm.

Horizon and locality.—All specimens are from the Santa Cruz Formation, Santa Cruz Province, Patagonia, Argentina. MLP 11-64 is probably from Monte León, MACN 9 is from Santa Cruz (date not specified but probably 1887), MACN 5988 is from Shehuén (1890–91), and MACN 646 and 669 are from Monte Observación (1890–91); all were collected by C. Ameghino.

Age.—Santacrucian.

Diagnosis.—Largest known Santacrucian species of Hathlyacyninae; slightly smaller than *herrerae;* diastems separating P_1 from C and P_2 smaller than in *A. herrerae.*

Comments.—The type of *Ictioborus destructor,* MACN 5988, is the largest known specimen of *Anatherium defossus.* The ramus anterior to the posterior root of the P_1 is missing, and this feature of preservation led Ameghino to believe that the P_1 was rudimentary and single rooted. Thus, he placed *destructor* in the genus *Ictioborus,* which he characterized as having a single-rooted, rudimentary P_1 (see p. 94).

MACN 5988 is a very old individual as evidenced by the deeply worn M_{1-2} in which the pulp cavities are exposed on M_1 and nearly so on M_2. This specimen has the most worn teeth of any animal in the Ameghino collection, and it may

FIG. 77. *Anatherium defossus* Ameghino, 1887 (Santacrucian). MACN 5988 (type of *Ictioborus destructor*), a fragment of a right mandibular ramus with posterior root of P_1, roots of P_{2-3}, and M_{1-2} complete but very worn: **top**, occlusal; **bottom**, labial views. Scale = 50 mm.

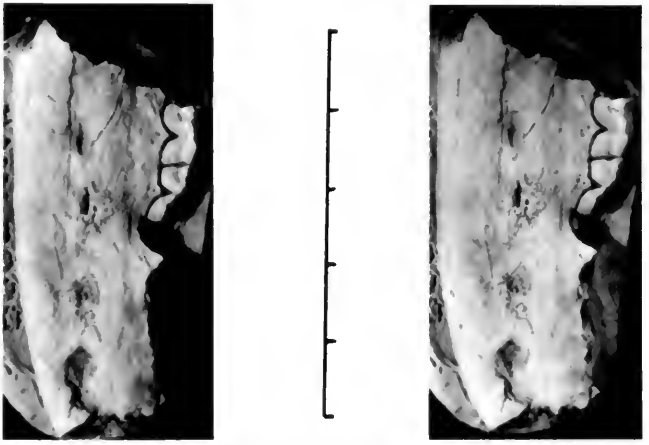

FIG. 78. *Anatherium defossus* Ameghino, 1887 (Santacrucian). Stereopairs of MACN 5988 (type of *Ictioborus destructor*), a fragment of a right mandibular ramus with posterior root of P_1, roots of P_{2-3}, M_{1-2} complete but very worn: labial view. Scale = 50 mm.

represent an aged male. Four mental foramina occur on the labial side of the ramus—a very large one below the P_2 and three smaller ones of similar size below the anterior roots of P_2, M_1, and M_2, respectively. This animal has the same pathological disorder as occurs in specimens of *Sipalocyon gracilis* (see p. 57), as evidenced by the irregular rugosities around the second and third most anterior mental foramina and along the inner surface of the symphysis.

Acyon? tricuspidatus was diagnosed by Ameghino (1887, p. 8) as having four tricuspate lower premolars. This, however, is not so—the P_3 crown on the type (MLP 11-64) was erroneously restored onto the broken base of the M_1, giving the impression that there were four premolars in this specimen. I have restored the P_3 into its proper position, and the species *tricuspidatus* now shows no differences with respect to other specimens here assigned to *A. defossus*.

Hathlyacyninae Indeterminate

Simpson (1948, pp. 48–49) recorded the presence of a number of fragmentary specimens and isolated teeth from beds of early Tertiary age in Patagonia. These could not be assigned to named taxa and themselves were inadequate to be made types of new species. Many, if not all, appear to represent generalized borhyaenids, and they may prove referable to the Hathlyacyninae. However, I can add little to Simpson's comments about these specimens, and they must remain in taxonomic limbo. The same is true for the unnamed specimens mentioned by Paula Couto (1970) from the Riochican fissure fills at São José de Itaboraí, Brazil.

Palaeocladosictis mosesi Paula Couto (1961, p. 332, fig. 12) from Itaboraí was based on what was called an upper M^1 or M^2 (MNRJ 2671-V). In the original description it was compared with *Cladosictis* and *Thylacodictis* (= *Sipalocyon*) and was thus associated with members of the Hathlyacyninae. This tooth is, however, not of a borhyaenid, but represents a DP^4 or P^4 of some sort of ungulate (Marshall, 1978, p. 70).

Summary of Evolution of Hathlyacyninae

Members of the borhyaenid subfamily Hathlyacyninae are known from beds of Riochican (late Paleocene) through Montehermosan (early Pliocene) age in Argentina and beds of Deseadan (early Oligocene) age in Bolivia. Eighteen species and 12 genera are recognized: *Patene simpsoni, P. coluapiensis, Procladosictis anomala, Pseudonotictis pusillus, Notictis ortizi, Perathereutes pungens, Borhyaenidium musteloides, B. riggsi, Sipalocyon externa, S. gracilis, S. obusta, Notocynus hermosicus, Notogale mitis, Cladosictis centralis, C. patagonica, Chasicostylus castroi, Anatherium herrerae,* and *A. defossus*.

Upper dentitions of various species showing relative proportions and size of the teeth are compared in Figure 79, and lower dentitions are compared in Figure 80. A summary of various characters, some diagnostic, for the genera are presented in Table 26. Size distributions as indicated by length of $M_{1\text{-}4}$ and length versus width of M_4 are compared in Figures 81 and 82, respectively. These plots demonstrate that absolute and/or relative size differences are sufficient in most cases to differentiate species of a given age.

Based largely on basicranial characters, the Hathlyacyninae have been shown (Marshall, 1978, p. 72, fig. 13) to be a monophyletic group relative to other

borhyaenid subfamilies. Dentally, hathlyacynines are the most generalized of known borhyaenids and share a number of features with their presumed didelphoid ancestors. Included, among other features, are a high incisor number; their generally small to medium size; their long, shallow, and generally gracile mandibular rami; symphysis ligamentous and rami unfused in adults; C weakly or moderately developed; presence of a metaconid in earliest forms (i.e., *Patene*); M_{1-3} typically with large-basined talonids; and a large protocone and wide stylar shelf on M^{1-3} in early forms.

The general evolutionary trend among hathlyacynines has been the increase in carnassial specializations resulting in loss of metaconid and reduction in size of protocone, stylar shelf, and talonid. A general trend of size increase also occurs, although some recognized lineages show size reduction and others show no significant size change. The general conclusion that can be made regarding the evolution of this group is that it has been extremely conservative with regard to the other borhyaenid subfamilies. Further, if sheer numbers of individuals and taxa are a gauge, then it has also been the most successful.

The recognized species of Hathlyacyninae are listed in Figure 83 in order of their chronostratigraphic occurrence and with an indication of their probable phylogenetic relationship. The proposed phylogeny is based largely on the data set in Table 26, although it includes consideration of other features discussed in the text. The character states that occur in *Patene* are regarded as plesiomorphic for the subfamily.

Patene simpsoni is the most generalized of known borhyaenids, and if more

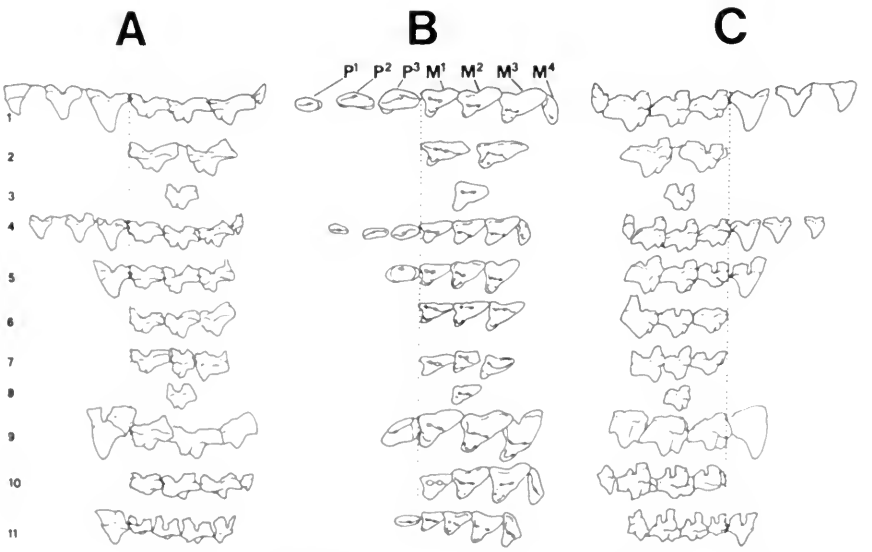

FIG. 79. Comparison of upper dentitions of various species of Hathlyacyninae showing relative size and proportions of teeth. All illustrations are drawn to same scale. **A**, labial; **B**, occlusal; **C**, lingual views. **1**, *Cladosictis patagonica;* **2**, *Chasicostylus castroi;* **3**, *Notogale mitis;* **4**, *Sipalocyon gracilis;* **5**, *Sipalocyon externa;* **6**, *Borhyaenidium riggsi;* **7**, *Borhyaenidium musteloides;* **8**, *Pseudonotictis pusillus;* **9**, *Procladosictis anomala;* **10**, *Patene coluapiensis;* **11**, *Patene simpsoni.*

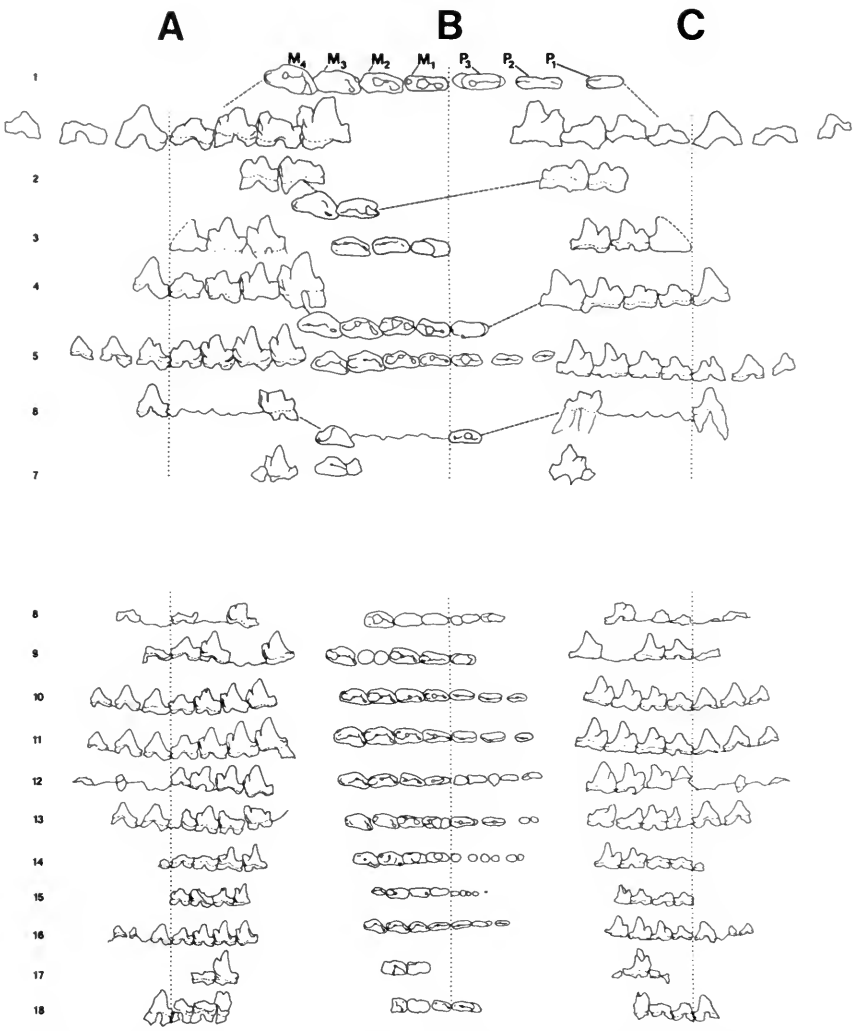

FIG. 80. Comparison of lower dentitions of various species of Hathlyacyninae showing relative size and proportions of teeth. All illustrations are drawn to same scale. **A,** labial; **B,** occlusal; **C,** lingual views. **1,** *Anatherium herrerae;* **2,** *Anatherium defossus;* **3,** *Chasicostylus castroi;* **4,** *Cladosictis patagonica;* **5,** *Cladosictis centralis;* **6 and 7,** *Notogale mitis;* **8,** *Notocynus hermosicus;* **9,** *Sipalocyon obusta;* **10 and 11,** *Sipalocyon gracilis;* **12,** *Borhyaenidium riggsi;* **13,** *Borhyaenidium musteloides;* **14,** *Perathereutes pungens;* **15,** *Notictis ortizi;* **16,** *Pseudonotictis pusillus;* **17 and 18,** *Patene simpsoni.*

specialized taxa like cf. *Nemolestes* sp. were not contemporaneous with it (see Marshall, 1978, p. 27), *P. simpsoni* would be an ideal prototype for the superfamily Borhyaenoidea. Nevertheless, *P. simpsoni* is structurally the most generalized and temporally the oldest of known Hathlyacyninae and may thus be regarded as representing the basal stock for the subfamily. *Patene simpsoni* is the only known species of Hathlyacyninae of Riochican age.

TABLE 26. Summary of various characters for genera of Hathlyacyninae.

Character	Patene	Pseudo-notictis	Notictis	Pera-thereutes	Borhyae-nidium	Procladosictis	Notogale	Sipalocyon	Notocynus	Cladosictis	Chasico-stylus	Ana-therium
1) Relative size within subfamily	small-medium	very small	very small	medium	medium	medium	medium	medium	medium	large	large	very large
2) Onentation of P_1 in jaw	straight	straight	set at 35° angle	slight (10%) angle	straight	...	straight	slight (10%) angle	straight	straight	...	straight
3) Diastems between C, P_1, and P_2	no	yes (very small)	no	yes	yes (very large)	...	no	yes (but small)	no	yes (large)	...	yes (very large)
4) Relative length of P_{2-3}	...	$P_2 < P_3$	...	...	$P_2 < P_3$	...	$P_2 \approx P_3$	$P_2 < P_3$	...	$P_2 \approx P_3$	...	$P_2 \approx P_3$
5) Metaconid	present (small on M_1, large on M_{2-4})	absent	absent	absent	absent	...	absent	absent	absent	absent	absent	absent
6) Talonid on M_{1-3}	large, basined	small, shallow basin	small, shallow basin	distinct and basined	small, not basined	...	well developed, with shallow basin	well developed, basined	well developed, basined	well developed, shallow basin	small but distinct, basined	small, not basined
7) Talonid on M_4	large, basined	very small, tiny basin but essentially cuspate	...	large, basined	small, cuspate	...	small, essentially cuspate	well developed, basined	...	very reduced, shallow basin or cuspate	...	very reduced, cuspate
8) Stylar shelf on M^{2-3}	large, well developed	very reduced	...	...	absent	very reduced	virtually absent	reduced but distinct on M^3	...	reduced but distinct on M^3	absent	...
9) Talon on M^{1-4}	large, basined	well developed, not basined	...	...	small, but distinct, cuspate	cuspate	moderately developed, very shallow basin	well developed, basined	...	moderately developed, shallow basin	small but, distinct, cuspate	...
10) Ectoflex on M^3	shallow but distinct	...	...	...	very shallow	very deep	shallow	very shallow	...	shallow	...	...
11) Relative length of M^{1-3}	$M^1 < M^2 < M^3$	...	...	...	$M^1 \leq M^2 \leq M^3$	$M^3 < M^1 < M^2$	$M^1 < M^2 < M^3$	$M^1 < M^2 \approx M^3$	...	$M^1 < M^2 < M^3$	...	...

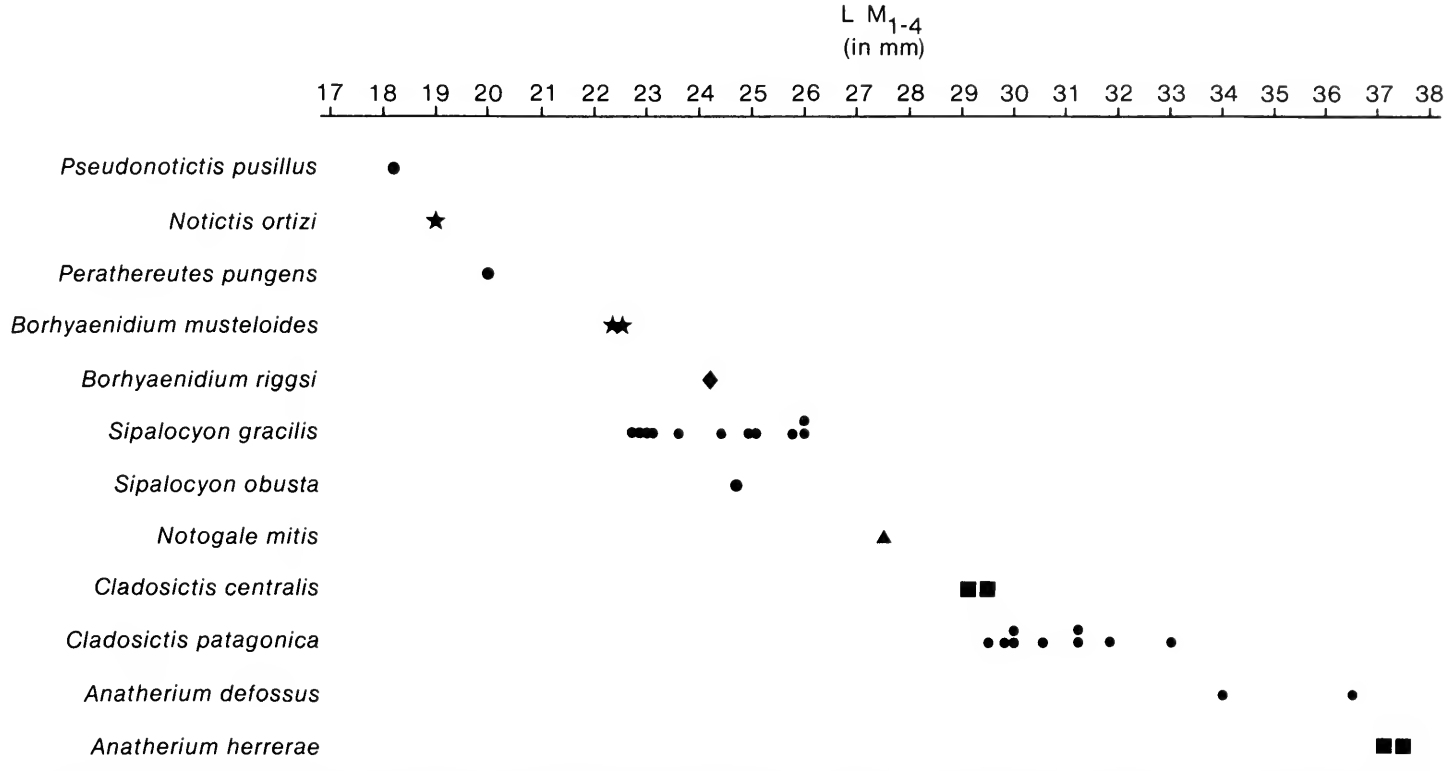

FIG. 81. Size distribution of various species of Hathlyacyninae as indicated by length of M_{1-4}. Symbols are: Deseadan (triangle), Colhuehuapian (squares), Santacrucian (circles), Huayquerian (stars), and Montehermosan (diamond).

The Casamayoran species *Patene coluapiensis* differs from *P. simpsoni* in being about one-fourth to one-third larger in linear tooth dimensions, in having relatively smaller protocones and a slightly narrower stylar shelf on M^{1-3}, a more reduced metacone on M^4, and a slightly deeper ectoflex on M^3. These taxa are very similar in other respects, and considering their occurrence in successive-aged beds, I recognize *P. coluapiensis* as the slightly larger and more specialized Casamayoran descendant of *P. simpsoni*.

Procladosictis anomala from beds of Mustersan age has a relatively smaller and cuspate protocone than in species of *Patene*, and the M^3 has a very deep ectoflex. The latter feature is not found in any other borhyaenid and excludes *P. anomala* as a potential ancestral form for any known later taxa. *Procladosictis anomala* is here regarded as a slightly larger, specialized, dead-end descendant of the Casamayoran species *Patene coluapiensis*.

A metaconid is definitely known only in *Patene simpsoni* and by inference in *P. coluapiensis* as well. An isolated lower molar possibly referable to the Mustersan genus *Procladosictis* also has a metaconid (see p. 18), whereas all known post-Mustersan hathlyacynines lack a metaconid. Loss of this structure thus occurred early in the evolutionary history of this group, although the exact time of loss cannot yet be firmly established. It is, however, assumed in the phylogeny proposed in Figure 83 that metaconid loss occurred independently at least two times within the Hathlyacyninae.

Pseudonotictis pusillus is the smallest species of borhyaenid known, being slightly smaller in most comparable linear tooth dimensions than the Riochican species *Patene simpsoni* (compare measurements in tables 1 and 2). *Pseudonotictis pusillus* differs from *Patene simpsoni* in having more advanced carnassial specializations (i.e., more reduced protocone, stylar shelf, and talonid; loss of metaconid; elongation of M_1; and increase in size and importance of postvallum-prevallid shear). These changes are nevertheless minor considering the time separating these species, and I choose to regard *Patene simpsoni* as the probable structural ancestor of *P. pusillus*.

Notictis ortizi is the smallest species of post-Santacrucian borhyaenid known and is very similar to *Pseudonotictis pusillus*. Both species are of similar size with virtually identical molar structure, with weakly developed canines, and with mental foramina of similar size, shape, and position. In *N. ortizi*, the premolars are absolutely and relatively smaller than in *P. pusillus*, and the premolar region is foreshortened, the premolars crowded, and the P_1 is set obliquely in the jaw. The differences in *N. ortizi* represent but slight specializations of features seen in *P. pusillus*, and an ancestral-descendant relationship for these species seems probable.

Perathereutes pungens from the Santacrucian is intermediate in size between the contemporaneous smaller *Pseudonotictis pusillus* and the larger *Sipalocyon gracilis*. I propose that *Perathereutes pungens* shared a common ancestry with *Pseudonotictis pusillus* and that this ancestor was characterized by somewhat reduced talonid basins, lack of a metaconid, and presence of small but distinct diastems between C, P_1, and P_2.

Perathereutes pungens is, in turn, here regarded as the most likely known ancestor for the Huayquerian species *Borhyaenidium musteloides*. Both species have P_1 set at a slight oblique angle in the jaw and separated from the C and P_2 by diastems, and the talonids (especially on M_4) are comparably more reduced relative to other similar-sized Hathlyacyninae. *Borhyaenidium musteloides* differs

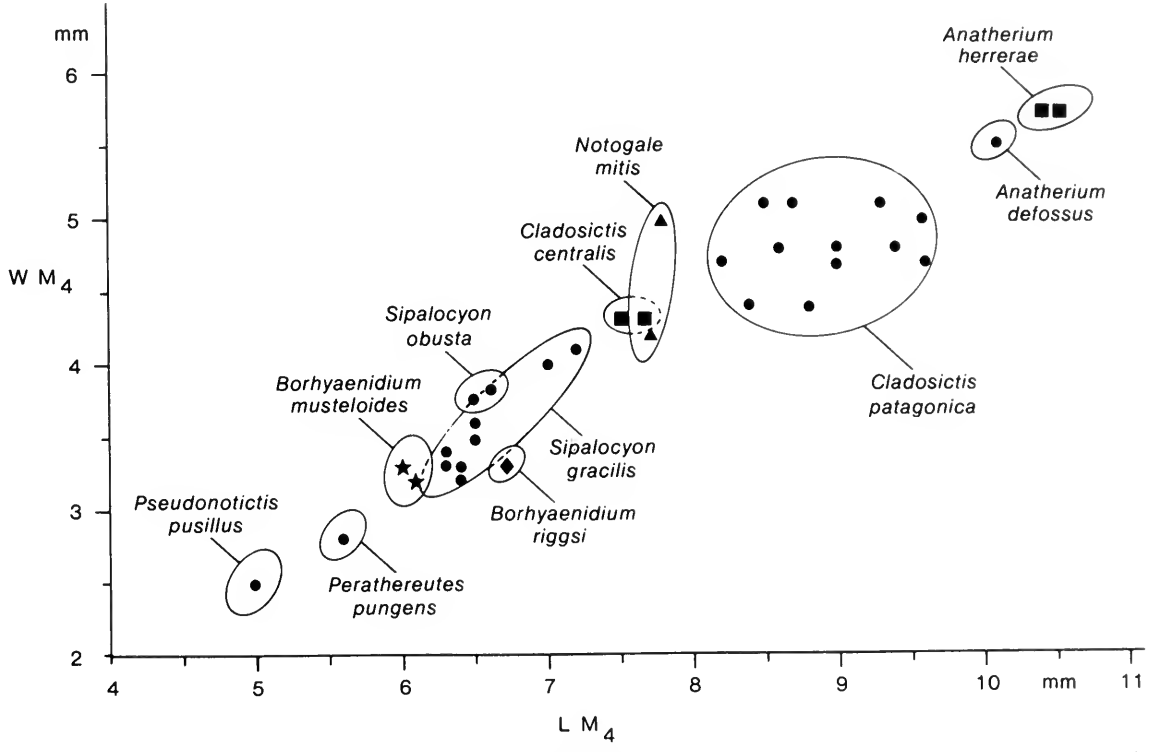

FIG. 82. Size distribution of various species of Hathlyacyninae as indicated by relationship of length and width of M_4. Symbols are: Deseadan (triangle), Colhuehuapian (squares), Santacrucian (circles), Huayquerian (stars), Montehermosan (diamond).

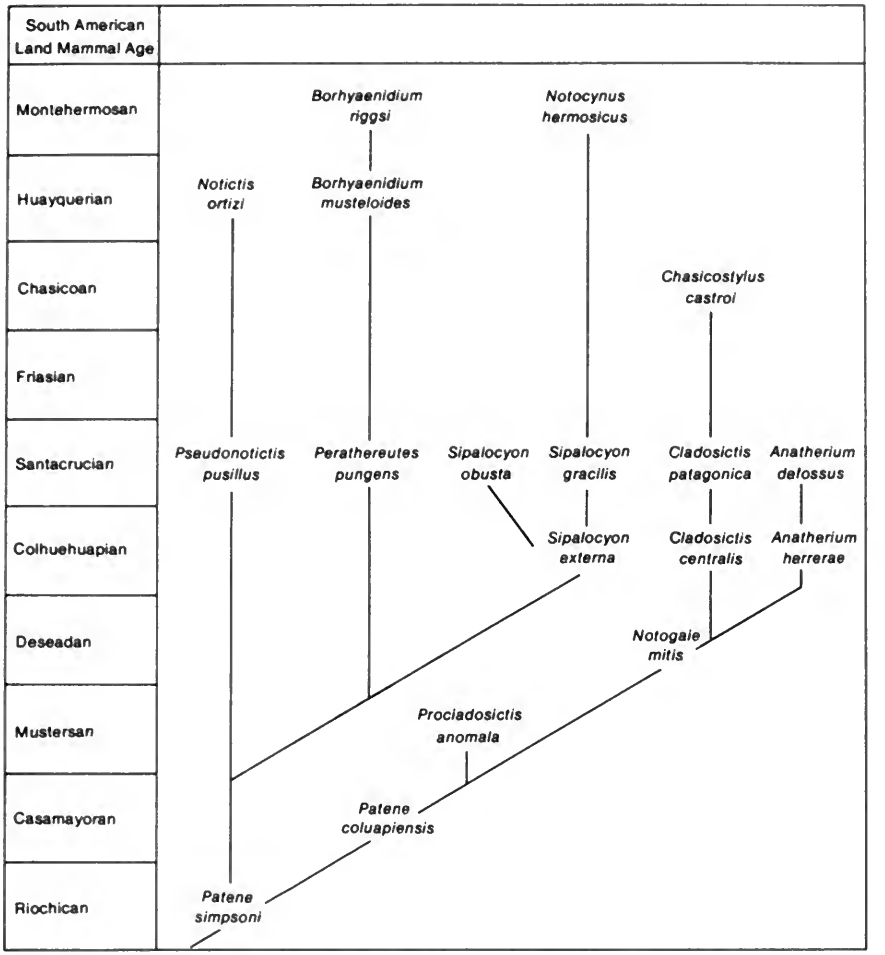

FIG. 83. Dendrogram showing probable phylogenetic relationships of the genera and species of Hathlyacyninae.

from *P. pungens* in being slightly larger in size and in the talonid basin being proportionately and absolutely more reduced.

The Montehermosan species *Borhyaenidium riggsi* differs from *B. musteloides* in having, in most cases, slightly larger linear tooth dimensions, a slightly larger M_4 talonid, and a slightly larger paracone. In other respects these species are inseparable, and they are regarded as representing a single evolutionary lineage.

It is proposed that *Perathereutes* and *Sipalocyon* shared a common ancestor characterized by a P_1 set at a slight angle relative to the rest of the tooth row, small diastems separating C, P_1, and P_2, and talonids on M_{1-4} being well developed and basined.

The Colhuehuapian species *Sipalocyon externa* is slightly smaller and more gracile than the Santacrucian species *S. gracilis*, but morphologically these species are virtually indistinguishable. Consequently, I recognize *S. externa* as the prob-

able Colhuehuapian ancestor of *S. gracilis*. The primary changes in this lineage include slight increase in size, shallowing of the ectoflex, and increase in size of metacrista on M^3.

Sipalocyon gracilis is the most abundant borhyaenid in the Santa Cruz fauna of Patagonia, southern Argentina. A contemporaneous species, *S. obusta*, is known only from its type and differs from the large comparative sample of *S. gracilis* in having a very shallow and gracile mandibular ramus and a very reduced talonid on M_4. In other respects *S. obusta* is indistinguishable from *S. gracilis*. *Sipalocyon obusta* is tentatively recognized as a valid species, although it may represent a variant individual of *S. gracilis*. Both *S. gracilis* and *S. obusta* can be easily derived from the Colhuehuapian species *S. externa*.

The Montehermosan species *Notocynus hermosicus* is very similar to *Sipalocyon gracilis;* both species are of comparable size, they have a small but distinct heel on P_2, M_3 has a very large and deeply basined talonid and a small anterobasal cingulum, and the size and proportions of the teeth and mandibular rami are virtually identical. These species differ in *N. hermosicus* having P_1 aligned in the same anteroposterior axis as the rest of the tooth row and not being set obliquely as in *S. gracilis* and in the P_1 in *N. hermosicus* not being separated from the C and P_2 by diastems. These differences are minor, and I regard *S. gracilis* as the probable Santacrucian ancestor of *N. hermosicus*.

The remaining Hathlyacyninae are recognized as monophyletic and can ultimately be derived from the Casamayoran species *Patene coluapiensis*. These taxa of the genera *Notogale, Cladosictis, Chasicostylus,* and *Anatherium* are of medium to large size, $P_2 \approx P_3$, metaconid is absent, talonid of M_4 is very small with a shallow basin or cuspate, stylar shelf is very reduced or absent, and talon on $M^{1\text{-}4}$ is moderately developed with a shallow basin or cuspate.

The Deseadan species *Notogale mitis* is a similar size to *Patene coluapiensis* and can be derived from the latter with a slight reduction in size of the protocone and stylar shelf. *Cladosictis* and *Anatherium* shared a post-Deseadan common ancestor that was of large size, had C, P_1, and P_2 separated by large diastems, and had more reduced protocones and talonid basins than *N. mitis*.

Cladosictis centralis from the Colhuehuapian is known only by a few specimens. These specimens are smaller than the large comparative sample of the Santacrucian *C. patagonica*. In other respects these species are inseparable, and I recognize *C. centralis* as the slightly smaller Colhuehuapian ancestor of *C. patagonica*.

The Chasicoan species *Chasicostylus castroi* is here regarded as a direct descendant of the Santacrucian species *Cladosictis patagonica*. These species differ in *C. castroi* being slightly larger in size, in having the upper and lower molars proportionately more elongated anteroposteriorly, in the upper molars having a larger parastyle that extends more anteriorly, in having the protocone set more anteriad relative to the para- and metacone, and in having a more elongated metacrista. These differences show *C. castroi* to have better developed shearing specializations than occur in *Cladosictis patagonica*.

The species of *Anatherium* are the largest members of Hathlyacyninae known, and the talonids of $M_{1\text{-}4}$ are more reduced than in species of *Cladosictis*. The Colhuehuapian species *A. herrerae* is the largest member of the genus, and the diastems separating P_1 from C and P_2 are larger than in the Santacrucian species *A. defossus*. Both *A. herrerae* and *A. defossus* are poorly known, and their specific separation will require reconsideration pending discovery of larger sample sizes.

For the present, *A. herrerae* is regarded as the slightly larger Colhuehuapian ancestor of *A. defossus*.

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