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The Deseadan, Early Oligocene, Marsupialia of South America

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ABSTRACT

Deseadan localities are briefly reviewed, and marsupials from Patagonian and Bolivian local faunas compared. Ten named species of marsupials are known from deposits of this age, four—*Notogale mitis* Ameghino, *Pharsophorus lacerans* Ameghino, *Pharsophorus? antiquus* Ameghino, *Proborhyaena gigantea* Ameghino—in the Borhyaenidae, and six—*Pseudhalmarhiphus guaraniticus* Ameghino, *Palaeothentes lucina* Ameghino, *P. boliviensis* n. sp., *P. chubutensis* Ameghino, *P. praecursor* Loomis, *Parabderites minusculus* Ameghino—in the Caenolestidae. In addition, there are two unnamed species of Borhyaenidae and one new species of Polydolopidae represented by material too fragmentary for formal description. The polydolopid, from Bolivia, is the latest recorded member of that family. *Notogale tenuis* Ameghino is regarded as a *nomen vanum*, and *Pharsophorus tenax* Ameghino is placed in the synonymy of *P. lacerans* Ameghino.

Notogale mitis is a possible descendant of *Patene* and an ancestor of *Sipalocyon* and, possibly, *Cladosictis*. A referred partial skull of *Pharsophorus lacerans*, from Bolivia, exhibits several resemblances to the saber-tooth thylacosmilids. *Pharsophorus? antiquus* may possibly be involved in the ancestry of *Arctodictis*. The gigantic *Proborhyaena* is the last recorded member of its subfamily. The Deseadan marks the first appearance of the Caenolestidae. *Pseudhalmarhiphus* may be ancestral to *Stilotherium*, *Parabderites minusculus* to *P. bicrispatus*, and several of the species of *Palaeothentes* show resemblances to later species of this long-lived genus. The absence of Didelphidae is a striking feature of the Deseadan fauna.

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INTRODUCTION

During Carlos Ameghino's seventh expedition to Patagonia, 1893-1894, he collected a Deseadan fauna from a locality or area known as La Flecha in Santa Cruz Province, Argentina (fig. 1). This site is situated a little distance to the south of the Inlet of the Río Deseado. The material collected during the expedition, which included some marsupials, formed the basis of Florentino Ameghino's first paper on the Deseadan (*Pyrotherium*) fauna, his "Première Contribution . . ." (Ameghino, 1895, pp. 603-606; Wood and Patterson, 1959, p. 283n). Several years later the French collector, André Tournouër (1903) made a collection of Deseadan fossils from this same locality (and elsewhere) and sent them to the Muséum Nationale d'Histoire Naturelle (MNHN), Paris. These collections were studied by Gaudry, who in 1906, on the basis of the collection from La Flecha proposed the name Deseado to replace Ameghino's faunal name of *Pyrotherium* beds. La Flecha then, is the type locality of the Deseadan (Wood and Patterson, 1959, p. 283n).

Between 1894-1896 Carlos Ameghino discovered and collected from Deseadan beds at the Great Barranca south of Lago Colhué-Huapi and at Cabeza Blanca. These materials formed the basis for Florentino's second contribution to the Deseadan fauna published in 1897. Additional marsupial taxa from the Deseadan beds of Patagonia were collected on several of Carlos' subsequent trips to these areas and were described by Florentino in 1899 and 1903. Tournouër (1903, p. 469) reported having collected a specimen of "*Epanorthus*" (= *Palaeothentes*) and "un Carnivore didelphe" from La Flecha. These specimens, now in the MNHN, are undescribed. F. B. Loomis of Amherst College visited Patagonia in 1911 and made a large collection of Deseadan mammals, including several good specimens of marsupials, from Cabeza Blanca (Loomis, 1914).

Subsequent to that time various workers have discussed Deseadan marsupials in taxonomic studies. Included are accounts of some Borhyaenidae (Cabrera, 1927; Chaffee, 1952), Abderitinae (Marshall, 1976b), and Caenolestinae (Marshall, 1976a). More recently Marshall (1978) has revised the borhyaenid subfamily Borhyaeninae, and included description of specimens from Pico Truncado and La Flecha made by the First Marshall Field Expedition to Patagonia under the leadership of E. S. Riggs in 1922-1924.

In 1968 Hoffstetter mentioned the occurrence of marsupials in the Salla (Deseadan) beds in the Salla-Luribay Basin of Bolivia. Bor-

hyaenidae were reportedly represented by the greater part of a cranium and associated mandible, tentatively referred to *Proborhyaena*, but to a form smaller than *P. gigantea*. Several teeth and other fragments attested to the existence of at least two other genera, one of medium size and the other smaller. Didelphids were reported as present but poorly represented.

Hoffstetter et al. (1971) reported marsupials from Deseadan age beds at Lacayani, Bolivia. These were represented by two mandibular fragments. More recently Hoffstetter (1976) reported that the marsupials in the Salla fauna from the Salla-Luribay Basin and Lacayani, included at least three genera of Borhyaenidae and possibly Didelphidae, although presence of the latter needed confirmation. All specimens upon which these reports were based are in the MNHN and none have as yet been described or illustrated.

In this paper we review all Deseadan Marsupialia in Argentinian (MACN, MLP) and North American (AC, AMNH, FMNH) collections. We also include description of new materials from the Salla-Luribay Basin, Provincia Loaza, Departamento La Paz, Bolivia in Princeton University.

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

AC	Amherst College, Massachusetts
AMNH	American Museum of Natural History, New York
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
MNHN	Muséum Nationale d'Histoire Naturelle, Paris, France
PU	Princeton University, Princeton, New Jersey

All measurements are in millimeters (mm.). Higher taxonomic categories for the Marsupialia follow those adopted by Clemens and Marshall (1976).

We are indebted to Dr. Donald Baird for permission to study the Salla collection in Princeton University. Illustration and publication have been aided by the Gordon Barbour fund of Princeton University.

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For access to pertinent collections and other courtesies we wish to thank Guillermo del Corro and José Gallardo, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, and Rosendo Pascual, Facultad de Ciencias Naturales y Museo de la Universidad Nacional de La Plata, La Plata, Argentina. Figures 4 and 5 are by Bill Peterson, the rest are by Elizabeth Liebman.

LOCALITIES

The following is a list of Deseadan fossil localities (fig. 1).

1. **La Flecha.** $47^{\circ} 54' S$, $66^{\circ} 15' W$. Located about 15-20 km. upriver and about 5 km. south of mouth of Río Deseado, Santa Cruz Province, Argentina. The fossil beds occur about 15 km. west of the Estancia now known as Ocho de Julio, and just southwest of the Puesto La Flecha, on the northern-most side of Lago Dulce. This is the type locality of the Deseado Formation (Tournouër, 1903, fig. 4; Bordas, 1945, profile 12; Feruglio, 1949, p. 60; Chaffee, 1952, p. 554, fig. 9, Loc. 10¹; Wood and Patterson, 1959, p. 283n).

2. **Cabeza Blanca** ("Loomis Locality"). $45^{\circ} 14' 04'' S$, $67^{\circ} 29' 80'' W$. This locality is a large peanut-shaped hill, about 5 km. southwest of the Estancia Venter, east of the Río Chico del Chubut, Chubut Province, Argentina. From this locality have come most of the Deseadan specimens in the Ameghino collection (MACN), and all those of the Loomis collection (AC), and many of those in Field Museum and the American Museum of Natural History (Simpson, 1948, p. 27, fig. 1, Loc. 6; 1967a, p. 69, fig. 3, Loc. 6; Chaffee, 1952, p. 555, fig. 9, Loc. 6).

3. **Pico Truncado.** $46^{\circ} 50' 40'' S$, $68^{\circ} 07' 20'' W$. Located in the large amphitheater on the southeastern slope of Cerro Pico Truncado, about 15 km. southwest of the Pueblo Pico Truncado, on the north

¹Chaffee (1952, pp. 554-555, fig. 9) shows a locality which he calls "La Flecha" (his Loc. 11) south and east of Pico Truncado, and north and west of Puerto Deseado. The true La Flecha locality is the same as his Loc. 10—"Río Deseado." Chaffee's Loc. 11 could represent the Cerro Alto locality of Riggs (unpub. field notes), but this is not certain.

FIG. 1. Map of Bolivia and parts of Argentina showing locations of mammal-bearing fossil localities (circles) discussed in text.

side of the Río Deseado, northern Santa Cruz Province, Argentina (Chaffee, 1952, p. 555, fig. 9, Loc. 7; Simpson, 1948, p. 27, fig. 1, Loc. 17; 1967a, p. 69, fig. 3, Loc. 17).

4. **Great Barranca.** 45° 42'S, 68° 42'W. Located about 3 km. directly south of Lago Colhué-Huapi, Chubut Province, Argentina (Simpson, 1948, fig. 1, Loc. 1; 1967a, fig. 3, Loc. 1).

5. **Neuquén.** The first discovery of a Deseadan mammal, *Pyrotherium romeroi*, was made west of the confluence of the río Limay with the Río Neuquén to form the Río Negro (Ameghino, 1906, pp. 90, 99, fig. 24). So far as we are aware, no subsequent work has been done at the locality.

6. **Rinconada de los Lopez** ("Scarritt Pocket"). 44° 40' S, 68° 25' W. The Rinconada de los Lopez is on the west side of the Meseta Canquel, between the Chubut Valley and the Colhué-Huapi Basin, central Chubut Province, Argentina. The "Scarritt Pocket" is on the southwestern portion of the Rinconada de los Lopez and on the west side of the Sierra Canquel (Chaffee, 1952, p. 555, fig. 9, Loc. 1).

7. **Paso de los Indios.** Laguna de los Machos, Departamento Paso de los Indios, Chubut Province, Argentina. This locality has yielded a small Deseadan faunule (Patterson and Pascual, 1968, p. 7).

8. **Laguna Payahilé.** 44° 30' S, 69° 00' W. Fossil beds of Deseadan age occur around, and especially to the north of Laguna Payahile, central Chubut Province, Argentina.

9. **Curuzú Cuatiá.** This locality, in Corrientes, Argentina, has yielded one specimen, the type of "*Ameghinotherium curuzucua-tiense*" Podestá (= *Trachytherus spegazzianus* Ameghino). As a note of minor historical interest, the red sandstones in which this fossil was found formed part of d'Orbigny's "Guaranitic Formation," a term improperly (by current standards) extended by Ameghino to include a number of late Cretaceous and early Tertiary rock units, including the Deseado.

10. **Ingeniero Jacobacci.** Río Negro Province, Argentina. A little known but evidently complex area as regards its Tertiary geology. Volkheimer (1973) mapped sediments of this age as Colloncuran on the basis of identifications of mammalian remains collected by him. Rocks of this age certainly occur in the area, but others do also. Specimens of *Palaeopeltis inornatus* (= *Orophodon hapaloides* Kraglievich and Rivas, 1951, *nec* Ameghino, 1895; *Pseudorophodon kraglievichi* Hoffstetter, 1954) and of an archaeohyracid attest to the presence of Deseadan deposits.

11. **Salla.** 17° 05" S, 67° 37" W. The locality is in the Salla-Luribay Basin, about 90 km. southeast of LaPaz, in the Serrania of Sicasica, at an elevation of about 4,000 m., Bolivia (see Hoffstetter, 1968; 1976, p. 7, fig. 2).

12. **Lacayani.** The locality is about 30 km. southeast of La Paz, and about 50 km. northwest of Luribay, Bolivia (see Hoffstetter *et al.*, 1971; Hoffstetter, 1976, p. 7, fig. 2).

13. **Tremembé.** The formation of this name, in the Taubaté Basin, São Paulo, Brazil (Paula Couto and Mezzalira, 1971, p. 475, fig. 1), has long been regarded as late Tertiary or Pleistocene on the basis of fossil remains, mainly fishes, consistent with but not diagnostic of such an age. A recent find of specimens of *Leontinia* (Paula Couto, *in* Paula Couto and Mezzalira, 1971) indicates a Deseadan dating (see also Patterson, *in press*).

For other possible, but at present dubious, localities for Deseadan mammals see Chaffee (1952, pp. 554-555).

Marsupialia have been recorded only from the following: La Flecha, Cabeza Blanca, Pico Truncado, Great Barranca, Rinconada de los Lope, Laguna Payahilé, Salla, and Lacayani.

AGE OF THE DESEADAN

Conventionally, the Deseadan land mammal age is considered Early Oligocene (e.g., Wood and Patterson, 1959; Patterson and Pascual, 1972). Recently Marshall *et al.* (1977) reported that a basalt conformably overlying rocks of Deseadan age at Pico Truncado gave a radiometric date of 33.6 mybp (KA 2917), and another from Cerro Blanco gave a date of 35.4 mybp (KA 2920). On the basis of these two radiometric dates these authors tentatively accepted 34.0 mybp as a terminal date for known Deseadan.¹ No basal dates for known Deseadan are yet available and the time period covered by this age is presently unknown.

Based on additional and younger radiometric dates from basalts at the Great Barranca south of Lago Colhué-Huapí and at Pico Truncado, Marshall *et al.* (1977) tentatively accept a date of 25.0 mybp as a basal age for known Colhuehuapian (Late Oligocene). The paleontological hiatus between known Deseadan and known Colhuehuapian is thus in the order of 9.0 my. Unfortunately, no

¹For the earlier Tertiary we follow the epoch boundaries of Berggren and Van Couvering (1974, fig. 1) who date the beginning of the Oligocene at 37.5 mybp.

TABLE 1. Number of specimens of each taxon recorded from each local fauna.

Taxa	Pico			Rinconada			Total
	La Flecha	Truncado	Great Barranca	Cabeza Blanca	Laguna Payahilé	de los Lopez	
<i>Notogale mitis</i>				3			15
<i>Proborhyaena gigantea</i>				1	1(1?)	2	4(3?)
<i>Pharsophorus lacerans</i>				6			9**
<i>Pharsophorus ? antiquus</i>	2	1	1				4
<i>Pharsophorus</i> sp.						1	1
Borhyaenidae g. and sp. indet.							3
<i>Pseudhalmarhiphus guaraniticus</i>				1		1***	1
<i>Palaeothentes lucina</i>				2			2
<i>Palaeothentes boliviensis</i> n. sp.							1
<i>Palaeothentes chubutensis</i>				1			1
<i>Palaeothentes praecursor</i>				1			1
<i>Palaeothentinae</i> g. and sp. indet.	1*						1
<i>Paraderites minusculus</i>				1			1
<i>Polydolopioidea</i> g. and sp. indet.						1	1
Totals	3	1	1	16	1(1?)	3	48

*Based on Tournouer (1903)

**One of these specimens is without locality data.

***Based on Hoffstetter et al. (1971).

radiometric dates are available for the Mustersan (conventionally Medial Eocene).

Of the Patagonian marsupial faunas of Deseadan age, the largest number of specimens (at least 16) are from the Cabeza Blanca, three from the Rinconada de los Lopez, one from Pico Truncado, three from La Flecha, one, possibly two, from Laguna Payahil, and one from the Great Barranca (table 1). An analysis of the relative ages of these local faunas, one to the other, based solely on comparison of the marsupials, is not possible at this time. Despite the lack of data needed for defining the relative ages of these faunas it is unlikely "that anyone would be prepared to assert that all Deseadan local faunas were exactly synchronous" (Patterson and Wood, in press).

The marsupial local faunas from Cabeza Blanca, Argentina and Salla, Bolivia are the most diverse and permit comparisons of their taxonomic differences and similarities. The most striking feature is that the two most common borhyaenid species, *Notogale mitis* and *Pharsophorus lacerans*, occur in both local faunas. If the species *Proborhyaena gigantea* is also present in the Salla local fauna, as suggested by two fragmentary maxillae, then three borhyaenid species are shared.

Palaeothentes boliviensis is slightly smaller than, but is structurally similar to *P. chubutensis* from Cabeza Blanca. The possibility exists that *P. boliviensis* is ancestral to *P. chubutensis*, making the fauna from Cabeza Blanca slightly later than that of Salla. It must be stressed that such an ancestral-descendant relationship cannot be demonstrated, although it does warrant consideration. It is of interest, in this regard, to note that Hartenberger (1975), based on a preliminary study of the rodents from these local faunas, also suggested that the Salla local fauna was somewhat earlier than that of Cabeza Blanca. A more detailed discussion of the relative ages of Deseadan local faunas is presented by Patterson and Wood (in press).

There is no doubt that the Bolivian faunas are referable to the Deseadan Land Mammal Age and aside from the marsupials contain mammalian species and genera inseparable from those in beds of Deseadan age in Patagonia (see faunal list given by Hoffstetter, 1976). It would appear that during the Deseadan there were few if any major barriers inhibiting dispersal of terrestrial mammals between Patagonia and Bolivia, areas separated by some 30 of latitude.

SYSTEMATICS

Order Marsupialia Illiger, 1811

Superfamily Borhyaenoidea (Ameghino, 1894) Simpson, 1930

Family Borhyaenidae Ameghino, 1894

Subfamily Hathlyacyninae Ameghino, 1894

Notogale Loomis, 1914*Notogale* Loomis, 1914, p. 216.*Type*.—? *Pharsophorus mitis* Ameghino, 1897.*Distribution*.—Deseadan, Patagonia, and Bolivia.*Diagnosis*.—As for the type and only known species.**Notogale mitis (Ameghino, 1897). Figures 2-7; Table 2**? *Pharsophorus mitis* Ameghino, 1897, p. 504.*Notogale mitis* Loomis, 1914, p. 216, figs. 142, 143.*Type*.—MACN 52-368, a fragment of a mandibular ramus with basal portions of $M_{2,3}$.

Hypodigm.—The type of AC 3060, a fragment of a left mandibular ramus with P_3 and M_4 present; AC 3117, a left maxillary fragment originally with part of M^2 , M^3 incomplete, and M^4 (M^4 now missing); PU 21867, a fragment of a right mandibular ramus with talonid of M_3 , M_4 complete; PU 21868, a fragment of a right mandibular ramus with M_3 (missing tip of protoconid); 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 ; 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^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).

Localities.—The type is probably, and the AC specimens are certainly, from Cabeza Blanca, Chubut Province, Argentina. PU 21996 is from Braniša 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 *Sipalocyon* from beds of Colhuehuapian and Santacruzian age of Argentina.

FIG. 2. *Notogale mitis* (Ameghino, 1897, p. 504). MACN 52-368 (type), a fragment of a right mandibular ramus with basal portions of $M_{2,3}$: a, lingual; b, occlusal; c, labial views. Scale = 10 mm.

I 4/3, C 1/1, P 3/3, M 4/4. Upper and lower P1 separated from C by small, but distinct, diastemata. P1-3 oriented along same axis as molar series, 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,

FIG. 3. *Notogale mitis* (Ameghino, 1897, p. 504). 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. 4. *Notogale mitis* (Ameghino, 1897, p. 504). 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 = 5 mm.

FIG. 5. *Notogale mitis* (Ameghino, 1897, p. 504). 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 = 5 mm.

united basally; parastyle small but distinct; styler 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; metaconid absent; talonids of M_{3-4} distinct, narrower than trigonids; talonid 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), 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. We have assumed that the larger tooth is more posterior in the series. We identify these teeth as $M_{2,3}$ although they could possibly, but less probably, repre-

FIG. 6. *Notogale mitis* (Ameghino, 1897, p. 504). 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 = 5 mm.

FIG. 7. *Notogale mitis* (Ameghino, 1897, p. 504). PU 21875, a fragment of a right maxillary with M^1 : a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

TABLE 2. Measurements of cheek teeth of *Notogale mitis*.

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	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
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	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
PU 21869	ca. 6.0	-----	ca. 7.3	-----	-----	-----	-----	-----	-----	3.8	-----	-----	-----	-----

*After Loomis (1914, p. 217)

sent M_{1-2} . 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 labelling 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. We have restored M_4 in its correct position (fig. 3).

In the same box with the type of *N. 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 a small borhyaenid with a rather generalized dentition, suggesting that it may have been a fox-like carnivore. *N. mitis* is similar in size to some large species of Pliocene-Pleistocene Didelphidae (Marshall, 1978) and it is conceivable that the unconfirmed reports of didelphids in the Salla fauna by Hoffstetter (1968, 1976) were based on fragmentary remains of this species. *N. mitis* is similar in size and structure to species of *Sipalocyon* from beds of Colhuehuapian and Santacruzian age and may well be ancestral to that genus, and/or to the larger *Cladosictis*.

Notogale tenuis* (Ameghino, 1897) *nomen vanum

?*Pharsophorus tenuis* Ameghino, 1897, p. 504.

Notogale tenuis Loomis, 1914, p. 217.

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 molar. It is, however, a premolar, 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 Palaeothentinae. In any case, this tooth is clearly not of a borhyaenid and the taxon is a *nomen vanum*.

Subfamily Borhyaeninae (Ameghino, 1894)

Cabrera, 1927

Pharsophorus Ameghino, 1897

Pharsophorus Ameghino, 1897, p. 502; Cabrera, 1927, p. 274; Simpson, 1948, p. 47.

Type.—*Pharsophorus lacerans* Ameghino, 1897, p. 503.

Distribution.—Deseadan, Patagonia, and Bolivia.

Diagnosis.— I_3^2 , C_1^1 , P_3^3 , M_4^4 ; comparable in size to species of *Borhyaena*. Incisors small, crowded, I_2 situated behind I_1 . Lower premolars increasing in size from P_1 to P_3 . P_1 implanted obliquely in jaw. P_{2-3} with well-developed posterobasal heel well separated from protoconid. P_3 large, higher than and inclined toward M_1 ; protoconid decidedly sloped posteriorly. Lower molars increasing gradually in size from M_1 to M_4 . Reduced but distinct talonid on M_{1-4} , decreasing in size relative to trigonid from M_1 to M_4 . Talonid of M_1 with distinct cusp, in M_2 small but basined, in M_{3-4} cuspsate. Metaconid lacking on M_1 . M_{2-4} with small metaconid and anterobasal cingulum; metaconid increasing in size from M_2 to M_4 . Large mental foramen below P_2 . M^{1-4} with small but distinct protocone and parastyle. M^{2-3} and probably M^1 with reduced but distinct ectocingulum.

Pharsophorus lacerans Ameghino, 1897. Figures 8-11; Tables 3-5.

Pharsophorus lacerans Ameghino, 1897, p. 503, figs. 79, 80; 1906, p. 352, fig. 183; Loomis, 1914, p. 214, fig. 139; Cabrera, 1927, p. 274; Simpson, 1948, p. 48; Marshall, 1978, p. 32.

Pharsophorus tenax Ameghino, 1897, p. 504; Loomis, 1914, p. 215, figs. 140, 141; Marshall, 1978, p. 33, figs. 5, 6.

Type.—MACN 52-391, greater part of a left mandibular ramus with roots of I_1 and I_3 and alveolus of I_2 , stump of C, roots of P_1 , P_2 missing tip of crown, P_3 - M_1 complete, and M_{2-4} present but partially broken.

Type of P. tenax.—An isolated lower M_1 , *fide* Ameghino. As the type is apparently lost, Marshall (1978) selected AC 3004 (greater part of a right mandibular ramus with roots of P_2 - M_1 , and M_{2-4} present but broken) as the neotype.

FIG. 8. *Pharsophorus lacerans* Ameghino, 1897, p. 503. MACN 52-391 (type), greater part of a left mandibular ramus with roots of I_1 and I_2 and alveolus of I_2 , stump of C, roots of P_1 , P_2 missing tip of crown, P_3 - M_1 complete, and M_{2-4} present but partially broken: a, lingual; b, occlusal; c, labial views. Scale = 3 cm.

FIG. 9. *Pharsophorus lacerans* Ameghino, 1897, p. 503. MACN 11652, a fragment of a left mandibular ramus with M_{1-3} : a, lingual; b, occlusal; c, labial views. Scale = 10 mm.

Hypodigm.—The types and neotype as above, and AC 3192, a left maxillary fragment with complete P^3 and M^{3-4} , and broken M^{1-2} ; MACN 52-388, base of a right lower canine; MACN 11652, a fragment of a left mandibular ramus with M_{1-3} ; MACN 11653, a fragment of a right mandibular ramus with posterior half of C alveolus, alveoli of P_1 , roots of P_2 , P_3 complete, roots of M_1 , M_{2-4} complete; PU 20551, medial portion of skull broken anterior to P^2 and posterior to postorbital process, with left and right P^2-M^1 (all somewhat broken)

FIG. 10. *Pharsophorus lacerans* Ameghino, 1897, p. 503. PU 20551, medial portion of skull broken anterior to P^2 and posterior to postorbital process, with left and right P^2-M^1 (all somewhat broken) and roots of M^2 : a, dorsal; b, ventral; c, frontal; d, left lateral views. Scale = 3 cm.

TABLE 3. Measurements of cheek teeth of *Pharsophorus lacerans*.

Specimen	C		P2		P3		M1		M2		M3		M4	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
Upper cheek teeth														
AC 3192	-----	-----	-----	-----	11.4	6.9	11.8	8.1	ca. 11.1	ca. 9.1	12.0	ca. 10.2	6.8	12.3
PU 20551(r)	-----	-----	ca. 10.3	5.5	10.4	7.7	10.1	9.2	-----	-----	-----	-----	-----	-----
PU 20551(l)	-----	-----	ca. 10.5	ca. 5.6	-----	-----	ca. 11.0	ca. 9.8	-----	-----	-----	-----	-----	-----
Lower cheek teeth														
MACN 52-391*	7.5	12.5	11.3	5.4	14.6	7.3	13.1	7.2	13.5	8.1	-----	8.7	16.5	10.3
MACN 11652	-----	-----	-----	-----	-----	-----	12.6	6.9	12.4	7.1	14.1	8.2	-----	-----
MACN 11653	-----	-----	11.0	4.7	11.9	6.2	-----	-----	12.3	7.4	14.0	7.9	15.4	8.9
AC 3004**	-----	-----	-----	-----	-----	-----	-----	-----	11.2	6.7	12.3	-----	13.9	8.7
PU 21865	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	ca. 12.7	-----	ca. 15.4	-----

*MACN 52-391 (type): L P_{1,3}, ca. 34.8 mm.; L M_{1,4}, 55.6 mm.; L P₁-M₄, ca. 90.2 mm.**Neotype of *P. tenax*.

and roots of M^2 ; and PU 21865, a fragment of a left mandibular ramus with posterior root of M_2 and M_{3-4} missing their lingual sides.

Localities.—The sites of collection of the types are not known, although the color and preservation of MACN 52-391 suggest provenance from Cabeza Blanca. MACN 11652 was collected at Cabeza Blanca by O. Gutierrez and L. G. Marshall in February, 1975. MACN 11653, is without locality data. The AC specimens were collected at Cabeza Blanca. PU 20551 and 21865 are from Salla, Bolivia and were collected by L. Braniša.

Age.—Deseadan.

Diagnosis.—Essentially as for genus, smaller than *P. ? antiquus*; similar in size to the Colhuehuapian *Borhyaena macrodonta*.

Pharsophorus tenax was considered by Marshall (1978, p. 33) to be a valid species, although poorly characterized. The neotype is the smallest in our mandibular series but, as shown in Table 3, the gap in molar size between it and the type of *P. lacerans*, the largest individual, is bridged by MACN 11652 and 11653. The size range is comparable to those shown by other similar sized borhyaenids, such as *Borhyaena tuberata*, for which good samples are on hand. On the evidence available we are unable to detect any differences of taxonomic significance between the Patagonian and Bolivian samples.

Description.—In PU 20551 the heel of P^3 is narrower than that of P^3 of AC 3192. The palate is unfenestrated and there is a broad nasolacrimal contact, as in other borhyaenids. A large, nearly circular infraorbital foramen opens over the middle of P^3 . The canine roots extend posteriorly to a point above the anterior edge of P^3 , resulting in inflation of the maxillaries in that region. The nasals are restricted transversely and the dorsal part of the rostrum is narrow transversely. The supraorbital bars are blunt, but distinct, and large rugose areas, marking sites of muscle attachment, occur on their dorsal surfaces and extend posteromedially, uniting to form the sagittal crest.

The lower incisors are small and crowded, their alveoli separated only by thin films of bone. I_1 and I_3 are on a line and I_2 is directly behind I_1 . I_1 is the smallest and I_2 the largest of the series. The canine is large, oval, and has a narrow but deep vertical groove on its inner face. The tooth was broken off not far above the gum line during life. This event occurred some time before death because the stump was to a considerable extent smoothed by abrasion. Although the pulp cavity was widely exposed, there is no sign of decay.

FIG. 11. *Pharsophorus lacerans* Ameghino, 1897, p. 503. PU 20551, detail of right P^2-M^1 : a, labial; b, occlusal; c, lingual views. Scale = 10 mm.

TABLE 4. Measurements of mandibular rami of *Pharsophorus lacerans*.

	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 52-391	40.0	14.5	42.5	17.0
AC 3004	31.2	13.3	34.6	14.9
PU 21865	----	----	31.0	15.6

All lower cheek teeth are two-rooted. P_1 is implanted obliquely, the anterior extremity facing anteroexternally. The protoconid of P_2 is largely missing, but enough of its posterior slope is preserved to reveal that the heel was quite distinct from it. The latter appears to have been fully as wide as the protoconid; it is highest at the center, where there is a small median cusp, and, sloping down on either side inconspicuous cingula run downward and forward from the cusp. P_3 has a large protoconid that slopes backward to a marked degree, the anterior root continuing the slope into the jaw. The base of the enamel is parallel to the alveolar border of the mandible, showing that this sloping is natural. Ameghino's figure incorrectly shows the base of the enamel to be inclined upward anteriorly, giving the false impression that the sloping was due to post-mortem displacement of the tooth. The heel is in general similar to that of P_2 , but is somewhat wider, with a smaller central cusp and less sloping sides. The premolars steadily increase in size from 1 to 3 .

M_1 is slightly shorter and wider than P_3 , and may have been approximately equal to it in height when unworn. The protoconid is large and central in position; the well-developed paraconid is anterior and only slightly internal to it. Both cusps are truncated by wear. An anteroexternal cuspule is present at the base of the paraconid. The base of the enamel on the external face is slightly smaller, but there is no definite cingulum. No trace of a metaconid is present. The talonid is wider than the trigonid and extends below it on the external face. There is a small hypoconid and a minute entoconid, but no basin, strictly speaking. The hypoconid is in line with the protoconid and the external surface of the talonid slopes sharply downward from it. The remaining molars increase in size posteriorly and, contrary to Ameghino's figure, are all incomplete, the protoconids of M_2 and 4 and the paraconid of M_3 having clearly been broken off prior to discovery of the specimen. The metaconids progressively increase in size posteriorly and the paraconids become more anterointernal in position. The anteroexternal cuspule at the base of the paraconid is very small on M_2 and absent on M_4 . The

TABLE 5. Measurements of PU 20551, *Pharsophorus lacerans*.

Width across palate between inner surfaces of anterior roots of P^2 's.	22.1
Same between protocones of M^1 's.	ca. 24.0
Length from anterior edge of right P^2 to posterior edge of right M^1	ca. 37.5
Dorsoventral diameter of right canine root above posterior root of P^2	15.0
Transverse diameter of right canine root above posterior root of P^2	7.4
Dorsoventral diameter of left canine root above posterior root of P^2	14.5
Transverse diameter of right canine root above posterior root of P^2	8.0
Width of naso-lacrimal contact (left side).	15.5
Width of naso-lacrimal contact (right side).	17.0
Diameter from surface of palate between P^2 's to dorsal edge of nasals.	39.0
Diameter of rostrum above P^2 's.	37.0
Diameter across postorbital processes.	56.7

talonid becomes progressively smaller; it is wider than the trigonid on M_1 and approximately equal to it in width on M_2 . On M_{2-3} the very small entoconid is higher than the hypoconid. A small but distinct basin occurs on the labial side of the talonid on M_{2-4} . This feature is lost in early stages of tooth wear, especially on M_{3-4} , as shown by its absence in MACN 52-391 and 11652, as compared with the younger MACN 11653.

The mandible is robust, and increases slightly in depth posteriorly below the cheek teeth. The symphysis is large, extending back to beneath the center of P_3 , only slightly rugose, and nearly flat. The coronoid process and the deep masseteric fossa are, as usual, posterior to M_4 . A large mental foramen occurs beneath the anterior portion of P_2 and there are three smaller foramina in a line behind it, beneath the posterior roots of P_2 , P_3 , and M_2 . Two vascular foramina are present beneath I_1 and I_3 on the anterior face of the symphysis, and a third, somewhat larger one, occurs a short distance below them.

The paraconid of M_3 , like the canine, was broken off prior to the death of the animal, since its stump, too, was clearly smoothed by subsequent wear. Here, again, there is no evidence of subsequent decay, although the pulp cavity was also exposed and the split extended well down into the anterior root. Injuries of this sort appear to have been rather common among the larger borhyaenids and suggest that at least some of these animals may have been bone crushers.

The astragalus that was figured in two views by Ameghino (1897, fig. 80), but not described by him, has not been found in the collections. This bone is certainly from a borhyaenid, but there is no positive evidence that it is attributable to *Pharsophorus*.

FIG. 12. *Plesiofelis schlosseri* Roth, 1903, p. 156. MLP 11-114 (type) a nearly complete left mandibular ramus with P_2-M_4 : a, labial; b, occlusal; c, lingual views. Scale = 3 cm.

Comments.—Cabrera (1927, p. 274) regarded the Mustersan genus *Plesiofelis* Roth, 1903 as a junior synonym of *Pharsophorus*, relegated *Plesiofelis schlosseri* Roth to the synonymy of *Pharsophorus lacerans*, and retained *Plesiofelis cretaceus* Roth as a distinct species of *Pharsophorus*.

Marshall (1978) has shown that *Pharsophorus* and *Plesiofelis* are quite distinct, valid genera. *Pharsophorus lacerans* (fig. 8) differs from *Plesiofelis schlosseri* (fig. 12) in the oblique implantation of P_1 ; in P_{2-3} being proportionately longer, narrower, and with the posterobasal heel proportionately larger; in a more gradual increase in size from M_1 to M_4 ; in more reduced talonid cusps; and in absence of a distinctly basined cingular shelf on lingual side of talonid. Taken separately these differences are not extreme, yet together they are sufficient to indicate that the taxa are distinct.

In addition, the provenance of the two described species of *Plesiofelis* was given by Roth (1903) as "Formación cretácea superior, Lago Musters (Territorio del Chubut)." Simpson (1936, 1948) has demonstrated that nearly all of Roth's specimens with this locality data are from the Mustersan horizon at Cerro del Humo. *P. schlosseri* is thus almost certainly Mustersan, despite the argument put forth by Cabrera (1927, p. 275) that it is from the Deseado horizon at the Great Barranca south of Lago Colhué-Huapi.

Ameghino (1897) was aware of the close similarity between species of *Pharsophorus* and species of Santacruzian *Borhyaena*. He noted that *P. lacerans* was similar to, but was slightly more massive than, *B. tuberosa*. The presence of a metaconid was also stressed as a diagnostic feature of *P. lacerans*. The size differences noted by Ameghino are of little value as the sample of *P. lacerans* falls within the range of the comparative samples of *Borhyaena tuberosa* and *B. macrodonta* given by Marshall (1978). Although *B. macrodonta* and *P. lacerans* are structurally quite similar, the latter is distinguished from *B. macrodonta* by the presence of a small metaconid on M_{2-4} and by a relatively larger talonid. As far as the dentition is concerned, an ancestral-descendant relationship for these taxa is plausible.

A complication arises, however, when the partial skull, PU 20551, is taken into consideration. This specimen differs decidedly from *Borhyaena* and other "dog-like" borhyaenids whose skulls are known in the marked posterior prolongation of the canine root, which extends back to a point above the posterior margin of P^3 ; the inflation of the maxillaries around the canines; the narrowing of the

rostrum anterior to P^3 ; the anterior narrowing of the nasals; the presence of a distinct postorbital process; and of a large, rugose postorbital ridge extending from it to the sagittal crest. If we are correct in an assignment of this specimen to *P. lacerans*, then an ancestral relationship to *Borhyaena* would not seem possible. In fact, there would appear to be no known form that could have fulfilled this role, the Mustersan *Plesiofelis* being already too specialized as regards the size gradient of the molars and the greater degree of talonid reduction (Marshall, 1978).

The most interesting point to be noted is that PU 20551 shows several resemblances to *Thylacosmilus*. Differences from *Borhyaena* noted above are approaches to thylacosmilid structure (Riggs, 1934). Derivation of the saber-tooth marsupials from a borhyaenid ancestry has generally been assumed, although undoubted transitional forms are so far unknown. Scott (1937, p. 711) suggested that the Casamayoran *Arminiheringia* might have been involved in the saber-tooth lineage, but Simpson (1948, p. 42) was sceptical as regards this possibility. PU 20551, whether or not it was involved in the ancestry, does, as far as the above features are concerned, demonstrate an intermediate condition between the two groups.

Pharsophorus? antiquus (Ameghino, 1895). Figures 13, 14.

?*Borhyaena antiqua* Ameghino, 1895, p. 655.

Proborhyaena antiqua Ameghino, 1897, p. 502; Loomis, 1914, p. 219.

Pharsophorus? antiquus Marshall, 1978, p. 36, fig. 7.

Type.—MACN 52-532, a nearly complete isolated right upper canine.

Hypodigm.—Type and FMNH P13633, crown of a right lower C; FMNH P 13800, an isolated right M^3 ; and MACN 52-384, an isolated left M_3 (?). We associate these specimens on the basis of size and their general agreement in structure with *P. lacerans*.

Localities.—The type is probably from La Flecha, Santa Cruz Province, Argentina. MACN 52-384 is labeled "Colhuapi Pyroth," which means the Deseadan horizon at the Great Barranca. FMNH P 13633 was collected at La Flecha, and FMNH P 13800 is from Pico Truncado.

Age.—Deseadan.

Diagnosis.—Very large, similar in size and structure to species of *Arctodictis* (Colhuehuapian and Santacruzian); larger and propor-

FIG. 13. *Pharsophorus? antiquus* (Ameghino, 1895, p. 655). MACN 52-384, an isolated left $M_3(?)$: a, labial; b, occlusal; c, lingual views. FMNH P 13800, an isolated right M^3 : d, labial; e, occlusal; f, lingual views. Scale = 10 mm.

tionately more robust than *Pharsophorus lacerans*.

Description.—On the upper canine a prominent longitudinal sulcus occurs along the lingual surface of the root. Total tooth height is 89.5 mm.; crown height, as measured on lingual side, is 35.0 mm.; anteroposterior length of base of crown is 23.7 mm., breadth is 16.2 mm. A large wear surface is present on the

anteromedial face of the crown, extending from its tip to about half the distance up the crown surface.

M³ is similar to that in species of *Arctodictis*. A small but distinct protocone is present, the paracone is reduced and is connate basally with the large metacone. A large parastyle is present, and extends, as a ridge, around the anterior and labial sides of the paracone. A weak ectocingulum and a shallow ectoflexus occur directly opposite the metacone. Measurements—maximum length of tooth, 16.2 mm.; maximum breadth, 13.3 mm.

On the lower canine a deep sulcus extends along the lingual surface and a shallower one along the labial surface of the root. These sulci extend onto the lowermost edge of the crown. Measurements—maximum length of tooth, 65.0 mm.; height of enamel portion of crown on labial side, 43.0 mm.; anteroposterior diameter at base of crown, 24.5 mm., breadth, 16.7 mm.

On M₃ the protoconid and paraconid are large and broad; the metaconid is small but distinct; the talonid is reduced and is composed of a small posterobasal cuspule with a cingular shelf extending from it along the labial surface. Measurements—maximum length of tooth, 16.0 mm.; maximum breadth, 10.8 mm.

Comments.—Ameghino based this species on what he considered to be a lower canine, although it is certainly an upper right. He was impressed by the similarity of this specimen to those of species of *Borhyaena* from the Santa Cruz Formation. He (1897, p. 502) was, however, hesitant in referring it to that genus, as the rest of the fauna with which it was associated differed "profoundly" from that of the Santacruzian fauna, and later referred this species to *Proborhyaena*, noting that it could be distinguished from *P. gigantea* by its smaller size.

The upper canine, MACN 52-532, is not only smaller than that of *P. gigantea* but has a distinct morphology. In the lower canine of *P. gigantea* the root is relatively straight and ribbing occurs over the entire root surface. Although upper canines of *P. gigantea* are not known, the upper and lower canines of other borhyaenids are basically similar.

MACN 52-532 is structurally similar to species of *Borhyaena*, to *Pharsophorus lacerans* and to species of *Arctodictis*. In fact, the canines of these three genera resemble each other closely. Canines of species of *Pharsophorus* and *Borhyaena* are virtually indistinguishable, while in *Arctodictis* they are relatively and absolutely larger

FIG. 14. *Pharsophorus? antiquus* (Ameghino, 1895, p. 655). FMNH P13633, crown of a right lower C: a, medial; b, dorsal; c, lateral views. Scale = 2 cm.

and more robust. MACN 52-532 is slightly larger than species of *Borhyaena*, suggesting possible affinities to species of *Arctodictis*.

The several isolated specimens from beds of Deseadan age here referred to *P.(?) antiquus* are, like the type, structurally similar to *Pharsophorus lacerans*, although larger. In view of the structural similarity of these specimens to *P. lacerans* and their occurrence in beds of similar age, we have tentatively referred them to *Pharsophorus*. Future reference of *P.(?) antiquus* to *Arctodictis* cannot be ruled out, although that genus lacks the metaconid, a cusp present in MACN 52-384. It is more likely that *P.(?) antiquus* is referable to a new genus, which cannot be adequately characterized on the basis of specimens at hand.

cf. *Pharsophorus* sp.

cf. *Pharsophorus* sp. Chaffee, 1952, p. 515; Marshall, 1978, p. 37, figs. 8-10.

Material.—AMNH 29591, an incomplete crushed juvenile skull with left and right C, left and right P¹, and unerupted P³; left P² and DP³ complete; various tooth fragments, left zygomatic arch, and a nearly complete left periotic.

Locality.—Rinconada de los Lopez in west side of Sierra Canquel, Chubut Province, Argentina. The specimen was collected from a level higher than the lake beds, from a breccia-filled dike near the top of the intrusive walls.

Age.—Deseadan.

Description.—The canines are erupting and only about 25.0 mm. of the crowns are exposed. The blades are narrow and weak relative to the size of the skull and premolars.

P¹ is set at an oblique angle in the jaw, a small and narrow posterobasal heel is present. P² is enormous compared to P¹. A large posterobasal heel is developed, which is elevated and cusped labially. P³ is larger than P². DP³ is almost complete, although the posterolabial corner is broken. Basically, it resembles a diminutive M¹, although the proportions are considerably different. There is a tiny cingular, crescentic protocone, a small parastyle, a larger paracone and a still larger metacone. Parastyle, paracone, and metacone are in a line.

The lingual half of the left M² is all that is known of the upper molars. It has a small but distinct protocone, a reduced paracone, a small but distinct parastyle, and a large metacone. What remains of the roots of the other molars suggest that M³ was erupted and M⁴ erupting. Measurements—maximum combined breadth of nasals = 58.0 mm., maximum length of nasals = 88.0 mm.; L DP³ = 11.9 mm., W DP³ = 8.0 mm.; L of right P¹ = 7.5 mm., W P¹ = 3.8 mm.; L of left P¹ = 7.6 mm., W P¹ = 4.0 mm.; L P² = 13.5 mm., W P² = 7.2 mm.

Comments.—The generic affinities of AMNH 29591 are quite uncertain. The animal is a juvenile and the canines have not yet attained their adult size. Complete molars, which are so important in borhyaenid taxonomy, are unknown. Largely on the basis of size, Chaffee (1952, p. 515) tentatively assigned this specimen to *Pharsophorus*. With reservations we have done likewise. This specimen is similar in size to *Pharsophorus lacerans* and appears to resemble that species more closely than other well known Deseadan species of Borhyaenidae.

Several features suggest, however, that AMNH 29591 might not

be referable to *Pharsophorus*. P^2 is considerably larger than P^3 in AMNH 29591, while in the lower dentition of *P. lacerans* (MACN 52-391) the relative size differences between P_1 and P_2 are less marked. Although P^3 of AMNH 29591 is not fully developed, it is larger and more robust than in other known species of Borhyaeninae. Affinities of this specimen with some or all of the elements assigned to *P.(?) antiquus* cannot be ruled out. In fact, the M^2 fragment of AMNH 29591 is similar in size and structure to the M^3 (FMNH P13800) assigned to *P.(?) antiquus*. AMNH 29591 may represent a new genus and species, but this cannot be decided on the basis of this specimen.

Subfamily Proborhyaeninae Ameghino, 1897, p. 501

Proborhyaena Ameghino 1897

Proborhyaena Ameghino 1897, p. 501.

Type.—*Proborhyaena gigantea* Ameghino 1897, p. 501.

Distribution.—Deseadan, Patagonia, and possibly Bolivia.

Diagnosis.—As for the type and only known species.

Proborhyaena gigantea Ameghino, 1897. Figures 15-17; Tables 6-9.

Proborhyaena gigantea Ameghino 1897, p. 501, fig. 78; Loomis, 1914, p. 218, fig. 144; Chaffee, 1952, p. 515, pl. 13.

Type.—MACN 52-382, a right mandibular ramus with alveoli of incisors, C complete, roots of P_1 , anterior root and posterior alveolus of P_2 , P_3 complete, M_1 present but worn, alveoli of $M_{2,3}$, and roots of M_4 .

Hypodigm.—The type and AMNH 29576, a right mandibular ramus with complete dentition (except for incisors), and associated root of left C, and complete left M_4 , and left $M^{2,3}$; MLP 71-XI-4-5, a fragment of a left mandibular ramus with M_1 complete but worn, and anterior root of M_2 ; MLP 73-VII-1-8, a fragment of a right mandibular ramus with alveoli of P_3 , M_1 complete, and anterior alveolus of M_2 .

Tentatively referred material.¹—MLP 71-XI-4-11 (-13), distal ends

¹Alvaro Mones and Martín Ubilla (Comun. Paleontol. Mus. Hist. Nat. de Montevideo, 1 (7), pp. 151-158) have recently reported and figured a left mandibular ramus with P_2 - M_4 of *Proborhyaena* cf. *P. gigantea* from the Fray Bentos Fm. at "paso del Cuello sobre el río Santa Lucía," Dept. of Canelones, Uruguay.

FIG. 15. *Proborhyaena gigantea* Ameghino, 1897, p. 501. MACN 52-382 (type), a right mandibular ramus with alveoli of incisors, C complete, roots of P_1 , anterior root and posterior alveolus of P_2 , P_3 complete, M_1 present but worn, alveoli of $M_{2,3}$, and roots of M_4 : a, labial; b, occlusal; c, lingual views. Scale = 50 mm.

FIG. 16. *Proborhyaena gigantea* Ameghino, 1897, p. 501. AMNH 29576, an isolated left M^2 : a, lingual; b, occlusal; c, labial views. Scale = 10 mm.

TABLE 6. Measurements of lower cheek teeth of *Proborhyaena gigantea*.

Specimen	P1		P2		P3		M1		M2		M3		M4		P1-M4
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	
MACN 52-382*	ca. 19.0	ca. 9.0	-----	-----	20.5	11.5	17.0	11.3	-----	-----	-----	-----	ca. 31.5	ca. 15.5	ca. 150.0
MLP 71-XI-4-5	-----	-----	-----	-----	-----	-----	18.0	10.4	-----	-----	-----	-----	-----	-----	-----
MLP 73-VII-1-8	-----	-----	-----	-----	-----	-----	17.0	10.8	-----	-----	-----	-----	-----	-----	-----
AMNH 29576(l)**	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	35.5	17.2	-----
AMNH 29576(r)**	18.7	9.6	19.0	10.7	22.5	14.5	19.4	12.3	22.1	13.9	27.0	15.4	35.7	17.5	165.0

*Anteroposterior diameter of C at alveolus, 29.5 mm.; transverse breadth of same, 19.0 mm.

**Anteroposterior diameter of left C at alveolus, 28.0 mm.; transverse breadth of same, 19.3 mm.

TABLE 7. Measurements of mandibular ramus of *Proborhyaena gigantea*.

	MACN 52-382	AMNH 29576
Depth of ramus below M_1	59.0	ca. 66.9
Breadth of ramus below M_1	26.5	ca. 29.0
Depth of ramus below M_4	64.0	ca. 74.0
Breadth of ramus below M_4	21.5	ca. 24.0
Symphysis		
Breadth	45.5	46.0
Length	92.0	89.0

of three metapodials with attached sesamoids; PU 21866, a fragment of a right maxillary with roots of $M^{1,3}$, and PU 21992, a fragment of a right maxillary with roots of M^3 ; these specimens agree in size with the Patagonian ones, but in the absence of any knowledge of crown structure no positive identification can be made.

Localities.—The type is without precise locality data, although probably from Cabeza Blanca. AMNH 29576 and MLP 73-VII-1-8 are from the Scarritt Pocket, Rinconada de los Lopez. MLP 71-XI-4-5 and 71-XI-7-11 (-13) were collected from "Zona Sud. Oriental Laguna Payahile." The PU specimens are from Salla, Bolivia.

Age.—Deseadan.

Diagnosis.—Largest known species of Borhyaenidae. $I_2^2 C_1^1 P_3^3 M_4^4$. Differing from *Arminiheringia* in larger size, in molars proportionately longer than wide, and in C implanted more perpendicularly.

Description.—The mandibular ramus is robust. The symphysis is fully fused and extends to a point below the P_3 - M_1 junction. Four well-developed mental foramina are present in the type, a small one below the anterior root of P_3 , a larger one below the anterior root of P_2 , and two others of equal size below M_1 , placed one above the other.

Alveoli of the two right incisors and that of the left medial one are preserved in the type. Both were of equal size and small compared with other species of Borhyaenidae, so far as can be judged from their shallow alveoli.

The canine is massive and set almost perpendicularly in the jaw. Posterodorsally a distinct concave wear facet is present and deep

FIG. 17. *Proborhyaena gigantea* Ameghino, 1897, p. 501. AMNH 29576, an isolated left M³: a, lingual; b, occlusal; c, labial views. Scale = 10 mm.

TABLE 8. Measurements of upper cheek teeth of *Proborhyaena gigantea* from Argentina compared with a specimen from Salla, Bolivia.

Specimen	M ¹		M ²		M ³	
	L	W	L	W	L	W
AMNH 29576	----	----	25.0	13.9	29.6	17.3
PU 21856	19.2*	15.0	22.8*	15.7*	----	19.6*

*Measurements taken on alveoli.

sulci extend down the sides of the tooth, one on the labial and another on the lingual surface. The root is relatively straight and is ribbed over its entire surface.

The premolars increase in size from P_1 to P_3 . P_1 and P_2 are single cusped and are implanted obliquely, with the anterior roots set labial to the posterior. P_3 has roots aligned in an anteroposterior direction and the crown carries a small posterobasal cusp or heel.

The molars increase in size from M_1 to M_4 . The talonid is reduced to a single cusp, which becomes progressively reduced from M_1 to M_4 , where it is merely a low vestige on the posterobasal edge of the protoconid. Protoconid and paraconid both increase in size from M_1 to M_4 , although the paraconid is larger relative to the protoconid in M_1 than in M_4 . The metaconid is much reduced and is distinguishable only on $M_{2,3}$; it lies on the posterolingual edge of the protoconid and after early stages of wear becomes united in a common shearing surface with the talonid cusp.

TABLE 9. Measurements of metapodials of *Proborhyaena gigantea*.

specimen	maximum transverse breadth, distal end	maximum dorsoventral depth, distal end
MLP 71-XI-4-11	27.0	22.5
MLP 71-XI-4-12	30.7	24.5
MLP 71-XI-4-13	25.0	----

On the upper molars an ectoflex is well developed on M^3 , but very weak on M^2 . The protocone is reduced to a swelling on the lingual side and for all practical purposes is absent. The paracone is reduced and the metacone very large. The metacrista is a prominent feature on all and a large parastyle is present on $M^{2,3}$.

The distal ends of the metapodials are very broad; a large keel bordered by two large sesamoids is present on the ventral surface.

Comments.—*Proborhyaena gigantea* is the largest and one of the

most specialized of known Borhyaenidae. In its gigantic size, presence of only two lower incisors in each ramus, oblique implantation of P_1 and P_2 , large proodont P_3 , and the parallel ribbing on the enormous perpendicular lower canines, this species is too specialized to be ancestral to any known borhyaenid found in beds of younger age. Ameghino's (1897, p. 502) erroneous reference of his ?*Borhyaena antiqua* to *Proborhyaena* has been discussed above (p. 68). Possible affinities of *Proborhyaena* and *Arminiheringia* have been discussed elsewhere (Marshall, 1978, p. 23).

Sinclair (1930, p. 38, pl. VIII, figs. 3-3A) described a fragment of a right mandibular ramus (FMNH P 13526), which he designated *Proborhyaena* sp. He stated that it came from the "Deseado Formation" and the "*Astraponotus* beds" (=Mustersan). Riggs and Patterson (1939, p. 149, n2) pointed out that this was in error and that the specimen had been collected from Colhué-Huapí beds at the Great Barranca south of Lago Colhué-Huapí. It is thus younger, not older than *Proborhyaena gigantea*; it has three incisors on each side of the mandibular ramus instead of two; it is smaller than *P. gigantea*; and the structure of the canine, mandibular ramus, and orientation of the premolars are quite different. This specimen is clearly not referable to *Proborhyaena*; it represents a Colhuehupian species of the genus *Arctodictis*, *A. sinclairi*, which is possibly ancestral to *A. munizi* from the Santacruzian (Marshall, 1978).

A specimen consisting of a cranium and associated mandible, identified as *Proborhyaena*, has been recorded from the Salla beds of the Salla-Luribay Basin, Bolivia (Hoffstetter, 1968, p. 1,095). This specimen is reportedly smaller than *P. gigantea*.

Borhyaenidae genus and species indet.

Two specimens of borhyaenids from the Salla fauna cannot be referred to any of the described species, and their fragmentary nature prevents precise identification. These are PU 21873, a fragment of a left premaxilla with roots of C and P_1 , and PU 21997, a fragment of a right mandibular ramus with roots of two teeth. These specimens represent an animal intermediate in size between *Notogale mitis* and *Pharsophorus lacerans*. Perhaps the specimen mentioned by Hoffstetter et al. (1971) from Lacayani, Bolivia, in which the crown of the M_4 had a length of 11.0 mm., should be included in this group. These specimens evidently represent a distinct and so far little known species of Deseadan borhyaenid.

Superfamily Caenolestoidea
(Trouessart, 1898) Osborn, 1910
Family Caenolestidae Trouessart, 1898
Subfamily Caenolestinae
(Trouessart, 1898) Sinclair, 1906

Pseudhalmarhiphus Ameghino, 1899a

Pseudhalmarhiphus Ameghino, 1899a.

Type.—*P. guaraniticus*.

Distribution.—Deseadan, Patagonia.

Diagnosis.—As for the type and only known species.

Pseudhalmarhiphus guaraniticus (Ameghino, 1899a)

Halmarhiphus guaraniticus Ameghino, 1899a, p. 7.

Halmarhiphus guaraniticus Ameghino, 1899b, p. 560, fig. 5.

Halmarhiphus (Pseudhalmarhiphus) guaraniticus Ameghino, 1902a, p. 424, fig. 5.

Pseudhalmarhiphus (Halmarhiphus) guaraniticus Ameghino, 1903, p. 83, fig. 2.

Pseudhalmarhiphus guaraniticus Loomis, 1914, p. 224; Reig, 1955, p. 61; Marshall, 1976a, p. 8.

Type.—Based on a fragment of a right mandibular ramus with $M_{1.2}$. M_2 figured by Ameghino, present whereabouts of type unknown.

Hypodigm.—Type only.

Locality.—Chubut Province, Argentina. No precise locality data are available.

Age.—Deseadan.

Description and diagnosis.—As figured by Ameghino, the trigonid of M_2 has two well-developed lingual cusps (paraconid and metaconid) separated by a deep valley. The trigonid is only slightly narrower than the talonid, and the cusps are sharp and high. Trigonid and talonid basins are deep and narrow, and the tooth is very narrow for its length. An anterobasal cingulum is also well developed, but not to the degree seen in species of *Pichipilus* and *Pliolestes* (Marshall, 1976a, p. 8). In all of these features *Pseudhalmarhiphus* agrees closely with species of *Stilotherium* from beds of Santacruzian age in Argentina.

Comments.—Ameghino (1899a, p. 7) gave the length of $M_{1.2}$ (his $M_{4.5}$) as 3.5 mm., and later (1899b; 1902a; 1903) figured M_2 in three views. The present whereabouts of this specimen, the type, is unknown. *P. guaraniticus* is the only caenolestine known from the

Deseadan, and is structurally similar, and possibly ancestral, to *Stilotherium* from beds of Santacruzian age (Marshall, 1976a, p. 8). *P. guaraniticus* is also the oldest known species surely referable to the Caenolestinae.

Progarzonia notostylopense Ameghino (1904, p. 260), collected from beds of Casamayoran age at the Great Barranca South of Lago Colhué-Huapi, was at one time referred to the Caenolestidae. The type, MACN 55-14, consists of a left mandibular ramus with a single rooted P_3 . Simpson (1967b, p. 9) has noted that this "animal may be a caenolestid, but in my opinion it is not adequately identifiable at any taxonomic level below class." We agree.

Subfamily Palaeothentinae Sinclair (1906)

Members of the subfamily Palaeothentinae are known from deposits of Deseadan through Santacruzian age. Although some 16 generic names for palaeothentines have been proposed (15 based initially on Santacruzian species), their status is extremely dubious. Apart from *Palaeothentes*, the first named, they include *Acdestis* Ameghino, 1887; *Epanorthus* Ameghino, 1889; *Dipilus* Ameghino, 1890; *Decastis* Ameghino, 1891; *Callomenus* Ameghino, 1891; *Essoprion* Ameghino, 1891; *Halmadromus* Ameghino, 1891; *Halmaselus* Ameghino, 1891; *Palaepanorthus* Ameghino, 1902; *Metriodromus* Ameghino, 1894; *Metaepanorthus* Ameghino, 1894; *Paraepanorthus* Ameghino, 1894; *Prepanorthus* Ameghino, 1894; *Cladoclinus* Ameghino, 1894; and *Pilchenia* Ameghino, 1903.

Most of the above genera and included species were distinguished on the basis of two characters—absolute size and relative size of P_3 compared to M_1 . In addition, supposed differences in proportions of M_{1-4} were occasionally noted.

Subsequent workers agreed that the Palaeothentinae were overly split at the generic and specific levels. Simpson (1945, p. 45), for example, tentatively recognized five genera of Palaeothentinae (*Palaeothentes*, *Pilchenia*, *Acdestis*, *Dipilus*, and *Halmadromus*). The other genera were either included as synonyms of one of these five or were regarded as *nomina vana*. As Simpson (1945, p. 42, 2n) noted, "Proper generic criteria for this group [Palaeothentinae] have not yet been worked out, and the published data are inadequate in several cases." All of these generic names are thus of dubious value at the present time and must be regarded as such until the entire subfamily is adequately revised. One of us (L.G.M.) has nearly com-

pleted a review of the Santacruzian taxa in which five species are recognized as valid: *P. minutus* Ameghino, 1887; *intermedius* Ameghino, 1887; *owenii* Ameghino, 1887; *lemoinei* Ameghino, 1887; and *aratae* Ameghino, 1887. These species can be all included in a single genus *Palaeothentes*. Adequate samples for each of these species are known and variation within each can be evaluated. Based upon this preliminary study, it was found that such characters as absolute size, relative size of P_3 to M_1 , and relative proportions of M_{1-4} are useful in diagnosing the different species but are of very dubious generic value. The characters dictate that either we recognize five distinct Santacruzian species of *Palaeothentes*, or we recognize five monotypic Santacruzian genera. For present purposes we choose the former alternative and have assigned (with some additional qualifications) the four Deseadan species of *Palaeothentinae* to the genus *Palaeothentes*. We are unable to detect any differences of generic significance between these and Santacruzian representatives of the genus.

Palaeothentes Ameghino, 1887

Palaeothentes Ameghino, 1887, p. 5.

Type.—*Palaeothentes aratae* Ameghino, 187, p. 5.

Distribution.—Deseadan, Colhuehuapian, and Santacruzian of Patagonia, and Deseadan of Bolivia.

Diagnosis.— $?/2$ $1/1$ $3/3$ $4/4$. P^{1-3} two-rooted; P^{1-2} very reduced in size and crown height; P^3 enormous, rivalling M^1 in size, with crown height equal to or greater than that of M^1 . Posterior end of crown much broader than anterior. Upper molars decreasing rapidly in size from M^1 to M^4 . Sharp cutting edge formed along labial sides of M^{1-2} extending onto P^3 . Labial sides of M^{1-2} much higher than lingual. M^1 with large posterolingual cusp, conferring rectangular shape to tooth; remnants of this cusp seen on M^2 , but not on M^3 or M^4 . Mandibular ramus typically long and relatively shallow. One large, laterally compressed incisor in each jaw followed by four tiny, single-rooted, vestigial teeth (presumably an incisor, a canine, and two premolars). P_3 either single rooted and styliform with a crown height much less than that of the M_1 , or very large, double rooted, and equal in height to trigonid crest of M_1 .

Lower molars decreasing rapidly in size from M_1 to M_4 . Trigonid region of M_1 greatly elongated, with paraconid set far anterior; crest connecting paraconid with protoconid blade-like. Trigonid of M_1 typically longer and narrower than talonid. Crista obliqua large,

FIG. 18. *Palaeothentes lucina* (Ameghino, 1903, p. 128). AC 3110, a left mandibular ramus with P_3 - M_4 : a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

well developed. M_{2-4} bunolophodont; trigonid and talonid regions of M_{2-3} distinct, M_4 usually ovate.

Palaeothentes lucina (Ameghino, 1903). Figure 18; Table 10.

Pilchenia lucina Ameghino, 1903, p. 128, fig. 49; 1904, p. 259 (said to be new in 1904, but publication in 1903 was prior and valid); Loomis, 1914, p. 222, fig. 146.

Type.—MACN 52-371, an isolated left M_3 .

Hypodigm.—Type and AC 3110, a left mandibular ramus with P_3 - M_4 complete.

Localities.—The type is from the "Piroteriense" and probably from Cabeza Blanca; AC 3110 is definitely from that locality.

Age.—Deseadan.

Diagnosis.—Compared with *P. chubutensis* and *P. boliviensis*, P_3 similar in relative length compared to M_1 , but considerably narrower and lower; larger than in *P. praecursor*. Decrease in size from M_1 to M_4 more gradual than in *P. chubutensis*.

Comments.—Ameghino erected "*Pilchenia*" *lucina* on an isolated molar which Loomis correctly interpreted as M_3 . Loomis assigned a second specimen (AC 3110), consisting of the greater part of a left mandibular ramus, to this species. We agree with this assignment.

When he proposed *Pilchenia*, Ameghino did not present criteria that would distinguish this from any of the 14 named Colhuehupian and Santacruzian genera of Palaeothentinae. We have compared AC 3110 with a large sample of Santacruzian taxa of *Palaeothentes* and find no reason to recognize it as distinct at the generic level and therefore assign *lucina* to that genus.

Ameghino (1903, p. 128) based "*Pilchenia*" *lobata* on a fragment of a right mandibular ramus with a complete M_2 (MACN 52-379). This specimen was collected from the "Notohippidense" (early Santacruzian) horizon at Karaiken, near the eastern end of Lago Argentino, Santa Cruz Province, Argentina. As noted by Marshall and Pascual (1976, p. 113), this specimen is clearly referable to *Palaeothentes* and is very similar to, and possibly conspecific with *P. lemoinei* from the Santa Cruz beds along the Atlantic coast between Río Gallegos in the south and Monte Leon in the north. The species *lobata* is placed in *Palaeothentes* (Marshall and Pascual, 1976).

***Palaeothentes boliviensis* new species.** Figure 19; Table 10.

Holotype.—PU 21977, a fragment of a right mandibular ramus with P_3 - M_1 (posterolingual corner of M_1 missing).

Hypodigm.—Type only.

Locality.—Salla-Luribay Basin (Braniša locality V-2), Bolivia.

Age.—Deseadan.

Etymology.—In reference to Bolivia, *boliviensis*.

Diagnosis.—Smaller than *P. chubutensis*; considerably larger and with more prominent and higher crowned P_3 than *P. lucina* and *P. praecursor*.

Description.—The double-rooted P_3 is very large relative to M_1 and is equal in height to the trigonid of M_1 ; the posterior end is much broader than the anterior, and a small cuspsule occurs on the anterior

FIG. 19. *Palaeothentes boliviensis* new species. PU 21977, a fragment of a right mandibular ramus with P_3 - M_1 (posterolingual corner of M_1 talonid is missing): a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

FIG. 20. *Palaeothentes chubutensis* (Ameghino, 1897, p. 500). MACN 52-378 (type), a right mandibular ramus with posterior root of P_2 , P_3 - M_2 , and M_4 relatively complete, roots of M_3 (all teeth are heavily worn): a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

edge about midway up the crown. The talonid of M_1 is only slightly lower than trigonid.

Comments.—The type of *Palaeothentes boliviensis* is the only palaeothentine known from the Salla fauna, and it is the only palaeothentine yet known outside Patagonia. In its relatively large size and high, broad P_3 , *P. boliviensis* shows closer affinities to *P. chubutensis* than to any other known Deseadan palaeothentine. Except for the very large Santacruzian species *P. aratae*, *P. boliviensis* is considerably larger than any other known Colhuehuapian or Santacruzian species of Palaeothentinae.

Palaeothentes chubutensis (Ameghino, 1897). Figure 20; Table 10.

Epanorthus chubutensis Ameghino, 1897, p. 500, fig. 77.

Palaeopanorthus chubutensis Ameghino, 1901, p. 77.

TABLE 10. Measurements of lower cheek teeth of Desoadan species of Palaeotheninae.

Specimen	P3		M1		M2		M3		M4		M1-4 P3-M4	
	L	W	L	W	L	W	L	W	L	W		
<i>Palaeotheres lucina</i>	---	---	---	---	---	---	2.4	1.8	---	---	---	---
MACN 52-371	2.5	1.5	4.3	2.1	2.9	2.1	2.5	2.0	1.7	1.6	11.8	12.7
AC 3110												
<i>Palaeotheres praecursor</i>	1.3**	---	5.0*	2.0*	3.5	2.2	---	---	---	---	---	---
AC 3020												
<i>Palaeotheres boliviensis</i> n.sp.	2.6	2.2	5.2	3.0	---	---	---	---	---	---	---	---
PU 21977												
<i>Palaeotheres chubutensis</i> ***	3.3	2.3	6.4	3.2	4.6	3.2	---	---	2.4	1.7	16.7	19.7
MACN 52-378												

*After Loomis (1914, p. 224)

**Measurement based on roots.

***Depth of mandibular ramus labial to M₁ = 12.0 mm.; width at same = 4.5 mm.

Palaeothentes chubutensis Loomis, 1914, p. 221, fig. 145.

Type.—MACN 52-378, a right mandibular ramus with posterior root of P_2 , P_3 - M_2 , and M_4 complete, roots of M_3 , all teeth being heavily worn.

Hypodigm.—Type only.

Locality.—Chubut Province, Argentina. The exact locality is not known, but it is probably from Cabeza Blanca.

Age.—Deseadan.

Diagnosis.—Largest known species of pre-Santacruzian Palaeothentinae. Differing from similar-sized Santacruzian *P. aratae* (e.g., MACN 14) in slightly deeper, more robust mandibular ramus and larger P_3 .

Description.— P_3 is a very large, double-rooted tooth, equal in height to the trigonid of M_1 , and is much wider anteriorly than posteriorly.

Comments.—*Palaeothentes chubutensis* is easily distinguished from other Deseadan Palaeothentinae by its large size and prominent P_3 . In *P. chubutensis*, as in the somewhat smaller *P. boliviensis*, P_3 is large, prominent, and equal in height to the trigonid of M_1 . *Palaeothentes lucina* and *P. praecursor* are much smaller than *P. chubutensis* and *P. boliviensis*, and have a proportionately smaller P_3 .

Ameghino (1897, fig. 77) figured the type of *P. chubutensis* in which M_3 was correctly illustrated as missing. Loomis (1914, fig. 145) redrafted Ameghino's figure and in so doing restored the missing tooth.

Palaeothentes praecursor (Loomis, 1914). Figure 21; Table 10.

Callomenus praecursor Loomis, 1914, p. 223, figs. 147, 148

Acdestis praecursor Pascual and Odreman Rivas, 1971, p. 383; Clemens and Marshall, 1976, p. 69.

Type.—AC 3020, a fragment of a right mandibular ramus with M_2 ; the crowns of P_3 and M_1 , originally present, have been lost since the specimen was figured by Loomis.

Hypodigm.—Type only.

Locality.—Cabeza Blanca, Chubut Province, Argentina.

Age.—Deseadan.

Diagnosis.— P_3 two rooted, very small compared with that of other Deseadan species; about half as high as M_1 . $M_{1,2}$ slightly larger than

FIG. 21. *Palaeothentes praecursor* (Loomis, 1914, p. 223). AC 3020 (type), a fragment of a right mandibular ramus with crown of M_2 and alveoli of P_2 - M_1 : a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

in *P. lucina*, considerably smaller than in *P. boliviensis* and *P. chubutensis*.

Comments.— $M_{1,2}$ of *P. praecursor* are heavily worn, preventing comparison of minor cusp morphology with *P. lucina*. The small size of the P_3 and large size of $M_{1,2}$ serve to separate the species.

Palaeothentes praecursor has the smallest P_3 of known Deseadan Palaeothentinae. In this feature it agrees well with Santacruzan species assigned by Ameghino to such genera as "*Acdestis*," "*Callomenus*," and "*Decastis*." In species of "*Acdestis*" the P_3 is typically small but two-rooted; while in "*Decastis*" (e.g., "*D. columnaris*"—MACN 5561) it is very reduced and definitely single rooted. Because of the structure of P_3 , Loomis assigned this species to "*Callomenus*."

The structure of P_3 is, however, quite variable in the Palaeothen-

tinae, and although a useful character in distinguishing species, it appears to lack generic utility. $M_{1,2}$ have the typical structure seen in species of *Palaeothentes*, and for these reasons we deem it more parsimonious to regard *praecursor*, at least for the present, as a member of this genus.

Subfamily Abderitinae Sinclair, 1906

Parabderites Ameghino, 1902b.

Parabderites Ameghino, 1902b, p. 121.

Type.—*Parabderites bicrispatus*

Distribution.—Deseadan and Colhuehuapian, Patagonia.

Diagnosis.—Jaw short, deep, but shallower, more gracile than in *Abderites*. Lower incisor large, laterally compressed, followed by four spaced, single-rooted, vestigial teeth, separated from P_3 by distinct diastema. P_3 large, double-rooted, blade-like with up to two serrations on each face and corresponding apical denticles. Trigonid of M_1 compressed transversely, blade-like with two distinct serrations on each face and corresponding apical denticles; talonid little modified, similar to that of M_2 . $M_{2,3}$ proportionately longer, narrower than in *Abderites*; trigonids and talonids distinct. M_2 basically quadrate, slightly broader anteriorly than posteriorly; two labial cusps, two lower lingual cusps. M_4 smaller than M_3 , oval in occlusal view.

Parabderites minusculus Ameghino, 1902c. Figure 22.

Parabderites minusculus Ameghino, 1902c, p. 43; Lomis, 1914, p. 224; Marshall, 1976b, p. 79, fig. 10.

Type.—MACN 52-380, a left mandibular ramus with P_3 - M_3 complete, and alveoli of M_4 .

Hypodigm.—Type only.

Locality.—Probably from Cabeza Blanca.

Age.—Deseadan.

Diagnosis.—Smallest known species of genus; further differing from Colhuehuapian *P. bicrispatus* in lacking serrations on P_3 , with P_3 and trigonid region of M_1 inclined forward at greater angle relative to main horizontal axis of ramus.

Comments.—This species has been discussed at length by Marshall (1976b, p. 79, fig. 10). *P. minusculus* is the oldest known species referable to the Abderitinae and is the only known Deseadan species of that subfamily.

FIG. 22. *Parabderites minusculus* Ameghino, 1902c, p. 43. MACN 52-380 (type), a left mandibular ramus with P_3 - M_3 , and alveoli of M_4 : a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

Superfamily Polydolopoidea Clemens and Marshall, 1976
 Family Polydolopidae Ameghino, 1897

Genus and species indet.

A single specimen, PU 21998, a fragment of a left mandibular ramus with the base of a large gliriform tooth, and roots of P_2 and P_3 , from Salla, Bolivia, is referable to this family (fig. 23). It is the latest known polydolopid.

FIG. 23. Polydolopid genus and species indet. PU 21998, a fragment of a left mandibular ramus with base of large gliriform tooth, and roots of P_2 and P_3 : a, labial; b, occlusal; c, lingual views. Scale = 10 mm.

The base of the gliriform tooth is narrow transversely (3.0 mm.) and deep dorsoventrally (5.5 mm.). It projects laterally from the jaw at an angle of 35° relative to a line drawn through the centers of P_2 and P_3 . A large, edentulous diastema separates this tooth from P_2 , which is very small, situated directly anterior to P_3 , and double rooted, the anterior root being smaller than the posterior. The base of P_2 is 2.7 mm. long and 1.8 mm. wide at the posterior end. As shown by the roots, P_3 is a large elongate tooth. Its base is about 9.6 mm. in length, the anterior root being longer (5.8 mm.) than the posterior (3.8 mm.), with both of about equal breadth (4.0 mm.). The mandibular symphysis is smooth, suggesting that the rami were loosely joined and probably capable of movements independent of each other. A small mental foramen occurs 4.0 mm. below the base of P_2 . The depth of the ramus below the middle of P_3 on the labial side is 14.0 mm., the breadth 6.8 mm.

Comparisons.—Included within the family Polydolopidae are five genera from the early Tertiary of South America. Four of these—*Amphidolops*, *Eudolops*, *Polydolops*, and *Seumadia*—are known only from Patagonia: *Eudolops* and *Amphidolops* from the Casamayoran (conventionally Early Eocene), *Seumadia* only from the Riochican (conventionally Late Paleocene), and *Polydolops* from Riochican through Mustersan (conventionally Mid Eocene) age (Simpson, 1948; Pascual and Odreman Rivas, 1971). The fifth, *Epidolops*, is known only from the Riochican Itaborai fauna near Rio de Janeiro, Brazil (Paula Couto, 1952).

In possessing three procumbent gliriform teeth in each lower jaw *Epidolops* differs markedly from all other known polydolopids which have only one. *Seumadia*, is known only from an isolated M^3 and therefore cannot be compared directly with the Salla specimen. *Amphidolops*, *Eudolops*, and *Polydolops* are known from referred upper and lower dentitions. *Polydolops*, *Amphidolops*, *Epidolops*, and PU 21998 are characterized by possession of a very large "plagiaulacoid" P_3 , while in *Eudolops* the shearing specialization of this tooth has been secondarily (?) lost and the tooth greatly reduced in size. Unfortunately, the lower dentition of *Amphidolops* anterior to M_1 is unknown and direct comparison of this taxon with the Salla polydolopid is not possible.

The Salla polydolopid can thus be compared directly only with species of *Polydolops*, the most abundant and, whether for this reason or another, the most varied of known polydolopid genera. These variations are, however, primarily in size, proportions, and

minor details of cuspule development. According to Simpson (1948), they involve no important morphological characters.

In size, PU 21998 is considerably larger than all known species of *Polydolops* of Riochican and Casamayoran age. The length of P_3 of Casamayoran and Riochican species has a known range of 4.0 mm. in *P. rothi*, to 7.8 mm. in *P. clavulus*, compared to 9.6 mm. in PU 21998. An extension of the time range of *Polydolops* to the Mustersan has been reported by Pascual and Odreman Rivas (1971, p. 381), but no description of the material has yet appeared, and comparison with PU 21998 is therefore not possible.

Classification of the Argentinian polydolopid specimens has proven difficult. Specimens are few, generally fragmentary, and associated upper and lower dentitions are unknown. More importantly, the types are not all comparable, and numerous names, applied to fragmentary materials, can neither be rejected nor validated (Simpson, 1948). In view of this situation and the fragmentary nature of PU 21998, affinities of the Bolivian form with other known genera cannot be firmly established. Of the five known genera, PU 21998 appears to be structurally most similar to *Polydolops*.

Species of *Abderites* also have a large "plagiaulacoid" tooth, but in that group it is M_1 , while in polydolopids it is P_3 (Paula Couto, 1952). In *Abderites* there are four tiny, spaced, single-rooted, vestigial teeth between the large gliriform tooth and M_1 , and M_1 is always preceded by a styliiform P_2 (Marshall, 1976b, p. 60). In polydolopids P_3 is preceded only by a two-rooted or incipiently two-rooted, peg-like P_2 , as in PU 21998.

In known beds of Casamayoran age, polydolopids are relatively abundant and are represented by some 10 nominal species (Simpson, 1948). Polydolopids are rare and represented only by a single specimen each in the Mustersan and Deseadan. It is interesting and probably significant that *Abderites*, a caenolestid structurally similar to polydolopids, first appears in beds of Colhuehuapian age (Marshall, 1976b), following the last appearance of polydolopids in the Deseadan.

DISCUSSION

The Deseadan was an interesting time in the history of vertebrate life in South America. At the close of this age various mammalian groups made their last appearance (e.g., pyrotheriids and isotemnids), and others their first (e.g., homalodotheriids, toxodontids,

mylodontids). More importantly, those foreign invaders, the rodents and primates, first occur in beds of this age.

Deseadan time marks for the Marsupialia a number of important changes, some of which may be linked with the appearance, disappearance or diversification of other groups.

The borhyaenid subfamily Proborhyaeninae reached large size in the early Tertiary. The last known member of this group, *Proborhyaena gigantea*, is the largest species of borhyaenid known, adults having skulls in excess of 2 ft. in length (Marshall, 1978). A possible explanation for the disappearance of this group exists. The other occupants of the terrestrial carnivore adaptive zone were members of a group of large cursorial ground birds, the Phororhacoidea. Three families, assorted into medium, large, and gigantic size groups by mammalian standards, are currently recognized. Phororhacoids are first known from beds of Deseadan age and ranged in South America through the Monterhermosan (conventionally Late Pliocene). Two of the families, Psilopteridae and Phororhacidae, were swift and rather lightly built, while the third, Brontornithidae (at present unknown subsequent to the Santacruzian), included ponderous forms with large massive beaks. The former two were evidently the dominant cursorial carnivores of their time (Patterson and Pascual, 1972, p. 262).

As suggested by Marshall (1978), the phororhacoids may have contributed to the disappearance of such large borhyaenids as *Proborhyaena*. This is clearly speculative, although it does appear that these birds either actively or passively replaced, at least in part, these large Borhyaenidae on the savanna-grasslands of southern South America.

Representatives of other borhyaenid subfamilies occur in the Deseadan, and some show affinities with taxa from earlier and later faunas. *Notogale mitis* is a small, generalized member of the subfamily Hathlyacyninae. It could have been derived from the Casamayoran *Patene coluapiensis*, and is apparently involved in the ancestry of *Sipalocyon* and perhaps that of *Cladosictis*, both genera known from the Colhuehuapian and Santacruzian. In the subfamily Borhyaeninae, *Pharsophorus lacerans* is of some interest in that certain cranial characters shown by a referred specimen exhibit some resemblance to structures encountered in the saber-tooth thylacosmilids, although dentally the species is close to *Borhyaena*. *Pharsophorus* (?) *antiquus* may be involved in the ancestry of *Arcotodictis*, although this relationship is very uncertain.

The Caenolestidae, including the subfamilies Caenolestinae, Palaeothentinae, and Abderitinae, make their first appearance in the Deseadan. The Caenolestinae are represented by one species, *Pseudhalmarhiphus guaraniticus*, the Palaeothentinae by four species of *Palaeothentes* (*P. lucina*, *P. chubutensis*, *P. praecursor*, and *P. boliviensis*), and the Abderitinae by *Parabderites minusculus*. This diversity indicates a considerable, but undocumented, adaptive radiation prior to the Deseadan. Some of these Deseadan caenolestids show close structural and presumably phylogenetic affinity with Colhuehuapian and Santacruzian taxa. *Pseudhalmarhiphus guaraniticus* may be involved in the ancestry of *Stilotherium dissimile* (Santacruzian); *Parabderites minusculus* is probably ancestral to *P. bicrispatus* (Colhuehuapian); *Palaeothentes chubutensis* makes at least an ideal structural ancestor for *P. aratae* (Santacruzian); *Palaeothentes lucina* shows strong affinity to *P. lobata* (Colhuehuapian) and *P. lemoinei* (Santacruzian); and *Palaeothentes praecursor* may be ancestral to *P. owenii* (Santacruzian). *P. boliviensis* does not appear to have left any known descendants in later faunas.

The Polydolopoidea declined in diversity after Casamayoran time (conventionally Early Eocene), and make their last appearance in the Deseadan of Bolivia. It is either coincidental or significant that this group's last appearance is concurrent with the first documented appearance of Rodentia in South America. It is generally agreed that polydolopids were somewhat rodent-like in structure and ecology, and may thus have been replaced by rodents in the Early Oligocene.

One of the most striking features of known Deseadan faunas is the apparent absence of Didelphidae. As noted above, Hoffstetter (1968, 1976) tentatively reported didelphids in the Salla fauna of Bolivia, although these reports are unconfirmed and may possibly have been based on fragmentary remains of the small borhyaenid, *Notogale mitis*. This species is abundant in the PU collection from Salla, but was not recorded as such by Hoffstetter. The report of a didelphid from La Flecha by Tournouër (1903) needs confirmation. The apparent absence of Didelphidae is puzzling, considering that members of the Didelphinae and Microbiotheriinae are known from earlier and later faunas. Their absence in Deseadan faunas is not entirely attributable to sampling bias, as very small Caenolestidae and Rodentia are known from beds of this age and at various localities.

For the most part, the Deseadan Marsupialia show closer affinities to taxa from later rather than from earlier faunas. In our opinion, this tends to convey a false impression. For example, Mustersan Marsupialia are known only from three taxa—*Plesiofelis schlosseri* (Borhyaeninae), *Procladosictis anomala* (Hathlyacyninae), and an undescribed polydolopoid. This scarcity prevents adequate comparison between the two faunas.

In contrast, marsupials are relatively abundant in Colhuehuapian and Santacruzian faunas. The diversity of taxa allow adequate comparisons to be made with those in the Deseadan, and in many cases phylogenetic lineages can be recognized. It should also be stressed that according to differences between Deseadan and Colhuehuapian mammals in general, the palaeontological hiatus between these ages was of less duration than the hiatus between the Mustersan and Deseadan (Pascual and Odreman Rivas, 1971, 1973).

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