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SYSTEMATICS OF THE SOUTH AMERICAN MARSUPIAL FAMILY CAENOLESTIDAE

LARRY G. MARSHALL

September 19, 1980

Publication 1310

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LARRY G. MARSHALL

*Assistant Curator of Fossil Mammals
Department of Geology
Field Museum of Natural History*

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ABSTRACT

The family CAENOLESTIDAE is, and according to the known fossil record always has been, endemic to South America. Three subfamilies are recognized. The CAENOLESTINAE includes the most generalized forms and is divisible into two tribes: the Caenolestini (Casamayoran—Early Eocene through Recent) includes *Caenolestes*, *Lestoros*, *Pseudhalmarhiphus*, *Stilotherium*, and *Rhyncholestes*; and the Pichipilini *new tribe* (Colhuehuapian—Late Oligocene through Montehermosan—Early Pliocene) includes *Pliolestes*, *Phonocdromus*, and *Pichipilus*. The ABDERITINAE includes the most specialized of known caenolestids and is also divisible into two tribes: the Parabderitini *new tribe* (Deseadan—Early Oligocene through Santacrucian—Early Miocene) includes *Parabderites*, and the Abderitini *new rank* (Colhuehuapian through Santacrucian) includes *Abderites* and *Pitheculites*. The subfamily PALAEOTHENTINAE (Deseadan through Santacrucian) is structurally intermediate between the other two subfamilies. A detailed systematic revision of the Palaeothentinae is given, and two genera are recognized—*Palaeothentes* with eight species (*P. minutus*, *P. primus*, *P. intermedius*, *P. lucina*, *P. lemoinei*, *P. boliviensis*, *P. chubutensis*, *P. aratae*) and *Acestis* with two species (*A. praecursor* and *A. oweni*). These species are distinguished largely on the basis of absolute size and on relative and absolute size differences between P_3 and M_1 .

Various aspects of ecology, behavior, dental specializations, and feeding habits of living Caenolestinae are discussed. Based on study of morphologically similar groups of living marsupials an attempt is made to establish the feeding habits and dietary preferences of members of the fossil subfamilies Palaeothentinae and Abderitinae.

The phylogenetic relationships of the caenolestid tribes and subfamilies are inferred using a cladistic analysis of shared derived character states, and all groups are shown to be monophyletic. The Caenolestini contains the most generalized forms with the highest number of plesiomorphic states and serves as a basal stock for the

family. The Palaeothentinae and Abderitinae are sister groups, and they and their common ancestors form the sister group of the Caenolestinae.

It is concluded that caenolestids evolved from a didelphoid ancestor in South America. This dichotomy occurred before Casamayoran time, whereas subfamilial differentiation within the Caenolestidae was a pre-Deseadan event. Caenolestids reached their known evolutionary climax in the mid-Tertiary (*i.e.*, Santacrucian time), when they were represented by the three subfamilies, five tribes, seven genera, and 11 species. In beds of that age, caenolestids are the most abundant and the most taxonomically diverse of the small Marsupialia. Although the factors influencing the times of origin, adaptive radiation, decline in diversity, and/or extinction of the various caenolestid groups are complex, it is shown that most of these events can be correlated with the appearance or disappearance of other mammalian groups.

INTRODUCTION

The Caenolestidae have been known to science since the latter part of the last century. Living forms occur along the west coast of South America from the Andes of Colombia and Venezuela in the north to southern Chile in the south. Although three genera and seven nominal species are known, these represent but relics of an impressive yet long subdued Tertiary radiation. In this study, I attempt to synthesize knowledge of the evolutionary history of the family Caenolestidae. I include discussion of living forms but am concerned mostly with their long-neglected fossil allies, the Abderitinae and especially the Palaeothentinae.

SCOPE OF STUDY

This study is concerned primarily with the family Caenolestidae and with the relationships of the included taxa. I have included consideration of previous and present views on the relationships of Caenolestidae with other marsupial groups to demonstrate that the included taxa form a monophyletic unit relative to other marsupial families. I have adopted the suprafamilial classification proposed by Clemens & Marshall (1976) and place the family Caenolestidae in the Superfamily Caenolestoidea, Order Marsupialia. This classification is not adopted in opposition to the views of Ride (1964) and Kirsch (1968, 1977a) that several orders be recognized within the Marsupialia. On the contrary, I concur that the Marsupialia should indeed be divided into several ordinal groups. However, most if not all of the orders recognized by those workers are explicitly paraphyletic. The families of Marsupialia are in need of a rigorous cladistic analysis to clarify their phylogenetic relationships and to establish monophyletic groups. This study is a step in that direction and is limited in scope to stabilizing nomenclature of included taxa and to defining the taxonomic limits of the family Caenolestidae.

This study includes a detailed systematic review of the caenolestid subfamily Palaeotheninae. Information on the other caenolestid subfamilies is abbreviated, although of such a nature as to permit an understanding of their interrelationships and of the relationships of included taxa. A diagnosis for each subfamily is presented along with a list of included taxa and synonymies. Because most of the taxa have never been adequately diagnosed or characterized, I have included some characters in the diagnosis the utility of which are yet to be tested. This approach is the preferred alternative to omitting characters that might have a diagnostic significance. Except for the Palaeotheninae, only original references for generic and specific synonymies within the other subfamilies are given, and no attempt has been made to give a complete listing of literature citations.

During the course of this study, I was able to examine first hand all

pertinent known fossil materials, including type and referred specimens. This work includes discussion and description of some new material but is essentially based on a reappraisal of previously known specimens and literature. All diagnoses of the family, subfamilies, tribes, genera, and species have been revised. This study represents an attempt to bring together in one place a modern, expanded, and synthetic treatment of these animals, the relationships of which are now better understood only in hindsight and through the pioneering efforts of a multitude of earlier workers.

TECHNIQUES OF STUDY

The identity of the teeth and of the dental formula employed in this study is based on the discussion on p. 112. In short, the basic marsupial formula is taken to be $I_1^1 \frac{2}{2} \frac{3}{3} \frac{4}{4} \frac{5}{0}$, C_1^1 , $P_1^1 \frac{2}{2} \frac{3}{3}$, $M_1^1 \frac{2}{2} \frac{3}{3} \frac{4}{4}$; the primitive caenolestid formula is $I_1^1 \frac{2}{2} \frac{3}{3} \frac{4}{4}$, C_1^1 , $P_1^1 \frac{2}{2} \frac{3}{3}$, $M_1^1 \frac{2}{2} \frac{3}{3} \frac{4}{4}$; and for Palaeothentinae it is $I_1^1 \frac{2}{2} \frac{3}{3}$, C_1^1 , $P_1^1 \frac{2}{2} \frac{3}{3}$, $M_1^1 \frac{2}{2} \frac{3}{3} \frac{4}{4}$. This conventional system for serial designation of the antepremolar teeth is intended to be descriptive and does not imply homology. However, homology is assumed for the premolars and molars, at least among the Marsupialia.

I initiated my revision of the Palaeothentinae by ignoring all available generic and specific names. I organized the specimens of Palaeothentinae into groups which I regarded as warranting specific recognition. These species I further organized into groups which I regarded as warranting generic recognition. At that point, I ascertained the type species and genera. Type specimens proved to be included in each group, and for this reason it was not necessary to erect new names.

The Argentine fossil localities mentioned below (fig. 1) are shown on maps and are discussed in greater detail in various papers as summarized by Marshall et al. (In press). The chronology and usage of South American Land Mammal Ages (fig. 2) follows Marshall et al. (In press).

Specimens were measured to the nearest 0.1 mm. when possible, using a pair of dial calipers. All measurements are in millimeters (mm.).

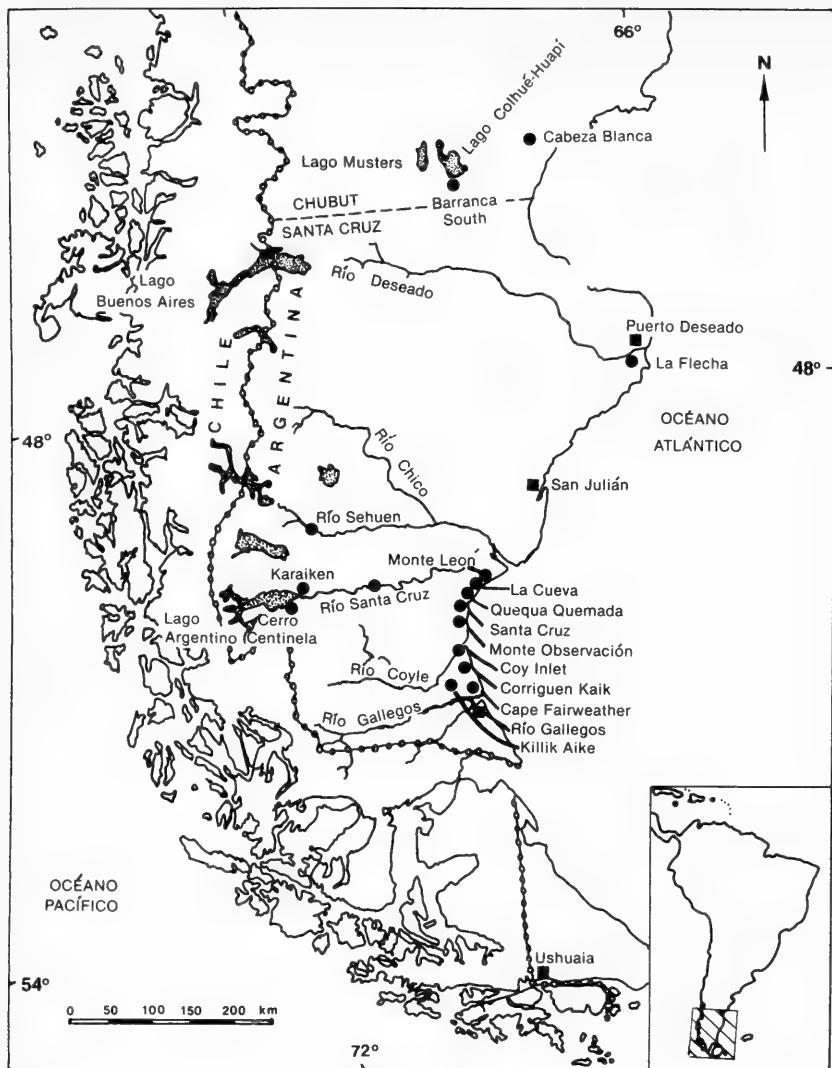
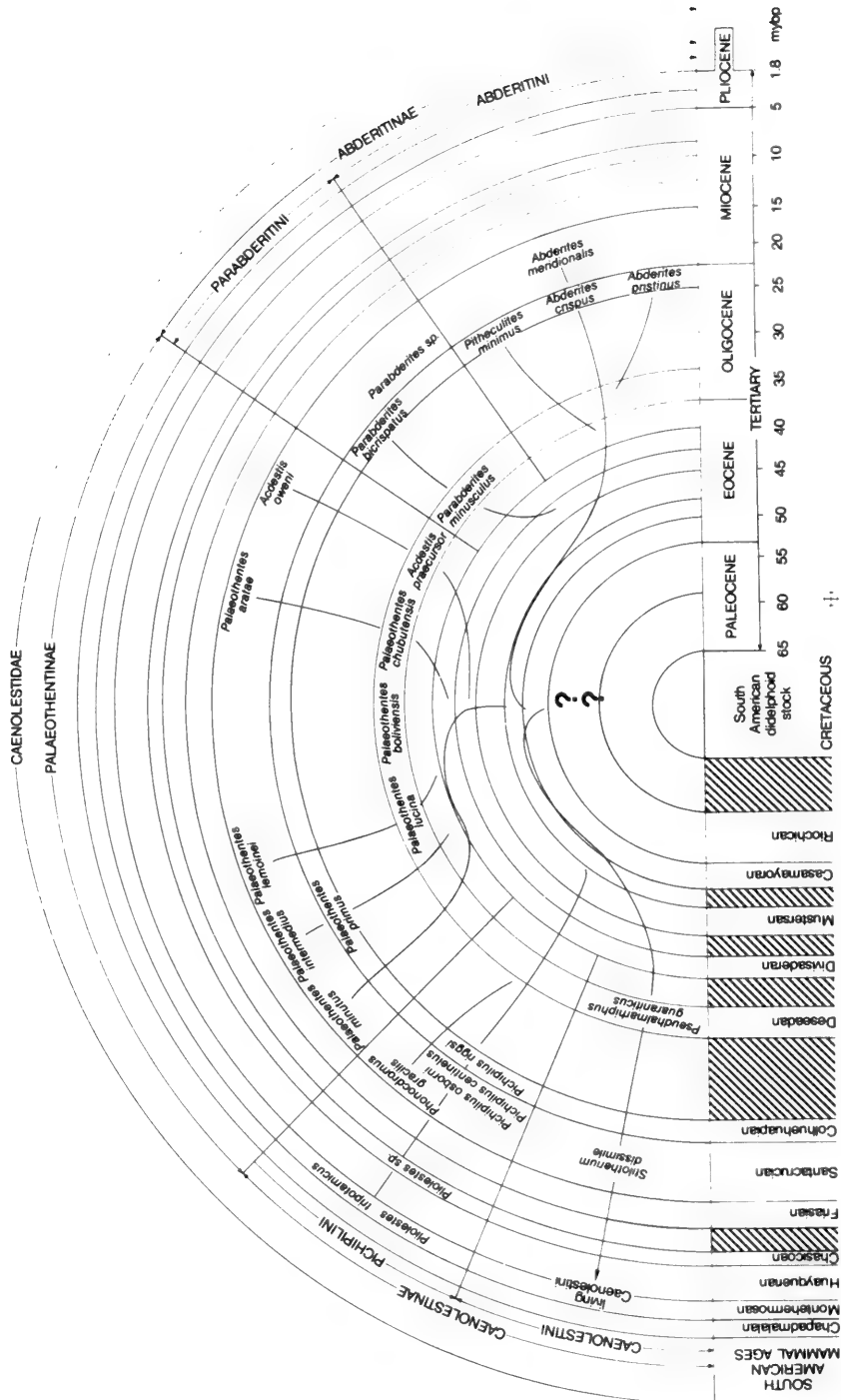


FIG. 1. Map of southern tip of South America showing vertebrate fossil localities (circles) discussed in text.

Opposite:

FIG. 2. Proposed phylogeny of the Caenolestidae. The phylogeny of the Palaeotheniinae is based on this study and that of the Abderitinae and Caenolestinae are based on Marshall (1976a and 1976b, respectively).



ABBREVIATIONS

The following abbreviations are used for specimens from institutional collections:

AC	Amherst College, Amherst, Massachusetts
AMNH	American Museum of Natural History, New York
BM(NH)	British Museum (Natural History), London, England
DGM	Divisão de Geologia e Mineralogia do Departamento Nacional da Produção Mineral, Rio de Janeiro, Brazil
FMNH	Field Museum of Natural History, Chicago
KUVP	University of Kansas, Department of Vertebrate Paleontology
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, Rio de Janeiro, Brazil
NMNH	National Museum of Natural History, Washington, D.C.
PU	Princeton University, Princeton, New Jersey

Abbreviations used in the 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.

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HISTORICAL REVIEW

The first reference to a living caenolestid was made by Tomes (1860) and was based on observation of a single juvenile specimen from Ecuador. The specimen was not then given a generic or specific name but was described as:

A small animal about the size of the Water shrew (*Sorex fodiens*), with external characters and incisor teeth so much like those of the Soricidae as to have led in the first instance to the belief that it was a placental Insectivore, perhaps in some degree resembling the *Solenodon* of Cuba. However, the existence of a small and rudimentary pouch sufficiently attests the implacental nature of the creature, which but for this must certainly, as far as external appearances go be regarded as one of the Soricidae.

Three years later Tomes (1863) named this animal *Hyracodon fuliginosus*, although he made no further reference to its marsupial affinity.

In 1887, Florentino Ameghino described and named a number of fossil taxa, some of which are now regarded as caenolestoids. These had been collected from the Santa Cruz Formation of Patagonia, southern Argentina, by his brother Carlos the previous year. Florentino immediately recognized the marsupial affinities of these taxa and placed them in two families. Within the Plagiaulacidae he included *Abderites meridionalis*, *Acestis Oweni*, *Palaeothentes Aratae*, *Palaeothentes Lemoinei*, *Palaeothentes pachygnathus*, *Palaeothentes intermedius*, *Palaeothentes pressiforatus*, and *Palaeothentes minutus*; and in Microbiotheriidae he included, along with two species of *Microbiotherium*, *Stilotherium dissimile*.

In 1889, F. Ameghino included *Stilotherium* in a superfamily Microbiotheria, family Microbiotheriidae, and in the superfamily Plagiaulacoidea he included (among other groups) a family Abderitidae with *Abderites* and a family Epanorthidae with *Acestis* and *Epanorthus*.

In subsequent years, F. Ameghino named additional fossil taxa and continued to acknowledge their marsupial affinity. In 1894, for example, he recognized several families, all of which he placed in his sub-

order Paucituberculata. These included the Abderitidae with *Abderites* and *Mannodon*; Decastidae with *Decastiis*, *Acestiis*, *Dipilus*, *Metricrodromus*, *Halmadromus*, and *Callomenus*; Epanorthidae with *Epanorthus*, *Metaepanorthus*, *Paraepanorthus*, *Prepanorthus*, *Halmaselus*, *Essoprion*, and *Pichipilus*; and Garzonidae with *Garzonina*, *Phonocrodromus*, *Parhalmarhiphus*, *Halmarhiphus*, *Stilotherium*, and *Cladoclinus*.

In 1895, a second specimen of extant Recent caenolestid, this one from Colombia, was sent to the British Museum. Thomas recognized its affinities with Tomes' *Hyracodon fuliginosus*, but since the new specimen was larger and different in appearance he gave it (1895a) a different specific name, *obscurus*. He placed this species, along with Tomes' *fuliginosus*, in a new genus, *Caenolestes*, because *Hyracodon* was preoccupied by *Hyracodon* Leidy (1856, p. 91), a genus of fossil Perissodactyla. Thomas (1895b) immediately recognized the affinities of *Caenolestes* with members of Ameghino's fossil families Abderitidae, Epanorthidae, Garzonidae, and Decastidae. Thomas (1895b, p. 875) concluded:

. . . after a careful examination of the characters of the different fossil genera, I am prepared to say that *Caenolestes* . . . falls into the Family, so that the name Epanorthidae must be used for its recent as well as fossil members.

He accordingly classified *Caenolestes* in the Order Marsupialia, Suborder Diprotodontia, family Epanorthidae.

F. Ameghino (1897) later noted:

M. Thomas est venu à La Plata, rapportant avec lui un crâne de *Caenolestes* que nous avons soigneusement comparé aux formes fossiles de Patagonie et nous avons pu reconnaître qu'il présente plus de rapports avec les Garzonidae qu'avec les Epanorthidae. Pourtant il est probable que le *Caenolestes* [sic] devra constituer le type d'une famille nouvelle.

Trouessart (1898, p. 1205), following Ameghino's (1897) suggestion, proposed a new family Caenolestidae to include only *Caenolestes*. Ameghino (1903) later included *Zygolestes* along with *Caenolestes* in the Caenolestidae, and he placed this family, along with the Abderitidae, Epanorthidae, and Garzonidae, in his suborder Paucituberculata (table 1).

Weber (1904) and Gregory (1910) recognized *Caenolestes* and its fossil allies as a distinct suborder, Paucituberculata, of Marsupialia. The other marsupials were included in the suborders Diprotodontia or Polyprotodontia. Thus, these workers recognized a tripartite division of Marsupialia.

Caenolestids are unique among marsupials in possessing, in combination, diprotodont modifications of their lower incisors, a polyproto-

TABLE 1. Subdivision of the Caenolestoidea (ss) as conceived by different workers.

Ameghino, 1903	Trouessart, 1905	Winge, 1923	Simpson, 1945	This study
Family Abderitidae	Family Abderitidae	Family Epanorthidae	Family Caenolestidae	Family Caenolestidae
<i>Abderites</i>	<i>Abderites</i>	[Tribe Microbiotheriini]	Subfamily Caenolestinae	Subfamily Caenolestinae
<i>Parabderites</i>	<i>Parabderites</i>	[<i>Microbiotherium</i>]	<i>Progarzonia</i>	Tribe Caenolestini
Family Epanorthidae	<i>Mannodon</i>	Tribe Caenolestini	<i>Pseudhalmarhiphus</i>	<i>Caenolestes</i>
<i>Epanorthus</i>	<i>Decastis</i>	<i>Halmatorhiphus</i> [sic]	<i>Garzonia</i>	<i>Lestoros</i>
<i>Palaeopanorthus</i>	<i>Acdestis</i>	<i>Caenolestes</i>	<i>Halmarhiphus</i>	<i>Pseudhalmarhiphus</i>
<i>Metaepanorthus</i> [sic]	<i>Dipilus</i>	<i>Orolestes</i>	<i>Stilotherium</i>	<i>Stilotherium</i>
<i>Prepanorthus</i>	<i>Metriodromus</i>	"Garzonia"	<i>Zygolestes</i>	<i>Rhyncholestes</i>
<i>Halmaselus</i>	<i>Halmadromus</i>	Tribe Epanorthini	<i>Caenolestes</i>	Tribe Pichipilini new
<i>Essoptron</i>	Family Epanorthidae	<i>Epanorthus</i>	<i>Orolestes</i>	<i>Ptilolestes</i>
<i>Pichipilus</i>	Subfamily Epanorthinae	("Palaeothenes")	<i>Rhyncholestes</i>	<i>Phonocdromus</i>
<i>Decastis</i>	<i>Callomenus</i>	"Decastis"	Subfamily Palaeotheninae	<i>Pichipilus</i>
<i>Acdestis</i> [sic]	<i>Epanorthus</i>	<i>Abderites</i>	<i>Palaeothenes</i>	Subfamily Palaeotheninae
<i>Dipilus</i>	<i>Palaeopanorthus</i>		<i>Pilchenia</i>	<i>Palaeothenes</i>
<i>Metriodromus</i>	<i>Metaepanorthus</i>		<i>Acdestis</i>	<i>Acdestis</i>
<i>Halmadromus</i>	<i>Paraepanorthus</i>		<i>Dipilus</i>	Subfamily Abderitinae
<i>Callomenus</i>	<i>Prepanorthus</i>		<i>Halmadromus</i>	Tribe Parabderitini new
<i>Pilchenia</i>	<i>Halmaselus</i>		Subfamily Abderitinae	<i>Parabderites</i>
Family Coenolestidae	<i>Essoptron</i>		<i>Parabderites</i>	Tribe Abderitini new
<i>Coenolestes</i>	<i>Pichilus</i> [sic]		<i>Micrabderites</i>	<i>Abderites</i>
<i>Zygolestes</i>	Family Garzonidae		<i>Abderites</i>	<i>Pitheculites</i>
Family Garzonidae	<i>Garzonia</i>			
<i>Garzonia</i>	<i>Phonocdromus</i>			
<i>Phonocdromus</i>	<i>Parhalmarhiphus</i>			
<i>Halmarhiphus</i>	<i>Halmarhiphus</i>			
<i>Parhalmarhiphus</i>	<i>Stilotherium</i>			
<i>Pseudhalmarhiphus</i>	<i>Cladoclinus</i>			
<i>Stilotherium</i>	Family Caenolestidae			
<i>Cladoclinus</i>	<i>Caenolestes</i>			
[<i>Telacodon</i>	<i>Zygolestes</i>			
<i>Butodon</i>				
[<i>Cinolestes?</i>]				

dont upper incisor formula, and quadrate molars. In attempting to establish caenolestid affinity, various workers have emphasized the special importance of one of these features over the other. The principal questions include: (1) are caenolestids indeed as distinct from diprotodonts and polyprotodonts as those groups are from each other, or (2) are caenolestids related by structure of their lower incisors to Australasian diprotodonts, or (3) by their upper incisor formula to polyprotodonts?

Bensley (1903) concluded that the similarities between *Caenolestes* and Australasian diprotodonts were the result of parallel or convergent evolution, and that the diprotodont specializations evolved independently in the two groups.

Sinclair (1905, p. 81; 1906, p. 443) and Scott (1913) believed, as did Ameghino and Thomas, that caenolestids were closely related phylogenetically to Australasian diprotodonts. This relationship was used as part of their evidence for existence of a former land connection between South America and Australia. Sinclair was firm in this view, but he did concede (1906, p. 443) that the striking similarities in dental structure displayed by these groups "may be explained by convergence."

Dederer (1909) and Broom (1911) emphasized the polyprotodont affinities of *Caenolestes* and maintained that apart from the diprotodont specializations of the lower incisors, it is a typical polyprotodont in all its cranial characters. Gregory (1910, p. 211) also maintained that the skull of *Caenolestes* shows no striking diprotodont characters, and he regarded it and its allies as a distinct suborder—"an offshoot of primitive polyprotodonts, which has paralleled the diprotodonts of Australia in certain characters of the dentition."

Based on an exhaustive monographic treatment of *Caenolestes*, Osgood (1921) concluded that caenolestids lay phylogenetically between the Australasian Peramelidae and Phalangeridae. The relationships "are best expressed by classifying . . . [*Caenolestes*] in the suborder Diprotodontia, family Palaeothentidae, subfamily Caenolestinae."

The issue of caenolestid affinity was in part clarified by Abbie's (1937) study of the marsupial brain. He demonstrated that Australasian Diprotodontia have a *fasciculus aberrans* in the anterior commissure of the brain, whereas Polyprotodontia lack this structure. Because Caenolestidae lack this structure, they must be assigned to the Polyprotodontia, but might still be regarded as ancestral to the Diprotodontia.

Ride (1962, p. 299) reviewed data bearing on the identity and homol-

ogy of the diprotodont incisors in caenolestids and Australasian phalangeroids. He concluded that the procumbent tooth in phalangeroids is probably the I_3 (by homology with that of didelphoids), whereas in caenolestids it is the I_1 or I_2 . This fact substantiated the view that the dental similarities between Phalangeroidea and Caenolestoidea are the result of convergence. Ride referred to the procumbent specializations in the Phalangeroidea as *diprotodonty* compared with *pseudodiprotodonty* in caenolestoids.

Further clarification of caenolestid affinity has resulted from study of sperm. Biggers & DeLamater (1965) have demonstrated that pairing of spermatozoa in the epididymes occurs in American didelphoids and caenolestids tested, but not in Australasian forms. Sperm pairing is an apomorphous condition among the Mammalia (see p. 116) and suggests that all living American marsupials form a monophyletic group. These workers further demonstrated that the morphology of the sperm in *Caenolestes* is quite different from those of the other marsupials tested.

Pascual & Herrera (1973, 1975) have presented arguments supporting the view that caenolestids are more closely related to microbiothere didelphoids than they are to any other known group. Winge (1923) had earlier promoted this view and included *Microbiotherium* in a tribe Microbiotheriini within the family Epanorthidae (see table 1).

Kirsch (e.g., 1971, in Hayman et al., 1971) compared sera of *Caenolestes obscurus* and *Lestoros inca* with members of all the families of living Marsupialia except the Thylacinidae. He (1977a, p. 92) concluded that the two caenolestids are more similar to each other than they are to any other marsupial group. The tests further indicated that:

. . . caenolestids have no greater similarity to any Australasian marsupial superfamily examined than to the [American] didelphids; in fact, the data suggest that caenolestids are less like any of the other superfamilies of marsupials than those superfamilies are like each other. Thus serology does not seem to support a separation of living marsupials into Australasian and American stocks, but suggests that the caenolestoids diverged from the principal line of marsupial evolution before the separation of didelphoids and Australasian marsupials. Such a conclusion, however, assumes that serological affinity strictly reflects propinquity of descent, and furthermore, because only two closely similar, modern genera of caenolestoids were studied, it leaves little allowance for variation within groups or for aberrant results (Hayman et al., 1971, pp. 194-195).

RELATIONSHIPS OF CAENOLESTIDAE AND POLYDOLOPIDAE

For many years it was conventional practice (*e.g.*, Simpson, 1945) to classify the families Caenolestidae and Polydolopidae in a superfamily Caenolestoidea. This practice was based in part on the belief that the sectorial or plagiaulacoid tooth was the first molar. Paula Couto (1952b) clearly demonstrated, however, that in polydolopids the sectorial tooth is the last premolar and not the first molar as is the case in those caenolestids with plagiaulacoid dentitions.

Thus, evolution of sectorial teeth is a convergent (or parallel) feature in these lineages. Because there was no convincing evidence to suggest that polydolopids were any closer phylogenetically to caenolestids than they are to didelphids, Clemens & Marshall (1976, p. 9) allocated the Polydolopidae to a separate superfamily, the Polydolopoidea. This left the Caenolestoidea an uncluttered and cohesive monophyletic group.

CLASSIFICATION

Six family-group names for caenolestoids have been proposed, and a synopsis of their establishment and usage is given in Table 2.

TABLE 2. Family-group names, type-genus of each nominal taxon, and type-species of each nominal genus (adopted from Marshall and Tedford, 1978, Table on p. 59).

Family-group name	Name of type-genus of nominal family-group taxon	Name of type-species of nominal type-genus, and how fixed
ABDERITIDAE Ameghino, 1889, pp. 268, 269 [as <i>Abderitesidae</i> (<i>sic</i>)]	<i>Abderites</i> Ameghino, 1887, p. 5.	<i>Abderites meridionalis</i> Ameghino, 1887, p. 5, by original designation
EPANORTHIDAE Ameghino, 1889, pp. 268, 270	<i>Epanorthus</i> Ameghino, 1889, p. 271 (replacement name for <i>Palaeothenes</i> Ameghino, 1887, p. 5)	<i>Palaeothenes aratae</i> Ameghino, 1887, p. 5, through <i>Palaeothenes</i> Ameghino, 1887, p. 5
GARZONIDAE Ameghino, 1891b, pp. 304, 307	<i>Garzonia</i> Ameghino, 1891b, p. 307 (subjective junior synonym of <i>Stilotherium</i> Ameghino, 1887, p. 7)	<i>Garzonia typica</i> Ameghino, 1891b, p. 307, under Article 68b
DECASTIDAE Ameghino, 1893b, p. 79	<i>Decastis</i> Ameghino, 1891b, p. 305 (subjective junior synonym of <i>Acestis</i> Ameghino, 1887, p. 5)	<i>Decastis columnaris</i> Ameghino, 1891b, p. 305, by original designation
CAENOLESTIDAE Trouessart, 1898, p. 1205	<i>Caenolestes</i> Thomas, 1895b, p. 875 (replacement name for <i>Hyracodon</i> Tomes, 1863 <i>non</i> Leidy, 1856)	<i>Hyracodon fuliginosus</i> Tomes, 1863, through <i>Hyracodon</i> Tomes, 1863, of which it is the type-species by monotypy
PALAEOTHENTIDAE (Sinclair, 1906, p. 417) Osgood, 1921, pp. 143, 151	<i>Palaeothenes</i> Ameghino, 1887, p. 5	<i>Palaeothenes aratae</i> Ameghino, 1887, p. 5, by subsequent designation by Clemens & Marshall, 1976, p. 72

ABDERITESIDAE was proposed by Ameghino (1889, pp. 268, 269) to include *Abderites* Ameghino, 1887. The spelling *Abderitesidae* was followed by Ameghino (1890, p. 174), although in later works he (*e.g.*, 1903, p. 159; 1906, p. 472) and all other workers used the spelling *Abderitidae*. For Greek nouns ending in *-tes*, the stem for forming family-group names is *-t*, alone (see Stoll et al., 1961, 1964, p. 133, example 16). Following the Code [Art. 11(e)(ii) and Art. 29(a)], *Abderitesidae* was an incorrect original spelling, and the change to *Abderitidae* was a "justified emendation" [see Stoll et al., 1961, 1964, Art. 33(a)(i)] and still dates from Ameghino, 1889. The incorrect spelling *Abderitesidae* has not been used in any zoological literature for more than 70 years. Sinclair (1906, p. 417) first recognized this group as a subfamily (*i.e.*, *Abderitinae*) of *Caenolestidae* Trouessart, 1898, p. 1205, and it has been regarded as such by all subsequent workers. *Abderitidae* has remained unused as a valid family-group name for the last 70 years.

EPANORTHIDAE was erected by Ameghino (1889, p. 272) to include *Epanorthus* and *Acdestis*. However, *Epanorthidae* Ameghino, 1889 is invalid because it is based on *Epanorthus* Ameghino, 1889, p. 271, an invalid replacement (see p. 54). *Epanorthidae* was last used as a valid senior synonym by Scott (1937, p. 717).

GARZONIDAE was proposed by Ameghino (1891b, pp. 304, 307) to include *Garzonia* and *Halmarhiphus*. *Garzonia* is now considered a junior synonym of *Stilotherium* Ameghino, 1887, p. 7 (see Reig, 1955, p. 62). Sinclair (1906, p. 417) included the *Garzonidae* within the *Caenolestinae*, and the name has remained unused as a senior family-group synonym for the last 70 years. The last use of *Garzonidae* as a valid name was by Ameghino (1906, p. 417). Loomis (1914, p. 219) used the names *Garzoninae* and *Caenolestinae* for the same group and thus considered them synonymous. He included both in the family *Caenolestidae*.

DECASTIDAE was proposed by Ameghino (1893b, p. 79) to include *Decastis*, *Acdestis* and *Dipilus*. *Decastis* Ameghino, 1891b is recognized as a junior synonym of *Acdestis* Ameghino, 1887 (see p. 91). Sinclair (1906, p. 417) included the *Decastidae* in the *Palaeothentinae*, and the name has remained unused as a senior synonym for the last 70 years.

CAENOLESTIDAE was proposed by Trouessart (1898, p. 1205) for *Caenolestes* only, and was first used as a subfamily by Sinclair (1906, p. 416).

PALAEOTHENTINAE was proposed by Sinclair (1906, p. 417) to

include *Palaeothenes*, *Callomenus*, and *Decastis*. It was raised to the rank of family by Osgood (1921, pp. 143, 151), but has remained unused as a senior synonym since that time.

Trouessart (1898, pp. 1200, 1202, 1204, 1205; 1905, pp. 839, 840, 843, 844) recognized four families within Thomas' (1895b) group Asyndactylia—the Abderitidae, Epanorthidae, Garzonidae, and Caenolestidae; Ameghino (1903, p. 159) recognized four families within his group Paucituberculata—the Abderitidae, Epanorthidae, Coenolestidae [*sic*], and Garzonidae; and Palmer (1904, pp. 876, 881, 882) recognized three families—the Abderitidae, Epanorthidae (which included Caenolestidae and Decastidae), and Garzonidae. Sinclair (1906, p. 416) recommended grouping “. . . all the Santa Cruz diprotodont marsupials in a single family, which may be called the Caenolestidae (Trouessart, 1898, p. 1205) from its only surviving and best known representative *Caenolestes*.” Within this family, Sinclair recognized three subfamilies—the Caenolestinae (with *Caenolestes*, *Halmarhiphus*, *Garzonia*), the Palaeotheninae (with *Palaeothenes*, *Callomenus*, *Decastis*), and the Abderitinae (with *Abderites*).

Sinclair's classification has been the one most commonly used for the last 70 years. However, no ratification has been given by subsequent workers that any of these supergeneric names are valid under the present code, and some certainly are not. They are, however, the names used almost universally in recent literature and are the most readily understood by any present student of marsupials or mammals in general (Simpson, 1970, p. 57n). Pertinent publications using this classification include Clemens & Marshall (1976, p. 10), Marshall (1976a, p. 83), Pascual & Herrera (1973, p. 44), Piveteau (1961, p. 619), Simpson (1930, p. 9; 1945, p. 44; 1970, p. 58), Zittel (1925, p. 27).

The following deviations from this usage are worthy of note. Thomas' (1895b, p. 875) practice of placing *Caenolestes* in the Epanorthidae was followed by Osborn (1910, p. 517). Osborn also recognized a superfamily Caenolestoidea, but no family Caenolestidae. Osgood (1921, p. 151) placed *Caenolestes* in the subfamily Caenolestinae, family Palaeothenidae. Winge (1923, p. 84) recognized one family, Epanorthidae, and included within it (among other groups) the Caenolestini (with *Halmatorhiphus* [*sic*], *Caenolestes*, *Garzonia*) and Epanorthini (with *Epanorthus*, *Callomenus*, *Decastis*, *Abderites*) (table 1). Scott (1937, pp. 717, 722) recognized one family, Epanorthidae, with three subfamilies—Caenolestinae, Epanorthinae, and Abderitinae.

If the Law of Priority is strictly applied, the names Caenolestidae

and Caenolestinae of the classification most commonly used for the last 70 years would have to be replaced by Abderitidae and Garzoninae. This usage would upset continuity and stability in nomenclature of this diverse and important group of South American mammals.

In view of this, Marshall & Tedford (1978, p. 58) submitted an application to the Commission to safeguard the family-group names Caenolestidae Trouessart, 1898, and Palaeothentidae (Sinclair, 1906) Osgood, 1921, from the threat to their stability represented by the prior names Abderitidae Ameghino, 1889, Epanorthidae Ameghino, 1889, Garzonidae Ameghino, 1891b, and Decastidae Ameghino, 1893b. They asked the Commission:

(1) to use its plenary powers to rule that the family-group names Abderitidae Ameghino, 1889, Garzonidae Ameghino, 1891b, and Decastidae Ameghino, 1893b, not be given nomenclatural precedence over the family-group names Caenolestidae Trouessart, 1898, and Palaeothentinae Sinclair, 1906;

(2) to place the following family-group names on the Official List of Family-Group Names in Zoology with the endorsements that:

- (a) Caenolestidae Trouessart, 1898, be given nomenclatural precedence over Abderitidae Ameghino, 1889, Garzonidae Ameghino, 1891b, and Decastidae Ameghino, 1893b;
- (b) Palaeothentinae Sinclair, 1906, be given nomenclatural precedence over Abderitidae Ameghino, 1889, Garzonidae Ameghino, 1891b, and Decastidae Ameghino, 1893b;
- (c) Abderitinae Ameghino, 1889, not be given nomenclatural precedence over Caenolestidae Trouessart, 1898, or Palaeothentinae Sinclair, 1906;
- (d) Garzonidae Ameghino, 1891b, not be given nomenclatural precedence over Caenolestidae Trouessart, 1898, or Palaeothentinae Sinclair, 1906;
- (e) Decastidae Ameghino, 1893b, not be given nomenclatural precedence over Caenolestidae Trouessart, 1898, or Palaeothentinae Sinclair, 1906;

(3) to place the following generic names on the Official List of Generic Names in Zoology:

- (a) *Caenolestes* Thomas, 1895a (gender, masculine);
- (b) *Palaeothentes* Ameghino, 1887 (gender, masculine);
- (c) *Abderites* Ameghino, 1887 (gender masculine);

- (d) *Garzonia* Ameghino, 1891b (gender, feminine);
 - (e) *Decastis* Ameghino, 1891b (gender, feminine);
- (4) to place the following specific names on the Official List of Specific Names in Zoology:
- (a) *fuliginosus* Tomes, 1863, as published in the binomen *Hyracodon fuliginosus* (name of type-species of *Caenolestes* Thomas, 1895a);
 - (b) *aratae* Ameghino, 1887, as published in the binomen *Palaeothentes aratae* (name of type-species of *Palaeothentes* Ameghino, 1887);
 - (c) *meridionalis* Ameghino 1887, as published in the binomen *Abderites meridionalis* (name of type-species of *Abderites* Ameghino, 1887);
 - (d) *typica* Ameghino, 1891b, as published in the binomen *Garzonia typica* (name of type-species of *Garzonia* Ameghino, 1891b);
 - (e) *columnaris* Ameghino, 1891b, as published in the binomen *Decastis columnaris* (name of type-species of *Decastis* Ameghino, 1891b).

In this study I adopt Sinclair's (1906) classification on the assumption that the Commission will use its plenary powers to endorse the recommendation of nomenclatural usage as requested by Marshall & Tedford (1978). This classification is used because it is the preferred one based on a careful consideration of the phylogenetic relationships of caenolestid genera and of their suprageneric groupings. The only addition to Sinclair's classification is in formal recognition of two tribes each of Caenolestinae and Abderitinae. This is based on my (1976b and 1976a, respectively) documentation of two major groupings within each of these subfamilies.

ECOLOGY

Living caenolestines prefer densely vegetated, cold, and wet forest habitats, ranging from sea level to elevations exceeding 14,000 ft. They prefer moist, often moss-covered slopes and ledges, well protected from cold winds, mist, and rain. In the high cold páramos of Colombia, Ecuador, and Perú they are typically found in the scrub adjacent to meadows (Osgood, 1921, p. 17; Collins, 1973, p. 169; Kirsch & Waller, 1979, p. 390).

BEHAVIOR

Caenolestines are terrestrial and crepuscular or nocturnal in habits. Young ones are agile climbers (Kirsch & Waller, 1979, p. 393), and the tail is used for this purpose. However, in no caenolestine is the tail truly prehensile, either in a ventral or in a dorsal direction. Kirsch & Waller (1979, p. 394) report that:

. . . an animal held dangling by the tip of the tail can swing itself ventrally, grasp the tail with the forepaws, and climb up "hand over hand"

A tripod stance—that is on the hind legs and tail—appears to be as common as a quadrupedal one in resting caenolestids. Often after a period of activity, which could be quite sustained (45 minutes for *C. obscurus* in the case of one session . . .), caenolestids would suddenly cease movement, close their eyes at least part way and drop the tip of the snout to the substrate. After a few minutes in this posture they seemed to revive and resumed activity. Another resting posture consisted of tucking the head between the forelegs while setting on the hindquarters. Once an animal (*C. obscurus*) was observed sitting on its hindlegs with its tail passed between them, much like a kangaroo. However, this posture was certainly not usual, nor were caenolestids ever observed to sleep or rest on their side . . . (Kirsch & Waller, 1979, p. 394).

Using a high-speed motion picture camera, Kirsch & Waller (1979, p. 394, fig. 1) photographed species of *Caenolestes* and *Lestoros*. The locomotion of these animals was observed to be typically symmetrical. At higher speeds they assumed a full bound, using the fore- and hind-legs nearly or exactly together. In all of the gaits observed by Kirsch & Waller the tail was used:

. . . as a balancing device on sloping or uneven surface, when it may be rotated violently to maintain the animal's equilibrium; on level ground it is usually held rigidly and curving slightly downward.

These workers did not observe any caenolestid adopt a saltatorial progression as Gregory (1922) suggested that they might do.

DENTAL SPECIALIZATIONS AND FEEDING HABITS

There is a marked regional differentiation of dentition in caenolestids. This reflects differences in function between the anterior and the posterior teeth. The lower dentition is characterized by an enlarged procumbent medial incisor (the I_1) and a reduced often rudimentary dentition between it and the P_3 or M_1 (fig. 6). This regional differentiation is influenced largely by selection for optimal designs for first acquiring, then breaking down food. The initial stages of feeding involve acquiring (ingesting) a bit of food and cutting it into manageable pieces before mastication. This usually involves the incisors, canines, and/or premolars. Food is then chewed (masticated) before swallowing, and this is accomplished primarily by the molar teeth. The differences in dental morphology can often be related to the physical properties of the foods (Kay & Hylander, 1978, p. 173).

Bensley (1903) suggested that diprotodonty may have originated as an adaptation for grasping and piercing small prey, probably insects. This view was reinforced by Osgood's (1921) report of mainly insect and arachnid remains in the stomachs of three specimens of *Caenolestes obscurus*.

Based on observation and study of living caenolestids killing prey, Kirsch (1977b) demonstrated that the original adaptive value of diprotodonty may be related to piercing and killing rather than grasping. Kirsch (1977b, p. 287) kept live specimens of *Caenolestes obscurus* from Colombia and fed them live newborn rats:

. . . [*C. obscurus*] did not use its incisors simply to grasp the rat, but made stabbing motions with the lower jaw. This rapier-like motion of the procumbent incisors was followed by manually shifting the young rat to the side of the mouth for actual ingestion and mastication by the cheek teeth; the incisors were never used to bite off pieces of the rat. Devouring the prey progressed in the normal marsupial manner, by first biting the head off and then proceeding posteriorly.

Drawings of this sequence traced from a film of a kill are shown by Kirsch (1977b, fig. 14).

These films demonstrate that *Caenolestes* is certainly competent to deal with vertebrate prey and suggest that the primary use of the diprotodont teeth is in killing. *C. obscurus* may well be an important small predator in its native habitat, for in south-

ern Colombia it occurs sympatrically with several species of cricetid rodents. I would suggest . . . [that diprotodonty] . . . is an effective adaptation for killing relatively large and vigorous prey (Kirsch, 1977b, p. 287).

Caenolestids would ordinarily pick up and hold small pieces [of meat] in the forepaws, but would tug on larger lumps with their incisors in order to pull off smaller bits. As this operation usually failed, they would chew off pieces with the cheek teeth; this as well as subsequent mastication was accompanied by a distinct clicking sound. As the labial cusps of caenolestid upper molars are much higher than the lingual, and the upper and lower molars form shearing surfaces in occlusion . . . , the clicking sounds probably are produced during shearing (Kirsch & Waller, 1979, p. 392).

Worms given to *C. convelatus* were held in the forepaws while the animal sat on its hindlegs and tail and fed the worms directly into the side of the mouth, making only occasional perfunctory nips with the incisors (Kirsch & Waller, 1979, p. 392).

Much speculation has been aroused by the peculiar lip flaps of caenolestids (Gregory, 1922; Lönnberg, 1921; Osgood, 1921), the various suggestions being that they hold, convey inwards, or eject food items. Our observations suggest that these structures help prevent the sensory vibrissae and fur at the side of the mouth from becoming clogged with blood and dirt, as might result from the caenolestids' method of feeding, and also prevent dirt from entering the mouth (Kirsch & Waller, 1979, p. 393).

Following a meal of rats, *C. obscurus* would rub its muzzle on the cage floor to remove some of the blood and wash off the rest by licking its forepaws and rubbing them over the snout. Other species of Caenolestidae also used the forepaws, either together or separately, in washing. Additionally, caenolestids use the tongue to wash the body fur and the hind feet to scratch. They frequently sit on the hind legs and tail during grooming and other operations (Kirsch & Waller, 1979, p. 393).

In Abderitinae the lower dentition is further characterized by a hypertrophied trenchant P_3 and/or M_1 (fig. 10). This type of dentition in which one or more of the lower cheek teeth is/are modified into large, simple, laterally compressed blades with serrated cutting edges has been termed *Plagiaulax-typus* or *plagiaulacoider Typus* by Abel (1931, pp. 326–328). This name was given in allusion to its occurrence in members of the multituberculate suborder Plagiaulacoidea. A *plagiaulacoid* type of dentition has evolved independently in a number of mammalian orders—twice in early Tertiary Primates (Carpolestidae and *Saxonella*—see Rose, 1975, p. 51), once in ptilodontoid multituberculates (see Simpson, 1933), and at least three times in marsupials (once each in Australian phalangeroids, in South American polydolopoids, and in caenolestoids—see Paula Couto, 1952b).

These blade-like specializations may involve more than one tooth as in multituberculates, which incorporate P_{2-4} or P_{3-4} , and in the caenolestoid *Parabderites*, which used P_3 - M_1 (figs. 8, 9). More typically, these specializations are restricted to a single lower tooth, such as the P_4 in carpolestids, the P_3 in *Saxonella*, the P_3 in phalangeroid and

polydolopoid marsupials, and the M_1 in Abderitini. Rose (1975, p. 51) has noted that the adaptive significance of the plagiaulacoid dentition may be basically similar in the varied types possessing it, but dissimilar upper dentitions in most of these mammals suggest that the function is variable. Eisenberg (1978) further cautioned that evaluation of dietary inferences should not be based solely on study of a single system such as tooth structure, but should be cross checked against other systems, such as morphology of the gut (*e.g.*, Vorontsov, 1962). Since this is not possible with fossil species, unequivocal interpretations of their feeding behavior may be impossible (Kay & Hylander, 1978, p. 174).

Based on his review of plagiaulacoid groups and of consideration of the feeding habits and food types of living plagiaulacoid forms, Simpson (1933) considered plagiaulacoidy an adaptation for herbivory, being especially efficient for dealing with coarse vegetation. Rose (1975, p. 62) has suggested that the plagiaulacoid tooth (in carpolestids at least) was used primarily during the puncture-crushing stage of mastication. He further suggested that the primary diet of these forms consisted of coarse herbage, fruits, and seeds. Most recently, Kay & Hylander (1978) have presented a competent and detailed analysis of the dentition and feeding adaptations of living phalangeroid marsupials. They conclude (p. 187) that a large plagiaulacoid tooth reflects increased ingestion and mastication of fibrous foods in this region. This includes hard-shelled insects, coarse leaves, stems, seeds, etc.

The best indication of the use and function of the plagiaulacoid dentition of the Abderitini comes from the study by Dimpel & Calaby (1972) of the feeding behavior, habits, and preferred food items of the living Australian "Mountain pigmy possum," *Burramys parvus*. This animal is similar in size to abderitines (especially to *Pitheculites*), and, except for the fact that the plagiaulacoid tooth in *Burramys* is the P_3 and in Abderitini it is the M_1 , the dentitions are almost identical (see Simpson, 1933, fig. 1C, *Abderites*; 1E, *Burramys*).

Dimpel & Calaby (1972, pp. 103–104) noted:

. . . the faeces of our first three specimens [of *Burramys parvus*] taken from the traps before the animals had fed, consisted largely of plant material, with some insect remains. With subsequent animals the faeces have contained mostly invertebrate remains, including worms, beetles, grasshoppers, and spiders. In captivity *Burramys* have been fed a variety of fruits and seeds such as sliced apple and pear, grapes, soaked raisins, walnut chips, raw peanuts, sunflower seeds, honey, and insects, such as meal-worm larvae and moths. All of these are readily eaten.

Feeding trials in the first couple of weeks of captivity indicated that a greater amount of fruit and seeds was eaten than insect material. . . . It is probable that in the wild, *Burramys* feed on whatever palatable fruits, seeds, or invertebrates are available.

Food is picked up with the incisors then transferred to and manipulated with the forepaws while the animal squats on its hind-quarters. The food may be held in one or both forepaws. The soft flesh of fruits is bitten off with the incisors and chewed with the molars. The skins are not eaten and *Burramys* have been observed holding pieces of apple and grape and removing the last fragment of flesh by pulling the skin with their forepaws against the lower incisors. Soft bodied insects such as moths are usually dealt with by the incisors. With insects having a hard cuticle such as meal-worm larvae the animal may begin biting with the incisors but usually the insect is held in the forepaws at the side of the mouth and chopped up with the sectorial premolars. Hard-shelled seeds such as sunflowers are invariably held at the side of the mouth and bitten with the premolars. Usually the seed case is opened with a single bite. Peanuts are mostly nibbled with the incisors but the premolars are used also to break up fragments.

. . . *Burramys* stores food in its nests. Only nuts and seeds are stored in these caches. Invertebrates are eaten when caught and if excess insects are provided they are never taken to the nests and stored. The nuts and seeds are held in front of the premolars, resting on the lower incisors. Animals may carry peanuts or sunflower seeds for as long as 15 minutes, and indulge in other activities such as scratching themselves or exploring their cages, before taking the food to their nests.

The dental specializations of Palaeothentinae are intermediate in virtually all respects between those of the more generalized Caenolestinae and the more specialized Abderitinae. Specializations seen in the Palaeothentinae compared with the Caenolestinae include relative enlargement in size of the protoconid-paraconid crest and of absolute size of M_1 , and the increase in size of the P^3 (figs. 11, 16, 17). Shear occurs between the labial side of the M_1 trigonid and the posterolingual surface of the P^3 . These shear specializations are accentuated in evolution of *Palaeotheres* by incorporation of the P_3 as a sectorial element, whereas in *Acdestis*, the P_3 is reduced in size and lacks a sectorial function.

Among the living Australasian phalangeroid marsupials, analogous dentitions to those of Palaeothentinae are found in *Petaurus*. This animal has an exceptionally small P_3 and is primarily gumivorous. The dentition of *Petaurus* is also similar to that of *Dactylopsila* which eats high proportions of soft plant foods and insect grubs (Kay & Hylander, 1978, p. 186).

Based on this analogy, the primary food items of Palaeothentinae probably included both leaves and soft-bodied insects. The feeding habits of this group thus appear to have been intermediate between the more carnivorous Caenolestinae and the apparently more herbivorous Abderitinae. Species of *Palaeotheres* were probably able to cope with slightly coarser items due to the relatively large, but unserrated P_3 , whereas species of *Acdestis* were confined by their relatively small P_3 to softer and more succulent items.

In Palaeothentinae and Abderitinae, the diprotodont incisors may have played a major role in incisal gnawing during food acquisition as is reported for living phalangeroids (Kay & Hylander, 1978, p. 186).

SYSTEMATICS

Order MARSUPIALIA Illiger, 1811, p. 75

Superfamily CAENOLESTOIDEA (Trouessart, 1898, p. 1205)
Osborn, 1910, p. 517 (=Paucituberculata Ameghino, 1894, p. 332;
Asyndactylia Thomas, 1895b, p. 870)

The diagnoses given by Ameghino (1898) for his order Paucituberculata and its included taxa are:

PAUCITUBERCULATA Ameghino.—Las muelas persistentes son cuadrangulares, con cuatro o cinco tubérculos principales y la séptima muela inferior siempre presente. Son numerosísimos en las formaciones eocenas y cretáceas de Sud América y tiene también algunos representantes en el Larámico de Norte América (*Cimolestes* Marsh, *Telacodon* Marsh y *Batodon* Marsh). Se ha encontrado recientemente un género vivo que habita Nueva Granada y Ecuador: el *Coenolestes* Thomas, con dos especies de talla muy reducida y aliado de los *Garzonidae* del Eoceno. Todos los representantes de este suborden son muy pequeños, comparables por el tamaño a lauchas y ratones. Las especies fósiles argentinas se distribuyen en tres familias: *Abderitidae*, *Epanorthidae* y *Garzonidae*.

ABDERITIDAE. Se distinguen por la cuarta muela inferior muy grande, cortante y rayada verticalmente; muelas anteriores de corona baja y aplastada como en *Stagodon*. Un solo género conocido: *Abderites* Ameghino, con varias especies: *Abderites meridionalis*, *crassiramis*, *altiramis*, *serratus*, *tenuissimus* Ameghino, todas del piso Santacrucense.

EPANORTHIDAE. Con la cuarta muela inferior un poco más grande que la quinta y cortante, pero no rayada verticalmente.* Todas las especies, a excepción de una sola: el *Epanorthus chubutensis*, son del piso Santacrucense. *Decastis* Ameghino, tercera muela inferior rudimentaria y con sola raíz en forma de columna: *Decastis columnaris* y *rurigenus* Ameghino. Parecido al anterior es *Acastis* Ameghino, con la tercera muela inferior igualmente pequeña, pero con dos raíces; tres especies: *Acastis Oweni*, *parvus* y *elatus* Ameghino. El género *Dipilus* Ameghino presenta la tercera muela inferior rudimentaria, la cuarta sumamente grande y cortante y la séptima atrofiada: *Dipilus Spegazzinii* y *Bergi* Ameghino. El género *Metriodromus* Ameghino presenta entre el incisivo hipertrofiado y la cuarta muela, sólo cuatro dientes stagodoniformes, en vez de cinco: *Metriodromus crassus*, *spectans* y *crassidens* Ameghino. *Halmadromus vagus* Ameghino, con sólo tres dientes inferiores stagodoniformes. *Callomenus* Ameghino, parecido al anterior, pero con la cuarta muela inferior birradiculada: *Callomenus intervalatus*, *ligatus* y *robustus* Ameghino. El género *Epanorthus* Ameghino, que sirve de tipo a la familia, tiene la cuarta muela inferior bien desarrollada, con dos raíces separadas y corona

conicocomprimida, sin tubérculos accesorios; los dientes stagodoniformes son en número de cuatro; comprende numerosas especies: *Epanorthus chubutensis* Ameghino, del Cretáceo de Patagonia, que es la sola especie de esta familia que no procede del piso Santacrucense; *Epanorthus Aratae*, *ambiguus*, *Lemoinei*, *pachygnathus*, *pressiforatus*, *simplex*, *lepidus*, *inaequalis* Ameghino. *Metaepanorthus* Ameghino, parecido al anterior, pero con la cuarta muela inferior provista de un tubérculo accesorio anterior y otro posterior: *Metaepanorthus intermedius*, *complicatus*, *Holmbergi* Ameghino. *Paraepanorthus minutus* Ameghino, presenta la cuarta muela inferior con un solo tubérculo accesorio adelante, es de tamaño muy pequeño y debió ser sumamente abundante, pues es el plagiaulacoidio que ha dejado más restos *Prepanorthus lanius* Ameghino, canino y primera a cuarta muelas superiores, inclusive, separadas una de otra y muy comprimidas en forma de hojas cortantes. *Halmaselus valens* Ameghino, con la tercera muela con dos raíces, como la cuarta. *Essopriion* Ameghino, primera muela inferior ausente y la cuarta bien desarrollada y con dos raíces distintas, dos especies: *Essopriion coruscus* y *consumptus* Ameghino. *Pichipilus* Ameghino, corona de las muelas inferiores con un pliegue profundo al lado interno que les da una forma semilunar o en arco de círculo, dos especies: *Pichipilus Osborni* y *exilis* Ameghino, ambas sumamente pequeñas.

*En la formación Patagónica del río Deseado y del lago Musters se han encontrado restos de las especies indeterminadas de los géneros *Abderites* y *Epanorthus*.—(Del «Suplemento: Adiciones y Correcciones»), página 7.)

GARZONIDAE. Segunda y tercera muela inferiores siempre birradiculadas; la cuarta inferior apenas un poco mayor que la quinta; cuarta a sexta inferiores bilobadas sobre el lado externo, con dos tubérculos externos y tres o cuatro sobre el lado interno; estas muelas presentan un gran parecido con las de los *Didelphys*. Todos los representantes conocidos de este grupo son excesivamente pequeños y hasta ahora exclusivos del piso Santacrucense. *Garzonia* Ameghino, segunda y tercera muelas inferiores birradiculadas, cuarta a sexta con dos tubérculos externos y tres internos y además un tubérculo rudimentario sobre el lado posterior, última inferior cónica y de una sola raíz, tres especies: *Garzonia typica*, *captiva* y *minima* Ameghino. El género *Phonocdromus* se distingue por las muelas inferiores cuarta a sexta con dos tubérculos externos y cuatro internos, ambas filas son separadas por un surco longitudinal, dos especies: *Phonocdromus patagonicus* y *gracilis* Ameghino, *Parhalmarhiphus annectens* Ameghino, muelas inferiores cuarta a sexta cuadrangulares, con cuatro tubérculos principales dispuestos por pares, dos adelante y dos atrás; última inferior cónicocolumnar. *Halmarhiphus* Ameghino, cuarta a sexta muelas inferiores con dos cúspides externas y tres internas, la anterior externa mucho más elevada que las otras, última muela inferior con dos raíces bien separadas, dos especies: *Halmarhiphus nanus* y *didelphoides* Ameghino.*

*Agréguese en el género *Halmarhiphus*: *Halmarhiphus guaraniticus*, n. sp., muelas inferiores con el tubérculo anterior externo de igual altura que el posterior externo y con un fuerte cigulo basal. Longitud del espacio ocupado por las cuarta y quinta muelas: 3.5 milímetros. Formación Guaranítica.—(Del «Suplemento: Adiciones y Correcciones»), página 7.)

El género *Stilotherium* Ameghino tiene once dientes en cada lado de la mandíbula inferior, el gran incisivo hipertrofiado, cuatro dientes unirradiculados stagodoniformes sumamente pequeños, dos dientes birradiculados de corona simple y cuatro muelas de corona complicada, cada muela con cuatro tubérculos dispuestos por pares, uno anterior y otro posterior, y un tubérculo impar anterior sobre el lado interno, unido al anterior externo por una cresta en arco de círculo, dos especies:

Stilotherium dissimile Ameghino, de tamaño diminuto y *Stilotherium grande* Ameghino, de tamaño cuatro veces mayor. *Cladoclinus Copei* Ameghino, caracterizado por la rama ascendente inclinada hacia atrás, formando una prolongación casi horizontal del borde alveolar.*

*A continuación del género *Cladoclinus* cóloquese el *Zygolestes paranensis* mencionado en la página 243; además *Zygolestes entrerrianus* n. sp., de talla doble que la del precedente. Longitud de la cuarta muela inferior: 3.5 milímetros. Formación Entrerriana.—(Ibidem: página 7). (Ver. página 714 de este tomo).

The family Caenolestidae and the subfamilies Caenolestinae, Palaeothentinae, and Abderitinae were diagnosed by Sinclair (1906, pp. 416–417) as follows:

Family: CAENOLESTIDAE.—Pes, so far as known (*Caenolestes*), non-syndactylous. Sectorials, when present, restricted to the posterior premolar above and the first molar below. Superior premolars three in number (*Palaeothenes*, *Caenolestes*), the anterior and median small, the posterior large and trenchant. Functional lower premolars 2-none. Vestigial teeth always present in the lower jaw. Molars rooted, brachyodont, tuberculo-sectorial or bunolophodont, undergoing progressive complication in the superior series by the addition of a hypocone. Hypertrophied lower incisors lanceolate with cutting edges enamel layer confined to the outer face.

First Subfamily: CAENOLESTINAE.—Dental formula $\frac{4,1,3}{1,4,3,2}$, 4 (*Caenolestes*). Sectorials not developed. First and second superior molars fully quadritubercular, third and fourth tritubercular (*Caenolestes*). Lower molars tuberculo-sectorial, approaching lophodont when worn. Median and posterior lower premolars double-rooted and functional. Genera: *Caenolestes*, *Halmarhipus*, *Garzonia*.

Second Subfamily: PALAEOTHENTINAE.—Dental formula $\frac{?;1,3}{1,4,3,1}$, 4. Posterior superior premolar and first lower molar sectorial in function. Sectorials unstriated. First upper molar fully quadritubercular, second with rudimentary hypocone, third and fourth tritubercular (*Palaeothenes*). Lower molars lophodont. M_1 with prominent metaconid. Posterior lower premolar double-rooted and functional or single-rooted and reduced. Genera: *Palaeothenes*, *Callomenus*, *Decastis*.

Third Subfamily: ABDERITINAE.—Dental formula $\frac{?;?;?}{?;?;?}$. First lower molar with protoconoid-paraconoid blade developed into a striated sectorial shear with serrate margin, greatly elevated above the general level of the tooth row. Metaconid absent on M_1 . Second, third and fourth lower molars bunolophodont. Functional lower premolars wanting in known Santa Cruz forms, the posterior tooth being single-rooted and vestigial. Genus: *Abderites*.

Revised diagnoses for the family Caenolestidae and the subfamilies and tribes follow.

- Family CAENOLESTIDAE Trouessart, 1898, p. 1205
 (Including Epanorthidae Ameghino, 1889, pp. 268, 270;
 Abderitesidae [sic] Ameghino, 1889, pp. 268, 269;
 Garzonidae Ameghino, 1891b, pp. 304, 307;
 Decastidae Ameghino, 1893b, p. 79;
 Palaeothenidae Osgood, 1921, pp. 143, 151)

Diagnosis.—Small size; I_{2-4}^{3-4} , C_1 , P_{2-3}^3 , M_4^4 ; mandibular rami unfused along symphysis; angular process of dentary is prominent and is strongly inflected; one large laterally compressed procumbent gliriform incisor in each lower jaw with enamel along only outer surface, followed by six to seven tiny, spaced vestigial teeth; M_{1-4}^{1-4} , with sharp reduction in size from M_1^1 to M_4^4 , M_4^4 reduced but not vestigial; hypocone present on M^{1-3} (large on M^1 , very small on M^3); M_1 modified into sectorial "plagiulacoid" blade in some groups; "intermediate conule" at inner base of metacone present in early and generalized forms; pes didactylous; palatal vacuities present; lack deciduous tooth (dP3); lack fasciculus aberrans in forebrain (simplicicommissural); lack superficial thymus; four or five mammae; adult females lack a pouch or marsupium; ossified epipubic bones present; sperm paired; sperm rectangular in shape; diploid chromosome number $2n = 14$.

Known range.—Caenolestids are and according to the known fossil record always have been endemic to South America.* Fossils are known from beds of Casamayoran, Deseadan, Colhuehuapian, Santa-crucian, Chasicuan, and Montehermosan age of Argentina, and from Deseadan age beds of Bolivia. Living forms range along the Andes Cordillera from southern Venezuela, through the uplands of Colombia, Ecuador and Peru, south to Llanquihue Province and Chiloé Island in southern Chile.

Comments.—The broader relationships of caenolestids with Australasian groups are discussed by Osgood (1921), Ride (1962), and Kirsch (1977a), and their relationships with other South American groups are discussed by Paula Couto (1952b) and Simpson (1928, 1930, 1933, 1970, 1971).

The documented occurrence of Caenolestidae in beds of Casamayoran age is based solely on an isolated lower molar (AMNH 28442), identified as an M_1 by Simpson (1948, p. 50). Simpson noted that this tooth has no shear specializations; the paraconid is reduced and is internal in position; the talonid is high and nearly bicuspid, with the entoconid about equal to the metaconid; and the hypoconulid is small and "sparlike."

This specimen was apparently broken subsequent to Simpson's study, and only the talonid remains (fig. 3). The entoconid is slightly larger than the hypoconid, and the hypoconulid is very reduced. This

*The African Miocene species *Palaeothenoides africanus* Stromer, 1932, was believed by its describer to be a caenolestoid and hence to have South American affinities. Butler & Hopwood (1957) and Patterson (1965) have shown, however, that this species is a member of the exclusively African placental family Macroscelididae.

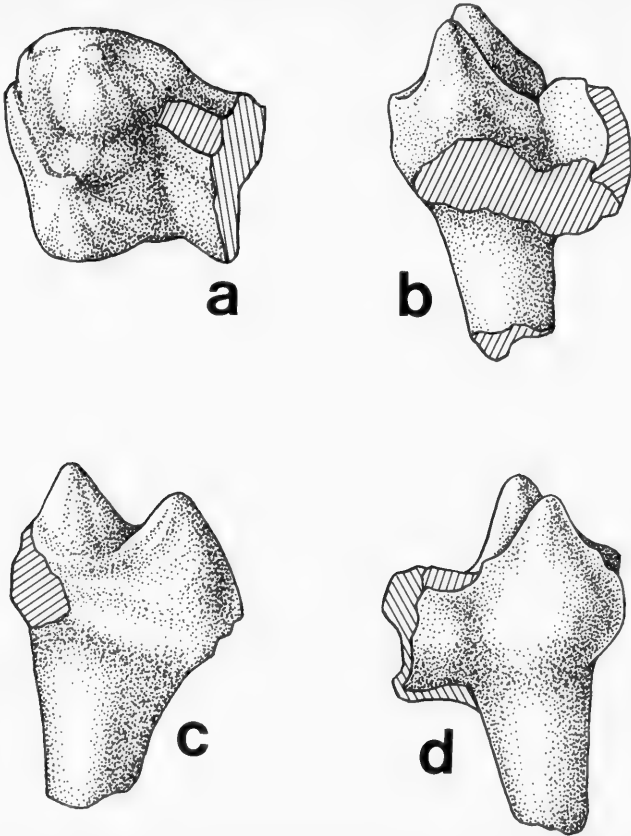


FIG. 3. *Caenolestid indet.* (Casamayoran). AMNH 28442, a nearly complete talonid of a right $M_1?$: a, occlusal; b, labial; c, posterior; d, lingual views. Scale = 25X.

specimen does indeed appear to represent a caenolestid and is probably a member of the subfamily Caenolestinae. Apart from this, little can be said of its phylogenetic significance.

Several South American fossil taxa once classified as caenolestids or believed to have had close caenolestid affinity have been shown to either be *nomina vana* or to belong elsewhere.

Progarzonia notostylopense Ameghino, 1904b, p. 260, was based on a fragment of a left mandibular ramus (MACN A55-14) with a single, two-rooted P_3 , 2.5 mm. in length, collected from beds of Casamayoran age from the Barranca south of Lago Colhué-Huapí (Simpson, 1948, p. 50; 1967a, 1967b, p. 9). Simpson (1967b, p. 9) concluded that:

. . . the animal may be a caenolestid, but in my opinion it is not adequately identifiable at any taxonomic level below the class.

?*Promysops primarius* Ameghino, 1902b, p. 36 (listed as *Promysops primarius* by Ameghino, 1903, p. 89, fig. 6; 1906, p. 363, fig. 209) was based on an isolated incisor (MACN A55-10) from the Musters Formation of Patagonia (no other data) (Simpson, 1948, p. 50; 1967b, p. 9). Simpson (1948, p. 50) noted that this incisor is:

. . . somewhat gliriform, with the crown enameled and the enamel not extending into the alveolus. It is perhaps from a caenolestid or a polydolopid, but even this is not certain.

He (1967b, p. 9) later concluded that:

. . . this specimen does not belong to *Promysops*, which is a [junior] synonym of [the polydolopoid genus] *Eudolops*. The specimen is not identifiable, and the specific name is a *nomen vanum*.

Zygolestes Ameghino, 1898, p. 243, was erected on the basis of specimens collected from the Entre Ríos Formation ("Mesopotamiense"), along the río Paraná, Entre Ríos Province, Argentina. These beds are now believed to be Late Tertiary (*i.e.*, Huayquerian and Montehermosan) in age (see Marshall et al., In press). Two species were recognized, and both were once placed in the Caenolestidae (see table 1). Reig (1957) restudied these specimens and demonstrated that they were both referable to the family Didelphidae. The type species, *Zygolestes paranensis* Ameghino, 1898, p. 243, was based on a left mandibular ramus with P_2 - M_4 (MACN 8889). The unique feature of this specimen (see Reig, 1957, p. 213, fig. 1) not found in other known Didelphidae is the small relative size of the P_3 compared with the much larger P_2 and M_1 . A referred species, *Zygolestes entrerrianus* Ameghino, 1899a, p. 7, was based on an isolated right M_1 (MACN 8888). Reig has shown this species to be referable to the living didelphid genus *Philander*.

Subfamily CAENOLESTINAE (Trouessart, 1898, p. 1205)

Sinclair, 1906, p. 416 (=Caenolestidae Trouessart, 1898, p. 1205, *sensu stricto*; Caenolestini Winge, 1923, p. 84)
(Including Garzonidae Ameghino, 1891b, p. 304)

Diagnosis.— I_{3-4}^4 , C_1 , P_3^3 , M_4^4 ; P_2 double rooted and functional; P_3 large, double rooted and equal to or greater than height of M_1 trigonid; M_{1-4}^1 tuberculo-sectorial, no lophs in unworn teeth; M_1 with prominent metaconid, trigonid, and talonid regions unmodified; M_{2-3} with distinct trigonids and talonids, talonid much larger in occlusal view than trigonid; "intermediate conule" present at inner base of metacone on M^{1-3} ; M^1 quadritubercular; neither P^3 , M^1 , P_2 , nor M_1 are developed

into sectorials; antorbital vacuity present between nasal, maxillary, and frontal.

Known range.—Casamayoran, Deseadan, Colhuehuapian, Santacrucian, Chasicosan, and Montehermosan of Argentina; Recent in Chile, Colombia, Ecuador, Perú, and Venezuela.

Comments.—Living Caenolestinae are reviewed by Osgood (1924) and discussed by Collins (1973), and fossil Caenolestinae are discussed by Reig (1955), Marshall (1976b), Pascual & Herrera (1973, 1975), and Marshall & Pascual (1977).

Tribe CAENOLESTINI (Trouessart, 1898, p. 1205)
Winge, 1923, p. 84

Diagnosis.—Differs from Pichipilini in trigonids of M_{2-3} having two large, distinct lingual cusps (paraconid and metaconid, respectively) separated by deep valley; trigonid basin distinct; talonid basin narrow and deep; absence of cuspule posterior to lingual trigonid cusp on M_{1-3} ; trigonid cusps notably higher than talonid cusps.

Known range.—Casamayoran, Deseadan, and Santacrucian of Argentina; Recent in Chile, Colombia, Ecuador, Perú, and Venezuela.

Includes.—

1. *Caenolestes* Thomas, 1895a, p. 367 [= *Hyracodon* Tomes, 1863, p. 50, *nec Hyracodon* Leidy, 1856, p. 91 (a genus of Perissodactyla)].
 - 1a. *Caenolestes caniventer* Anthony, 1921, p. 6. Recent—known only from El Chiral, Cordillera Occidental, El Oro, Ecuador.
 - 1b. *Caenolestes convelatus* Anthony, 1924, p. 1. Recent—known only from Aloag and Las Máquinas, Cordillera Occidental, Ecuador.
 - 1c. *Caenolestes fuliginosus* (Tomes, 1863, p. 51). Recent—known only from Andes of Ecuador.
 - 1d. *Caenolestes obscurus* Thomas, 1895a, p. 367. Recent—known only from Bogotá northward along the Cordillera Oriental to the Páramo de Tama on Venezuelan-Colombian border.
 - 1e. *Caenolestes tatei* Anthony, 1923, p. 1. Recent—known only from Molleturo, Azuay, Cordillera Occidental, Ecuador.
2. *Lestoros* Oehser, 1934, p. 240 [= *Orolestes* Thomas, 1917, p. 3, *nec Orolestes* MacLachlan, 1895, p. 21 (a genus of dragonfly); *Cryptolestes* Tate, 1934, p. 154, *nec Cryptolestes* Ganglebauer, 1899, p. 608 (a subgenus of Coleoptera)].
 - 2a. *Lestoros inca* (Thomas, 1917, p. 3). Recent—known only from southern Perú.

3. *Pseudhalmarhiphus* Ameghino, 1899a, p. 7.
 - 3a. *Pseudhalmarhiphus guaraniticus* (Ameghino, 1899a, p. 7). De-seadan.
4. *Stilotherium* Ameghino, 1887, p. 7 [Including *Garzonina* Ameghino, 1891b, p. 307; *Halmarhiphus* Ameghino, 1891b, p. 308 (*partim*); *Parhalmarhiphus* Ameghino, 1894, p. 356].
 - 4a. *Stilotherium dissimile* Ameghino, 1887, p. 7 [Including *Garzonina typica* Ameghino, 1891b, p. 307; *Garzonina annectens* (*partim*) Ameghino, 1891b, p. 307; *Pichipilus exilis* Ameghino, 1891b, p. 307; *Garzonina captiva* Ameghino, 1891b, p. 308; *Garzonina minima* Ameghino, 1891b, p. 308; *Halmarhiphus dideloides* (*sic*) (*partim*) Ameghino, 1891b, p. 308; *Halmarhiphus nanus* (*partim*) Ameghino, 1891b, p. 308; *Phonocdromus patagonicus* (*partim*) Ameghino, 1894, p. 355.] Santacrucian.
5. *Rhyncholestes* Osgood, 1924, p. 169.
 - 5a. *Rhyncholestes raphanurus* Osgood, 1924, p. 170. Recent—known only from forests of Llanquihue Province and Chiloe Island, southern Chile.

Remarks.—Included within the Caenolestini are the most generalized of known Caenolestidae. They represent the prototype group from which evolved the Pichipilini and the subfamilies Palaeothentinae and Abderitinae. The Caenolestini have the longest known record of any caenolestid group, extending from Casamayoran to Recent.

Pseudhalmarhiphus guaraniticus was erected by Ameghino (1899a, p. 7) on the basis of a fragment of a right mandibular ramus with M_{1-2} . The present whereabouts of this, the type specimen, is not known, although Ameghino (1899b, p. 560, fig. 5; 1902d, p. 424, fig. 5; 1903, p. 83, fig. 2) did figure the M_2 in three views. As figured by Ameghino, the M_2 trigonid 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; the trigonid and talonid basins are deep and narrow, and the tooth is very narrow for its length; and a well-developed anterobasal cingulum is present. Ameghino (1899a, p. 7) gave the length of M_{1-2} (his M_{4-5}) as 3.5 mm. In all of these features, *Pseudhalmarhiphus* is structurally similar to and is probably directly ancestral to *Stilotherium dissimile* (Marshall, 1976b, p. 58).

Stilotherium dissimile (figs. 4, 5) is the most abundant caenolestine in the Santacrucian fauna of Argentina. Reig (1955, p. 62) noted that he was unable to locate the type; therefore, he selected MACN 8464 (fig. 6) as neotype. However, Ameghino recorded in his catalogue that

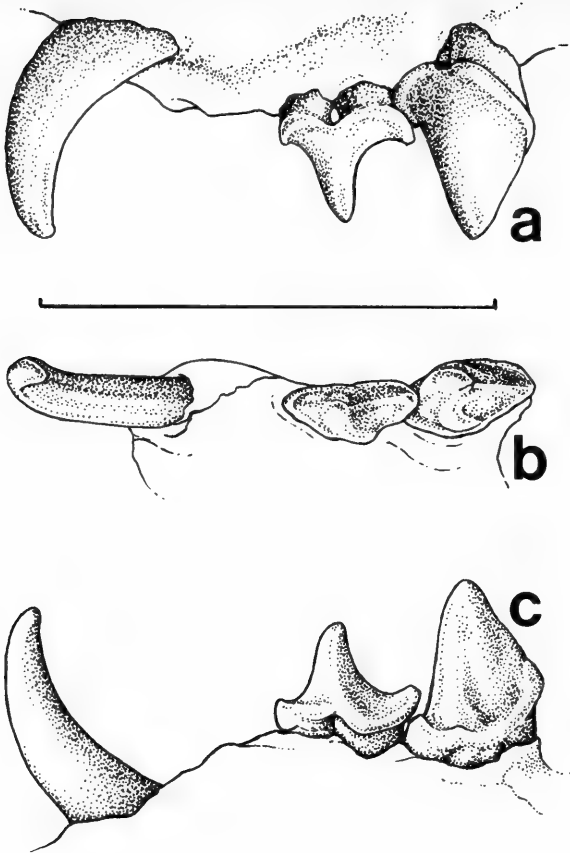


FIG. 4. *Stilotheerium dissimile* Ameghino, 1887, p. 7 (Santacrucian). MACN 8427, a fragment of a rostrum with left C, P², and P³ (same individual as in fig. 5): a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

MACN 5723, a fragment of a right mandibular ramus with crowns of P₂₋₃ and bases of M₁₋₂, is the "Tipo," and this specimen agrees perfectly with the original description. MACN 5723 is recorded as being collected by Carlos Ameghino in 1890-91, whereas the species *S. dissimile* was named four years earlier in 1887.* Whether this specimen is

*There are many uncertainties regarding Carlos Ameghino's 1887 collection. It is very likely that all of it did not end up in the MLP, but that Florentino diverted a substantial portion to the MACN. There may have been several shipments from Carlos, of which the first one or two went to the MLP and served as the basis for Florentino's *Enumeración sistemática . . .* of 1887, whereas the last one or two provided the basis for his monograph

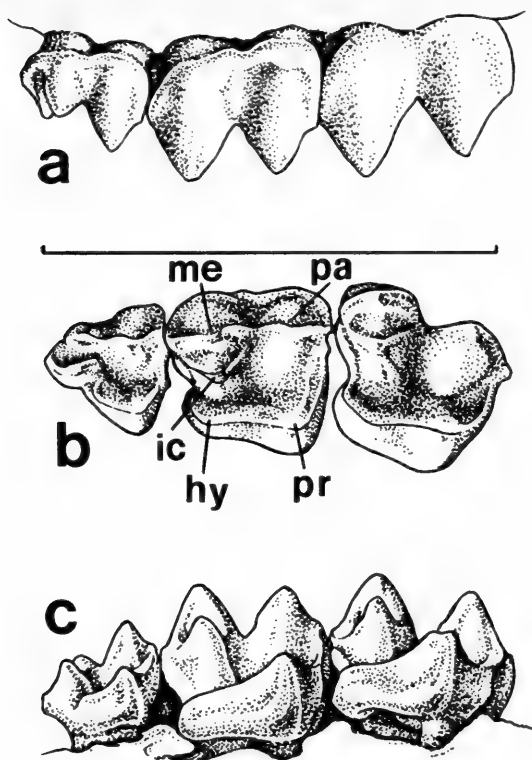


FIG. 5. *Stilotherium dissimile* Ameghino, 1887, p. 7 (Santacrucian). MACN 8426, a fragment of a right maxillary with M^{2-3} , and MACN 8231, an isolated right M^1 (same individual as in fig. 4): a, labial; b, occlusal; c, lingual views. Scale = 5 mm. Abbreviations are: pr, protocone; pa, paracone; me, metacone; ic, intermediate conule; hy, hypocone.

of 1889 and went into the Ameghino Collection in the MACN, in which Bryan Patterson (*pers. comm.*) and myself have seen some of the specimens there figured.

The evidence for this, as pointed out by Bryan Patterson (*written communication*, Oct., 1975), is as follows. F. Ameghino resigned from the MLP on Jan. 17, 1888 (see Ameghino, 1889, p. xiv), the culmination of a progressive deterioration of relations with the director Alceides Moreno, who thereupon barred Ameghino from the collections of that institution. In February, 1888, Florentino began work on the "*Contribución . . .*" and finished 14 months later (see Ameghino, 1889, p. vii), around April, 1889, as the publication date was May 20 (1889, p. iv). His principal artist, Z. Bommert, worked for eight straight months on that paper (see Atlas, pp. v-vi). In the course of this immense labor, Bommert illustrated 74 of 120-odd species described in Ameghino (1887) and all of the 11 additional species described in Ameghino (1889). Where did the material for all of this come from? Certainly not from the MLP, because Moreno would never have allowed

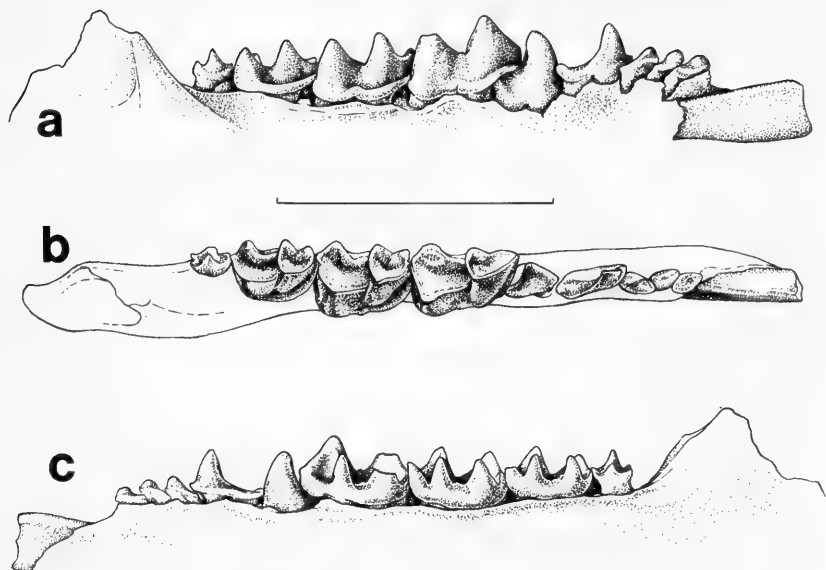


FIG. 6. *Stilotherium dissimile* Ameghino, 1887, p. 7 (Santacrucian). MACN 8464 (neotype), a right mandibular ramus with complete dentition, missing only tip of I_1 : a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

access, and Ameghino specifically stated (1889, pp. xiii–xiv) that Moreno was indeed responsible for the fact that a number of species were not figured. Not, it would seem from Carlos' expedition of 1888–89, unless an unreported detour to the Río Santa Cruz was made, which seems unlikely as there would have been no reason to keep it quiet, both brothers being by then no longer in the employ of the MLP.

In dealing with F. Ameghino, it is sometimes necessary to employ what may be termed textual criticism, which in this instance compels one to the belief that all of the 1887 collection did not end up in the MLP. This was not simple robbery, at least in Florentino's eyes. He had taken Moreno's measure and found him wanting, both as a man and as a paleontologist. Ameghino may have decided that Science would be better served with part of the collection in his possession—and, if he did, events have largely proved him correct. Also, as one who had crucially aided the expedition of 1887 in various ways (see 1889, p. xiv), Ameghino may well have thought he had a moral right to take such action. In any event, the type of *Stilotherium dissimile* may well have been included among those specimens "diverted" to the MACN.

Rosendo Pascual has also noted that after the MLP collections were closed to Florentino, Carlos went back to Patagonia and recollected the same localities that he worked in 1886–87. Some of these new specimens came to be labeled as types, in the MACN, of species that he described in 1887.

This was Florentino's way of being able to refer to types, despite the fact that the real types were in the MLP. Many of these supplemental MACN types were collected by Carlos during his field season of 1890–91. Such may be the case of MACN 5723.

in fact the type, and the dating in the catalogue is in error, or whether this specimen is itself a neotype selected by Ameghino in 1891 is not known. Reig's neotype is certainly more complete than the type of Ameghino (*sensu* his catalogue), and in this respect it is a much more useful specimen. Because there is some doubt as to the validity of MACN 5723 being the true "Tipo," I follow Reig and recognize MACN 8464 as the valid neotype (also see Marshall, 1976b, pp. 62-63 for discussion on this point).

Most of the synonymies recognized here for *Stilotherium dissimile* were originally suggested by Reig (1955). My only modification from his scheme is in recognizing *Garzonia typica* Ameghino, 1891b, p. 307 (type species of the genus) as a junior synonym of *S. dissimile*. Reig (1955, p. 64) recognized "*G.*" *typica* as a valid species of *Stilotherium* and noted that *S. dissimile* and *S. typicum* were virtually identical in size and structure and surely differed only in the greater depth of the mandibular ramus in the latter. On the primary basis of this one character he recommended tentatively regarding these taxa as distinct, and I (1976b, p. 62) later followed this suggestion. Upon restudy of all pertinent material, I now see no justification for recognizing these taxa as distinct and here formally recognize them as synonymous. In addition, I formally recognize *Pichipilus exilis* Ameghino, 1891b, p. 307, as a junior synonym of *S. dissimile*. *P. exilis* was based on a fragment of a left mandibular ramus (MACN 5698) with alveoli of M_2 and M_4 , and M_3 present but very worn.

A second species of *Stilotherium*, *S. grande*, was erected by Ameghino (1894, p. 358) on the basis of what he believed to be a right lower molar. Reig (1955, p. 64) was unable to locate the type, but concluded that based on Ameghino's description the species was not related to *Stilotherium* nor was it a caenolestid. While in the MACN in 1976, I was fortunate to relocate the type (MACN 8468) in the Ameghino collection. I gave a cast of this to P. Hershkovitz for study, and he has demonstrated (*unpubl.*) that it represents the dP_4 of the primate genus *Homunculus* and proposes to recognize it as a valid species of that genus.

The validity of the three genera—*Garzonia*, *Halmarhiphus*, *Parhalmarhiphus*—included in synonymy with *Stilotherium* was also discussed by Reig (1955), the conclusions of which are substantiated by my own studies. Reig (1955, p. 63) noted that *Halmarhiphus didelphoides* was based on four partial mandibular rami (MACN 5716, 5717, 5718, 5719) of which the first (considered the type in the MACN catalogue) and the latter two are microbiotheres, whereas MACN 5717

is inseparable from *S. dissimile*. *Halmarhiphus nanus* (the genotype) was based on three partial mandibular rami of which one (MACN 5720—considered the type in the MACN catalogue) is inseparable from *S. dissimile*, another (MACN 5721) is probably a microbiothere, and the third is an edentulous mandibular ramus that on the basis of its size may be referred to *Phonocdromus gracilis*.

The type species of *Parhalmarhiphus* Ameghino, 1894, p. 357, is "*Garzonia*" *annectens* Ameghino, 1891b, p. 307. The type of that species (MACN 5703) is a left mandibular ramus with M_{1-3} that is inseparable from specimens of *S. dissimile*. However, the generic diagnosis of *Parhalmarhiphus* appears to have been based largely on two other specimens—MACN 5704 and 5705—of which the first is an indeterminate caenolestid, and the second is a microbiothere. Consequently, the genus *Parhalmarhiphus* has no validity (Reig, 1955, p. 63).

The living Caenolestini are grouped into three genera—*Caenolestes*, *Lestoros*, *Rhyncholestes*—with five named species in the first and one each in the others (Osgood, 1924). It is generally agreed among Recent marsupial workers that the genus *Caenolestes* is overly split, and three of the nominal species are known only from or near their type locality. In addition, the genera *Caenolestes* and *Lestoros* are questionably separable. Simpson (1970, p. 41n) has suggested that placing of the "genera" as three species would be a better arrangement. Many additional species of Caenolestinae have been collected since the time of Osgood's study, and the living forms are clearly in need of a rigorous systematic revision.

Tribe PICHIPILINI *new tribe*

Diagnosis.—Differs from Caenolestini in trigonids being narrower than talonids; single, large lingual trigonid cusp that is bifid in unworn teeth (paraconid very reduced); trigonid cusps equal to or only slightly higher than talonid cusps; talonid basin broad and relatively shallow; cuspule present posterior to lingual trigonid cusp on M_{1-3} ; P_3 small in some taxa (*Pliolestes*), but large in others (*Phonocdromus*, *Pichipilus*).

Known range.—Colhuehupian, Santacrucian, Chasicuan, and Montehermosan of Argentina.

Includes.—

1. *Pliolestes* Reig, 1955, p. 66.
 - 1a. *Pliolestes tripotamicus* Reig, 1955, p. 67. Montehermosan.
2. *Phonocdromus* Ameghino, 1894, p. 355.
 - 2a. *Phonocdromus gracilis* Ameghino, 1894, p. 356. Santacrucian.

3. *Pichipilus* Ameghino, 1890, p. 155.3a. *Pichipilus osborni* Ameghino, 1890, p. 155. Santacrucian.3b. *Pichipilus riggsi* (Simpson, 1932, p. 4). Colhuehuapian.3c. *Pichipilus centinelus* Marshall and Pascual, 1977, p. 102. Early Santacrucian ("Notohipidense" horizon).

Comments.—Within the Pichipilini are several mid- to late Tertiary taxa that include the largest and the smallest of known Caenolestinae. In certain features of molar morphology (*i.e.*, reduced size of paraconid on M_{2-3} ; trigonid cusps equal to or only slightly higher than talonid cusps; talonid basin broad and relatively shallow) they resemble Palaeothentinae.

The oldest known species is *Pichipilus riggsi* from the Colhuehuapian of Patagonia. This species was originally placed by Simpson (1932, p. 4, fig. 2) in the genus *Halmarhiphus*. Reig (1955, p. 61) later noted that it does not belong in *Halmarhiphus*, is possibly referable to *Phonocdromus* or, more fundamentally, to a new genus. The generic affinities of the species *riggsi* were clarified upon the redescription of the Santacrucian species *Pichipilus osborni* by Marshall (1976b) and the discovery and description of a new early Santacrucian species of *Pichipilus*, *P. centinelus* by Marshall & Pascual (1977). The species *riggsi* was formally placed in *Pichipilus* by Marshall & Pascual (1977). The three known species of *Pichipilus* appear to represent an evolutionary lineage characterized by slight size increase, going from the smallest species *P. centinelus* in the Colhuehuapian to the largest species *P. osborni* in the later Santacrucian, and with the early Santacrucian *P. centineulus* representing an intermediate form in size, structure, and time.

Pliolestes tripotamicus was erected by Reig (1955, p. 67, fig. 3) on the basis of specimens from beds of Montehermosan age in Argentina. The species was based on a fragment of a left mandibular ramus (MACN 9971) with P_3 and M_2 present and alveoli of P_{1-2} , M_{1-2} , and part of M_4 . Pascual & Herrera (1973, p. 42) later described additional specimens of that species and referred a specimen (MMP 975M) from the Arroyo Chasicó Fm. (Chasicóan Age) to *Pliolestes* sp.

Species of *Pichipilus* and *Pliolestes* share a large number of features: both are similar in size; anterobasal cingulum is large and broad; trigonid has two major cusps, with the lingual cusp set anterior relative to the labial cusp; trigonid is much narrower than the talonid; talonid basin is broad and shallow; small hypoconulid present just posterior to entoconid and joined with hypoconid by a low posterocingular ridge; and overall proportions of known molar teeth are similar. In *Pichipilus*,

the P_3 is small (*i.e.*, it is about $\frac{1}{2}$ the height of M_1 trigonid), and the lingual corner of the anterobasal cingulum continues onto the anterior surface of the trigonid as a small ridge, whereas in *Pliolestes* the P_3 is about the same height as the M_1 trigonid, and there is no ridge along the anterior surface of the trigonid. Because of these similarities, *Pichipilus* represents an ideal morphological ancestor for *Pliolestes*, and the last two features may be considered derived in *Pliolestes*. *Pichipilus* and *Pliolestes* are the largest known genera of Caenolestinae.

Phonocdromus gracilis is the smallest known species of Caenolestinae (fig. 7) and is further distinguished from *Pichipilus* and *Pliolestes*

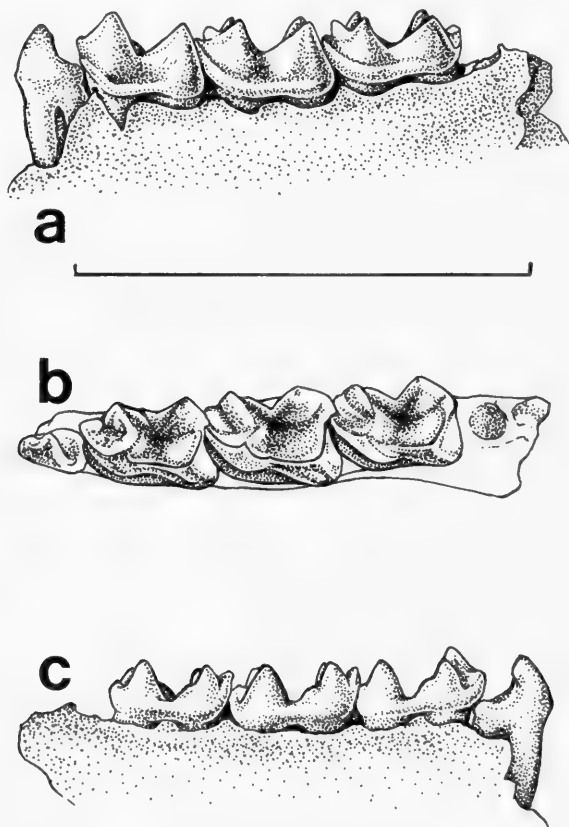


FIG. 7. *Phonocdromus gracilis* Ameghino, 1894, p. 356 (Santacrucian). MACN 8457 (lectotype), a fragment of a left mandibular ramus with P_3 - M_3 complete, alveoli of M_4 : a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

in its molars being proportionately narrower and more elongated anteroposteriorly; in the anterobasal cingulum being proportionately narrower and less well developed; in the M_2 trigonid being proportionately not as narrow as the talonid; and in the M_3 trigonid being almost as wide as the talonid (not distinctly narrower as in *Pichipilus osborni*).

Subfamily ABDERITINAE (Ameghino, 1889, pp. 268, 269)

Sinclair, 1906, p. 417

(Including Abderitesidae [sic]

Ameghino, 1889, pp. 268, 269;

Epanorthini Winge, 1923, p. 84 [partim])

Diagnosis.— $I_2^?$, $C_1^?$, $P_3^?$, $M_4^?$; mandibular ramus short and deep; large procumbent incisor (I_1) followed by four tiny, spaced, single-rooted vestigial teeth (I_2 , C , P_1 , P_2); P_2 single rooted; M_1 lacks metaconid, trigonid transversely compressed, greatly elevated above rest of tooth row, and modified into "plagiaulacoid" shear-blade with serrated edge along crest joining protoconid and paraconid; M_{2-3}^{2-3} bunolophodont, distinct lophs connect primary labial and lingual cusps; M_{2-3} lack paraconid, trigonid and talonid of subequal size in occlusal view and in height in lateral view, trigonid and talonid basins shallow; no trace of "intermediate conule" on M^{1-3} ; small cusp present anterior to paracone on M^3 ; sectorials— $P^3(?) / P_3-M_1$ trigonid or M^1 / M_1 trigonid.

Known range.—Deseadan, Colhuehuapian, and Santacrucian, Santa Cruz and Chubut Provinces, Patagonia, southern Argentina.

Comments.—The species and genera of Abderitinae are reviewed by Marshall (1976a).

Tribe PARABDERITINI *new tribe*

Diagnosis.—Mandibular ramus shallower and more gracile than in Abderitini; P_2 separated from P_3 by distinct diastema; P_3 large, double rooted, and blade-like, with simple serrated edge (up to two serrations on each surface and corresponding apical denticles, with a smaller anterior and a larger posterior); M_1 shear-blade, with two distinct serrations on each surface and corresponding apical denticles; M_1 talonid unmodified and similar to that on M_2 ; M_{2-3} proportionately longer and narrower than in Abderitini, and trigonids and talonids of M_{2-3} distinct; distinct cuspule absent just anterior to paracone on M^3 ; sectorials— $P^3(?) / P_3-M_1$ trigonid.

Known range.—Deseadan, Colhuehuapian, and early Santacrucian, Santa Cruz and Chubut Provinces, Patagonia, southern Argentina.

Includes.—

1. *Parabderites* Ameghino, 1902c, p. 121 [Including *Tideus* Ameghino,

1890, p. 157, *nec Tydeus* Koch, 1837, Table II (Arachnida), *nec Sauvage*, 1870, p. 23 (Pisces), *Tydaeus* Ameghino, 1893a, p. 15; *Mannodon* Ameghino, 1893a, p. 15.]

1a. *Parabderites bicrispatus* Ameghino, 1902c, p. 121. Colhuehuapian.

1b. *Parabderites minusculus* Ameghino, 1902b, p. 43 Deseadan.

Comments.—Within the Parabderitini is included one genus, *Parabderites*, with two species, *P. minusculus* (fig. 8) and *P. bicris-*

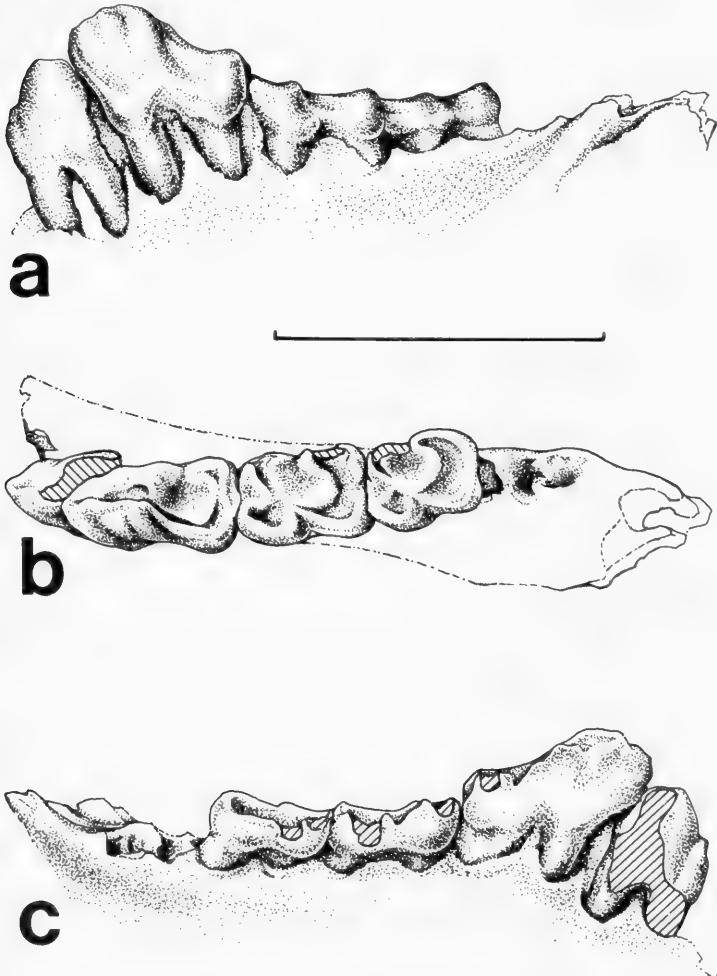


FIG. 8. *Parabderites minusculus* Ameghino, 1902b, p. 43 (Deseadan). MACN 52-380 (type), a left mandibular ramus with P_3 - M_3 , and alveoli of M_2 : a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

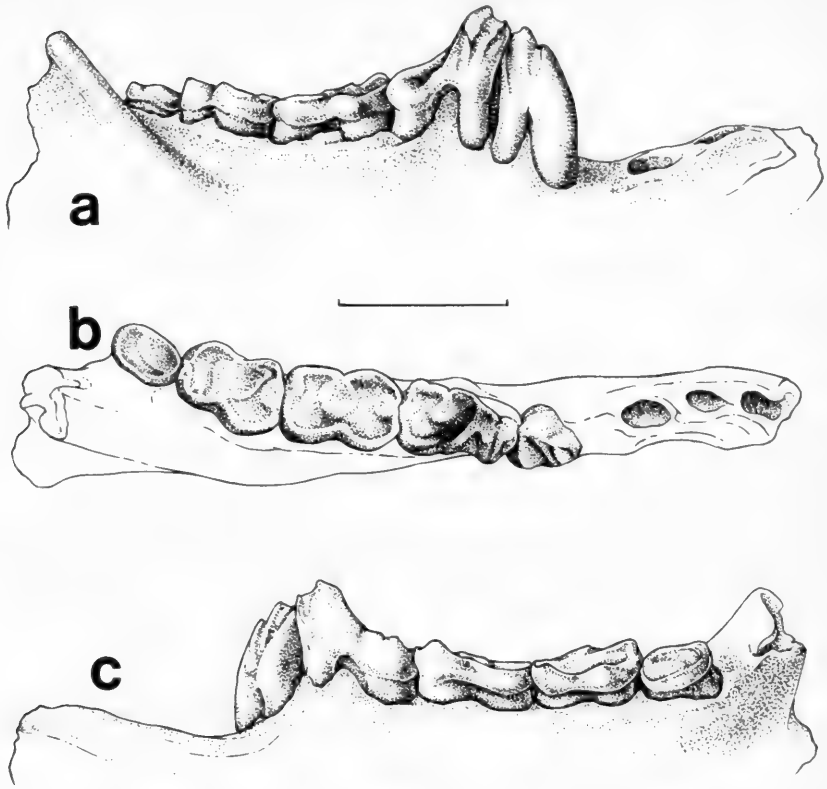


FIG. 9. *Parabderites bicrispatus* Ameghino, 1902c, p. 121 (Colhuehuapian). MACN 52-45 (type), greater part of a right mandibular ramus with alveoli of C-P₂, P₃-M₄ complete but worn: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

patus (fig. 9). *Parabderites minusculus* is the smallest of the two and is the only abderitine of Deseadan age. It is known only from its type (MACN 52-380), a left mandibular ramus with P₃-M₃ and alveoli of M₄ (see Marshall, 1976a, p. 79, fig. 10; Patterson & Marshall, 1978, p. 89, fig. 22).

The Colhuehuapian species *P. bicrispatus* is known from several specimens, including partial upper and relatively complete lower dentitions (see Marshall, 1976a, p. 76). It differs from *P. minusculus* in being larger in size, in having two distinct serrations on labial and lingual sides of P₃ (P₃ of *P. minusculus* has no serrations), and in the P₃ and trigonid region of M₁ being inclined forward at less of an angle relative to the main horizontal axis of the mandibular ramus.

No morphological characters are present in *P. minusculus* that would exclude it as an ancestor of *P. bicrispatus*. The change from one to the other involves increase in size, development of serrations on the P_3 , and the orientation of the P_3 and trigonid region of the M_1 into a more vertical position. It is thus possible to regard *P. minusculus* as the Deseadan ancestor of *P. bicrispatus*.

An isolated left M_2 (MACN 52-375b) and a fragment of a right mandibular ramus with roots of M_{1-4} (MLP 68-1-17-205) identified as *Parabderites* sp. are known from the "Notohipidense" horizon (early Santacrucian) at Karaiken and Cerro Centinela near the eastern edge of Lago Argentino, Patagonia (see Marshall, 1976a, p. 79, fig. 11; Marshall & Pascual, 1977, p. 115, fig. 7). Both specimens are intermediate in size between *P. minusculus* and *P. bicrispatus*, but because they are found in beds younger than either of those species, they cannot represent a phylogenetic intermediate form. The poorly known "Notohipidense" population of *Parabderites* thus may have evolved directly from a form similar to *P. minusculus* or from a post-*P. minusculus*—pre-*P. bicrispatus* population of that genus.

The above molar (MACN 52-375b) referred by Marshall (1976a, p. 81) to *Parabderites* sp. was referred by Ameghino (see below) to his species *Tideus trisulcatus* and *Mannodon trisulcatus*. To clarify the previous taxonomic history of this tooth it is necessary to review the history of these names.

Tideus trisulcatus was erected by Ameghino (1890, p. 157) on the basis of a tip of a "lower incisor," described as having three longitudinal sulci and being similar in size and shape to species of *Abderites*. It was placed in the Plagiaulacoidea. The type of *T. trisulcatus* (MACN 52-375a) does not, however, appear to represent a mammal, but its true affinities are not known. It can be described for all practical purposes as a sliver of reddish-brown bone, with two deep longitudinal sulci (not three as indicated by Ameghino), that measures 7.6 mm. in length. The type is thus indeterminate, and the generic and specific names are *nomina vana*.

Ameghino (1893a, p. 15) replaced the name *Tideus* with *Mannodon* on the ground that it was doubly preoccupied by *Tydaeus* (misprint for *Tydeus* Koch, 1837, a genus of Arachnida; Sauvage, 1870, a genus of Pisces). The former spelling is, however, different from *Tydeus* and this does not constitute preoccupation under the present Code. The name *Tideus* is thus technically valid.

Ameghino (1893a, p. 15) also noted that *Mannodon trisulcatus* was the first genus of Plagiaulacidae known from Patagonia in which the

“lower molar” was constructed similar to multituberculates. The lower molar he referred to was MACN 52-375b, which he later figured (1903, p. 110, fig. 28) and listed as coming from the “Notohipidense” horizon in the figure caption. Ameghino’s concept of *Tideus trisulcatus* (= *Mannodon trisulcatus*) was essentially based around this specimen, and the type (*i.e.*, the dubious lower incisor—MACN 52-375a) is not discussed further by him except for a brief statement (1898, p. 185) to its Santacrucian age. The most detailed description of this species and one based solely on MACN 52-375b (the M_2) is given by Ameghino in 1894 (p. 340). In essence, the name *Tideus trisulcatus* was used by Ameghino with reference to the type (MACN 52-375a), whereas the name *Mannodon trisulcatus* was applied to the M_2 (MACN 52-375b). The M_2 , however, is not the type that is a *nomen vanum*, and there are no problems of preoccupation of the generic name *Parabderites* Ameghino, 1902c, by the older names *Tideus* Ameghino, 1890, or *Mannodon* Ameghino, 1893a.

Tribe ABDERITINI (Ameghino, 1889, pp. 268, 269) *new rank*
(= *Abderitesidae* [*sic*] Ameghino, 1889, pp. 268, 269)

Diagnosis.—Mandibular ramus short and deep; P_2 not separated from P_3 by distinct diastema; P_3 single rooted, styliform, and set in notch in anterobasal edge of M_1 ; M_1 shear-blade more highly specialized than in *Parabderitini* and with three to six apical denticles and corresponding labial and lingual serrations, and talonid very reduced but basined with lingual side enclosed by prominent, anteroposteriorly compressed entoconid; M_{2-4} proportionately shorter and broader than in *Parabderitini*, and trigonids and talonids poorly differentiated in worn teeth; M_3 slightly smaller than M_2 , and of similar shape and structure; M^1 blade-like with serrated anterior edge; M^{2-4} with two distinct labial cusps (which are connected basally, forming a well-developed anteroposterior crest), and two lower lingual cusps; distinct cuspule occurs just anterior to paracone on M^3 ; sectorials— M^1/M_1 trigonid (fig. 10).

Known range.—Colhuehuapian and Santacrucian, Santa Cruz and Chubut Provinces, Patagonia, southern Argentina.

Includes.—

1. *Abderites* Ameghino, 1887, p. 5 [Including *Homunculites* Ameghino, 1902c, p. 73].
 - 1a. *Abderites crispus* Ameghino, 1902c, p. 120 [Including *Abderites crispulus* Ameghino, 1902c, p. 120; *Parabderites invelatus* Ameghino, 1902c, p. 122]. Colhuehuapian.

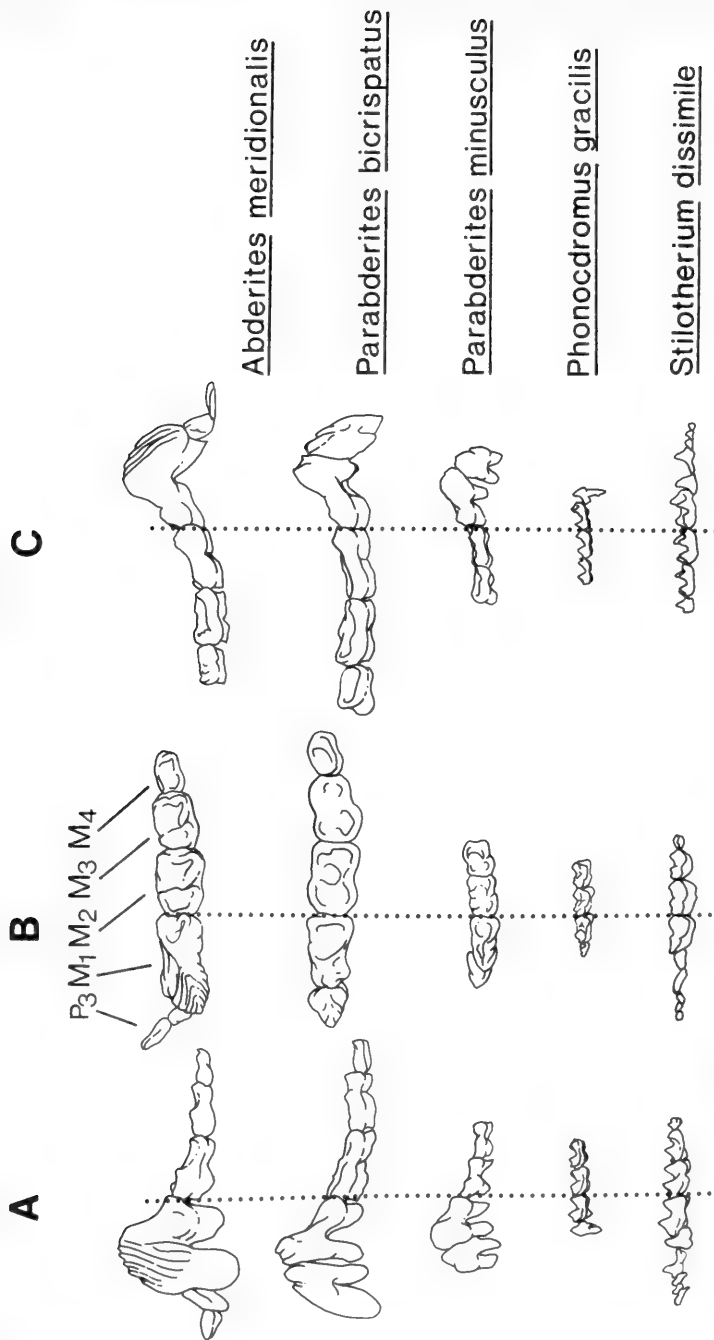


FIG. 10. Comparison of lower dentitions of various species of fossil Caenolestidae showing relative size and proportions of teeth. All illustrations are drawn to same scale. **A**, labial; **B**, occlusal; **C**, lingual views.

- 1b. *Abderites meridionalis* Ameghino, 1887, p. 5 [Including *Abderites crasignathus* (sic) Ameghino, 1891a, p. 248; *Abderites crassiramis* Ameghino, 1893b, p. 80; *Abderites serratus* Ameghino, 1891a, p. 248; *Abderites tenuissimus* Ameghino, 1891b, p. 304]. Santacrucian.
- 1c. *Abderites pristinus* (Ameghino, 1902c, p. 73). Colhuehuapian.
2. *Pitheculites* Ameghino, 1902c, p. 74 [Including *Eomannodon* Ameghino, 1902c, p. 119; *Micrabderites* Simpson, 1932, p. 6].
- 2a. *Pitheculites minimus* Ameghino, 1902c, p. 74 [Including *Eomannodon multituberculatus* (sic) Ameghino, 1902c, p. 119; *Micrabderites williamsi* Simpson, 1932, p. 6]. Colhuehuapian.

Comments.—Included within the Abderitini are several mid-Tertiary taxa that are characterized by possession of a large "plagiolacoid" M_1 with a serrated cutting edge and with P_3 very reduced, peg-like, and set into a notch in the anterobasal edge of the M_1 .

Pitheculites minimus from the Colhuehuapian of Patagonia is the smallest known species of Abderitini. It differs from species of *Abderites* in its smaller size and in the M_1 blade having fewer striae [three occur in *Pitheculites* (AMNH 29661) compared with six in *Abderites*] (Marshall, 1976a, p. 72).

Three species of *Abderites* are recognized—*A. crispus* and *A. pristinus* of Colhuehuapian age and *A. meridionalis* (fig. 11) of Santacrucian age. *Abderites crispus* and *A. meridionalis* are represented by large sample sizes, and the numerous characters that can be compared show them to be quite similar. In *A. crispus*, the M_1^1 is larger in length and breadth, M_{2-4}^2 are smaller and the lophi connecting the labial and lingual cusps are not as well developed, the M^2 is proportionately shorter, and the labial crests in M^{2-3} are proportionately stronger than in *A. meridionalis*.

I recognize *A. crispus* as the probable Colhuehuapian ancestor of *A. meridionalis*. The primary changes from one to the other include increase in size of M_{2-4}^2 , slight reduction in length and breadth of M_1^1 , size reduction of labial crests on M^{2-3} , increase in size of lophi connecting labial and lingual cusps, and proportionate increase in length of M^2 . These changes are minor, and there is little problem in deriving one from the other.

The type of *A. pristinus* (MACN 52-34), a fragment of a left mandibular ramus with M_2 complete and alveoli of P_3 , M_1 and M_{3-4} , is all that is known of this species, and little can be said about its affinities with other species of *Abderites*. *Abderites pristinus* has a larger M_2 and a more gracile mandibular ramus than either *A. crispus* or *A.*

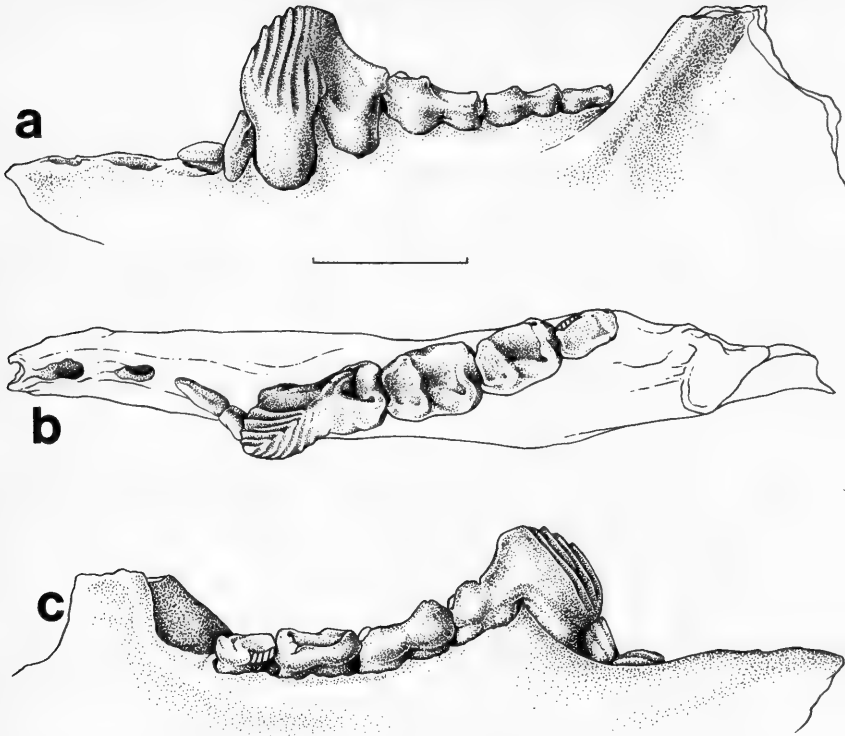


FIG. 11. *Abderites meridionalis* Ameghino, 1887, p. 5 (Santacrucian). MACN 2037, a left mandibular ramus with alveoli of C-P₁, P₂-M₃ complete, M₄ missing anterolingual corner: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

meridionalis. It is certainly distinct from the other Colhuehuapian species *A. crispus*, and it does not appear to be involved in the ancestry of *A. meridionalis*.

The dentitions of *A. crispus* and *P. minimus* are similar in the weak development of the lophos connecting the lingual and labial cusps, in the shorter and more quadrate structure of M² as compared to the more elongated M² in *A. meridionalis*, and in the large and prominent structure of the labial crest in M² and M³ (especially M²). These features are all slightly modified in the Santacrucian *A. meridionalis*, and their joint occurrence in the two Colhuehuapian taxa suggest that they represent character states shared by a common *Pitheculites-Abderites* ancestor.

Abderites altiramis Ameghino, 1894, p. 304, was based on a right mandibular ramus (MACN 8250) with the anterior alveolus and talonid of M₃ and both roots of M₄, collected from the Santa Cruz beds of Patagonia. This specimen was earlier figured by Ameghino (1889, pl. 1,

figs. 10–10b) as “*Epanorthus*” *aratae* and has been shown by Marshall (1976a, p. 72) to be a borhyaenid. The name *Abderites altiramis* represents a junior synonym of the borhyaenid species *Perathereutes pungens* Ameghino, 1891b.

A specimen (MLP 68-1-17-210), consisting of a fragment of a left mandibular ramus with alveoli and/or roots of most of the teeth, collected from the “Notohipidense” horizon (early Santacrucian) of Patagonia has been identified as *Abderites* sp. by Marshall & Pascual (1977, p. 113).

Pascual & Odreman Rivas (1971, p. 396) include *Abderites* sp. in a faunal list of Friasian mammals. However, no specimens of *Abderites* have as yet been described from beds of Friasian age, and this report needs confirmation and documentation.

Willard (1966, p. 73, pl. 65, fig. 6) identified a partial edentulous left mandibular ramus with seven alveoli as *Abderites* sp. Judging from the photograph presented by Willard, this specimen is a member of the family Didelphidae as evidenced by the seven posterior alveoli that are of subequal size and shape. In *Abderites*, these alveoli decrease rapidly in size from front to back. The specimen is listed as coming from the “upper Inuya” of Peru. These beds are presently regarded as Late Tertiary (cf. Huayquerian and/or Montehermosan) in age (Marshall et al., in press).

Subfamily PALAEOThENTINAE Sinclair, 1906, p. 417

(Including Epanorthidae Ameghino, 1889,
pp. 268, 270, *sensu stricto*;

Epanorthini Winge, 1923, p. 84 [*partim*];

Decastidae Ameghino, 1893b, p. 79;

Epanorthinae Trouessart, 1905, p. 840;

Palaeothentidae Osgood, 1921, pp. 143, 151)

Diagnosis.— I_2^3 , C_1 , $P_{(2-3)}^3$, M_4^1 ; mandibular ramus long and relatively shallow, but deeper and relatively shorter than in Caenolestinae; two mental foramina are typically present, one below P_2 and another below M_1 , sometimes a third occurs between these below anterior root of M_1 ; large procumbent and lanceolate I_1 followed by three or four tiny, vestigial teeth (I_2 , C , P_1 , P_2); P_2 either double or single rooted; P_3 either single rooted and styliform with a crown height less than $\frac{1}{2}$ that of M_1 , or large, double rooted, and equal to or greater than height of M_1 trigonid (intermediate sizes also occur); M_1 with trigonid region (crest connecting protoconid and paraconid) elongated and with paraconid set far anteriorly, metaconid large and well developed; M_{2-3}^{2-3} brachyo-

dent, no distinct lophos in unworn teeth; trigonid and talonid regions of M_{2-3} distinct and subequal in size in occlusal view and in height in lateral view, trigonid and talonid basins shallow, paraconid absent; P^{1-2} very reduced in size and crown height; P^2 laterally compressed with prominent central cusp and smaller anterior and posterior accessory cusps; P^3 enormous, rivalling M^1 in size in some taxa, and with crown height equal to or greater than that of M^1 ; posterior end of P^3 crown much broader than anterior and with posterolingual cingular shelf; anterior root of P^3 is much narrower transversely than posterior root; sharp cutting edge formed along labial sides of M^{1-2} and extending onto P^3 ; M^1 with cingular shelf along anterior edge of paracone; "intermediate conule" weakly developed in unworn M^{1-3} only in *P. minutus*; anterior ends of M^{1-3} much broader than posterior ends; sectorials-posterointernal surface of P^3 shears against labial surface of M_1 trigonid; no trace of antorbital vacuity as in Caenolestinae.

Known range.—Deseadan, Colhuehuapian, and Santacrucian of Patagonia, southern Argentina; Deseadan of Bolivia.

Comments.—Although 16 generic names for palaeothentines have been proposed (15 based initially on Santacrucian species), their status has been viewed as extremely dubious. This is due to the fact that many of the type specimens were never figured, and diagnoses for the most part were inadequate. The group has also suffered from neglect, and the included genera and species were last reviewed by Ameghino (1898).

Apart from *Palaeothentes* Ameghino, 1887, the first named, the genera include *Acestis* Ameghino, 1887; *Epanorthus* Ameghino, 1889 (a replacement name for *Palaeothentes*); *Dipilus* Ameghino, 1890; *Decastis* Ameghino, 1891; *Callomenus* Ameghino, 1891; *Essoprion* Ameghino, 1891; *Halmadromus* Ameghino, 1891; *Halmaselus* Ameghino, 1891; *Palaepanorthus* Ameghino, 1902c; *Metriodromus* Ameghino, 1894; *Metaepanorthus* Ameghino, 1894; *Paraepanorthus* Ameghino, 1894; *Prepanorthus* Ameghino, 1894; *Cladoclinus* Ameghino, 1894; and *Pilchenia* Ameghino, 1903.

Subsequent workers agreed that the Palaeothentinae were overly split at the generic and specific levels. Simpson (1945, p. 45), for example, tentatively recognized only five genera (*Palaeothentes*, *Pilchenia*, *Acestis*, *Dipilus*, and *Halmadromus*). The others were either included as synonyms of one of these five or were regarded *nomina vana*. As Simpson (1945, p. 42, 2n) noted:

Proper generic criteria for this group have not yet been worked out, and the published data are inadequate in several cases.

All of the genera and included species were erected on lower dentitions and were distinguished in large part on the basis of overall size, number of antemolar teeth, absolute size and/or number of roots on P_3 , relative size of P_3 and M_1 , and presence, absence, and/or relative size of accessory cuspules on P_3^* (see p. 29 for quote from Ameghino, 1898). Supposed differences in proportions of M_{1-4} were also occasionally noted. These criteria alone or together are adequate if one is working with entire dentitions, but for most taxa this was not the case. In addition, Ameghino made no attempt to evaluate individual variation within a species, and the taxonomic limits of the species and genera were never subjected to rigorous cross evaluation based on large sample sizes.

Palaeothentes Ameghino, 1887

Palaeothentes Moreno, 1882, p. 122 (*nomen nudum*).

Palaeothentes Ameghino, 1887, p. 5.

Epanorthus Ameghino, 1889, p. 271; to replace *Palaeothentes*.

Essoprion Ameghino, 1891b, p. 306.

Halmadromus Ameghino, 1891b, p. 306.

Halmaselus Ameghino, 1891b, p. 306.

Palaepanorthus Ameghino, 1902c, p. 123.

Metriodromus Ameghino, 1894, p. 342.

*Metaepanorthus*** Ameghino, 1894, p. 348.

*Paraepanorthus*** Ameghino, 1894, p. 349.

Prepanorthus Ameghino, 1894, p. 350.

Cladoclinus Ameghino, 1894, p. 358.

Pilchenia Ameghino, 1903, p. 128.

Type of *Palaeothentes*.—*P. aratae* Ameghino, 1887, p. 5.

Type of *Epanorthus*.—*E. aratae* (Ameghino, 1889, p. 272).

Type of *Essoprion*.—*E. coruscus* Ameghino, 1891b, p. 306.

Type of *Halmadromus*.—*H. vagus* Ameghino, 1891b, p. 306.

Type of *Halmaselus*.—*H. valens* Ameghino, 1891b, p. 306.

Type of *Palaepanorthus*.—*P. primus* Ameghino, 1902c, p. 123.

Type of *Metriodromus*.—*M. arenarus* Ameghino, 1894, p. 343.

Type of *Metaepanorthus*.—*M. intermedius* Ameghino, 1887, p. 6.

*For example, *Metaepanorthus* was characterized by the presence of a well-defined anterior and posterior accessory cuspule on P_3 , and *Paraepanorthus*, by the occurrence of the anterior cuspule only.

**In accordance with Articles 27 and 32c of the International Code of Zoological Nomenclature (Stoll et al., 1961, 1964) the diacritic mark is dropped from the names originally spelled *Metaëpanorthus* and *Paraëpanorthus*.

Type of Paraepanorthus.—*P. minutus* (Ameghino, 1894, p. 350).

Type of Prepanorthus.—*P. lanius* Ameghino, 1894, p. 351.

Type of Cladoclinus.—*C. copei* Ameghino, 1894, p. 359.

Type of Pilchenia.—*P. lucina* Ameghino, 1903, p. 128.

Diagnosis.—Small to very large Palaeothentinae: I_2^3 , C_1^1 , P_3^3 , M_4^4 ; P_2 reduced relative to P_3 and double or single rooted; P_3 large, double rooted (posterior root is always larger than anterior root), and always greater than $\frac{1}{2}$ height of M_1 trigonid; anterobasal cuspule present on P_3 ; paraconid bifurcated on M_1 ; M_1 protoconid is generally slightly higher than paraconid in unworn teeth compared with species of *Acdestis* in which they are generally more subequal in height; anterolabial cingula weakly developed on M_{1-2} ; anterobasal cuspule on P^3 well developed in unworn teeth; size decrease from M_2^2 to M_4^4 more gradual than in species of *Acdestis*.

Known range.—Deseadan, Colhuehuapian, and Santacrucian of Patagonia, southern Argentina; Deseadan of Bolivia.

Comments.—The name "*Palaeothentes aratae* Mor." was published in a list of names by Doering (1882, p. 455) and is a *nomen nudum*. In the same year Moreno (1882, p. 116) published the name *Palaeotentes* (also spelled by him *Palaeothentes*) *aratae* but this too is a *nomen nudum*. It is impossible to establish which name appeared first. A valid definition of this genus and species was first published by Ameghino (1887, p. 5) under the name *Palaeothentes*. In 1889 Ameghino (p. 271) decided that the spelling *Palaeothentes* was "impossible" and that the generic name should have been written *Palaeoteuthis* and hence was preoccupied by *Palaeoteuthis* D'Orbigny (1850, p. 327), an extinct genus of dibranchiate cephalopod. On these grounds, Ameghino (1889, p. 271) proposed the generic name *Epanorthus* to replace *Palaeothentes* Ameghino, 1887. But the spelling *Palaeothentes* was original, intentional, and has priority and *ipso facto* is the correct spelling regardless of its etymology; it cannot be preoccupied by the quite different name *Palaeoteuthis* (Simpson, 1945, p. 45n). Indeed, Sinclair (1906, p. 416) has already argued that *Epanorthus*:

. . . can no longer be retained either for a genus or to designate a family [Epanorthidae].

There is no possible origin for the name *Palaeothentes*. Palmer (1904) gave "*thereutes*, hunter" as the origin and probably got that from Ameghino. However, it is impossible to get *-thentes* or anything like it from *-thereutes*.

Palaeothentes, when described in 1887 (and redescribed in 1889 when *Epanorthus* was proposed to replace it), contained six species, although no type-species was designated on either occasion. Clemens & Marshall (1976, p. 72) were the first to designate a type-species when they chose *P. aratae*, the first species described.

Eight species of *Palaeothentes* are here recognized: three (*P. lucina*, *P. boliviensis*, *P. chubutensis*) are known from beds of Deseadan age, one (*P. primus*) is from beds of Colhuehuapian age, and four (*P. minutus*, *P. intermedius*, *P. lemoinei*, *P. aratae*) are from the Santacrucian.

These species are distinguished primarily on the basis of absolute size and on minor size differences of the P_3 relative to the M_1 (figs. 12–17). For example, in length of M_{1-4} (fig. 12) all species for a given Age are readily separable one from the other. This is also true for plots of $L P_3$ vs. $L M_1$ (fig. 13), $L M_1$ vs. $W M_1$ (fig. 14), and $L M_1$ vs. $L M_2$ (fig. 15). These plots are based for the most part on large sample sizes, and they show that absolute and/or relative size differences alone are ample to readily differentiate the species.

***Palaeothentes minutus* Ameghino, 1887. Figures 18–20; Tables 3–5.**

Palaeothentes minutus Ameghino, 1887, p. 6; Sinclair, 1906, p. 432, pl. 63, figs. 1, 4–5a, pl. 64, fig. 2; Schlosser, 1925, p. 27, figs. 40B, 42.

Epanorthus minutus Ameghino, 1889, p. 274, pl. 1, fig. 16; 1893b, p. 78, fig. 1.

Paraepanorthus minutus Ameghino, 1894, p. 350, fig. 40; 1897, p. 500, fig. 76; 1898, p. 186, fig. 50h; 1904a, p. 45, fig. 30; 1905, p. 17, figs. 18, 19; Rusconi, 1933, p. 247, fig. 4.

Paraepanorthus (Epanorthus) minutus Ameghino, 1903, p. 141, figs. 62, 95, 96.

Dipilus bergii Ameghino, 1890, p. 155; 1894, p. 342; 1898, p. 186.

Halmaselus valens Ameghino, 1891b, p. 306; 1894, p. 351; 1898, p. 186.

Essopriion consumptus Ameghino, 1891b, p. 306; 1894, p. 351; 1898, p. 186.

Essopriion coruscus Ameghino, 1891b, p. 306; 1894, p. 351; 1898, p. 186.

Epanorthus simplex Ameghino, 1894, p. 347.

Cladoclinus copei Ameghino, 1894, p. 359; 1903, p. 117, fig. 35; Reig, 1955, p. 64.

Epanorthus delicatus Ameghino, 1894, in Roger, 1896, p. 19 (*nomen nudum*).

Palaeothentes delicatus Simpson, 1930, p. 57 (*nomen nudum*).

Metaepanorthus complicatus Ameghino, 1894, p. 348; 1898, p. 186.

Epanorthus complicatus Roger, 1896, p. 19.

Palaeothentes complicatus Sinclair, 1906, p. 455.

Prepanorthus lanius Ameghino, 1894, p. 351.

Type of Palaeothentes minutus.—MACN 15, a right mandibular ramus with alveoli of I_2 - P_2 , and P_3 - M_4 complete (listed as type in Ameghino's catalogue).

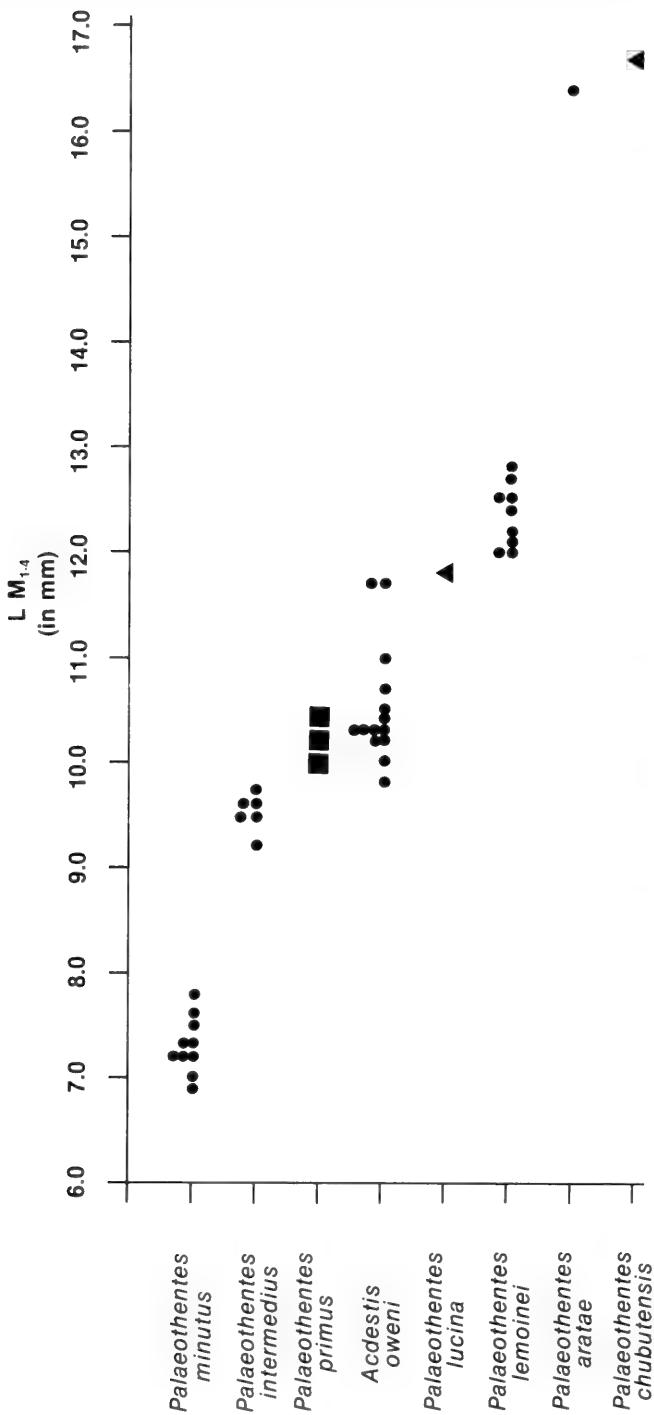


FIG. 12. Size distribution of various species of Palaeotheninae as indicated by length of M_{1-4} . Symbols are: Deseadan (triangles), Colhuehuapian (squares), Santacrucian (circles).

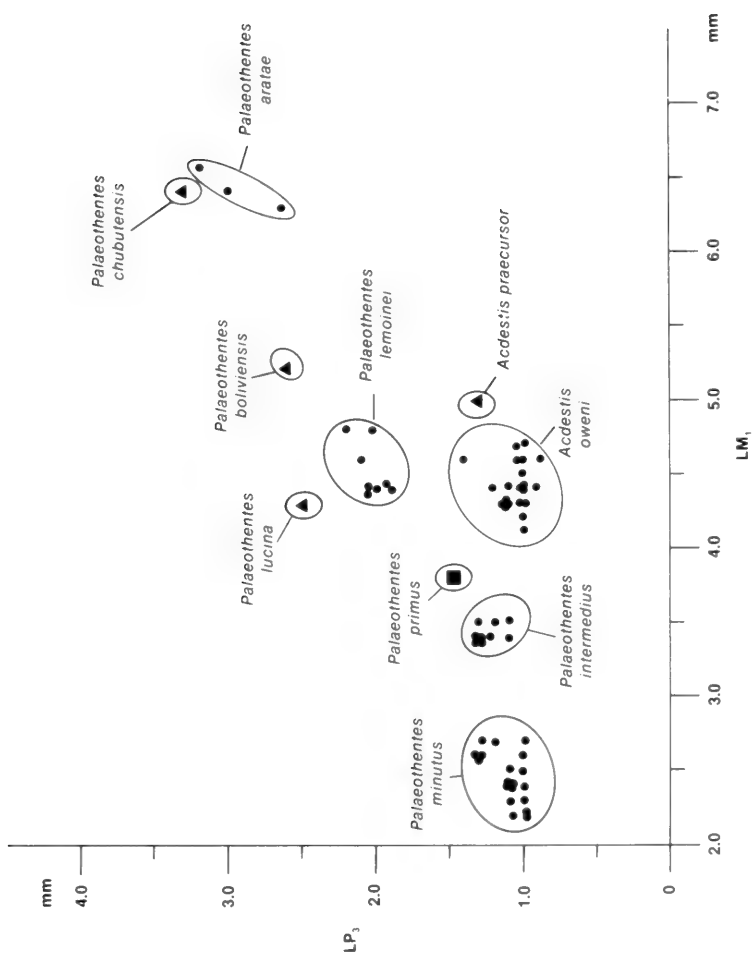


FIG. 13. Size distribution of various species of Palaeotheninae as indicated by relationship of length of P_3 and M_1 . Symbols are: Deseadan (triangles), Colhuehuapian (squares), and Santacrucian (circles).

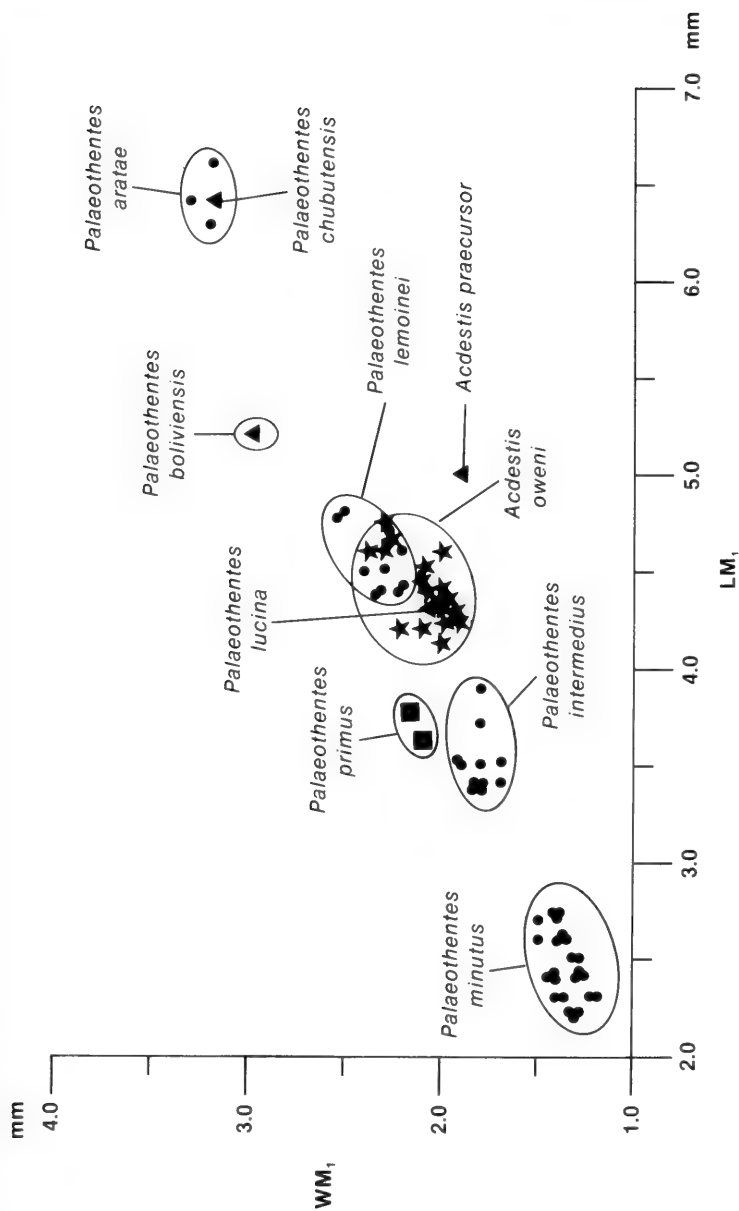


FIG. 14. Size distribution of various species of Palaeotheninae as indicated by relationship of length and width of M_1 . Symbols are: Deseadan (triangles), Colhuehuapian (squares), Santacrucian (circles); stars represent Santacrucian species *Accestis oweni*.

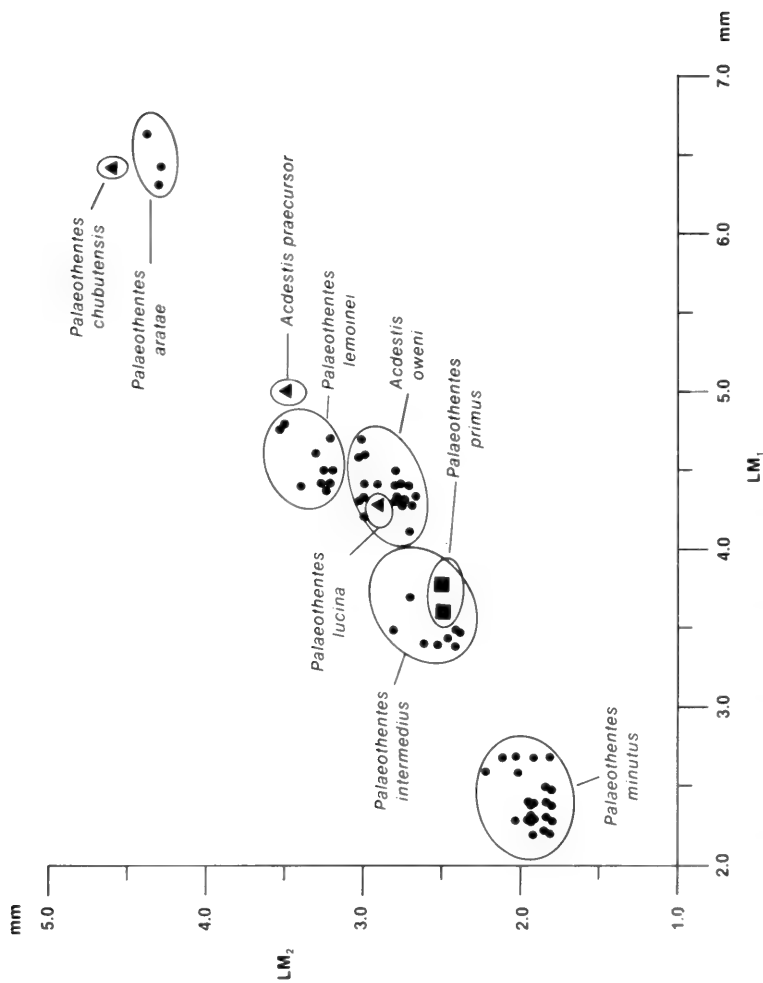


FIG. 15. Size distribution of various species of Palaeotheninae as indicated by relationship of length of M_1 and M_2 . Symbols are: Deseadian (triangles), Colhuahuapian (squares), Santacrucian (circles).

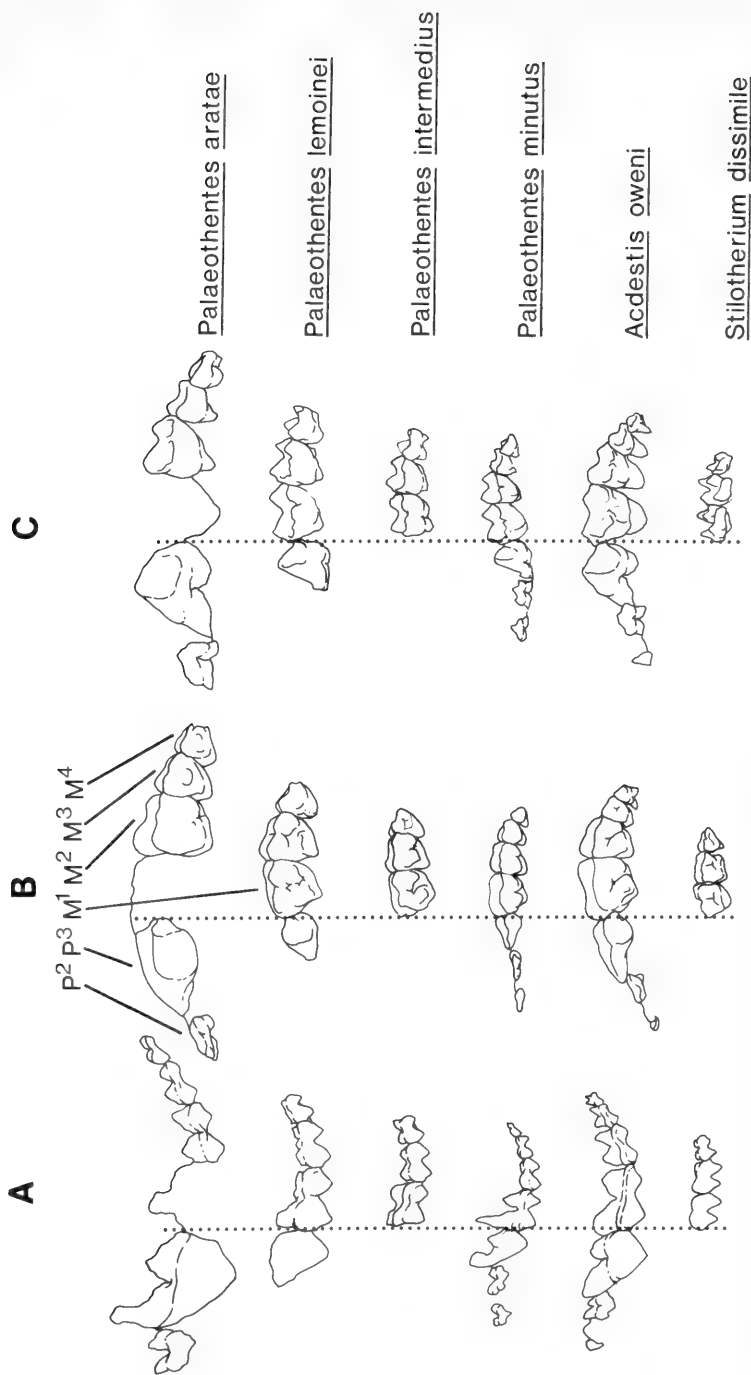


FIG. 16. Comparison of upper dentitions of various species of fossil Caenolestidae showing relative size and proportions of teeth. All illustrations are drawn to same scale. **A**, labial; **B**, occlusal; **C**, lingual views.

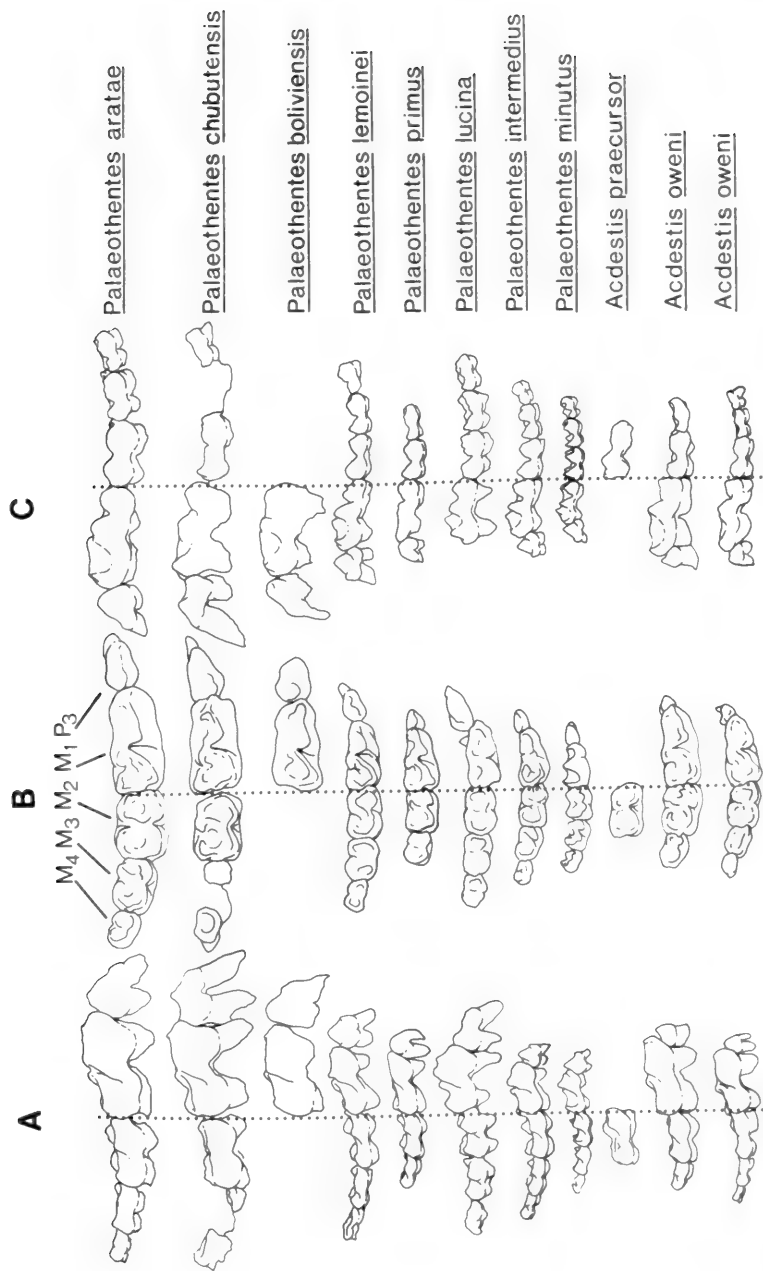


FIG. 17. Comparison of lower dentitions of various species of Palaeotheninae showing relative size and proportions of teeth. All illustrations are drawn to same scale. **A**, labial; **B**, occlusal; **C**, lingual views.

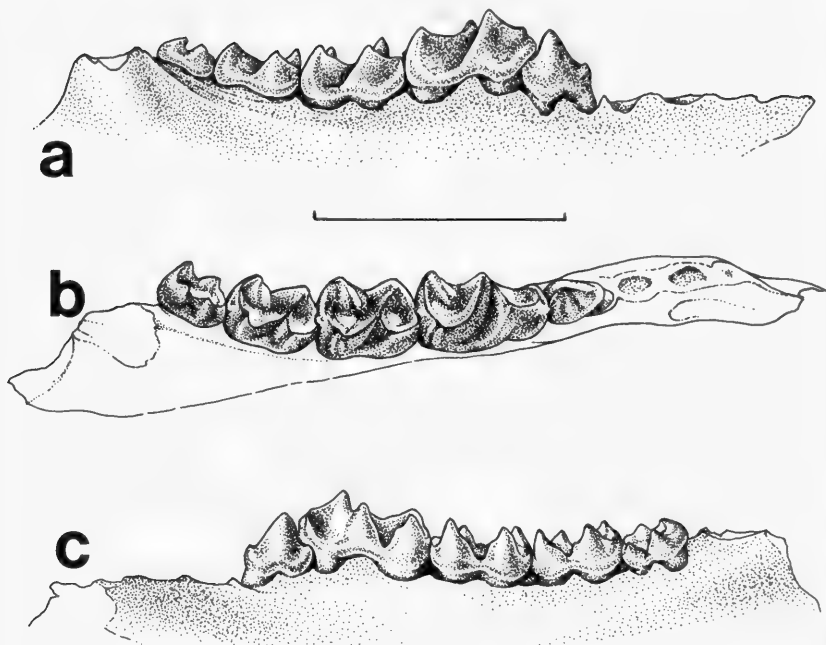


FIG. 18. *Palaeotheres minutus* Ameghino, 1887, p. 6 (Santacrucian). MACN 15 (type), a right mandibular ramus with alveoli of I_2 - P_2 , and P_3 - M_1 complete: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

Type of Dipilus bergii.—MACN 2041, a fragment of a left mandibular ramus with P_3 - M_2 .

Type of Halmaselus valens.—MACN 6595, a fragment of a right mandibular ramus with alveoli of C - P_2 , P_3 - M_2 complete (the alveoli of the P_2 show this tooth to have been double rooted, a character not visible if the tooth were present).

Type of Essoprion consumptus.—MACN 5697, a fragment of a right mandibular ramus with alveoli of I_2 - P_2 , P_3 - M_1 complete, and trigonid of M_2 present.

Type of Essoprion coruscus.—MACN 5696, a fragment of a right mandibular ramus with alveoli of C - M_1 , and M_2 complete.

Type of Epanorthus simplex.—MACN 5677, a fragment of a left mandibular ramus with alveoli of P_{1-2} , and P_3 - M_2 complete (listed as type in Ameghino's catalogue).

Type of Epanorthus delicatus.—MACN 5690, a fragment of a left mandibular ramus with alveoli of M_2 , and M_{3-4} complete.

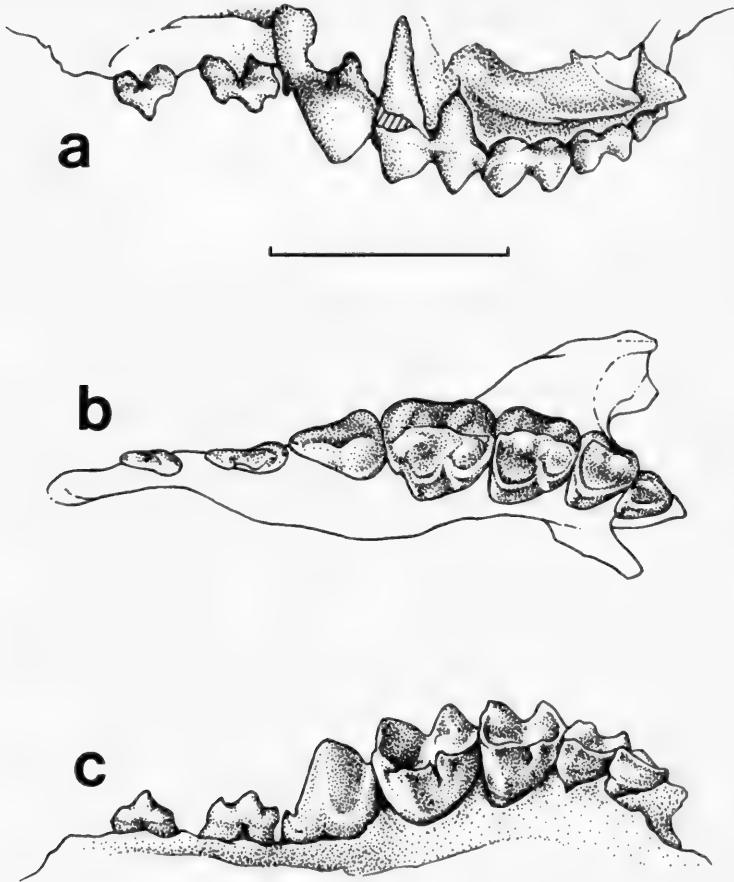


FIG. 19. *Palaeotheres minutus* Ameghino, 1887, p. 6 (Santacrucian). MACN 10245, a left maxillary fragment with P¹-M⁴ complete: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

Type of Epanorthus complicatus.—MACN 5671, a nearly complete left mandibular ramus with base of I₁, alveoli of I₂-P₂, P₃ complete, alveoli of M₁, and M₂₋₄ complete.

Type of Prepanorthus lanius.—MACN 8323-8328 [8323, a fragment of a right maxillary with M¹⁻³ complete; 8324, a fragment of a left maxillary with M²⁻³ complete, and alveoli of M¹ and M⁴; 8325, a fragment of a right maxillary with P¹⁻³ complete; 8326, two isolated upper incisors; 8327, three isolated upper molars; 8328, a pelvic fragment with acetabulum (all of a single associated individual)].

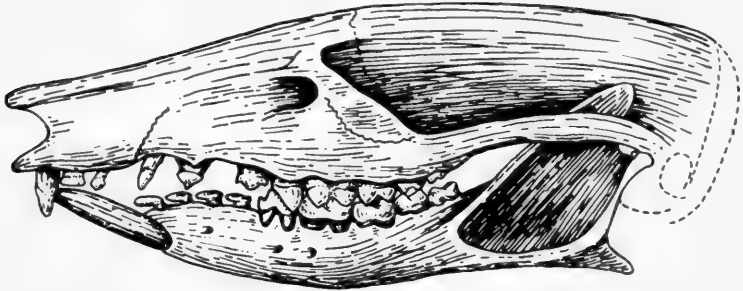


FIG. 20. *Palaeothenes minutus* Ameghino, 1887, p. 6. Left lateral view of skull. Redrafted from Ameghino (1897, fig. 76; 1903, figs. 62, 95; 1904a, fig. 30). This figure was drawn by Florentino Ameghino and is apparently based in total or at least in part on MACN 8271. Scale = 3 X natural size.

Type of Cladoclinus copei.—MACN 8469, a fragment of a right mandibular ramus with M_4 complete.

Hypodigm.—The 10 types and MACN 2042, a fragment of a right mandibular ramus with M_{3-4} (possible cotype of *Dipilus bergii*); MACN 5672, a fragment of an innominate (supposedly of same individual as type of *Epanorthus complicatus*, MACN 5671); MACN 5673, a right mandibular ramus with P_3 - M_2 ; MACN 5674, a right mandibular ramus with P_3 ; MACN 5675, a right mandibular ramus with P_3 - M_2 ; MACN 5674, a right mandibular ramus with P_3 ; MACN 5675, a right mandibular ramus with P_3 ; MACN 5676, a fragment of a right mandibular ramus with P_3 - M_1 ; MACN 8271, partial skull with attached mandible with complete dentition, including incisors (this is probably the specimen used by Ameghino to reconstruct the skull that he illustrated—see Ameghino, 1897, fig. 76; 1903, figs. 62, 95; 1904a, fig. 30—as it is the most complete specimen of that element yet known); MACN 8297, a nearly complete right mandibular ramus with dentition; MACN 8298, nearly complete left mandibular ramus with dentition (this specimen was figured by Ameghino, 1894, fig. 40; 1898, fig. 50h; 1903, fig. 96—it is the same individual as 8297); MACN 8300, a left mandibular ramus with P_3 complete, alveoli of M_1 , and M_{2-4} complete; MACN 8306, a right mandibular ramus with M_{1-4} complete; MACN 8307, a right mandibular ramus with P_3 - M_4 complete; MACN 8308, a right mandibular ramus with M_{2-4} complete; MACN 8309, a right ramus with M_{2-4} complete; MACN 8310, a left mandibular ramus with M_{1-2} complete; MACN 8321, a right maxillary fragment with P^3 - M^3 complete; MACN 8330a, a fragment of a left mandibular ramus with P_3 - M_3 complete; MACN 8330b, a fragment of a right mandibular ramus with I_1 - M_1 (same individual as 8330a); MACN 8331, a left mandibular ramus with I_1 - M_2

TABLE 3. Measurements of upper cheek teeth of *Palaeothenes minutus*.

	P3		M1		M2		M3		M4		M ¹⁻⁴		P ³ -M ¹	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
MACN 8323	2.0	1.9	1.7	1.9	1.1	1.7
MACN 8324	1.6	2.0	1.0	1.6
MACN 8355	2.1	2.0	1.6	2.0	1.0	1.7	0.8	1.3	5.8	1.3
MACN 10245	1.9	1.3	2.3	2.2	1.7	2.1	1.0	1.7	0.9	1.3	6.3	1.3	8.0	7.7
PU 15709	1.6	1.1	2.3	1.8	1.9	1.8	1.3	1.5	0.9	1.2	6.0	1.2
PU 15999	1.9	2.0	1.3	1.6

TABLE 4. Measurements of lower cheek teeth of *Palaeotheres minutus*.

	P ₃		M ₁		M ₂		M ₃		M ₄		M1-4	P3-M4
	L	W	L	W	L	W	L	W	L	W	L	L
MACN 15	1.1	0.8	2.4	1.3	1.8	1.4	1.5	1.2	1.0	0.9	7.5	8.6
MACN 2041	1.0	0.9	2.7	1.4	1.9	1.5
MACN 2042	1.4	1.2	1.0	0.9
MACN 5671	1.0	0.9	2.0	1.4	1.5	1.1	0.9	0.9	7.2	8.6
MACN 5673	1.1	0.8	2.2	1.3	1.8	1.4
MACN 5674	1.1	0.8
MACN 5675	1.0	0.9
MACN 5676	1.1	0.9	2.4	1.4
MACN 5677	1.1	0.8	2.4	1.3	1.9	1.5
MACN 5690	1.5	1.2	1.0	0.8
MACN 5696	2.0	1.3
MACN 5697	1.0	0.8	2.4	1.4
MACN 6595	1.0	0.8	2.2	1.3	1.9	1.3
MACN 8297	1.0	0.7	2.2	1.3	1.8	1.4	1.4	1.2	1.0	0.8	7.3	8.2
MACN 8298	1.0	0.8	2.3	1.2	1.8	1.3	1.5	1.2	1.0	0.8	7.2	8.3
MACN 8306	2.3	1.4	1.9	1.4	1.5	1.2	1.0	0.9	7.6	...
MACN 8307	2.4	1.3	1.9	1.3	1.4	1.1	1.0	0.8	7.2	...
MACN 8308	2.0	1.4	1.4	1.2	1.0	0.9
MACN 8309	2.0	1.4	1.4	1.2	1.0	0.9
MACN 8310	2.3	1.2	1.8	1.4
MACN 8330a	1.0	0.8	2.5	1.3	1.8	1.4	1.5	1.2	7.2ca	8.1ca
MACN 8330b	1.0	0.8	2.6	1.4
MACN 8331	1.1	0.9	2.4	1.4	1.8	1.4
MACN 8376	1.1	0.8	2.5	1.3	1.8	1.3	1.4	1.2	0.9	0.9	7.3	8.4
MACN 8469	1.0	0.8
PU 15068	1.3	1.0	2.7	1.5	2.0	1.5	1.7	1.3
PU 15706	1.3	0.8	2.2	1.5	1.8	1.3	1.1	0.9	7.0ca	...
PU 15707	1.3	0.9	2.6	1.5	2.2	1.5
PU 15708	1.2	0.8	2.7	1.4	2.1	1.5	1.7	1.2	7.0ca	...
PU 15709	1.3	0.8	1.8	1.3	1.1	0.9
KUVP 655(I)	1.3	0.9	2.6	1.4	1.7	1.2	1.1	1.0
KUVP 655(II)	1.3	0.9	2.6	1.4	2.0	1.4	1.6	1.2	1.1	1.0	6.9	...
AMNH 9122	1.1	0.9	2.3	1.4	2.0	1.3

TABLE 5. Statistics for some cheek teeth of *Palaeothenes minutus*.

Dimension		N	OR	x	s	CV
UPPER CHEEK TEETH						
P ³	L	2	1.6-1.9	1.75	0.21	12.00
	W	2	1.1-1.3	1.20	0.14	11.67
M ¹	L	4	2.0-2.3	2.18	0.15	6.88
	W	4	1.8-2.2	1.98	0.17	8.59
M ²	L	6	1.6-1.9	1.73	0.14	8.09
	W	6	1.8-2.1	1.97	0.10	5.08
M ³	L	6	1.0-1.3	1.12	0.15	13.39
	W	6	1.5-1.7	1.63	0.08	4.91
M ⁴	L	3	0.8-0.9	0.87	0.06	6.90
	W	3	1.2-1.3	1.27	0.06	4.72
M ¹⁻⁴	L	3	5.8-6.3	6.03	0.25	4.15
P ³ -M ⁴	L	2	7.7-8.0	7.85	0.21	2.68
LOWER CHEEK TEETH						
P ₃	L	24	1.0-1.3	1.12	0.12	10.71
	W	24	0.7-1.0	0.84	0.07	8.33
M ₁	L	23	2.2-2.7	2.45	0.17	6.94
	W	23	1.2-1.5	1.36	0.08	5.88
M ₂	L	24	1.8-2.2	1.93	0.13	6.74
	W	25	1.3-1.5	1.40	0.07	5.00
M ₃	L	19	1.4-1.8	1.54	0.14	9.09
	W	19	1.1-1.3	1.21	0.06	4.96
M ₄	L	17	0.9-1.1	1.01	0.06	5.94
	W	18	0.8-1.0	0.88	0.06	6.82
M ₁₋₄	L	12	6.9-7.8	7.27	0.26	3.58
P ₃ -M ₄	L	6	8.1-8.6	8.37	0.21	2.51

complete; MACN 8355, rostral and palatal region of skull with partial dentition; MACN 8372, partial skull with attached mandible (mandible has greater part of dentition but lacks incisors; left half of skull with P¹-M⁴ complete); MACN 8376, a left mandibular ramus with P₃-M₁ complete; MACN 8377, a left mandibular ramus with P₃-M₁ (same individual as 8376); MACN 10245, a left maxillary fragment with P¹-M⁴ complete (labeled *D. spegazzinii*); MACN 10246, rostral part of skull with partial dentition; AMNH 9122, a fragment of a left mandibular ramus with P₃-M₂ complete; AMNH 9599, a left mandibular ramus with M₁₋₄ complete; KUVF 655, a left mandibular ramus with I₁-C complete, alveoli of P₁-P₂ and P₃-M₄ complete, and an associated right mandibular ramus with I₁, alveoli of I₂-P₁, P₂ complete, and P₃-M₄ complete (only M₂ is broken between trigonid and talonid); PU 15068, a fragment of a right mandibular ramus with P₃-M₃ complete, and alveoli of M₄; PU 15624, an incomplete mandibular ramus; PU 15706, a left mandibular ramus with I₁, alveoli of I₂-P₁, P₂ complete, P₃ complete, roots of M₁,

M₂₋₄ complete; PU 15707, a fragment of a right mandibular ramus with base of I₁, alveoli of I₂-P₂, P₃-M₂ complete; PU 15708, a left mandibular ramus with I₁, alveoli of I₂-P₂, and P₃-M₄ complete (only posterior edge of M₄ is broken); PU 15709, a fragment of a right mandibular ramus with I₁-C, a fragment of a left mandibular ramus with I₁, alveoli of I₂-P₂, P₃ complete, anterior half of M₁ present, alveoli of M₂, M₃₋₄ complete, and an associated fragment of a left maxillary with P³-M⁴ complete; and PU 15999, a fragment of a right maxillary with M²⁻³ complete; MLP 11-51, a fragment of a left mandibular ramus with M₂₋₃ complete and alveoli of M₄; MLP 11-55a, a fragment of a left mandibular ramus with M₁₋₂ complete, and roots of M₃; MLP 11-123, a fragment of a left mandibular ramus with P₃-M₃ complete, and alveoli of M₄; MLP 11-124, a fragment of a right mandibular ramus with alveoli of P₂-M₁, and with M₂ complete; MLP 11-128, a fragment of a left mandibular ramus with P₃ complete, and alveoli of P₁₋₂ and M₁. (In addition to the above, Ameghino, 1889, pl. 1, fig. 16, figured a fragment of a mandibular ramus with M₁₋₃, and in 1905, figs. 18, 19, he figured an astragalus and calcaneum, respectively. I have not been able to locate or identify these specimens in the Ameghino collection in the MACN.)

Horizon and locality.—All of the specimens are from the Santa Cruz Formation, Santa Cruz Province, southern Argentina, and their localities of collection are as follows: *Killik Aike* PU 15068 (collected by O. A. Peterson, 1896), PU 15624 (collected by J. B. Hatcher, 1898), PU 15706 (collected by H. Felton, 1899), PU 15707, 15708, 15709 (collected by H. Felton, 1899); [*La*] *Cueva* MACN 8297, 8298, 8300, 8469, 10246 (collected by C. Ameghino, 1892-93); *Santa Cruz* MACN 15, MLP 11-51, 11-55a, 11-123, 11-124, 11-128; *Sehuen* MACN 5677 (collected by C. Ameghino, 1890-91); *Río Gallegos* AMNH 9122, 9599 (collected by B. Brown, 1899); *Monte Observación* MACN 8323-28, 8321 (collected by C. Ameghino, 1891-92), MACN 5671, 5672, 5673, 5674, 5675, 5676, 5690, 5696, 5697, 6595, 8306, 8307, 8308, 8309, 8310 (collected by C. Ameghino, 1890-91); *south side of Río Santa Cruz, 60 miles below Lago Argentino* PU 15999 (collected by J. B. Hatcher, 1897); KUVF 655, collected in 1904 by H. T. Martin from his "Loc. S.A. 2."; MACN 2041 and 2042, collected by C. Ameghino, 1889-90 (locality not specified); MACN 10245, collected by C. Ameghino, 1898 (locality not specified); all other specimens are without collection or locality data.

Age.—Santacrucian.

Diagnosis.—Smallest and most generalized of known Palaeotheriinae; molars relatively narrower and more trenchant than in other known species; P₂ double rooted in some specimens; P₃ large, double

rooted and = or > height of M_1 ; anterobasal cuspule on P_3 large; P^1 double rooted; anterobasal cuspule on P^3 large; differs from contemporaneous *P. intermedius* in being smaller in size with a relatively larger P_3 and with relatively narrower and more trenchant molars (fig. 17).

Comments.—Ameghino (1897, fig. 76; 1903, figs. 62, 95; 1904a, fig. 30) figured a nearly complete skull of *Palaeothenetes minutus*, lacking only the basicranial region. This illustration is apparently based in total or at least in part on MACN 8271 and is here reproduced in Figure 20. The rostral portion of the skull in MACN 8271 is no longer intact, and the illustration thus documents our only knowledge of the upper incisors and canine of the Palaeothenetinae.

As seen in Figure 20, there are three single-rooted upper incisors designated I^1 , I^2 , I^3 . The I^1 is largest and is proodont; I^2 is lower and is elongated anteroposteriorly; and I^3 is slightly higher than I^2 and is button shaped. The I^1 and I^2 are similar to those in living Caenolestinae, whereas the I^3 is more elongated and is thus more similar to I^2 in living forms. The C is similar to the I^3 , but is slightly larger.

Palaeothenetes primus (Ameghino, 1902c). Figure 21; Tables 6, 7.

Palaeapanorthus primus Ameghino, 1902a, p. 77 (*nomen nudum*); 1902c, p. 123.

Type.—MACN 52-373a, a nearly complete edentulous left mandibular ramus.

Hypodigm.—MACN 52-370c, a fragment of a right mandibular ramus with alveoli of P_2 , and P_3 complete; MACN 52-373b, a fragment of a left mandibular ramus with roots of P_3 , M_{1-3} complete, and alveoli of M_4 (possible cotype); MACN 52-373c, a complete lower left I_1 ; MACN 52-373d, root of a lower I_1 ; MACN 52-377a, a right mandibular ramus with alveoli of P_2 , P_3 - M_3 complete, and alveoli of M_4 ; MMP M-944, a right mandibular ramus with alveoli of I_1 - P_2 , roots of P_3 - M_1 and M_{2-4} complete; MLP 77-VI-13-2, a fragment of a right mandibular ramus with M_{1-2} very worn; MLP 77-VI-13-16, a fragment of a left mandibular ramus with M_{1-2} complete; MLP 77-VI-13-17, a right mandibular ramus with P_3 - M_4 complete; MLP 77-VI-13-22, a left mandibular ramus with alveoli of C- P_2 and M_1 and M_4 , and with P_3 and M_{2-3} complete.

Horizon and locality.—All specimens are from the Colhué-Huapí Formation at the Barranca south of Lago Colhué-Huapí, Chubut Province, Argentina. The MACN specimens were collected by C. Ameghino; the MMP specimen (labeled "frente a estacion ferrocarril La Parada") was collected by G. Scaglia, Contreras, and J. Hernández in 1964; the MLP specimens were collected by E. Herrera.

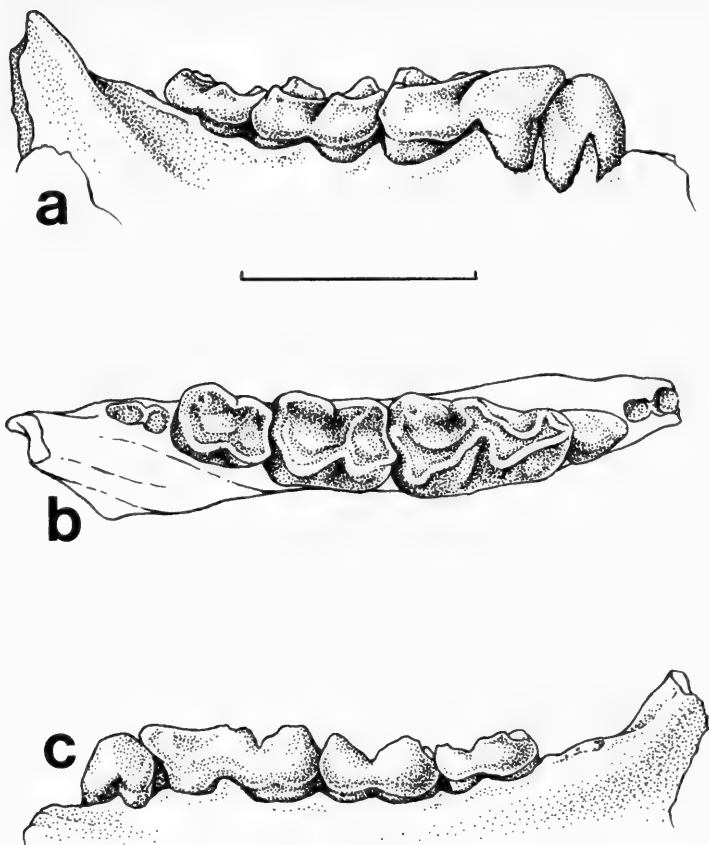


FIG. 21. *Palaeothenes primus* Ameghino, 1902c, p. 123 (Colhuehuapian). MACN 52-377a, a right mandibular ramus with alveoli of P_2 and M_4 , and P_3 - M_3 complete: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

Age.—Colhuehuapian.

Diagnosis.—Small to medium-sized palaeothenine; P_3 large, double rooted and = or < height of M_1 ; differs from *Palaeothenes intermedius* in having slightly larger linear molar dimensions and in a relatively larger P_3 ; differs from *Acelestis oweni* in having a much larger P_3 (fig. 17).

Comments.—In the same box containing the type (MACN 52-377a) is another specimen (MACN 52-377b), a fragment of a left mandibular ramus with alveoli of M_{3-4} . The M_4 alveoli of this specimen are larger than in known specimens of *Palaeothenes primus*; differences in the posterior part of the mandible suggest that it is not referable to that

TABLE 6. Measurements of lower cheek teeth of *Palaeothenes primus*.

	P3		M1		M2		M3		M4		M1-4		P3-M4		
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	
MACN 52-370c	1.5	1.3	
MACN 52-373a	10.2ca	11.8ca	
MACN 52-373b	3.6	2.1	2.5	1.9	2.0	1.5	10.0	...	10.4	11.2ca	
MACN 52-377a	1.5	1.2	3.8	2.2	2.5	2.1	1.9	1.6	11.4	
MMP M-944	2.7	2.1	2.0	1.5	1.4	1.2	12.0ca

TABLE 7. Statistics for some lower cheek teeth of *Palaeotheres primus*.

Dimension		N	OR	x	s	CV
P ₃	L	2	1.5	1.50
	W	2	1.2-1.3	1.25	0.07	5.60
M ₁	L	2	3.6-3.8	3.70	0.14	3.78
	W	2	2.1-2.2	2.15	0.07	3.26
M ₂	L	3	2.5-2.7	2.57	0.12	4.67
	W	3	1.9-2.1	2.03	0.12	5.91
M ₃	L	3	1.9-2.0	1.97	0.06	3.05
	W	3	1.5-1.6	1.53	0.06	3.92
M ₄	L	1	1.4	1.40
	W	1	1.2	1.20
M ₁₋₄	L	3	10.0-10.4	10.20	0.20	1.96
P ₃ -M ₄	L	4	11.2-12.0	11.60	0.37	3.19

species. Ameghino made no specific reference to this specimen, and it is so fragmentary as to be virtually indeterminate. The name *Palaepanorthus secundus* was included, along with *Palaepanorthus primus*, by Ameghino (1902a, p. 77) in a faunal list of Colhuehuapian species. This species was not then nor was it subsequently described, and the name is a *nomen nudum*. As a point of speculation, Ameghino may have coined this name for MACN 52-377b, but later decided not to, or simply forgot to, formally describe it.

Palaeotheres intermedius Ameghino, 1887. Figures 22, 23; Tables 8, 9.

Palaeotheres intermedius Ameghino, 1887, p. 6 (not Sinclair, 1906, p. 430, pl. 63, figs. 3, 7, pl. 64, figs. 1, 1a); Schlosser, 1925, p. 27, fig. 40A; Simpson, 1930, p. 58.

Epanorthus intermedius Ameghino, 1889, p. 274, pl. 1, fig. 15.

Metaepanorthus intermedius Ameghino, 1894, p. 348.

Epanorthus lepidus Ameghino, 1891b, p. 305; 1894, p. 348.

Palaeotheres lepidus Sinclair, 1906, p. 431, pl. 62, figs. 6, 6a.

Epanorthus inaequalis Ameghino, 1891b, p. 305; 1894, p. 348; 1898, p. 186.

Palaeotheres inaequalis Sinclair, 1906, p. 455.

Halmadromus vagus Ameghino, 1891b, p. 306; 1894, p. 344; 1898, p. 186; Palmer, 1904, p. 307.

Metriodromus arenarus Ameghino, 1894, p. 343.

Dipilus arenarus Clemens & Marshall, 1976, p. 70.

Metriodromus crassidens Ameghino, 1898, p. 186.

Dipilus crassidens Clemens & Marshall, 1976, p. 71.

Epanorthus lemoinei (partim) Ameghino, 1894, figs. 36, 37; 1898, figs. 50e, f.

Type of Palaeotheres intermedius.—MACN 2, a fragment of a right mandibular ramus with P₃-M₃ complete (figured by Ameghino, 1889, pl. 1, fig. 15).

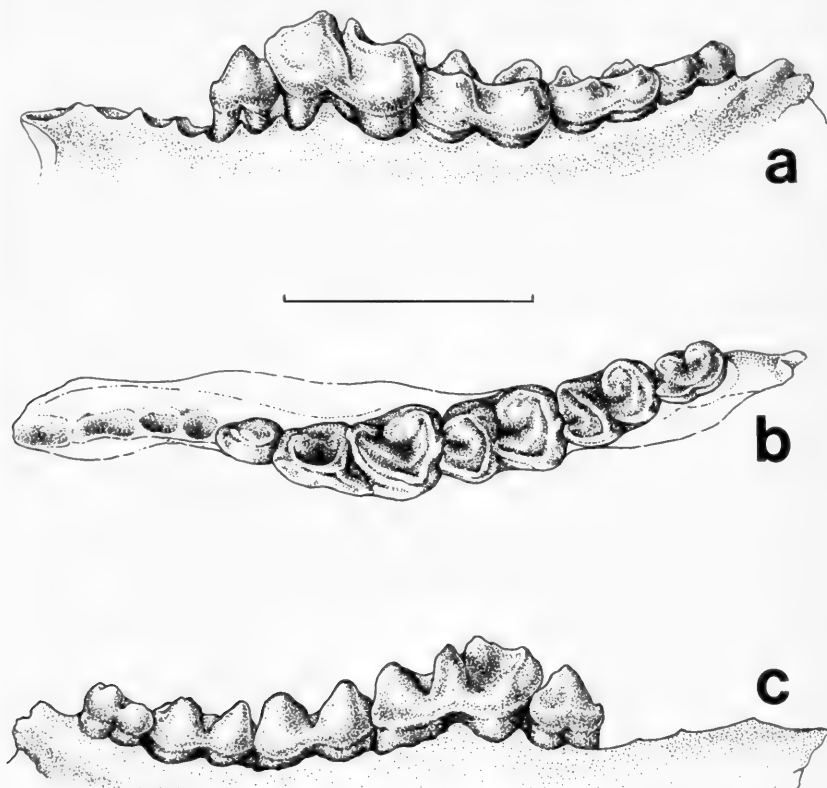


FIG. 22. *Palaeothentes intermedius* Ameghino, 1887, p. 6 (Santacrucian). MACN 5678 (type of "*Epanorthus lepidus*"), a left mandibular ramus with alveoli of C-P₂, and P₃-M₄ complete: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

Type of Epanorthus lepidus.—MACN 5678, a left mandibular ramus with P₃-M₄ complete (listed as type in Ameghino's catalogue).

Type of Epanorthus inaequalis.—MACN 5689, a fragment of a left mandibular ramus with M₁ complete, and alveoli of M₂₋₄.

Type of Halmadromus vagus.—MACN 5694, a fragment of a left mandibular ramus with alveoli of P₃-M₃.

Type of Metriodromus arenarus.—MACN 5699, a fragment of a right mandibular ramus with M₃ complete, and alveoli of M₂ and M₄.

Type of Metriodromus crassidens.—MACN 8508, a right mandibular ramus with P₃ and M₂ complete, and alveoli of M₁ and M₃₋₄.

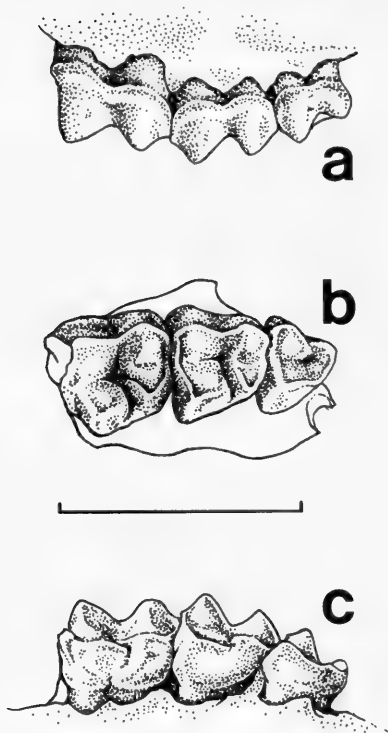


FIG. 23. *Palaeotheres intermedius* Ameghino, 1887, p. 6 (Santacrucian). MACN 5646, a fragment of a left maxillary with M^{1-3} complete: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

Hypodigm.—The six types and MACN 2063, a fragment of a left mandibular ramus with M_{1-2} complete (listed as type of *E. intermedius* in Ameghino's catalogue and a possible cotype); MACN 5582, a nearly complete right mandibular ramus with I_1 and P_3 - M_3 complete; MACN 5584, a fragment of a right mandibular ramus with roots of M_1 and anterior half of M_2 , and talonid of M_2 and M_{3-4} complete; MACN 5585, a fragment of a right mandibular ramus with alveoli of M_1 and M_{2-4} complete; MACN 5646, a fragment of a left maxillary with M^{1-3} complete (figured as *P. lemoinei* by Ameghino, 1894, figs. 36, 37; 1898, figs. 50e, f); MACN 5681, a fragment of a right mandibular ramus with alveoli of I_2 - P_2 and P_3 - M_1 complete; MACN 5682, a fragment of a left mandibular ramus with P_3 - M_1 complete; MACN 5683, a fragment of a left mandibular ramus with P_3 and M_2 complete, and alveoli of M_1 ;

TABLE 8. Measurements of cheek teeth of *Palaeothenes intermedius*.

	P3		M1		M2		M3		M4		M1-4		P3-M4	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
UPPER CHEEK TEETH														
MACN 5646	2.3	2.5	2.0	2.5	1.6	2.0
LOWER CHEEK TEETH														
MACN 2	1.3	1.2	3.5	1.8	2.4	2.0	2.0	1.5	9.2ca	...	10.6ca	...
MACN 2063	3.7	1.8	2.7	2.0
MACN 5582	1.3	1.0	3.4	1.8	2.6	1.9	2.1	1.5	9.6ca	...	10.7ca	...
MACN 5584	1.9	1.9	1.5	1.3	1.1
MACN 5585	2.5	1.8	1.8	1.5	1.3	1.0
MACN 5678	1.1	1.0	3.5	1.9	2.8	1.8	2.0	1.3	1.1	1.0	9.5	...	10.5	...
MACN 5681	1.3	1.2	3.4	1.8
MACN 5682	1.2	1.1	3.5	1.9
MACN 5683	1.2	1.0	2.5	1.9
MACN 5689	3.9	1.8
MACN 5699	1.8	1.5
MACN 8296	1.1	0.9	3.4	1.7
MACN 8302	2.5	1.8	1.5	1.3	1.1
MACN 8311	2.5	1.8	2.0	1.4
MACN 8508	1.2	1.0	2.7	2.0	10.9ca	...
NMNH 5937	1.3	0.8	3.4	...	2.5	1.8	10.7ca	...
AMNH 9597	1.3	0.9	3.4	1.8	2.4	1.8	1.9	1.5	9.6ca
AMNH 9598	3.5	1.7	2.4	1.8	1.8	1.4	9.5ca
AMNH 9600	1.3	1.0	3.4	1.8	2.4	1.8	1.8	1.5

TABLE 9. Statistics for some lower cheek teeth of *Palaeotheres intermedius*.

Dimension		N	OR	x	s	CV
P ₃	L	11	1.1-1.3	1.24	0.08	6.45
	W	11	0.8-1.2	1.01	0.12	11.88
M ₁	L	12	3.4-3.9	3.50	0.15	4.29
	W	11	1.7-1.9	1.80	0.06	3.33
M ₂	L	13	2.4-2.8	2.53	0.13	5.14
	W	14	1.8-2.0	1.86	0.08	4.30
M ₃	L	11	1.5-2.1	1.87	0.16	8.56
	W	11	1.3-1.5	1.45	0.08	5.52
M ₄	L	4	1.1-1.3	1.20	0.12	10.00
	W	3	1.0-1.1	1.03	0.06	5.83
M ₁₋₄	L	6	9.2-9.7	9.52	0.17	1.79
P ₃ -M ₄	L	5	10.5-10.9	10.68	0.15	1.40

MACN 8296, a fragment of a left mandibular ramus with P₃-M₁ complete, and trigonid of M₂ (very worn) (labeled *E. simplex*); MACN 8302, a right mandibular ramus with base of I₁, alveoli of C-M₁, and M₂₋₄ complete (labeled *M. intermedius*); MACN 8311, a fragment of a left mandibular ramus with alveoli of M₁ and M₄, and M₂₋₃ complete (labeled *M. complicatus*); NMNH 5937 (= AMNH 9596), a right mandibular ramus with P₃ complete, M₁ missing labial surface, M₂ complete, and roots of M₃₋₄; AMNH 9597, a right mandibular ramus with P₃-M₃ complete (figured by Sinclair, 1906, pl. 63, fig. 6); AMNH 9598, a left mandibular ramus with posterior half of P₃, M₁₋₃ complete, and alveoli of M₄; AMNH 9600, a left mandibular ramus with P₃-M₃ complete; MLP 11-48, a fragment of a left mandibular ramus with M₁₋₃ complete and alveoli of M₄; MLP 11-53, a fragment of a right mandibular ramus with posterior root of P₃ and anterior root of M₁, talonid of M₁ and M₂ complete but very worn; MLP 11-127, a fragment of a right mandibular ramus with M₂₋₄ complete; MLP 11-131, a fragment of a right mandibular ramus with P₃-M₁; MLP 55-XII-13-150, a right mandibular ramus with P₃-M₃ complete and alveoli of M₄.

Horizon and locality.—All specimens are from the Santa Cruz Formation, Santa Cruz Province, Patagonia, southern Argentina, and their localities of collection are as follows: *Santa Cruz* MACN 2, MLP 11-127, 11-131; *Sehuen* MACN 5689 (collected by C. Ameghino, 1890-91); [*La*] *Cueva* MACN 8302, 8508 (collected by C. Ameghino, 1892-93); *Monte Observación* MACN 5582, 5584, 5585, 5646, 5678, 5681, 5682, 5683, 5694, 5699, 8311 (collected by C. Ameghino, 1890-91), MACN 8296 (collected by C. Ameghino, 1891-92); *Rio Gallegos* NMNH 5937, AMNH 9597, 9598, 9600 (collected by B. Brown, 1899); *Monte León*

MLP 55-XII-13-150; MACN 2063 (collected in 1889-90, no additional locality data); MLP 11-48, 11-53 (no data).

Age.—Santacrucian.

Diagnosis.—Small to medium-sized palaeothentine; P_3 large, double rooted, less than height of M_1 ; differs from *Palaeothentes primus* in being slightly smaller in size and with a smaller P_3 ; differs from *P. minutus* in being larger and with a slightly smaller P_3 ; differs from *Acestis oweni* in being slightly smaller in linear tooth dimensions and with a much larger P_3 (fig. 17).

Comments.—*Palaeothentes intermedius* has slightly larger linear molar dimensions and a relatively larger P_3 than the Colhuehuapian species *P. primus*. These differences are minor, and the two species appear to represent a single phylogenetic lineage. I therefore recognize *P. primus* as the probable Colhuehuapian ancestor of *P. intermedius*.

Palaeothentes lucina (Ameghino, 1903). Figure 24; Table 10.

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

Palaeothentes lucina Patterson & Marshall, 1978, p. 82, fig. 18.

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

Hypodigm.—Type and AC 3110, a left mandibular ramus with P_3 missing anterior tip, and M_{1-4} nearly complete.

Horizon and locality.—The type is from the "Piroteriense," Probably from Cabeza Blanca; AC 3110 is definitely from that locality.

Age.—Deseadan.

Diagnosis.—Compared with *Palaeothentes chubutensis* and *P. boliviensis*, P_3 similar in relative length compared to M_1 , but considerably narrower and lower; larger than in *Acestis praecursor*; decrease in size from M_1 to M_4 more gradual than in *P. chubutensis*; differs from *P. lemoinei* in being slightly smaller in overall linear tooth dimensions but with a larger P_3 (fig. 17).

Comments.—Ameghino erected *Pilchenia lucina* on an isolated molar that Loomis (1914) 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. I agree with this assignment.

When he proposed *Pilchenia*, Ameghino did not present criteria that would distinguish it from any of the 15 named Colhuehuapian and Santacrucian genera of Palaeothentinae. I have compared AC 3110 with a large sample of Santacrucian species of *Palaeothentes* and find no reason to recognize it as distinct at the generic level; I therefore assign *lucina* to that genus.

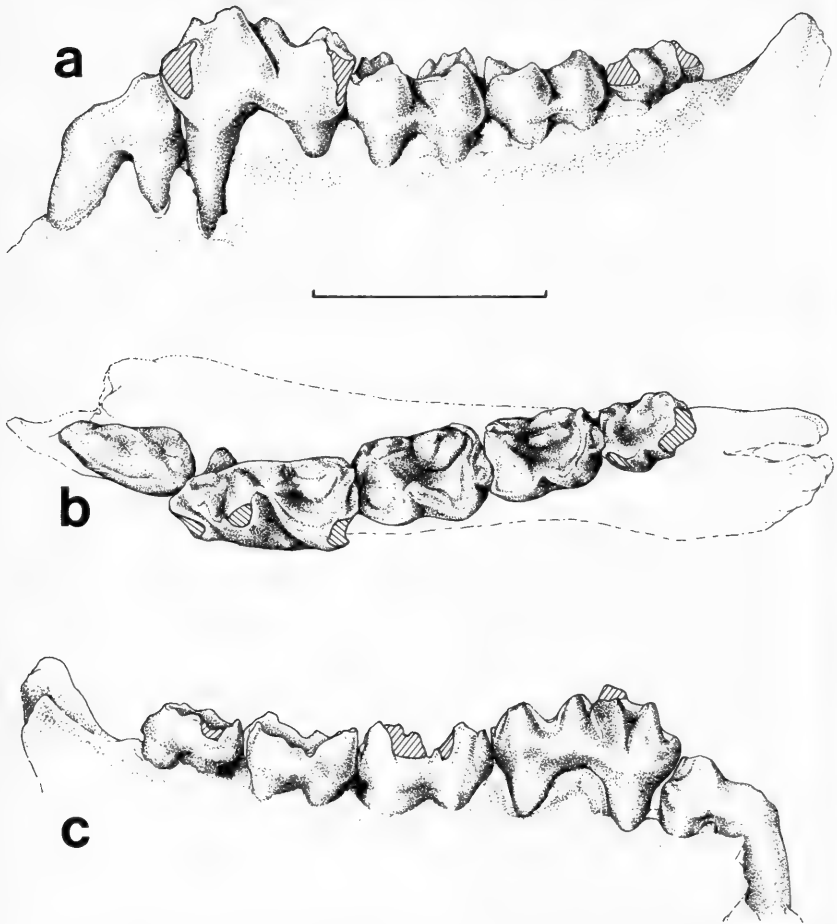


FIG. 24. *Palaeothenes lucina* (Ameghino, 1903, p. 128) (Deseadan). AC 3110, a left mandibular ramus with P_3 - M_4 : a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

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 "Notohipidense" (early Santacrucian) horizon at Karaiken, near the eastern end of Lago Argentino, Santa Cruz Province, Argentina. As noted by Marshall & Pascual (1977, p. 113), this specimen is clearly referable to *Palaeothenes* and is here regarded as conspecific with *P. lemoinei* from the Santa Cruz beds along the Atlantic coast between Río Gallegos in the south and Monte León in the north.

TABLE 10. Measurements of lower cheek teeth of Desmodontinae species of Palaeothentinae (after Patterson & Marshall, 1978, table 10).

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

*Measurements based on roots.

**After Loomis (1914, p. 224).

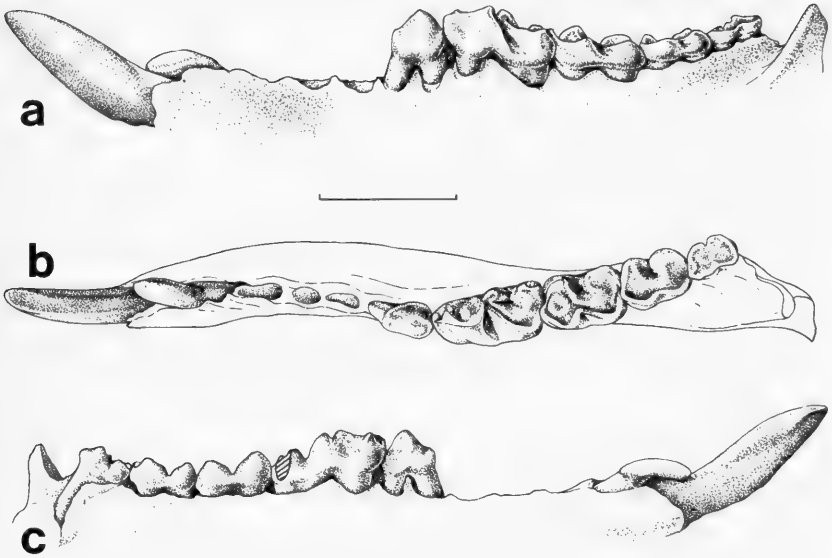


FIG. 25. *Palaeothenes lemoinei* Ameghino, 1887, p. 6 (Santacrucian). MACN 8293, a nearly complete left mandibular ramus with alveoli of C-P₂, and I₁₋₂ and P₃₋₄ complete: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

***Palaeothenes lemoinei* Ameghino, 1887. Figures 25, 26; Tables 11-13.**

Palaeothenes lemoinei Ameghino, 1887, p. 6.

Epanorthus lemoinei Ameghino, 1889, p. 273, pl. 1, figs. 13, 14; 1890, fig. 7; 1894, p. 346, fig. 38; 1898, p. 186, fig. 50 g.

Epanorthus ambiguus Ameghino, 1891b, p. 305; 1894, p. 347; 1898, p. 186.

Palaeothenes ambiguus Sinclair, 1906, p. 454.

Epanorthus holmbergi Ameghino, 1890, p. 157, fig. 8.

Metaepanorthus holmbergi Ameghino, 1894, p. 349, fig. 39; 1898, p. 186; 1903, p. 172 (partim); Schlosser, 1925, p. 27, fig. 51A, B.

Palaeothenes holmbergi Sinclair, 1906, p. 455.

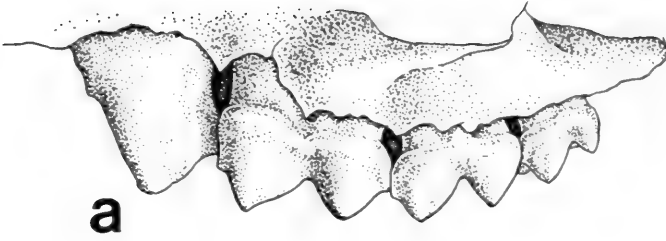
Callomenus ligatus Ameghino, 1903, p. 88 (partim, figs. 10 & 46 are referable to *P. lemoinei*).

Pilchenia lobata Ameghino, 1903, p. 128, fig. 50; 1904b, p. 259 (said to be new in 1904, but publication in 1903 was prior and valid).

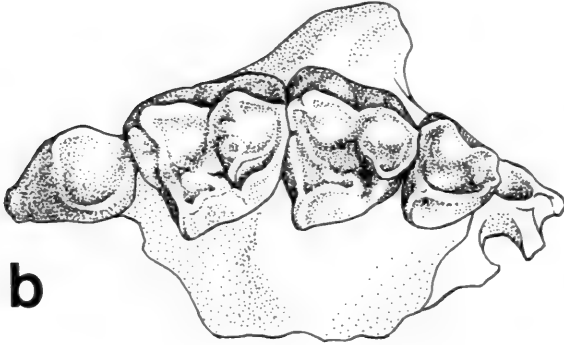
Palaeothenes lobata Marshall & Pascual, 1977, p. 111, fig. 6.

Type of Palaeothenes lemoinei.—MACN 3, a right mandibular ramus with M₁₋₄ complete but worn (figured by Ameghino, 1889, pl. 1, fig. 13; 1890, fig. 7; 1894, fig. 38; 1898, fig. 50g).

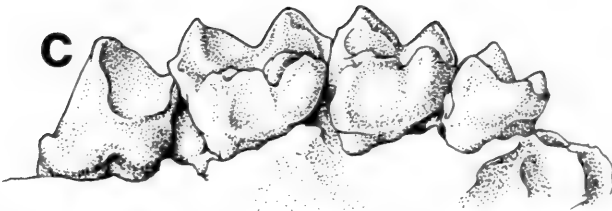
Type of Epanorthus ambiguus.—MACN 5565, a fragment of a right mandibular ramus with M₂₋₄ complete.



a



b



c

FIG. 26. *Palaeotheres lemoinei* Ameghino, 1887, p. 6 (Santacrucian). MACN 5568, a fragment of a left maxillary with P³-M³ complete, and alveoli of M¹: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 5 mm.

TABLE 11. Measurements of upper cheek teeth of *Palaeotheres lemoinei*.

	P ³		M ¹		M ²		M ³		M ⁴		M ¹⁻⁴	
	L	W	L	W	L	W	L	W	L	W	L	W
MACN 5568	3.0	2.0	3.7	3.3	2.7	3.6	1.9	2.6
MACN 5576	3.5	3.6	2.9	3.4
MACN 5577	3.8	3.4	2.9	3.7	1.9	2.7	1.5	2.0	10.0	...
MACN 5578	3.3	2.2	3.8	3.3

TABLE 12. Measurements of lower cheek teeth of *Palaeotheres lemoinei*.

	P ₃		M ₁		M ₂		M ₃		M ₄		M ₁₋₄		P ₃ -M ₄	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
MACN 3	4.5	2.4	3.2	2.5	2.6	2.1	1.9	1.4	12.2	1.4
MACN 2071	1.9	1.3	4.4	2.3	3.2	2.3	2.5	2.0	1.6	1.4	12.0	1.4	14.0	...
MACN 5565	3.5	2.6	2.6	2.2	1.9	1.6
MACN 5570	2.2	1.6	3.2	2.4	2.5	2.0	12.4ca	1.5	14.4ca	...
MACN 5571	4.7	2.3	3.2	2.3	2.6	2.0	1.9	1.5	12.5	1.5
MACN 5572	2.0	1.3	4.4	2.3
MACN 8259	3.3	2.4	2.6	2.0
MACN 8291	2.2	1.4	4.8	2.5	3.5	2.6	2.8	2.1	12.7	1.5	15.0	...
MACN 8292	2.0	1.4	4.8	2.5	3.5	2.5	2.5	2.1	1.6	1.5	12.8	1.5	14.5	...
MACN 8293	2.0	1.5	4.4	2.2	3.2	2.3	2.5	2.0	1.8	1.3	12.0	1.3	14.0	...
MACN 8294	4.5	2.3	3.2	2.4	2.6	2.0	12.1
MACN 8295	2.1	1.5	4.6	2.2	3.3	2.4	2.6	2.0	1.8	1.5	12.5	1.5	14.6	...
MACN 10244	1.9	1.4	4.4	2.3	3.4	2.5
MACN 52-379	3.4	2.5
FMNH P15264	2.0	1.3	4.4	2.2	3.2
MLP 68-1-17-208	3.5	2.4	2.5	1.9
MLP 68-1-17-209	3.7	2.5	2.6	2.0

TABLE 13. Statistics for some cheek tooth dimensions of *Palaeothenes lemoinei*.

Dimension		N	OR	x	s	CV
UPPER CHEEK TEETH						
P ³	L	2	3.0-3.3	3.15	0.21	6.67
	W	2	2.0-2.2	2.10	0.14	6.67
M ¹	L	4	3.5-3.8	3.70	0.14	3.78
	W	4	3.3-3.6	3.40	0.14	4.12
M ²	L	3	2.7-2.9	2.83	0.12	4.24
	W	3	3.4-3.7	3.57	0.15	4.20
M ³	L	2	1.9	1.9
	W	2	2.6-2.7	2.65	0.07	2.64
M ⁴	L	1	1.5	1.5
	W	1	2.0	2.0
M ¹⁻⁴	L	1	10.0	10.0
LOWER CHEEK TEETH						
P ₃	L	9	1.9-2.2	2.03	0.11	5.42
	W	9	1.3-1.6	1.41	0.11	7.80
M ₁	L	11	4.4-4.8	4.54	0.16	3.52
	W	11	2.2-2.5	2.32	0.11	4.74
M ₂	L	16	3.2-3.7	3.34	0.16	4.79
	W	15	2.3-2.6	2.44	0.10	4.10
M ₃	L	13	2.5-2.8	2.58	0.08	3.10
	W	13	1.9-2.2	2.03	0.08	3.94
M ₄	L	7	1.6-1.9	1.79	0.13	7.26
	W	7	1.3-1.6	1.46	0.10	6.85
M ₁₋₄	L	9	12.0-12.8	12.36	0.30	2.43
P ₃ -M ₄	L	6	14.0-15.0	14.42	0.38	2.64

Type of Epanorthus holmbergi.—MACN 2071, originally a right mandibular ramus with P₃-M₄ complete [now in two parts—anterior with P₃ through trigonid of M₂, posterior with M₃₋₄ complete; anterior part, which had I₁ and diastema with alveoli of I₂-P₂ has been lost since specimen was figured by Ameghino (1890, fig. 8; 1894, fig. 39)].

Type of Pilchenia lobata.—MACN 52-379, a fragment of a right mandibular ramus with M₂.

Hypodigm.—The four types and FMNH P15264, a fragment of a left mandibular ramus with P₃-M₁ complete, and M₂ missing posterolabial corner; MACN 4, a fragment of an M¹ (figured by Ameghino, 1889, pl. 1, fig. 14); MACN 5568, a fragment of a left maxillary with P³-M³ complete and alveoli of M⁴; MACN 5570, a left mandibular ramus with P₃-M₄ complete (crown of M₁ broken); MACN 5571, a fragment of a left mandibular ramus with M₁₋₄ complete; MACN 5572, a fragment of a right mandibular ramus with P₃-M₁ complete; MACN 5576, a fragment of a right maxillary with M¹⁻² complete; MACN 5577, a fragment of a left maxillary with M¹⁻⁴ complete; MACN 5578, a fragment of a right

maxillary with P^3-M^1 , and alveoli of M^2 ; MACN 8259, a fragment of a right mandibular ramus with M_{2-3} (M_3 is now loose from mandible; originally referred in literature to *C. ligatus*—figured by Ameghino, 1903, figs. 10, 46); MACN 8291, a left mandibular ramus with P_1-M_4 complete but worn (labeled *E. ambiguus*); MACN 8292, a right mandibular ramus with P_3-M_4 (labeled *E. ambiguus*); MACN 8293, a nearly complete left mandibular ramus with nearly complete dentition (labeled *E. lemoinei*); MACN 8294, a right mandibular ramus with P_3-M_3 complete, and roots of M_4 (labeled *E. lemoinei*); MACN 8295, a left mandibular ramus with complete I_1 , alveoli of I_2-P_2 , and P_3-M_4 complete; MACN 10244, a right mandibular ramus with base of I_1 , alveoli of I_2-P_2 , and P_3-M_2 complete; MLP 11-52, a fragment of a right mandibular ramus with alveoli of M_1 , M_2 complete, alveoli of M_{3-4} ; MLP 11-56, a fragment of a right mandibular ramus with alveoli of $C-P_2$ and with P_3 complete; MLP 11-129, a fragment of a right mandibular ramus with I_1 and P_3 complete, and alveoli of I_2-P_2 ; MLP 55-XII-13-147, a fragment of a left mandibular ramus with P_2-M_1 complete; MLP 68-1-17-208, a fragment of a right mandibular ramus with M_{2-3} complete and roots of M_4 ; and MLP 68-1-17-209, a fragment of a right mandibular ramus with M_{2-3} complete, but broken.

Horizon and locality.—All specimens are from the Santa Cruz Formation, Santa Cruz Province, Patagonia, southern Argentina, and their localities of collection are as follows: *Corriguen-Kaik* MACN 8291 (collected by C. Ameghino, 1892-93); [*La*] *Cueva* MACN 8292, 8294, 8295 (collected by C. Ameghino, 1892-93); *Santa Cruz* MACN 3, 4, MLP 11-129; *Quequa-Quemada* MACN 8293 (collected by C. Ameghino, 1892-93); *Sehuen* MACN 5565, 5568 (collected by C. Ameghino, 1890-91); *Monte León* MLP 55-XII-13-147; *Monte Observación* MACN 5570, 5571, 5572, 5576, 5577, 5578 (collected by C. Ameghino, 1890-91); MACN 10244 (collected by C. Ameghino, 1891-92); *12 miles North of Cape Fairweather* FMNH P15264; *Karaiken* MACN 52-379 (collected by C. Ameghino, 1889); *Cerro Centinela* MLP 68-1-17-208, 68-1-17-209 (collected by R. Pascual and O. E. Odreman Rivas, 1968); MACN 2071 (collected in 1889-90—no locality data); MACN 8259, MLP 11-52, 11-56 (no data).

Age.—Santacrucian.

Diagnosis.—Medium to large-sized palaeothentine; $P_3 \approx$ in height to M_1 ; M^3 larger than in *Acestis oweni* and with relatively larger hypocone; intermediate in size between contemporaneous *P. intermedius* and *P. aratae*; differs from Deseadan *P. lucina* in being slightly larger in overall linear tooth dimensions but with a smaller P_3 (fig. 17).

Comments.—*Palaeothenes lemoinei* is similar in size and structure to the Deseadan species *P. lucina*. They differ in the latter being slightly smaller in overall linear tooth dimensions and in having an absolutely larger P_3 . These differences are, however, minor, and these species are here regarded as representing a single phylogenetic lineage. I recognize *P. lucina* as the probable Deseadan ancestor of *P. lemoinei*.

Palaeothenes boliviensis Patterson & Marshall, 1978. Figure 27; Table 10.

Palaeothenes boliviensis Patterson & Marshall, 1978, p. 83, fig. 19.

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

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

Age.—Deseadan.

Diagnosis.—Large palaeothenine; $P_3 \approx$ in height to M_1 trigonid; smaller than *Palaeothenes chubutensis*; considerably larger and with more prominent and higher-crowned P_3 than contemporaneous *P. lucina* and *Acestis praecursor* (fig. 17).

Comments.—*Palaeothenes boliviensis* is the only palaeothenine known from the Salla fauna, and it is the the only palaeothenine yet known outside of 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 palaeothenine. Except for the very large Santacrucian species *P. aratae*, *P. boliviensis* is considerably larger than any other known Colhuehuapian or Santacrucian palaeothenine.

Palaeothenes chubutensis (Ameghino, 1897). Figure 28; Table 10.

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

Palaepanorthus chubutensis Ameghino, 1902a, p. 77.

Palaeothenes chubutensis Loomis, 1914, p. 221, fig. 145; Patterson & Marshall, 1978, p. 85, fig. 20.

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

Hypodigm.—Type only.

Horizon and locality.—Chubut Province, Argentina; exact locality is not known, but probably from Cabeza Blanca.

Age.—Deseadan.

Diagnosis.—Largest known species of pre-Santacrucian Palaeotheninae; $P_3 \approx$ in height to M_1 trigonid; differs from similar-sized Santacrucian *Palaeothenes aratae* in having a slightly deeper, more robust mandibular ramus and a large P_3 (fig. 17).

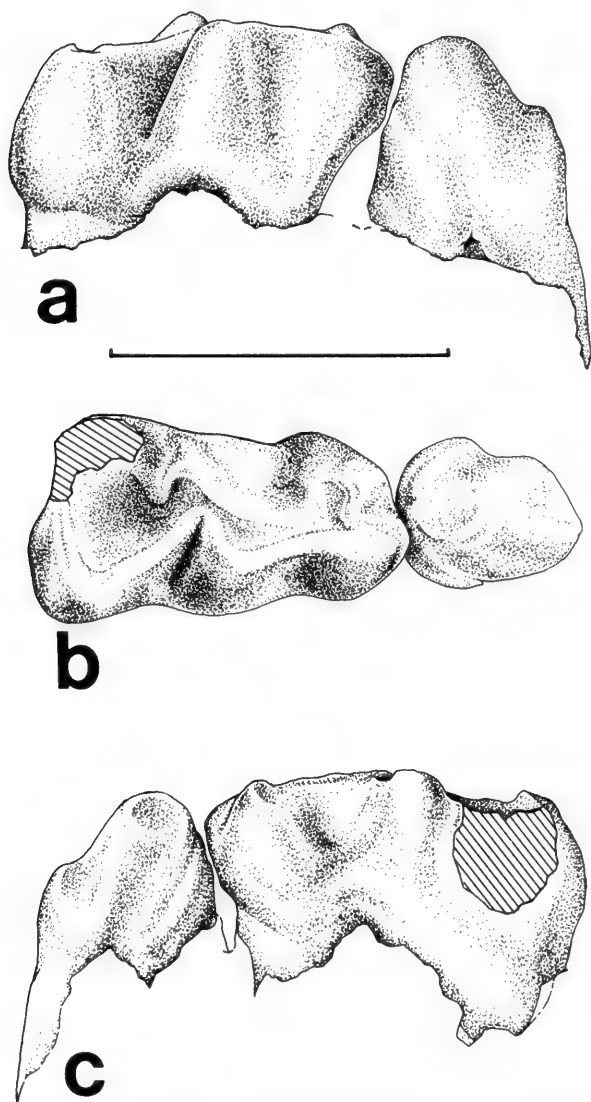


FIG. 27. *Palaeotheres boliviensis* Patterson & Marshall, 1978, p. 83 (Deseadan). PU 21977 (type), a fragment of a right mandibular ramus with P₃-M₁ (posterolingual corner of M₁ talonid is missing): a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

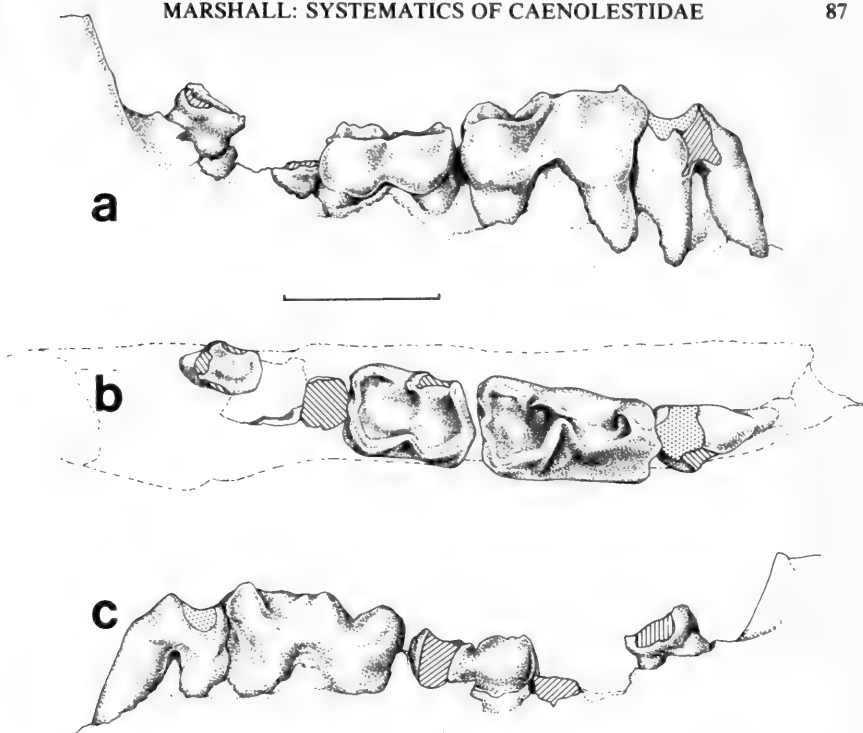


FIG. 28. *Palaeothenes chubutensis* (Ameghino, 1897, p. 500) (Deseadan). MACN 52-378 (type), a right mandibular ramus with posterior root of P_2 , P_3 - M_2 , and M_4 relatively complete, and roots of M_3 (all teeth are heavily worn): a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

Comments.—Ameghino (1897, fig. 77) figured the type of *Palaeothenes 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.

***Palaeothenes aratae* Ameghino, 1887. Figures 29, 30; Tables 14, 15.**

Palaeothenes aratae Moreno, 1882, p. 122 (*nomen nudum*).

Palaeothenes aratae Ameghino, 1887, p. 5; Sinclair, 1906, p. 428, text-fig. 8, pl. 63, figs. 2, 2a; J. L. Kraglievich, 1953, p. 54, fig. 6D.

Epanorthus aratae Ameghino, 1889, p. 272, pl. 1, figs. 10-12; 1894, p. 347.

Type.—MACN 14, a right mandibular ramus with alveoli of P_{1-2} , P_3 - M_4 complete (figured by Sinclair, 1906, text-fig. 8; J. L. Kraglievich, 1953, fig. 6D).

Hypodigm.—MACN 1340 (cast), a right mandibular ramus with roots of P_{1-3} , M_{1-2} present but worn, and roots of M_{3-4} (figured by Ameghino, 1889, pl. 1, fig. 11-11a; original probably in MLP); MACN

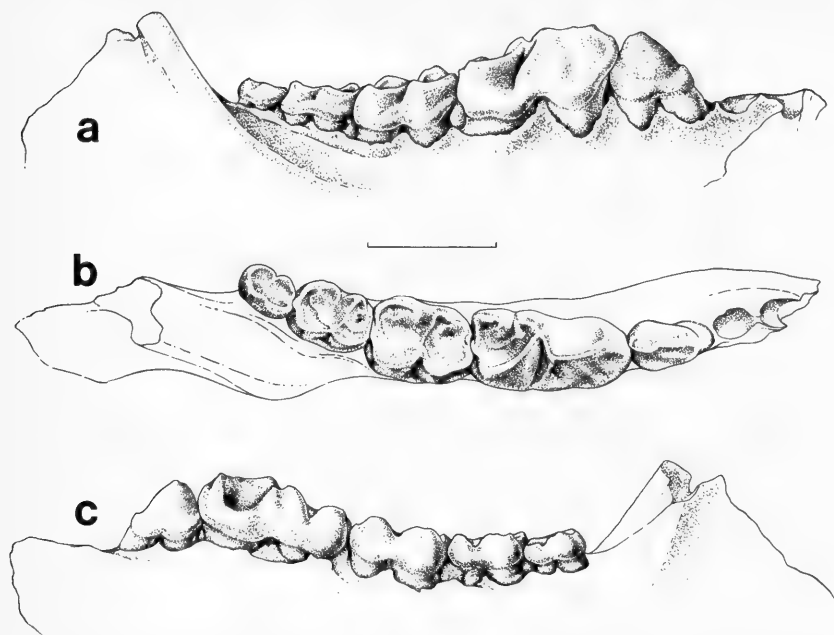


FIG. 29. *Palaeothenetes aratae* Ameghino, 1887, p. 5 (Santacrucean). MACN 14 (type), a right mandibular ramus with alveoli of P_{1-2} , and P_3 - M_4 complete: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

5563, a fragment of a left mandibular ramus with P_3 - M_2 complete, and MACN 5564, a complete associated left I_1 ; MACN 5566, a fragment of a left mandibular ramus with P_3 ; MACN 8289, a right maxillary fragment with roots of P^{1-2} , space for P^3 , and M^{1-3} complete; MACN 8290, a fragment of a right mandibular ramus with alveoli of I_2 - P_2 (which decrease in size anteriorly), P_3 - M_3 complete, and alveoli of M_4 ; AMNH 9549, a right maxillary fragment with alveoli of P^1 , P^{2-3} complete, alveoli of M^1 , and M^{2-4} complete; MLP 11-93, a fragment of a right mandibular ramus with trigonid of M_3 present and roots of C - M_1 , talonid of M_2 , and M_{3-4} .

Horizon and locality.—All specimens are from the Santa Cruz Formation, Santa Cruz Province, Patagonia, southern Argentina, and their localities of collection are as follows: *Santa Cruz* MACN 14 (collected by C. Ameghino, 1890-91); *Sehuen* MACN 5563, 5564, 5566, 8289 (collected by C. Ameghino, 1890-91); *Monte Observación* MACN 8290 (collected by C. Ameghino, 1890-91); *Río Gallegos* AMNH 9549 (collected by B. Brown, 1899); MACN 1340 and MLP 11-93 (without locality data).

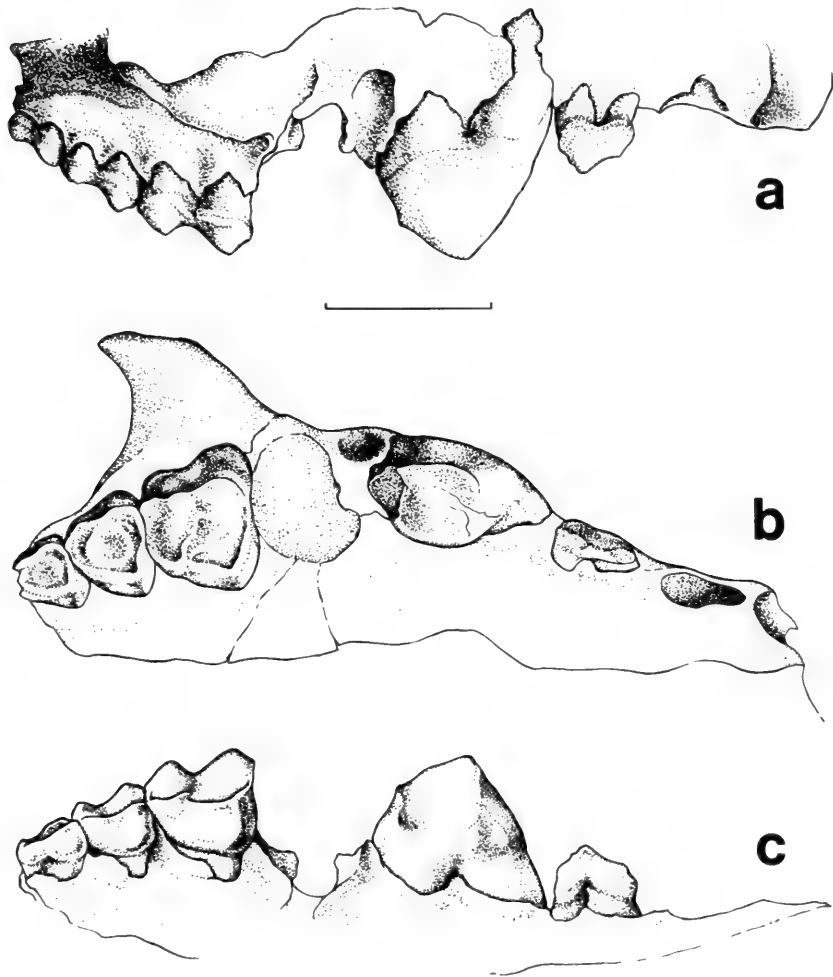


FIG. 30. *Palaeothentes aratae* Ameghino, 1887, p. 5 (Santacrucian). AMNH 9549, a right maxillary fragment with alveoli of P^1 and M^1 , and P^{2-3} and M^{2-4} complete: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

Age.—Santacrucian.

Diagnosis.—Largest known species of Santacrucian palaeothentine and only known species with single-rooted P^1 ; $P_3 \approx$ in height to M_1 trigonid; teeth anterior to P_3^3 are more spaced than in other species; differs from similar-sized Deseadan *P. chubutensis* in having a slightly shallower and less robust mandibular ramus and a slightly smaller P_3 (fig. 17).

TABLE 14. Measurements of cheek teeth of *Palaeotherium aratae*.

	P3		M1		M2		M3		M4		M1-4		P3-M4	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
UPPER CHEEK TEETH														
MACN 8289	4.4	4.3	3.6	4.4	2.3	3.0
AMNH 9549*	5.3	3.4	3.5	4.6	2.5	3.3	2.0	2.4	16.5
LOWER CHEEK TEETH														
MACN 14	3.0	2.1	6.4	3.3	4.3	3.2	3.1	2.5	2.2	1.8	16.4	18.8
MACN 5563	3.2	2.3	6.6	3.2	4.4	3.2
MACN 5566	2.9	2.0
MACN 8290	2.6	2.0	6.3	3.2	4.3	3.1	3.1	2.5

*p2L = 2.3, W = 1.4.

TABLE 15. Statistics for some lower cheek teeth of *Palaeothentes aratae*.

Dimension		N	OR	x	s	CV
P ₃	L	4	2.6-3.2	2.93	0.25	8.53
	W	4	2.0-2.3	2.10	0.14	6.67
M ₁	L	3	6.3-6.6	6.43	0.15	2.33
	W	3	3.2-3.3	3.23	0.06	1.86
M ₂	L	3	4.3-4.4	4.33	0.06	1.39
	W	3	3.1-3.2	3.17	0.06	1.89
M ₃	L	2	3.1	3.1
	W	2	2.5	2.5

Comments.—The specimen figured by Ameghino (1889, pl. 1, fig. 10-10b) as *Epanorthus aratae* is MACN 8250. It was later made the type of *Abderites altiramis* by Ameghino (1894, p. 304) and was characterized as being almost twice as large as *Abderites crassiramis*. The specimen is, however, not an abderitine, but a small borhyaenid. The size of the roots of M₃₋₄ and structure of the M₃ talonid agree perfectly with the type of *Perathereutes pungens* (MACN 684), which is also of Santacrucian age. The ramus of *A. altiramis* is slightly shallower and more gracile than that of *P. pungens*, but these differences are minor, and they surely represent no more than individual variation within a single species. The name *A. altiramis* thus represents a junior synonym of *Perathereutes pungens* Ameghino, 1891b, the latter having three years date of priority over the former (see Marshall, 1976a, p. 72). In addition, the cranial roof fragment (MACN 1074) figured as *Epanorthus aratae* by Ameghino (1889, pl. 1, figs. 12-12a) is not of a marsupial, but more probably represents a dasypodid edentate.

Palaeothentes aratae is very similar to the Deseadan *P. chubutensis* and can be regarded as a direct descendant of that species. The primary changes involved in this lineage include a slight reduction in size and robustness of the mandibular ramus and in size of the P₃.

Acdestis Ameghino, 1887

Acdestis Ameghino, 1887, p. 5.

Dipilus Ameghino, 1890, p. 153.

Decastis Ameghino, 1891b, p. 305.

Callomenus Ameghino, 1891b, p. 306.

Type of Acdestis.—*A. oweni* Ameghino, 1887, p. 5.

Type of Dipilus.—*D. spegazzinii* Ameghino, 1890, p. 154.

Type of Decastis.—*D. columnaris* Ameghino, 1891b, p. 305.

Type of Callomenus.—*C. intervalatus* Ameghino, 1891b, p. 306.

Diagnosis.—Medium-sized Palaeotheninae; I_2^2 , C_1^2 , P_{2-3}^2 , M_4^1 [three or four teeth (I_2 , C , P_1 , P_2) on diastema between I_1 and P_3 ; P_2 sometimes lost]; P_3 very small and ranging from double rooted and $\frac{1}{2}$ height of M_1 trigonid to single rooted and less than $\frac{1}{2}$ height of M_1 trigonid; anterobasal cuspule absent on P_3 ; M_1 paraconid not bifurcated; anterobasal cuspule on P^3 very tiny; hint of development of styler area especially labial to M^2 paracone and less so labial to M^1 and M^2 metacone; size decrease from M_2^2 to M_4^1 sharper, and M_1 relatively larger and narrower than in species of *Palaeothenes*.

Known range.—Deseadan and Santacrucian of Patagonia, southern Argentina.

***Accestis praecursor* (Loomis, 1914). Figure 31; Table 10.**

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

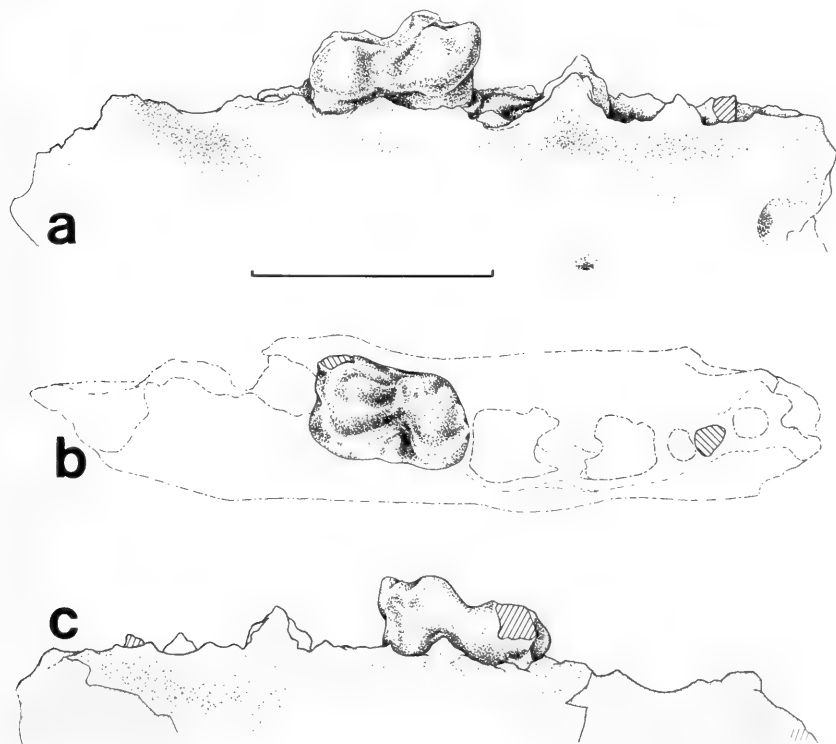


FIG. 31. *Palaeothenes praecursor* (Loomis, 1914, p. 223) (Deseadan). AC 3020 (type), a fragment of a right mandibular ramus with crown of M_2 and alveoli of P_2 - M_1 ; a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

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

Palaeothentes praecursor Patterson & Marshall, 1978, p. 87, fig. 21.

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.

Horizon and locality.—Cabeza Blanca, Chubut Province, Argentina.

Age.—Deseadan.

Diagnosis.— P_3 double rooted, very small compared with that of other Deseadan species, about half as high as M_1 trigonid; M_{1-2} slightly larger than in *Palaeothentes lucina*, considerably smaller than in *P. boliviensis* and *P. chubutensis*; M_1 and M_2 slightly longer than in Santacrucian species *Acdestis oweni* (fig. 17).

Comments.— M_{1-2} of *Acdestis praecursor* are heavily worn, preventing comparison of minor cusp morphology with *Palaeothentes lucina*. The smaller size of M_{1-2} and larger size of P_3 in the latter serve to separate these species. *Acdestis praecursor* has the smallest P_3 of any known Deseadan Palaeothentinae.

***Acdestis oweni* Ameghino, 1887. Figures 32-34; Tables 16-18.**

Acdestis oweni Ameghino, 1887, p. 5; 1889, p. 270, pl. 1, fig. 9; 1890, p. 153, fig. 4; 1894, p. 342, fig. 33; 1898, p. 186, fig. 50d; 1903, p. 171, fig. 98.

Dipilus spegazzinii Ameghino, 1890, p. 154, figs. 5, 6; 1894, p. 342, figs. 34, 35; 1898, p. 186, fig. 50a, b.

Dipilus spegazzinianus Ameghino, 1903, pp. 157, 172, figs. 79, 99.

Acdestis elatus Ameghino, 1891b, p. 304; 1894, p. 342; 1898, p. 186.

Acdestis parvus Ameghino, 1891b, p. 305; 1894, p. 342; 1898, p. 186.

Callomenus intervalatus Ameghino, 1891b, p. 306; 1894, p. 344.

Callomenus ligatus Ameghino, 1894, p. 344; 1903, p. 88 (*partim*), fig. 5 (figs. 10 & 46 are referable to *Palaeothentes lemoinei*); Sinclair, 1906, p. 435, pl. 64, figs. 5, 5a.

Callomenus robustus Ameghino, 1894, p. 344; 1903, pp. 116, 120, figs. 34, 38; Schlosser, 1925, p. 28, fig. 43.

Decastis columnaris Ameghino, 1891b, p. 305; 1893b, p. 79, fig. 3; 1894, p. 341, fig. 32; 1898, fig. 50c; 1903, p. 171, fig. 97; Sinclair, 1906, p. 437, pl. 64, figs. 4, 4a, 6, 6a.

Decastis rurigenus Ameghino, 1891b, p. 305; 1894, p. 342; 1898, p. 186; Sinclair, 1906, p. 452.

Dipilus rurigenus Clemens & Marshall, 1976, p. 71.

Metriodromus spectans Ameghino, 1894, p. 343; 1898, p. 186.

Dipilus spectans Clemens & Marshall, 1976, p. 71.

Metaepanorthus holmbergi Ameghino, 1903, p. 172 (*partim*), fig. 100.

Palaeothentes intermedius Sinclair, 1906, p. 430, pl. 63, figs. 3, 7, pl. 64, figs. 1, 1a.

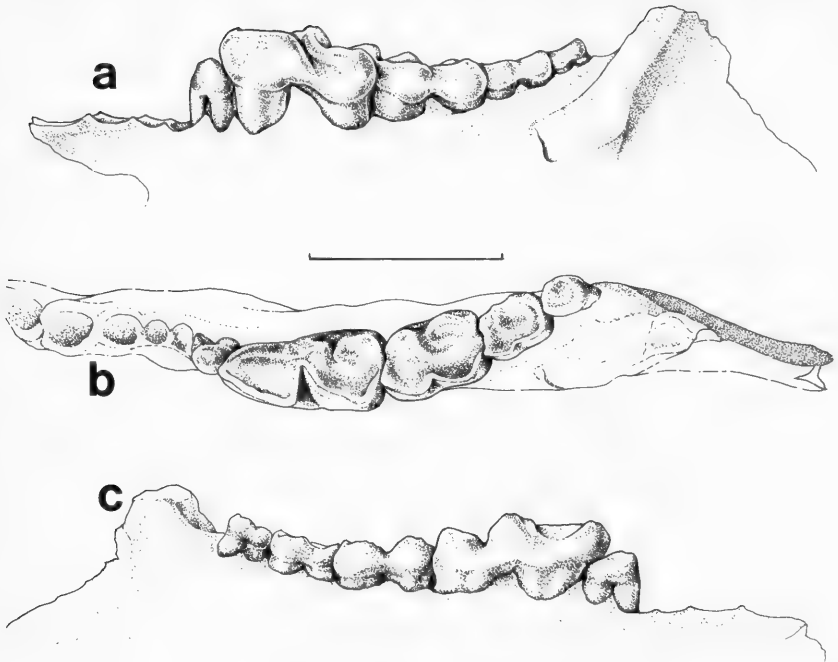


FIG. 32. *Acdestis oweni* Ameghino, 1887, p. 5 (Santacrucian). MACN 5559 (type of "*Acdestis elatus*"), a left mandibular ramus with alveoli of I_2 - P_2 , and P_3 - M_1 complete: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

Type of Acdestis oweni.—MACN 1379, a fragment of a right mandibular ramus with root of I_1 , alveoli of I_2 - P_2 , P_3 - M_1 complete, and trigonid of M_2 present (figured by Ameghino, 1889, pl. 1, fig. 9-9e; 1890, fig. 4; 1894, fig. 33; 1898, fig. 50d; and probably 1903, fig. 98—in the latter four publications, the jaw was partially restored by the artist, with I_1 - P_2 being added).

Type of Dipilus spagazzinii.—MACN 2038, a left mandibular ramus (greatly restored) with complete I_1 - P_1 , P_3 - M_2 complete, in position of M_3 trigonid is a reversed right M_1 talonid (the jaw is completely restored in this area, resulting in an increase and exaggeration of distance from M_1 to M_4), posterior half of M_3 and all of M_4 are complete (figured by Ameghino, 1890, figs. 5, 6; 1894, figs. 34, 35; 1898, fig. 50a, b; 1903, figs. 79, 99—the P_3 is actually larger relative to the M_1 than appears as figured; crown of P_3 is actually about twice the size of the crowns of I_2 - P_2).

Type of Acdestis elatus.—MACN 5559, a left mandibular ramus with alveoli of I_2 - P_2 , and P_3 - M_4 complete.

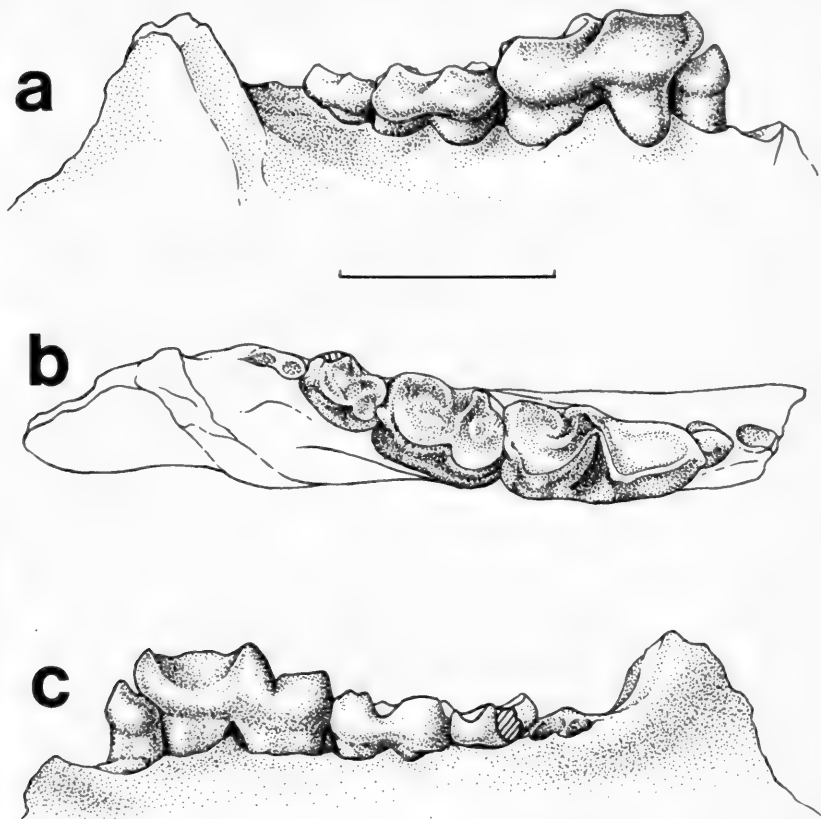


FIG. 33. *Acestis oweni* Ameghino, 1887, p. 5 (Santacrucian). MACN 5561 (type of "*Decastis columnaris*"), a right mandibular ramus with alveoli of P_2 and M_4 , and P_3 - M_3 complete: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

Type of Acestis parvus.—MACN 5553, a nearly complete mandible with left and right rami articulated; left ramus with base of I_1 , alveoli of I_2 - P_2 , and P_3 - M_4 complete; right ramus of I_1 , alveoli of I_2 - P_2 , P_3 - M_2 complete, and alveoli of $M_{3,4}$ (MACN 5554, a vertebra, and MACN 5555, a diaphysis of a humerus, are of same individual).

Type of Callomenus intervalatus.—MACN 5693, a fragment of a right mandibular ramus with three alveoli on preserved portion of diastema (probably C- P_2), roots of P_3 , and $M_{1,2}$ present but very worn.

Lectotype of Callomenus ligatus.—MACN 8257, a left mandibular ramus with alveoli of I_1 - P_2 , P_3 - M_3 complete (specimen matches all measurements in original description perfectly, and it is the only probable cotype with the M_3 as indicated in original description).

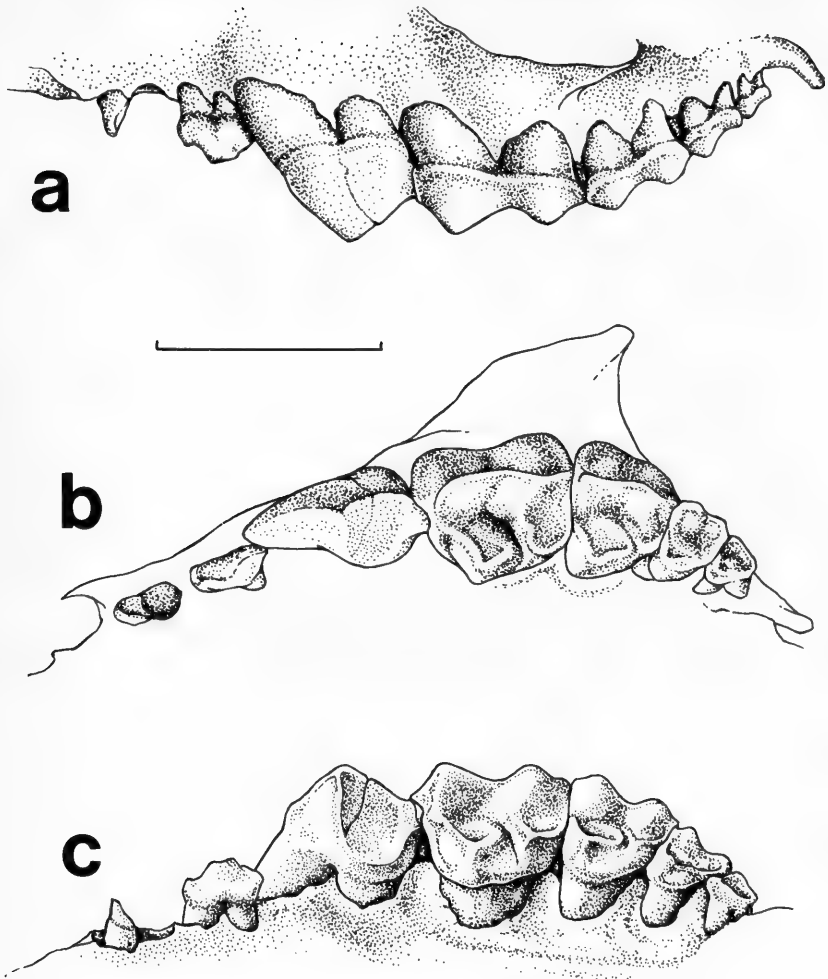


FIG. 34. *Acastis oweni* Ameghino, 1887, p. 5 (Santacrucian). PU 15225, left maxillary with alveoli of C and part of P¹, and P²-M¹ complete: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

Type of Callomenus robustus.—MACN 8260, a left mandibular ramus with P₃-M₂ complete (but very worn), and roots of M₃₋₄ (listed as type on card with specimen but not in Ameghino's catalogue—it does, however, fit original description perfectly).

Type of Decastis columnaris.—MACN 5561, a right mandibular ramus with P₃-M₃ complete (figured by Ameghino, 1893b, fig. 3; 1894, fig. 32; 1898, fig. 50c; 1903, fig. 97).

TABLE 16. Measurements of upper cheek teeth of *Acdestis oweni*.

	P3		M1		M2		M3		M4		M1-4		P3-M4	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
MACN 5645	3.0	2.1	3.3	3.4	2.4	3.0	1.3	1.8	0.8	1.2	8.5	10.8	8.5	10.8
MACN 8312 (l)	3.0	2.0	3.5	3.4	2.5	3.2	1.3	1.9	8.4ca	10.5ca	8.4ca	10.5ca
MACN 8312 (r)	2.9	2.1	3.4	3.3	2.4	3.2	1.1	2.0	0.8	1.3	8.5	10.7	8.5	10.7
FMNH P13160	3.1	2.2	3.5	3.3	2.6	3.1	1.3	2.0	0.8	1.3	8.4	11.0	8.4	11.0
AMNH 9550	3.1	2.3	3.7	3.4	2.5	3.2
PU 15225 (l)*	3.1	2.4	3.7	3.3	2.5	3.2	1.3	2.0	0.9	1.3	8.6	11.1	8.6	11.1
PU 15225 (r)	3.0	2.3	3.6	3.3	2.4	3.1	1.2	2.0	0.9	1.3	8.5	11.1	8.5	11.1
PU 15952**	3.0	2.2	3.7	3.2	2.6	3.1	1.3	2.0	1.0	1.3	8.5	...	8.5	...

*P²L = 2.0, W = 1.0.

**P²L = 2.0, W = 1.1.

TABLE 17. Measurements of lower cheek teeth of *Acedesis oweni*.

	P3		M1		M2		M3		M4		M1-4		P3-M4	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
MACN 1379	1.0	1.0	4.6	2.3
MACN 2038	0.9	0.8	4.6	2.0	3.0	2.0
MACN 2039	4.3	2.0	2.7	1.9
MACN 2040	4.2	2.2
MACN 5549	4.3	2.0	2.9	2.0	1.8	1.6	1.0	1.0	1.0	10.7
MACN 5550	1.1	1.0	4.3	2.0	2.7	2.1	1.8	1.5	9.8
MACN 5551	4.2	2.1	3.0	2.0	1.7	1.4	0.9	1.0
MACN 5552	1.0	1.0	4.3	2.2
MACN 5553 (l)	1.0	0.8	4.5	2.1	2.8	1.9	1.8	1.4	0.9	0.9	10.2	11.2
MACN 5553 (r)	1.1	0.9	4.4	2.0	3.0	2.0	10.3ca	11.2ca
MACN 5556	1.0	1.0	4.2	2.0
MACN 5557	1.0	0.8	4.4	2.0	2.8	1.8
MACN 5558	2.8	1.8	1.7	1.3	0.8	0.9
MACN 5559	1.1	1.0	4.3	2.1	3.0	2.0	1.8	1.6	1.0	1.0	10.3	11.0
MACN 5560	1.1	1.0	4.3	2.0	3.0	2.0	1.9	1.5	1.0	1.0	10.3	11.4
MACN 5561	1.0	1.0	4.7	2.3	3.0	2.3	1.9	1.6ca	1.0ca	1.0	11.0	11.5
MACN 5562	1.0	0.9	4.1	2.0	2.7	2.0	1.7	1.4	10.0ca	10.3ca
MACN 5693	2.2	3.0	2.2
MACN 8251	1.0	1.0
MACN 8253	1.0	0.9	4.3	2.1	2.7	1.9
MACN 8254	1.7	1.5
MACN 8255	1.0	0.8	4.4	2.1
MACN 8256	1.0	0.9	4.7	2.3	3.0	2.2
MACN 8257	0.9	0.9	4.4	2.1	2.9	2.0	1.7	1.4
MACN 8258	1.2	1.1
MACN 8260	1.5	1.2	4.6	2.3	11.5ca	12.5ca
MACN 10236	1.0	1.0	4.6	2.4	3.0	2.3	1.9	1.7	11.5ca	12.5ca
FMNH P13160 (l)	1.1	0.9	4.3	2.2	2.8	2.0	1.7	1.5	0.9	1.0	10.5	11.1
FMNH P13160 (r)	2.1	1.7	1.5	1.0	1.0
AMNH 9124 (l)	4.3	2.1	2.8	2.0
AMNH 9124 (r)	4.3	2.1	2.7	2.0	1.7	1.5	10.2ca
PU 15066	1.2	0.9	4.4	2.1	2.7	2.1	1.8	1.6	10.3ca	11.2ca

TABLE 18. Statistics for some cheek tooth dimensions of *Acdestis oweni*.

Dimension		N	OR	x	s	CV
UPPER CHEEK TEETH						
P ³	L	8	2.9-3.1	3.03	0.07	2.31
	W	8	2.0-2.4	2.20	0.13	5.91
M ¹	L	8	3.3-3.7	3.55	0.15	4.23
	W	8	3.2-3.4	3.33	0.07	2.10
M ²	L	8	2.4-2.6	2.49	0.08	3.21
	W	8	3.0-3.2	3.14	0.07	2.23
M ³	L	7	1.1-1.3	1.26	0.08	6.45
	W	7	1.8-2.0	1.96	0.08	4.08
M ⁴	L	6	0.8-1.0	0.87	0.08	9.20
	W	6	1.2-1.3	1.28	0.04	3.13
M ¹⁻⁴	L	7	8.4-8.6	8.49	0.07	0.82
P ³ -M ⁴	L	6	10.5-11.1	10.87	0.24	2.21
LOWER CHEEK TEETH						
P ₃	L	23	0.9-1.5	1.05	0.12	11.43
	W	23	0.8-1.2	0.95	0.10	10.53
M ₁	L	27	4.1-4.7	4.39	0.16	3.64
	W	28	2.0-2.4	2.12	0.12	5.66
M ₂	L	23	2.7-3.0	2.86	0.13	4.55
	W	24	1.8-2.3	2.03	0.13	6.40
M ₃	L	16	1.7-1.9	1.77	0.08	4.52
	W	16	1.3-1.7	1.50	0.10	6.67
M ₄	L	9	0.8-1.0	0.94	0.07	7.45
	W	9	0.9-1.0	0.98	0.04	4.08
M ₁₋₄	L	14	10.3-12.5	10.50	0.51	4.86
P ₃ -M ₄	L	11	10.3-12.5	11.37	0.64	5.63

Type of Decastis rurigenus.—MACN 5562, a right mandibular ramus with P₃-M₃ complete, and roots of M₄ (listed as type in Ameghino's catalogue).

Type of Metriodromus spectans.—MACN 8254, a right mandibular ramus with M₃ complete, and alveoli of rest of dentition.

Hypodigm.—The ten types and MACN 2039, a fragment of a left mandibular ramus with M₁₋₂ (labeled *D. spegazzinii*); MACN 2040, a fragment of a left mandibular ramus with M₁ (labeled *D. spegazzinii*); MACN 5546, a fragment of a right mandibular ramus with alveoli of M₂, and M₃₋₄ complete; MACN 5547, a fragment of a left mandibular ramus with roots of P₁, and P₂-M₂ complete but worn; MACN 5548a, a fragment of a right mandibular ramus with alveoli of I₂-P₂, P₃-M₁ complete, and roots of M₂; MACN 5548b, a fragment of a right mandibular ramus with alveoli of P₃, and M₁₋₂ complete but worn; MACN 5549, a left mandibular ramus with M₁₋₄; MACN 5550, a left mandibular ramus with P₃-M₃; MACN 5551, a left mandibular ramus with M₁₋₄; MACN

5552, a right mandibular ramus with P_3 - M_1 complete, and trigonid of M_2 ; MACN 5556, a fragment of a right mandibular ramus with P_3 - M_1 ; MACN 5557, a fragment of a left mandibular ramus with P_3 - M_2 ; MACN 5558, a fragment of a left mandibular ramus with M_{2-4} ; MACN 5560, a left mandibular ramus with P_3 - M_4 complete; MACN 5645, a right maxillary fragment with P^2 - M^4 (labeled *M. intermedius*); MACN 8251, a right mandibular ramus with P_3 complete, and alveoli of rest of teeth (labeled *D. rurigenus*); MACN 8253, a fragment of a right mandibular ramus with P_3 - M_2 (labeled *D. rurigenus*); MACN 8255, a fragment of a left mandibular ramus with P_3 - M_1 complete (labeled *C. ligatus* and a possible cotype of that species); MACN 8256, a fragment of a right mandibular ramus with I_1 , and P_3 - M_2 complete (labeled *C. ligatus* and a possible cotype of that species); MACN 8258a, a fragment of a left mandibular ramus with I_1 - P_3 complete (possible cotype of *C. ligatus*); MACN 8258b, an isolated right lower I_1 (figured by Ameghino, 1903, fig. 5, and possible cotype of *C. ligatus*); MACN 8312, palate of skull with right P^3 - M^4 , and left P^1 - M^3 complete [figured by Ameghino (1903, fig. 100) as *E. holmbergi*] (labeled *M. holmbergii*); MACN 10236, a left mandibular ramus with P_3 - M_3 complete, and roots of M_4 (labeled *A. elatus*); FMNH P13160, a partial skull with right P^3 - M^4 complete, a partial right mandibular ramus with talonid of M_2 , and all of M_{3-4} complete, and a partial left mandibular ramus with P_3 - M_4 complete (all of a single associated individual); AMNH 9124, a partial left mandibular ramus with M_{1-2} complete, and an associated partial right ramus with M_{1-3} complete, and alveoli of M_4 ; AMNH 9550, a partial left maxillary with P^3 - M^2 complete; AMNH 9594, a partial right mandibular ramus with base of I_1 , and P_2 and M_{1-2} complete; PU 15066, a right mandibular ramus with base of I_1 , alveoli of I_2 - P_1 , P_3 - M_3 complete, and roots of M_4 ; PU 15225, a partial skull with much of upper dentition; PU 15710, a partial left mandibular ramus with P_3 - M_2 complete, and roots of M_{3-4} ; PU 15952, a fragment of a right maxillary with roots of P^1 and P^2 - M^4 complete; [I was unable to find or identify the specimen figured by Ameghino (1903, figs. 34, 38) as *Callomenus robustus*, although it is clearly referable to *A. oweni*]; MLP 11-50, a fragment of a left mandibular ramus with M_{2-4} complete; MLP 11-72, a right mandibular ramus with alveoli of P_3 (two rooted), M_{1-3} complete but very worn, and alveoli of M_4 ; MLP 11-73, a right mandibular ramus with roots of P_{1-2} , P_3 complete (two rooted), alveoli of M_1 , and M_{2-4} complete.

Horizon and locality.—All specimens are from the Santa Cruz Formation, Santa Cruz Province, Patagonia, southern Argentina, and their localities of collection are as follows: [La] Cueva MACN 8251, 8253,

8254, 8255, 8256, 8260, 8312 (collected by C. Ameghino, 1892-93); *Coy Inlet* PU 15710 (collected by O. A. Peterson, 1899); *Killik Aike* PU 15066 (collected by O. A. Peterson, 1896), PU 15952 (collected by O. A. Peterson, 1899); *La Costa, 2 miles west of Coy Inlet* FMNH P13160 (collected by J. B. Abbott, 1923-24); *5 miles South of Coy Inlet* PU15225 (collected by O. A. Peterson, 1896); *Santa Cruz* MACN 1379; *Río Gallegos* AMNH 9124, 9550, 9594 (collected by B. Brown, 1899); *Sehuen* MACN 5553, 5645 (collected by C. Ameghino, 1890-91); *Monte Observación* MACN 5546, 5547, 5548a, 5548b, 5549, 5550, 5551, 5552, 5556, 5557, 5558, 5559, 5560, 5561, 5562, 5693 (collected by C. Ameghino, 1890-91), MACN 8257, 8258a, 8258b (collected by C. Ameghino, 1892-93); MACN 2038, 2039, 2040 (1889-90, no other data); MACN 10236, MLP 11-50, 11-72, 11-73 (no data).

Age.—Santacrucian.

Diagnosis.— M_1 and M_2 are slightly shorter than in Deseadan species *Acelestis praecursor*; smallest P_3 relative to M_1 of all known Santacrucian Palaeothentinae.

Description.—Two partial skulls of *Acelestis oweni* are known—PU 15225 and FMNH 13160. The former was described and figured by Sinclair (1906, pp. 427-428, pl. 63, fig. 3, pl. 64, figs. 1, 1a) as *Palaeothentes intermedius*.

The braincase is large, bulbous, and widely expanded posteriorly. There are no postorbital processes, but the weak temporal ridges converge posteriorly to form a low sagittal crest. Between the anterior edge of the orbits, the frontals form a broad flat plane. The frontals have a broad sutural contact with the maxillaries at a point dorso-anterior to the anterior edge of the orbit.

The nasals are broad and pointed posteriorly, and they decrease rapidly in width anteriorly. Unlike known fossil (*i.e.*, *Pichipilus*) and all living Caenolestinae, there is no trace of an antorbital vacuity between the nasal, maxillary, and frontal. The premaxillaries resemble those of living Caenolestinae in having a narrow extension between the maxillary and nasal (see Sinclair, 1906, pl. 63, figs. 3, 14, pl. 64, fig. 1a). The lacrimal is largely confined to the orbit with only a small facial contribution along the anterodorsal edge. The lacrimal duct opens within the rim of the orbit and supports a small but distinct lacrimal tubercle. A large infraorbital canal opens above the anterior root of the P^3 .

The anterior margin of the orbit is well defined and is modified into a sharp rim. The jugal extends posteriorly and forms the anterior edge of the glenoid fossa. The squamosal portion of the zygomatic arch is not

inflated as it is in some Australian phalangeroids (*e.g.*, *Petaurus*). The alisphenoid is slightly inflated and forms an ossified contribution to the auditory bulla anteriorly.

The palate is deeply concave anteroposteriorly and transversely and is perforated by two large anteroposteriorly elongated palatal vacuities. The latter extend from a point opposite the anterior extremity of M^1 to a point posterior to M^4 . Small nutrient canals perforate the bony portion of the palate. The palatal-narial border is thickened, ridge-like, and elevated to a height equal to that of the occlusal surfaces of M^{1-4} .

Comments.—A marked amount of variation occurs in the size and the number of antemolar teeth in *Acdestis oweni*. In all specimens except MACN 8260,* the P_3 is very small relative to the M_1 . In MACN 1379, 5553, 5559 (fig. 32), 5562, 5693, 8257, and PU 15066 the P_3 is clearly double rooted; in MACN 2038 it appears to be single rooted (although it may be incipiently double rooted and have a figure 8-shaped root); in MACN 8254 it appears to be single rooted as evidenced by the figure 8-shaped alveolus, with the anterior part being smaller than the posterior (a double root with a single alveolus is suggested); and in MACN 5561 (fig. 33) it is *definitely* single rooted. When double rooted, the posterior root is always larger than the anterior root.

The diastema is complete in MACN 1379, 5553, 5559, 8254, 8257, and PU 15066. In the former three specimens there are four tiny, single-rooted teeth (I_2 , C, P_1 , P_2) or their alveoli on the diastema anterior to the P_3 , and in all cases the last (P_2) is the smallest, and in MACN 5553 (and MACN 5562) its alveolus is confluent with the anterior alveolus of the P_3 . In the latter three specimens there are only three tiny alveoli anterior to the P_3 (probably I_2 , C, P_1), and it appears that the one just anterior to the P_3 (the P_2) was lost. In MACN 5693 a small diastema occurs just anterior to the P_3 , which is then followed by three tiny teeth (presumably P_1 , C, I_1)—this space presumably marks the site of a former fourth tooth (the P_2), whereas in MACN 8254 there is a tiny lingual depression between the P_3 alveolus and that anterior to it (the P_1 ?) that could represent the remnant alveolus of the missing P_2 . In MACN 2038, 5561, and 8260 there are three rudimentary teeth on the diastema, but the anterior ends of these diastemas are broken away and with it may have been lost a fourth rudimentary tooth (the I_2).

*In MACN 8260 the P_3 is double rooted and is somewhat larger (table 17) than in other specimens. It is reminiscent of specimens of the slightly larger *Palaeothenes lemoinei*, although in that species the P_3 is much larger (compare specimens in fig. 17). In length of M_{1-4} , MACN 8260 falls within the range of other specimens assigned to *A. oweni* (table 17), and it is smaller than those assigned to *P. lemoinei* (table 13).

The Deseadan *Acestis praecursor* and the Santacrucian *A. oweni* are the only species of *Acestis* known. Their only real difference is in the slightly larger size of the lower molars in *A. praecursor*. It is possible to envision *A. praecursor* as the Deseadan ancestor of *A. oweni* if a slight diminution in size occurred in this lineage. Alternatively, these species may represent independent derivations from a common pre-Deseadan ancestor. I favor the first view as there is no conflicting evidence against such a lineage relationship.

PALAEOTHENTINAE—INDETERMINATE

I was unable to locate the types of two of Ameghino's 1887 species of *Palaeotheres*, *P. pachygnathus* and *P. pressiforatus*. As a result I am neither able to determine their validity nor their systematic position with regard to the other named species. Both species were erected on specimens collected by Carlos Ameghino from the Santa Cruz Formation of Patagonia. The types should be in the MLP although neither could be located in the collections of that institution. A catalogue card in the MLP for specimen 11-32 bears the name of one of these species (*P. pachygnathus*), although neither I nor Rosendo Pascual could locate the specimen. Several possibilities regarding the fate of these types exist: (1) they are lost; (2) they are temporarily misplaced; (3) they are among known MLP specimens but are not recognized as the types; or (4) they were taken by Ameghino to the MACN and are now in the Ameghino Collection of that institution (see footnote, p. 36). Whatever the case, I here regard these species as *nomina vana*.

The original descriptions and pertinent literature citations for these species follow:

1. *Palaeotheres pachygnathus* sp. n.—Talla todavía menor, pero relativamente más robusto (than *P. lemoinei*).—Parte sinfisaria de la mandíbula, muy espesa.—Cara externa de la rama horizontal debajo del pm.₄, muy convexa.—Largo del pm.₄ 4mm.—Largo del pm.₃ pm.₄ y m.₁ —0.0095. —Alto de la rama horizontal debajo del pm.₄, 6 mm. (Ameghino, 1887, p. 6).

*Palaeotheres pachygnathus** [sic] Ameghino, 1887, p. 6.

*Epanorthus pachygnathus** [sic] Ameghino, 1889, p. 273; 1894, p. 347; 1898, p. 186.

Palaeotheres pachygnathus Sinclair, 1906, p. 454; Simpson, 1930, p. 58.

2. *Palaeotheres pressiforatus*, sp. n.—Tamaño más considerable que el de la especie precedente (*P. intermedius*), comparable al del *Palaeotheres Lemoinei*.—Los dos agujeros mentonarios de cada rama mandibular, muy próximos entre sí, el anterior debajo de la parte posterior del pm.₂, y el posterior debajo de la segunda raíz del pm.₃, a sólo 3 mm. de distancia.—Alto de la rama horizontal debajo del pm.₃, 6 mm. (Ameghino, 1887, p. 6).

*Despite the fact that Ameghino repeatedly spelled the trivial name *pachygnathus* this seems such an obvious *lapsus calami* that it seems permissible to accept the corrected form [*pachygnathus*] (Simpson, 1930, p. 58).

Palaeothenes pressiforatus Ameghino, 1887, p. 6.

Epanorthus pressiforatus Ameghino, 1889, p. 274; 1894, p. 347; 1898, p. 186.

PALAEOTHENTINAE—UNIDENTIFIED

In the summer of 1976, I visited the British Museum (Natural History), London, and made a brief survey of south American fossil marsupials in the collection of that institution. Nine specimens were labeled *Epanorthus* sp. and are clearly referable to the subfamily Palaeotheninae. I did not then study these specimens in any detail nor have I had the opportunity to do so for this present review. I list these specimens here for the sake of completeness—BM(NH) M5685, 5686, 5687, 5688 (all presented by F. Ameghino in 1895); 7267, 7326 (both purchased from R. Damon in 1899); 11724, 11725, 11726 (collection of W. E. Balston purchased by J. R. Gregory & Co., August, 1919).

Other known specimens of palaeothenines not seen by me include: AMNH 9592, a partial left mandibular ramus with P_3 and M_{3-4} (collected by B. Brown from the Río Gallegos in 1899); PU 15072, a fragment of a maxillary (collected by J. B. Hatcher and O. A. Peterson in 1897 from the Río Chalia, 30 miles east of the cordillera); PU 15513, upper teeth (collected by O. A. Peterson in 1899 from Coy Inlet); and PU 15559, an edentulous left lower jaw (no collection data). All of the above specimens are from the Santa Cruz Formation of Patagonia.

Tournouër (1903, p. 469) reported "un *Epanorthus*" from beds of Deseadan age at La Flecha on the south side of the mouth of the Río Deseado, and specimens of *Abderites meridionalis*, *Epanorthus*, and *Garzonia* from beds of Santacrucian age at Monte León. These specimens are in the MNHN and have neither been described nor figured.

SUMMARY OF EVOLUTION OF PALAEOTHENTINAE

Members of subfamily Palaeotheninae are known from beds of Deseadan through Santacrucian age in Patagonia, southern Argentina, and in beds of Deseadan age in Bolivia. Two genera, *Palaeothenes* and *Acdestis*, are recognized.

Palaeothenes is the most generalized of the two, and it most closely approximates the basal stock for the subfamily and in turn the ancestor of Caenolestini. Species of *Palaeothenes* are distinguished from those of *Acdestis* in their possession of a large two-rooted P_3 that is greater than $\frac{1}{2}$ the height of the M_1 ; in a relatively longer, less crowded diastema; and in the presence of a bifurcated paraconid on the M_1 . In the latter feature, the paraconid region branches into two small crests. One extends lingually perpendicular to the main axis of the tooth. A second crest extends anteriorly, linking the protoconid-paraconid shear crest

of the M_1 trigonid with the cutting edge of the large P_3 . This crest furnishes continuation of the shearing surface between the P_3 and the protoconid-paraconid crest of the M_1 (figs. 16, 17).

The smallest and most generalized of the known species of *Palaeotheres* (and of the Palaeotherinae) is *P. minutus*. This species retains several features found only in ancestral Caenolestini (e.g., an "intermediate conule" on unworn upper molars and a two-rooted P_2 in some specimens), and it serves as a proto- or morphotype from which may be derived all other known species of Palaeotherinae and for that matter Abderitinae.

The next largest species is *P. intermedius*. It has slightly larger linear molar dimensions and a relatively larger P_3 than the Colhuehuapian species *P. primus*, but these differences are minor, and the two species appear to represent a single phylogenetic lineage. I therefore recognize *P. primus* as the Colhuehuapian ancestor of *P. intermedius*.

The Deseadan species *P. lucina* is of medium-large size and differs from the Santacrucian species *P. lemoinei* in being slightly smaller in overall linear tooth dimensions but in having an absolutely larger P_3 . These species also appear to form a phylogenetic lineage, and the former is here regarded as representing the Deseadan ancestor of the latter.

Palaeotheres boliviensis is of large size and is known only from a single specimen from the Deseadan Salla fauna of Bolivia. It does not appear to be related ancestrally to any known later species. Based on its large size and its high, broad P_3 , *P. boliviensis* shows closer affinities to the Deseadan species *P. chubutensis* than to any other known Deseadan palaeotherine. This suggests that these species shared a common ancestor more recent than those shared with other Palaeotherinae.

The Deseadan species *P. chubutensis* and the Santacrucian *P. aratae* are the two largest species of Palaeotherinae (and Caenolestidae) known. The former differs from the latter in having a slightly deeper, more robust mandibular ramus and a slightly larger P_3 , but these differences are minor and their range of variation within each species is not yet known. There is little problem in regarding *P. chubutensis* as the Deseadan ancestor of *P. aratae*. *Palaeotheres aratae* further differs from other palaeotherines in having a single-rooted P^1 . This state may have existed in the ancestral *P. chubutensis*, but the upper dentition of that species is not yet known.

Species of *Acestis* share a number of apomorphic states not found in species of *Palaeotheres*. The jaw and especially the diastema in

TABLE 19. Summary of some diagnostic characters of known species of Palaeothentinae.

Character	Palaeothentes minutus	Palaeothentes prinus	Palaeothentes intermedius	Adestis praecursor	Adestis oweni	Palaeothentes lucina	Palaeothentes kemoini	Palaeothentes bolivianis	Palaeothentes chubutensis	Palaeothentes aratae
1. Relative average over-all size (see fig. 17)	small	small-medium	small-medium	medium	medium	medium-large	medium-large	large	very large	very large
2. Number of teeth between I_1 and P_3	four	four	four	(unknown)	three or four	(unknown)	four	(unknown)	(unknown)	(unknown)
3. P_2 number of roots	one or two	one	one	one	one	(unknown)	one	(unknown)	(unknown)	one
4. Size of P_3	large, double rooted, = or > in height than M_1	large, double rooted, height of M_1	large, double rooted, < height than M_1	very small, double rooted, about $\frac{1}{2}$ height of M_1	very small, double or single rooted, $\frac{1}{2}$ height or less than that of M_1	*large, double rooted, height to M_1	large, height to M_1	large, height to M_1	large, height to M_1	large, height to M_1
5. Anterobasal cuspule on P_3	present	present	present	absent	absent	present	present	present	present	present
6. Paraconid	bifurcated	bifurcated	bifurcated	not bifurcated	not bifurcated	bifurcated	bifurcated	bifurcated	bifurcated	bifurcated
7. P_1 number of roots	two	(unknown)	(unknown)	(unknown)	two	(unknown)	(unknown)	(unknown)	(unknown)	one
8. Anterobasal cuspule on P_1	large	(unknown)	(unknown)	(unknown)	very tiny	(unknown)	present	(unknown)	(unknown)	present
9. Styliar area (base of crown swollen labially)	only hint	(unknown)	absent	(unknown)	hint of development especially labial to M^2 paracone; less so labial to M^1 and M^2 metacone	(unknown)	absent	(unknown)	(unknown)	hint of development labial to M^2 paracone

*Broken in only known specimen.

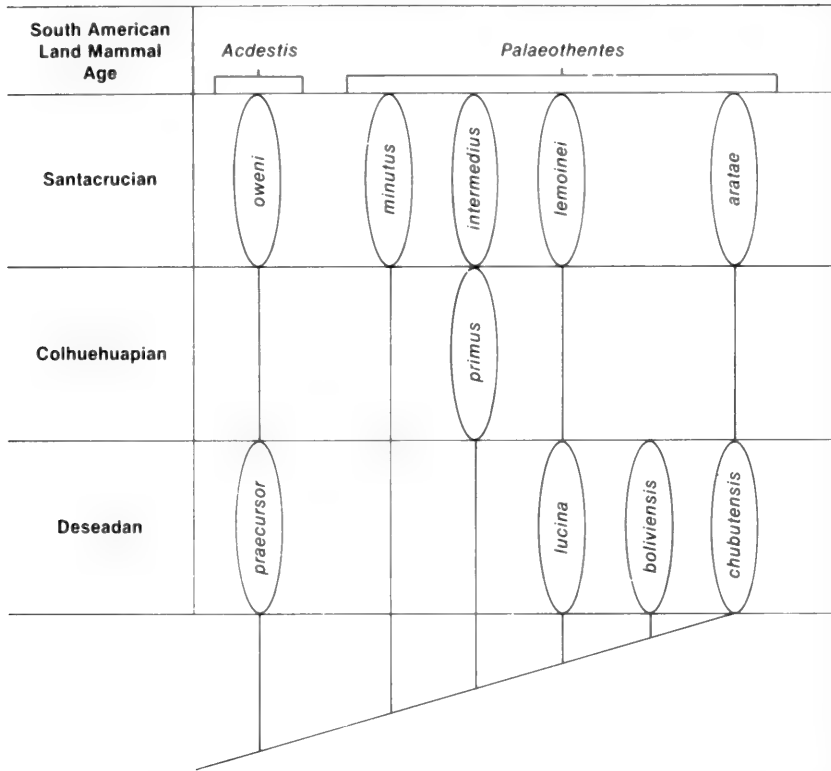


FIG. 35. Dendrogram showing probable phylogenetic relationships of the genera and species of Palaeotheninae. Only relative positions of pre-Deseadan common ancestors are indicated.

Acestoris is foreshortened, resulting in a crowding of the antemolar teeth. A consequence of this is loss in some specimens of the P_2 and in a significant reduction in size of the P_3 . The P_3 is less than $\frac{1}{2}$ the height of the M_1 trigonid in all specimens; it may be single or double rooted, and it tends to be tucked under the anterior edge of the M_1 trigonid. The M_1 becomes relatively larger than the other cheek teeth, and the size decrease from M_1 to M_4 is sharper than in species of *Palaeothenes*. The paraconid on the M_1 is not bifurcated as in species of *Palaeothenes*, an important feature for distinguishing isolated M_1 's of such similar-sized contemporary species as *Acestoris oweni* and *Palaeothenes intermedius*. In the upper molars, the styler area is swollen especially labial to the M^2 paracone and also, but less so, labial to the M^1 and M^2 metacone.

Two species of *Acestis* are recognized, the Deseadan *A. praecursor* and the Santacrucian *A. oweni*. *Acestis praecursor* differs from *A. oweni* only in the M_1 and M_2 being slightly longer. In other respects these species are inseparable. I regard them as representing a single evolutionary lineage and recognize *A. praecursor* as the slightly larger Deseadan ancestor of *A. oweni*.

Some diagnostic characters for the species of Palaeothentinae are listed and compared in Table 19. The character states that occur in *Palaeothentes* are regarded as plesiomorphic, those in *Acestis*, as apomorphic. The probable phylogenetic relationships of the two genera and 10 species are shown in Figure 35. This suggested phylogeny is based on the data set in Table 19, and for want of better characters I have regarded size increase as an important apomorphy in several instances.

PHYLOGENETIC SYSTEMATICS

METHODOLOGY

Cladistic analysis is a procedure for inferring phylogeny as branching sequences in evolutionary time. Extensive discussions of this method are given by Hennig (1966), Brundin (1966, 1968), Kavanaugh (1972), Ashlock (1974), and Andersen (1978). The fundamental premise of cladistics is that relatedness is demonstrated by shared, derived (synapomorphous) character states, not by shared primitive (symplesiomorphous) ones. The methods used here for determining if a character is plesiomorphic (primitive), symplesiomorphic (primitive and possessed by more than one species), apomorphic (derived), or synapomorphic (derived and possessed by more than one species) largely conform with those of Schaeffer et al. (1972). Use of such terms as *sister-group*, *monophyly*, *morphocline*, *polarity*, *character state*, *convergent evolution*, and *parallel evolution* follow the definitions of Hecht (1976), Hecht & Edwards (1976), and Kirsch (1977a).

Establishment of polarity is therefore the most important problem in the analysis of a morphocline or transformation series. The parts of these sequences must be evolutionary homologues. For a series of comparisons there can be only one primitive state, and criteria for determining the primitive state must be rigidly followed.

One method for determining whether a character is primitive or derived for a particular taxon is by application of the *principle of commonality* (Schaeffer et al., 1972). If a character or suite of characters is found in the majority or in all members of the group under consideration, it is concluded that the character was present in the common ancestor of that group and was not independently derived in each instance of its occurrence. The unique origin of this character state is the most parsimonious explanation for its distribution, and the cladogram requiring the fewest steps or changes is preferred (Hecht, 1976, p. 340; Ashlock, 1974, p. 83). Any variation from the inferred primitive state is regarded as a derived state.

Doubts have been expressed concerning the validity of the "common is primitive" postulate, and contentions that a rare state is primitive may involve appeals to character state distribution in a wider range of taxa of different levels of cladistic relatedness. This fact leads to a second method for establishing plesiomorphy, *out-group comparison*. For this, a minimum of three groups must be used—the two or more taxa under consideration and an out-group consisting of some other taxon or taxa hypothesized to be related to these two. If a character or suite of characters is found to be unique to one of the two taxa not in the out-group, two possibilities must be considered: (1) the character(s) evolved from a simpler, more primitive condition in only one of the groups; or (2) the character(s) was present in the common ancestor, but was secondarily lost in one of the two groups. Decisions concerning these choices can be made following comparisons with one or more out-groups (Reig et al., In prep.).

Decisions about the relative plesiomorphy or apomorphy of character states may also be tempered by knowledge of what sorts of changes are possible for a given character. For example, improbable polarities, such as the resurrection of complex structures from lost or reduced states, can be given low probability of occurrence (Hecht, 1976, p. 341).

Once the primitive state of a character has been inferred, the apomorphous states may be ordered corresponding to the likely evolutionary sequence and this series used to infer the relationships of the taxa in which those states co-occur. The transformation of a sequence may be simply linear and be expressed as in the stepwise four-character state morphocline $a \rightarrow b \rightarrow c \rightarrow d$, or it may be complexly branching. These alternatives can only be determined empirically by sequential comparison of the cladograms suggested by each series of character states. The degree of concordance or discordance between characters suggests the extent of convergence or parallelism in those characters. Ordinarily, one begins an analysis with three or four taxa likely to be closely related and determines their cladistic relatedness by means of the best-established character morphoclines. All types of branching patterns should be examined, and the simplest pattern may not necessarily be the correct one for any given character. Clearly, for more than a few characters, the number of possible cladograms is very large, particularly when some character-sequences do not give concordant cladograms due to convergence, to parallelism, or to mistaken homologies. The greater the concordance between different cladograms, the more likelihood that the original hypothesis of relatedness was correct (Hecht, 1976, p. 341; Reig et al., In prep.).

CHARACTER ANALYSIS

Discussions of the phylogenetic relationships of caenolestid subfamilies have been based on an array of characters that have not previously been analyzed in a cladistic framework. An attempt is made to treat all useful or potentially useful characters for which data are available. The analysis for each character is presented in an abbreviated form, with extensive literature citations to more detailed coverage.

Two basic groups of characters may be recognized. Hard part features, like bones and teeth, are based on an analysis of both living and fossil forms, employing both the principle of commonality and out-group comparison. Inference of the distribution of soft part features is based largely on the application of the principle of commonality. It is assumed, with reservations but in the absence of conflicting (or any) data, that the states of soft part features in living Caenolestini are the same in all fossil Caenolestidae.

I have selected 12 characters for analysis and have arranged them in the general order of head, dentition, and postcranial. Most of the characters are unique and distinct, but others represent "complexes" that I have attempted to isolate into component parts.

An analysis of each of these characters follows.

1. *Antorbital vacuity*.—An *antorbital vacuity*, bounded by the nasal, frontal, and maxillary occurs on each side of the face directly above the infraorbital foramen in all living Caenolestini (see Osgood, 1924, pl. 23) and in a fossil species of Pichipilini, *Pichipilus centinelus* (see Marshall & Pascual, 1977, p. 104, fig. 4). As seen in living species, this vacuity opens into the large sinus between the nasoturbinale and the maxillary. Its relations to the overlying dermal tissues are simple, and no glandular or other special development is apparent (Osgood, 1921, p. 107).

A vacuity of this type does not occur in the two known skulls of the palaeothenine *Acdestis oweni* (see p. 101) nor in any other known marsupial group. Among placentals, a vacuity in this part of the skull is found only among ungulates (Osgood, 1921, p. 107). Among Marsupialia in general and Caenolestidae in particular, an antorbital vacuity is regarded as an apomorphy for the subfamily Caenolestinae, since it occurs in all known skulls in members of both recognized tribes.

2. *Palatal vacuities*.—The palate in marsupials is often perforated by three sets of palatal vacuities or fenestrae adjacent to the palatal midline. Because of the widespread occurrence of these vacuities in marsupials, their presence is generally regarded (e.g., Tyndale-Biscoe, 1973) as plesiomorphous for the group.

Large palatal vacuities occur in all living Caenolestini (see Osgood, 1924), in the fossil *Pichipilus centinelus* (see Marshall & Pascual, 1977, p. 104), and in the two known skulls of the palaeothenine *Acdestis oweni* (see p. 102). Based on the traditional view, the presence of palatal vacuities in caenolestids would thus be regarded as a retained primitive marsupial character.

Elsewhere, I reviewed the distribution of palatal vacuities in marsupials in particular (1977, p. 415) and in mammals in general (1979b, p. 377). In the former study I was led to conclude that palatal vacuities may have evolved independently in various marsupial lineages. In the latter study I concluded that a solid, unfenestrated palate was plesiomorphic for mammals in general and prototherians, therians, metatherians, and eutherians in particular.

The relevant point for this study is that all known caenolestids have a fenestrated palate and that nothing can be said about the interrelationships of caenolestid taxa based on this character. At the family level, the occurrence of a fenestrated palate can be regarded as a plesiomorphic feature.

3. *Brain*.—All marsupial groups, except for Australasian diprotodonts (=Phalangeroidea *sensu* Ride, 1962, p. 301), show the same pattern of commissural connections as do monotremes, and this arrangement probably also occurred in the common therian ancestor of marsupials and placentals. In this basic arrangement there are two large fiber bundles interconnecting pallial structures of the two cerebral hemispheres, the dorsal or *hippocampal commissure* and the ventral or *anterior commissure*.

In Australasian diprotodonts a third bundle of neocortical commissural fibers is added, the *fasciculus aberrans*. Ride (1962, p. 301), following Abbie (1939), used the term *duplicommissural* for the presence of a fasciculus aberrans in the forebrain and *simplicicommissural* for the lack of this structure. The former condition is regarded as apomorphic for Phalangeroidea and the latter condition as plesiomorphic (for review of pertinent literature on this point see Marshall, 1979b, p. 374).

The brains of *Caenolestes* and *Lestoros* were studied by Obenchain (1925), and they lack a fasciculus aberrans (Abbie, 1937, 1939). They are therefore plesiomorphic for this feature.

4. *Dental formula*.—The most generalized of living marsupials, the American Didelphidae, have a dental formula of $I_3^1, C_1^1, P_3^3, M_4^4$. This is the highest number of teeth known for any fossil or living marsupial, and all specializations involving reduction in other marsupial groups

may be derived from this formula. This formula is regarded as plesiomorphic for Marsupialia (Marshall, 1979b, p. 388).

Many attempts have been made to identify homologous teeth in marsupials and placentals, and this has resulted in a plethora of symbolic and ordering systems, and in conflicting dental terminology. The issue is still debated, and no one system has yet been agreed upon. The most recent attempt to stabilize this issue is that of Archer (1978).

It is not my intention to enter this debate by accepting one controversial system over any other. I therefore use the following conventional system for serial designation of the teeth in the Marsupialia; for the incisors and canine it is intended to be descriptive and does not imply homology although for the premolars and molars homology is implied: $I_1^1 \frac{2}{2} \frac{3}{3} \frac{4}{4} \frac{5}{5}$, C_1^1 , $P_1^1 \frac{2}{2} \frac{3}{3}$, $M_1^1 \frac{2}{2} \frac{3}{3} \frac{4}{4}$. Any deviation from this formula is regarded as a derived condition.

Attempts to establish homologies of the antemolar (*sensu* Ride, 1962, p. 297) dentition between caenolestids and didelphoids are given by Osgood (1921, p. 112) and Ride (1962, p. 297). The homologies of the upper incisors and of the lower antemolar teeth of caenolestids are difficult to establish because nothing is yet known of the dental embryology of this group. Attempts to establish homology have thus been based on study of adult specimens, living and fossil.

Individuals of *Caenolestes* have as many as eight antemolar teeth (Bensley, 1903, p. 124, pl. 5, fig. 38; Osgood, 1921, p. 112) and thus retain the plesiomorphic number for Marsupialia. A specimen of *Stilotherium dissimile* ("Garzonia") is reported by Sinclair (1906, p. 417) to have nine lower antemolar teeth. Ride (1962, p. 298) has opted to regard this number as an individual peculiarity, pending confirmation of the consistency of its occurrence. If, however, this number is not aberrant, the lower dental formula may be I_5, C_1, P_3, M_4 , since the maximum number of premolars in any known didelphoid is three, and the canine is always single (*ibid.*). This would indicate that the lower incisor number in caenolestids was either increased from 4 to 5 and the condition should be regarded as an apomorphy, or that the primitive marsupial number was 5. The latter possibility has been discussed in more detail by Ride (1962).

Archer (1978, p. 163) studied over 150 specimens of the three living genera of Caenolestinae and found no evidence of a milk tooth or of tooth replacement of any sort. In addition, there is no evidence for tooth replacement in any fossil caenolestid. Archer (*ibid.*) concluded:

If tooth replacement of the sort which occurs in other marsupial orders does occur in caenolestoids, it must occur very early in ontogenetic development. . . . If tooth

replacement does not occur, then it is possible that caenolestoids represent a unique order of marsupials all members of which have no more than seven postcanine cheek teeth.

The apparent loss of this tooth in caenolestids is thus regarded as an apomorphic feature for members of this family. It is tempting to speculate that the extra antemolar tooth in the specimen of *Stilotherium* discussed above represents the retained deciduous tooth.

The least number of lower incisors possessed by *Stilotherium* is four, and in *Caenolestes* it is three. Assuming caenolestids have the same number of tooth germs as other marsupials, the lower procumbent incisor is almost certainly developed from the first incisor germ, or the I_1 , by homology with didelphoids (Ride, 1962, p. 298).

The plesiomorphic incisor formula for the Caenolestidae is here taken to be $\frac{4}{4}$. Reduction to $\frac{3}{3}$ in some Caenolestinae and to $\frac{2}{2}$ in Palaeothentinae and presumably this (or a lower) number in Abderitinae are considered apomorphous states. Likewise, the presence of only two lower premolars in some specimens of *Acestis oweni* is regarded as derived from the higher condition of three. In this case, the reduction apparently involves loss of the P_2 (see p. 102). The following serial designations are used for the various subfamilies of Caenolestidae (parentheses indicate absence of teeth in some included taxa or individuals):

Caenolestidae	$I_1^1 \frac{2}{2} \frac{3}{(3)} \frac{4}{4}$	C_1^1	$P_1^1 \frac{2}{2} \frac{3}{(3)}$	$M_1^1 \frac{2}{2} \frac{3}{3} \frac{4}{4}$
Caenolestinae	$I_1^1 \frac{2}{2} \frac{3}{3} \frac{4}{(4)}$	C_1^1	$P_1^1 \frac{2}{2} \frac{3}{3}$	$M_1^1 \frac{2}{2} \frac{3}{3} \frac{4}{4}$
Abderitinae	$I_1^1 \frac{?}{2} \frac{0}{0} \frac{0}{0}$	$C_1^?$	$P_1^? \frac{2}{2} \frac{3}{3}$	$M_1^1 \frac{2}{2} \frac{3}{3} \frac{4}{4}$
Palaeothentinae	$I_1^1 \frac{2}{2} \frac{3}{3} \frac{0}{0}$	C_1^1	$P_1^1 \frac{2}{2} \frac{3}{(3)}$	$M_1^1 \frac{2}{2} \frac{3}{3} \frac{4}{4}$

5. *Dental specializations.*—In late Cretaceous members of the Didelphidae (see Clemens, 1966) and in most living forms (see Reig et al., In prep.), the incisors are unspecialized and are similar in size; the premolars are well developed, trenchant, and double rooted; and the molars are well developed and tuberculo-sectorial in structure. The M_4 is subequal in size to the M_3 , and a well-developed styler shelf with distinct cusps is present on the upper molars. This type of tooth structure is regarded as plesiomorphic for the Marsupialia (Archer, 1976).

Derived states for the family Caenolestidae include development of a hypocone (this term is used without implication of homology) on M^{1-3} ; increase in size and development of a procumbent, lanceolate, diprotodont I_1 ; reduction in size of most other antemolar teeth; presence in unworn teeth of a small but high and distinct "intermediate conule" (*sensu* Osgood, 1921, p. 120) at the inner base of the metacone on M^{1-3} ;

and the reduction in size of the M4. Further specializations within the family are discussed on p. 23.

6. *Teat number*.—Within the Marsupialia, the number and distribution of teats vary greatly. In the South American didelphoid *Monodelphis*, up to 27 teats are distributed over the inguinal, abdominal, and pectoral areas (Thomas, 1888; Reig et al., In prep.; Thomas, 1888, figured a specimen of *Monodelphis henseli* with 25 teats, but mentioned one in the text that had 27). The lowest number occurs in species of *Notoryctes*, *Distoechurus*, *Phascolarctos*, and *Vombatus* that have two teats (Osgood, 1921, p. 75).

The primitive teat number for Marsupialia is believed by Bresslau (1912, 1920) to be 25, and he concluded that all specializations involve a reduction in this number. Of the 26 genera listed by Osgood (1921), four had two teats, 10 had four, and the remaining 12 had a number higher than seven. In *Caenolestes* there are four mammae—two on each side of the abdomen inside the thighs (Osgood, 1921, p. 75); *Lestoros* has four mammae (Collins, 1973, p. 173); and *Rhyncholestes* has five mammae—two inguinal on each side and one midventral slightly in advance of them (Osgood, 1924, p. 169). The low teat number in living Caenolestinae is thus regarded as a derived state.

7. *Pouch or "marsupium"*.—Elsewhere, I (1979b, p. 383) reviewed information on the distribution and degree of development of a pouch or *marsupium* in mammals. Based on that study I concluded, as some others before me, that it is probable that the earliest marsupials, and the immediate ancestors of marsupials and placentals, did not have a pouch. Thus, a pouch apparently developed independently in various marsupial lineages and in the echidna as an adaptation for special mechanical and/or locomotory needs.

There is some disagreement about the occurrence of a pouch in living caenolestines. Tomes (1860, p. 213) wrote that his specimen of "*Hyracodon*" (= *Caenolestes fuliginosus* (as he later designated it) possessed ". . . a small and rudimentary pouch . . .," a feature that has not been remarked on by subsequent workers even though lactating females have been examined (Osgood, 1921, p. 21; Kirsch & Waller, 1979, p. 394). The measurements given in Tomes' (1863) description clearly indicate that the type specimen is a juvenile (Kirsch & Waller, 1979, p. 394). This has caused Osgood (1921) and Kirsch & Waller (1979) to suggest that the pouch may be a juvenile feature in caenolestids. In any event, it can only be concluded that a pouch is not developed in adult female caenolestids, a condition regarded as plesiomorphic for the Marsupialia. The state of this character is, of

course, unknown in the fossil subfamilies Palaeothentinae and Abderitinae.

8. *Epipubic bones*.—Ossified epipubic (=prepubic or “marsupial”) bones are present in both sexes of monotremes, in tritylodont therapsids, in Cretaceous multituberculates, and possibly in triconodonts and pantotheres. They are absent in placentals. Epipubic bones are present in both sexes of living marsupials, except *Notoryctes* and *Thylacinus* in which they are cartilaginous and vestigial, and in South American borhyaenids in which they are apparently altogether absent (Marshall, 1977, p. 419; 1979b, p. 385, and references therein). The presence of large ossified epipubic bones in living caenolestines (a complete pelvis is not known in fossil taxa) thus represents a retained primitive mammalian feature for the group.

9. *Sperm pairing*.—The phenomenon in which two sperm are united by juxtaposition of the shorter portions of the two heads was first observed in *Didelphis marsupialis* by Selenka (1887), who referred to them as “copulating” spermatozoa. This term was subsequently used by Korph (1902), who made the crucial observation that the “copulation” occurs only after the gametes reach the epididymes. Wilson (1928) objected to the term “copulating,” and instead introduced the term “conjugating.” Biggers & DeLamater (1965, p. 403) noted, however, that the term “conjugating” has acquired a specific meaning in biology with reference to the union of gametes in unicellular organisms. For this reason these authors, and those subsequent to them, preferred the simple descriptive word “pairing” to describe this phenomenon.

Biggers & Creed (1962) noted that pairing of spermatozoa is a normal occurrence in the epididymes of the North American opossum, *Didelphis virginiana*. Subsequent work by Biggers & DeLamater (1965) has shown that pairing occurs in the epididymes of all species of American marsupials investigated; both in members of the Didelphidae (*Didelphis*, *Philander*, *Chironectes*, *Monodelphis*, *Metachirus*, *Marmosa*, and *Caluromys*), and in Caenolestidae (*Caenolestes*) (see Biggers & DeLamater, 1965, p. 403, Table 1). The sperm remained paired in the vaginae of females after copulation (Tyndale-Biscoe, 1973, p. 15), suggesting that the bond between them is quite firm. In no instance was pairing observed in sections of the testes, indicating, once again, that the pairing takes place in the epididymes.

Biggers & DeLamater (1965) presented data indicating the incidence of pairing within species. Out of 92 specimens of *Didelphis marsupialis*, 88 (95.7%) had sperm that were paired, and out of 56 specimens of *Philander opossum*, 54 (96.5%) had sperm that were paired.

The fact that sperm pairing has been observed in all species (but not every individual) of American marsupials examined, including two families, indicates that these marsupials are derived from a common ancestral stock that had already evolved the pairing phenomenon. Thus, pairing of spermatozoa, whatever its function, must have become established early in the evolutionary history of the American group of marsupials (Biggers & DeLamater, 1965, p. 404).

The pairing of spermatozoa in the epididymes or in sections of the testes has not been observed in any species of Australasian marsupials yet investigated. These include species of *Sminthopsis*, *Neophascogale*, *Antechinus*, *Acrobates*, *Eudromicia*, *Trichosurus*, *Vombatus*, *Perameles*, *Peroryctes*, *Wallabia*, *Megaleia*, and *Macropus* (Biggers & DeLamater, 1965, p. 403, table 2).

Because pairing of spermatozoa is not known in any eutherian (Tyndale-Biscoe, 1973, p. 16), nor in any Australasian marsupial, it would appear that non-pairing represents the primitive condition; the pairing phenomenon as occurs in the American marsupials is derived.*

10. *Sperm morphology*.—Three distinct morphological types of spermatozoa have been observed in American marsupials. The first type, described by Biggers & Creed (1962), occurs in species of *Didelphis*, *Monodelphis*, *Philander*, *Metachirus*, *Chironectes*, and *Marmosa* (Biggers & DeLamater, 1965, p. 403, fig. 1). A second morphology was found only in *Caluromys*, in which the spermatozoa possess saucer-shaped heads with the mid-piece inserted into the convex side, and the acrosome lying in the concave side. Pairing occurs by apposition of the two concave sides (Biggers & DeLamater, 1965, p. 403, fig. 2). The third type was observed in *Caenolestes*, in which the spermatozoa are very rectilinear in shape with a niche on one side from which the mid-piece arises. Pairing occurs by apposition of the edges opposite the insertion of the mid-piece (Biggers & DeLamater, 1965, p. 403, fig. 3).

The spermatozoa of each of five Australasian marsupial families (Macropodidae, Phalangeridae, Dasyuridae, Peramelidae, and Phascolarctidae) were investigated by Hughes (1965). The morphologies of

*I must caution that this conclusion is based on a variable character, and cladists have been notoriously unable to deal with the problem of variations of this type. An alternative interpretation to this conclusion is that the marsupial(s) that entered Australia, probably, via a sweepstakes route, could have been an individual(s) that by chance did not have pairing sperm. Thus, the founder effect could be used to favor the view that Australasian marsupials were derived from ancestors in which pairing sperm was present at some frequency. I think this possibility is unlikely, but it does warrant consideration.

the spermatozoa (including dimensions of the head, flagellum, and fine structure) of members of each family were distinct from those of other families. In the wombat, *Vombatus ursinus*, and the koala, *Phascolarctos cinereus*, the morphology of the sperm, particularly of the heads, differs strikingly from that of any other marsupial sperm described. In both species, the proximal portion of the sperm head bears a strongly recurved hook not described for other marsupial sperm, and the flagellum is inserted into a notch on one side of the distal portion of the head (Hughes, 1965, p. 541, pl. 1, fig. 1; figs. 1a, b). The position of the hook in *Vombatus* is not an artifact of fixation, because it was observed in living spermatozoa from the epididymes of several specimens (*ibid.*).

Study of marsupial sperm morphology thus indicates that no special similarity exists between any American and any Australasian groups. Further, the sperm morphology of *Caenolestes* is distinct from that of members of the family Didelphidae. Unfortunately, the ancestral state of marsupial sperm morphology cannot yet be inferred on the basis of available data.

11. *Karyotype*.—Several authors have discussed the question of the original marsupial karyotype, and it is now generally agreed that a diploid number of 14 is primitive for metatherians (Reig et al., 1977; Reig et al., In prep.). The latter authors based their conclusions on a cladistic analysis of all available data. The karyotype is known in four species of two caenolestid genera, *Caenolestes* and *Lestoros*, and in all the diploid number is $2n = 14$ (Hayman et al., 1971; Kirsch, 1977c). Thus, caenolestids are plesiomorphic in chromosome number.

12. *Structure of pes*.—In the pes of living and fossil American marsupials and Australasian Dasyuroidea (*sensu* Ride, 1962, p. 301), digits three and four are commonly subequal, are slightly larger than digits two and five, and are quite separate from the latter. This type of pes has been termed *didactyly* (Gr. *di-*, prefix meaning two or double; *-daktylos*, a finger or toe) and *eleutherodactyly* (Gr. *eleutheros-*, free or not bound) and is regarded by most workers (e.g., Ride, 1962) as the plesiomorphic state for marsupials.

In sharp contrast, the Australasian groups Perameloidea and Phalangerioidea (*sensu* Ride, 1962, p. 301) have digits two and three reduced in size relative to digits four and five, and digits two and three are enclosed basally in a common skin sheath. In some species and groups these digits are bound together for the whole of their length with exception of their distal joints and claws. Digits two and three are generally slender and are markedly shorter than digit four, the domi-

nant toe in the hind foot. This condition has been termed *syndactyly* (Gr. *syn-*, together).

Some authors (*e.g.*, Kirsch, 1977a, fig. 20) have noted that some American didelphids show an approach to the syndactylous condition seen in Australasian groups. However, in those didelphids having relatively reduced digits two and three, these toes are not enclosed in a skin sheath. The "true" syndactylous condition thus occurs among marsupials only in the Australasian groups and is the apomorphic state for this feature.

As described by Osgood (1921), Boas (1933), Lönnberg (1921, p. 76, pl. 1, fig. 4), and Thomas (1895a, b), the pes of *Caenolestes* is relatively long, narrow, and didactylous. The hallux is short, is set at a slight angle to the rest of the foot, and is not opposable. It scarcely reaches the end of the second metatarsal of the second digit, and its functional importance is minimal. Digits two through five are subequal, although the third and fourth are a bit longer than the second and fifth, and all bear well-developed curved claws.

Gregory (1910, p. 211) maintained that in caenolestids:

the pes is entirely eleutherodactylous and shows no trace of the syndactyly so characteristic of the [Australasian] Diprotodontia.

He further concluded that the pes, as in smaller Australasian *Dasyuridae*, is modified for terrestrial and cursorial habits.

Osgood (1921, p. 21) noted that in some specimens of *Caenolestes* available to him for study

the third and fourth digits are connected at the base by an integumentary web which is slightly more extensive than that between the other digits, but this is scarcely to be regarded as a tendency toward syndactyly.

Lönnberg (1921, p. 77) also noted that in a specimen of *Caenolestes obscurus* that he studied, the fourth and fifth digits on the right hind foot were united along their whole length in a skin sheath. Both examples are of anomalous individuals, but well illustrate the ease with which two toes may become united or nearly so.

Little is known of the postcranial anatomy of fossil caenolestids. Ameghino (1894) described the feet of Santacrucian representatives of his suborder *Paucituberculata* as follows:

The four limbs were almost equal in length, but the hind feet were longer than the fore. They were plantigrade, with five toes on the hind feet and probably also on the fore feet, with all the toes well developed and without the least trace of syndactyly (translated from Spanish by Sinclair, 1906, p. 418).

Figures substantiating these observations were not given nor were descriptions of postcranial materials presented. The only described post-

cranial material of fossil Caenolestidae are by Sinclair (1906, p. 423). These include the distal end of a right scapula, a left humerus, a left radius, and a left ulna, all attributed to "*Garzonia patagonica*" (= *Stilotherium dissimile*).

In summary, caenolestids have a didactylous pes and are therefore plesiomorphic in this feature.

SYNOPSIS OF THE CHARACTERS

The distribution of the characters and their states is summarized in Table 20. An important feature of this analysis is that the family Caenolestidae, although clearly a monophyletic group as shown by features of the dentition (*e.g.*, development of diprotodonty; presence of a hypocone on M^{1-3} ; presence of an "intermediate conule" at base of metacone in M^{1-3} ; emphasis of M_1 in mastication) is largely defined by retention of characters here considered primitive for the Marsupialia (*e.g.*, lack of a fasciculus aberrans in forebrain; lack of a pouch; presence of ossified epipubic bones; diploid chromosome number of $2n = 14$; didactylous pes). Some characters distinguish caenolestids from some or all other marsupial groups, but the polarity is either not surely known (*e.g.*, sperm morphology) or the polarity of change is not clearly understood with respect to all other marsupial groups (*e.g.*, presence of large palatal vacuities; reduction of teat number to 5 or 4). Some characters establish definite phylogenetic affinity with other marsupial groups (*e.g.*, sperm pairing in caenolestids and didelphoids shows living American marsupials to be a monophyletic group), and some characters distinguish one caenolestid subfamily from another (*e.g.*, presence of an antorbital vacuity in Caenolestinae; number of incisors; certain structural features of premolars and molars).

Osgood (1921, pp. 111, 151), based on a detailed study of *Caenolestes*, listed several features not discussed above in which it differs from other living non-caenolestid marsupials. These include: (1) presence of a large mastoid foramen in adults; (2) a long, narrow carotid canal between the petrous periotic and basioccipital; (3) floor of braincase very wide between sphenoidal fissures; (4) mastoid large and broadly exposed laterally; (5) olfactory fossa relatively large and wide; (6) very short pubic symphysis; (7) extended articular surface of trochlea of humerus; (8) sesamoid in tendon of *m. extensor cruris* [among marsupials a patella is reported elsewhere only in perameloids (Winge, 1923) and borhyaenoids (Sinclair, 1906)]; and (9) stomach with three marked divisions (the cardiac gland of the stomach has a counterpart only in *Phascolarctos* and *Vombatus*).

TABLE 20. Summary of some diagnostic characters of the tribes and subfamilies of Caenolestidae.

Character	I		II		III		IV	
	Plesiomorphic state for Marsupialia	Caenolestini	Caenolestinae	Pichipilini	Palaeothentinae	Paraberitini	Aberitinae	Aberitini
1. Antorbital vacuity between nasal, frontal, and maxillary	absent	present	present	present	absent	(unknown)	(unknown)	(unknown)
2. Palatal vacuities	absent	present	present	present	present	(unknown)	(unknown)	(unknown)
3. Brain	fasciculus aberrans absent	fasciculus aberrans absent	fasciculus aberrans absent	(unknown)	(unknown)	(unknown)	(unknown)	(unknown)
4. Dental formula	I_1^1, C_1, P_3^3, M_1^1	$I_{3-4}^4, C_1, P_3^3, M_1^1$	$I_{3-4}^4, C_1, P_3^3, M_1^1$	$I_{3-4}^4, C_1, P_3^3, M_1^1$	$I_2^2, C_1, P_{2-3}^3, M_1^1$	I_2^2, C_1, P_3^3, M_1^1	I_2^2, C_1, P_3^3, M_1^1	I_2^2, C_1, P_3^3, M_1^1
5. Dental specializations	unspecialized	diprotodont	diprotodont	diprotodont	diprotodont	diprotodont	diprotodont	diprotodont
a. Incisors	two	two	two	two	one or two	one	one	one
b. Number of roots on P_2	two	two	two	two	one or two	one	one	one

TABLE 20. *Continued.*

Character	I		II		III		IV	
	Plesiomorphic state for Marsupialia	IIa Caenolestini	IIb Pichipilini	Caenolestinae	Palaeotheninae	IVa Paraderitini	IVb Abderitini	
c. Size and structure of P ₃	large, two rooted, of equal or greater height than M ₁	large, two rooted, of equal or greater height than M ₁	large, two rooted, of equal or less height than M ₁	either large, two rooted, and possibly higher than M ₁ ; or small, single rooted, and less than ½ height of M ₁ [intermediate sizes occur]	large, two rooted and blade-like (<i>Parabderites minusculus</i> has an unserrated blade as in <i>Palaeotheres</i> , whereas in <i>Parabderites bicristatus</i> , it is serrated)	very small, single rooted styliform, and set in notch in anterobasal edge of M ₁		
d. Antemolar teeth	large and functional	greatly reduced in size	greatly reduced in size	greatly reduced in size	greatly reduced in size	greatly reduced in size	greatly reduced in size	
e. Molar structure (in general)	tuberculo-sectorial; stylar shelf present	tuberculo-sectorial (no lophs in unworn teeth); stylar shelf absent	tuberculo-sectorial (no lophs in unworn teeth); stylar shelf absent	brachyodont (no distinct lophs in unworn teeth); stylar shelf absent	bunolophodont (distinct lophs connect primary labial and lingual cusps in unworn teeth); stylar shelf absent	bunolophodont (distinct lophs connect primary labial and lingual cusps in unworn teeth); stylar shelf absent	bunolophodont (distinct lophs connect primary labial and lingual cusps in unworn teeth); distinct accessory cusps present anterior to anterolabial cusp); stylar shelf absent	

TABLE 20. Continued.

Character	I		II		III	IV	
	Plesiomorphic state for Marsupialia	Caenolestinae	Caenolestinae	Pichipillini	Palaeotheninae	IVa Paraberitini	IVb Abderitini
f. Hypococone on M ¹⁻³	absent	present	present	present	present	present	present
g. Relative size of molars	gradual size increase from M ₁ to M ₃	sharp size decrease from M ₁ to M ₃	sharp size decrease from M ₁ to M ₃	sharp size decrease from M ₁ to M ₃	sharp size decrease from M ₁ to M ₃	sharp size decrease from M ₁ to M ₃	sharp size decrease from M ₁ to M ₃
h. "Inter-mediate conule" at base of metacone	absent (homology not established)	present in unworn teeth	present in unworn teeth	present in unworn teeth	present in unworn teeth only in <i>Palaeothenes minutus</i>	no trace	no trace
i. Structure of M ₁	trigonid and talonid regions distinct and unmodified; metaconid present	trigonid and talonid regions distinct and unmodified; metaconid present	trigonid and talonid regions distinct and little modified; metaconid present	trigonid (protocnid-paraconid crest) elongated but not blade-like; talonid little modified (large and distinct); metaconid present	trigonid large, blade-like and greatly elevated above rest of tooth row; metaconid absent; talonids large and distinct	trigonids very large, blade-like with serrated edges and greatly elevated above rest of tooth row; metaconid absent; talonids very reduced	

TABLE 20. *Continued.*

Character	I		II		III		IV	
	Plesiomorphic state for Marsupialia	IIa Caenolestini	IIb Pichipilini	Palaeothentinae	IVa Paraberitini	IVb Abderitini	IVc Abderitinae	IVd Abderitini
j. Paraconid on M_2 - M_3	large and distinct	large and distinct	very reduced	absent (lost)	absent (lost)	absent (lost)	absent (lost)	absent (lost)
k. Structure of M^1	tribosphenic	quadrotubercular	quadrotubercular	quadrotubercular	quadrotubercular	(unknown)	blade-like with serrated edges	blade-like with serrated edges
l. Sectorials	not developed	not developed	not developed	P^3	P^3	$P^3(?)$	M^4 (serrated)	M^4 (serrated)
m. Trigonid and talonid regions on M_{2-3}	distinct and subequal in size in basins distinct; trigonid cusps notably higher than talonid cusps; absence of cuspsules posterior to lingual trigonid cusp	distinct, and talonid much larger in occlusal view, larger in occlusal view than trigonid; trigonid basin distinct; talonid basin narrow and deep; trigonid cusps notably higher than talonid cusps; absence of cuspsules posterior to lingual trigonid cusp	distinct, and talonid much larger in occlusal view than trigonid; trigonid cusps equal to or only slightly higher than talonid cusps; talonid basin broad and relatively shallow; cuspsule present posterior to lingual trigonid cusp	distinct, subequal in size in occlusal view and in height in lateral view; trigonid and talonid basins shallow	M_1 , trigonid	P_3 - M_1 , trigonid (both serrated in later forms)	M_1 , trigonid (serrated)	typically difficult to differentiate and subequal in size in occlusal view and in height in lateral view; trigonid and talonid basins shallow

TABLE 20. *Continued.*

Character	I		II		III		IV	
	Plesiomorphic state for Marsupialia	IIa	Caenolestinae	IIb	Palaeothentinae	IVa	IVb	
6. Teat number	27 (more or less)	4 or 5	(unknown)	Pichipilini	(unknown)	Paraberitini	Abderitini	
7. Pouch or "marsupium"	absent	absent	(unknown)		(unknown)	(unknown)	(unknown)	
8. Ossified epipubic bones	present	present	(unknown)		(unknown)	(unknown)	(unknown)	
9. Sperm pairing	"unpaired"	"paired"	(unknown)		(unknown)	(unknown)	(unknown)	
10. Sperm morphology	ancestral state not yet established	rectilinear with notch on one side from which mid-piece arises	(unknown)		(unknown)	(unknown)	(unknown)	
11. Karyotype	2n = 14	2n = 14	(unknown)		(unknown)	(unknown)	(unknown)	
12. Pes	didactylous	didactylous	(unknown)		(unknown)	(unknown)	(unknown)	

The polarity of each of these characters needs to be firmly established, although they appear to be potentially useful in phylogenetic studies. If nothing else, they reaffirm the uniqueness of caenolestids compared with other marsupial groups. I list these here for the sake of completeness, but do not attempt a cladistic analysis of them at this time.

PHYLOGENETIC RELATIONSHIPS OF CAENOLESTID SUBFAMILIES

Three major monophyletic lineages occur among known fossil and living Caenolestidae. These are regarded as warranting subfamilial recognition and include the Caenolestinae, Palaeothentinae, and Abderitinae. These subfamilies share a number of apomorphies that distinguish them from some or from all other marsupial groups, and the joint possession of these apomorphies establish the monophyletic origin of the family Caenolestidae. These apomorphies include: reduction in incisor number to at most 4; palatal vacuities present; diprotodonty; most antemolar teeth greatly reduced in size; hypocone present on M^{1-3} ; loss of styler shelf; sharp size decrease of molars from M_1 to M_4 ; "intermediate conule" present at inner base of metacone in unworn M^{1-3} ; M_1 quadritubercular; talonids of $M_{2,3}$ much larger in occlusal view than trigonids; teats five or four in number; sperm paired; and sperm rectilinear, with notch on one side from which mid-piece arises. The unique position of caenolestids among the Marsupialia is further established by studies of serum proteins (Kirsch, 1977a).

The one uniquely derived character of great importance in phylogenetic inference is the occurrence of sperm "pairing" in caenolestids and didelphoids. This feature clearly shows the American marsupials to be a monophyletic group relative to those in Australasia, and it further clarifies the major trichotomy in marsupial phylogeny implied by the serological studies of Kirsch (1977a, fig. 23).

Two tribes of Caenolestinae, the Caenolestini and Pichipilini, are recognized. Members of the Caenolestini are the most generalized of caenolestids, and they retain the larger number of states regarded as plesiomorphic for the Marsupialia. This tribe has the longest geological range of any caenolestid group (Casamayoran to Recent), and it represents the basal stock from which may be derived the Pichipilini and the subfamilies Palaeothentinae and Abderitinae. The plesiomorphic states possessed by Caenolestini include: P_2 with two roots; P_3 large, two rooted, and of equal or greater height than M_1 ; trigonid and talonid regions of M_1 distinct and unmodified; the paraconid on $M_{2,3}$ large and distinct. Members of the Caenolestini possess no apomorphous states

not shared with Pichipilini; they are distinguished from Pichipilini by possession of plesiomorphic states of the subfamily.

Apomorphous states possessed by Pichipilini, which separate them from Caenolestini, include: P_3 of equal or less height than M_1 ; paraconid very reduced on M_{2-3} ; trigonids narrower than talonids; trigonid cusps equal to or only slightly higher than talonid cusps; talonid basin broad and relatively shallow; and cuspule present posterior to lingual trigonid cusp on M_{1-3} .

The common possession of an antorbital vacuity between the nasal, frontal, and maxillary in both Caenolestini and Pichipilini is a unique apomorphy that establishes the Caenolestinae as a monophyletic group.

The subfamilies Palaeothentinae and Abderitinae are monophyletic and shared a common ancestor that possessed the following apomorphies: incisor number reduced to $\frac{3}{2}$, mandibular ramus relatively shorter and deeper than in Caenolestini; molars brachyodont; protoconid-paraconid crest on M_1 trigonid becomes elongated but not blade-like; sectorial occlusion developed between posterolingual edge of enlarged P^3 and protoconid-paraconid crest of M_1 trigonid; paraconid is reduced in size and is virtually lost on M_{2-3} ; trigonid and talonid regions of M_{2-3} subequal in size in occlusal view and in height in lateral view; and talonid basin shallow.

The Palaeothentinae retained most of these features without change, but are further distinguished from Abderitinae in hypertrophy of the P^3 . Some Palaeothentinae (*i.e.*, species of *Acdestis*) have the additional apomorphies of a single-rooted P_2 , and the P_3 is small, sometimes single rooted, and less than $\frac{1}{2}$ the height of M_1 .

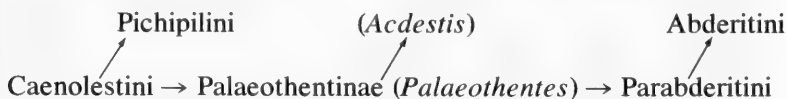
Some Palaeothentinae retain features shared with Caenolestini, but which are lost in other Palaeothentinae and in all Abderitinae. In *Palaeothentes minutus* these include: presence of an "intermediate conule" in unworn M^{1-3} ; P_2 double rooted in some specimens; P_3 equal to or greater in height than M_1 ; and retention of the "stamp" of a tuberculo-sectorial dentition. *Palaeothentes minutus* thus forms a link between the subfamilies Caenolestinae and Palaeothentinae.

Two tribes of Abderitinae, the Parabderitini and Abderitini, are recognized. The Abderitinae are a monophyletic group as indicated by the common possession of the following apomorphies: P_2 single rooted; molars bunolophodont; "intermediate conule" completely lost; trigonid of M_1 large, blade-like with serrated edge, and greatly elevated above rest of tooth row; and metaconid lost from M_1 .

The Parabderitini retained the large P_3 as occurs in most Palaeotheninae and Caenolestini and incorporated it as a sectorial. The sectorials in Parabderitini include $P^3(?)$ above and the P_3 and trigonid of M_1 below. The P_2 is separated from the P_3 by a distinct diastema in Parabderitini, but not in Abderitini or in Palaeotheninae or Caenolestinae. Thus, the dental specializations seen in *Parabderites* simply represent further development of those occurring in the genus *Palaeothenes* among the Palaeotheninae.

The Abderitini represent the most specialized of known caenolestids and are distinguished by possession of the following apomorphies: P_3 very small, single rooted, styliform, and set in notch in anterobasal edge of M_1 ; distinct accessory cuspule present anterior to paracone on M^{2-3} ; M^1 blade-like and with a serrated edge and talonid very reduced; sectorials are M^1 above and trigonid of M_1 below; and trigonid and talonid regions of M_{2-3} are typically difficult to differentiate.

Sinclair (1906, pp. 417-418) adduced evidence to show that the plagiulacoid M_1 in *Abderites* was derived from a tuberculo-sectorial M_1 as occurs in such caenolestines as *Caenolestes*. He further suggested that the structural change passed through an intermediate stage as seen in some Palaeotheninae. These views are ratified by the present study. The tribes and subfamilies of Caenolestidae form a structural series, and one group is readily derivable from another. It is thus possible to construct an evolutionary series based on known morphologic types. In the following diagram, change occurs from left to right along the horizontal axis, and dorsodextrally along the vertical axis:



One implication of the foregoing analysis is that size reduction of the P_3 occurred independently in all three subfamilies. In the Caenolestinae it occurred in the Pichipilini (*Pliolestes*), in the Palaeotheninae it occurred in *Acdestis*, and in the Abderitinae it occurred in the Abderitini. This size reduction is regarded as a convergent feature in which the ancestral form had, in all cases, a large two-rooted P_3 . Thus, *Abderites* did not evolve from an ancestral palaeothenine such as *Acdestis*, but from a form with a large, two-rooted P_3 like *Palaeothenes*.

The time of the didelphoid-caenolestoid dichotomy is not certain and is open to broad speculation. Based on present knowledge, two points appear certain; one that the split occurred in South America, and two that the Caenolestidae are, in the strictest sense, monophyletic.

The earliest record of fossil marsupials in South America comes from the Laguna Umayo local fauna in Perú, considered to be of Late Cretaceous age (*vide* Sigé, 1972). The marsupial fauna includes two species of didelphoids (Sigé, 1972; Crochet, 1979). These animals are known exclusively from a few isolated or broken tooth fragments. The diversity of this fauna has yet to be determined, and absence of forms known from later faunas carries little significance at this time. Absence of caenolestids does not necessarily indicate that they were not present at this locality or that they did not exist elsewhere.

Caenolestids are also unknown in the rich Riochican fauna of Itaboraí, Brazil, in which many small marsupials are found. However, one Riochican species, *Derorhynchus singularis* Paula Couto (1952a, p. 15) displays a number of features that are reminiscent of living caenolestids. These include: a slender elongated mandibular ramus; a long symphysis; a well-developed, procumbent, laterally compressed, and probably very elongate I₁; and in general reduction in size of antemolar teeth on the symphysis. Paula Couto (1952a, p. 15) concluded that this species was convergent with caenolestids, and he accordingly classified it in the family Didelphidae, subfamily Didelphinae.

It must be stressed that of the 13 genera and 14 species of marsupials referred by Paula Couto (1952a, 1961, 1962, 1970) to the Didelphidae, all are based on preliminary original descriptions. He neither attempted to evaluate the relationships of these forms among each other, nor to compare them with possible ancestral forms from the Late Cretaceous of North America or with contemporaneous or later taxa elsewhere. As a result, the taxonomic diversity of these forms has not yet been fully realized. Simpson (1971, p. 112) has noted, and I agree, that at least subfamilial division is warranted, but these divisions have not yet been established. These didelphoids seem to be as varied as the didelphoids from the Lance Formation of North America that Clemens (1966) puts in three families, one with two subfamilies.

It is now generally agreed that all Cenozoic marsupial groups evolved from didelphoids or didelphoid-like ancestors. It is thus important to understand the phylogenetic relationships of these Riochican forms with each other and with other groups. These Riochican didelphoids represent the earliest documented radiation of marsupials in South America, and they provide a "key" to understanding the phylogenetic relationships of all other South American marsupial groups.

The critical point with regard to this study is that ancestral forms for the family Caenolestidae *may* exist among known Riochican didelphoids, but if so they have not been recognized as such. This will

only be possible pending a detailed phylogenetic study of these Riochican taxa. All that can be said for now is that caenolestids are not known or are not recognized in beds of pre-Casamayoran age.

Caenolestids are first known from a single isolated partial lower molar from beds of Casamayoran age in Patagonia. Little can be said about the affinities of this tooth with other caenolestids or with other marsupial groups. This tooth is however the oldest specimen of the family Caenolestidae yet known, and it records a minimal age for the appearance of this family.

The fossil record of caenolestids begins, for all practical purposes, in the Deseadan. Relatively complete representatives of each of the three subfamilies have been found in beds of this age in Argentina. Further, a member of the Palaeothentinae is known from the Deseadan of Bolivia. The three subfamilies are clearly distinguishable at this time, indicating an earlier radiation for the family.

The above data indicate that a member of the generalized caenolestid subfamily Caenolestinae was present by Casamayoran time and that the more specialized subfamilies Palaeothentinae and Abderitinae (which are derivatives of the Caenolestinae) are present in the Deseadan. The didelphoid-caenolestoid dichotomy clearly occurred before the Casamayoran, whereas subfamily differentiation within the Caenolestidae was a pre-Deseadan event.

The cladogram in Figure 36 is a graphic summary of the above relationships, based upon an analysis of shared-derived character states.

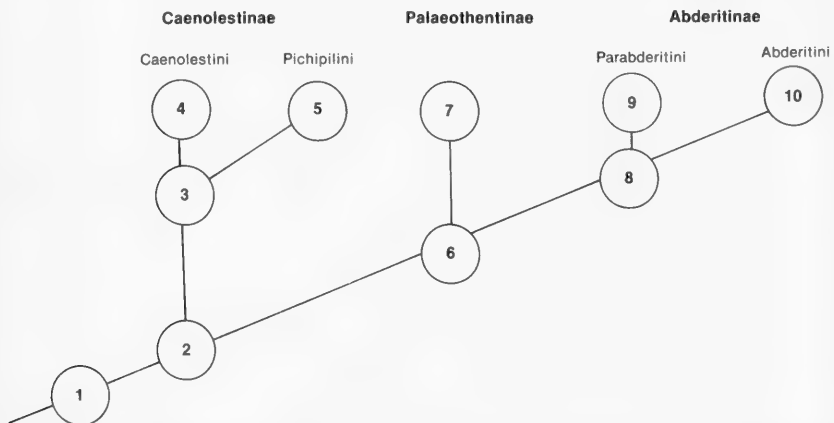


FIG. 36. Cladogram showing probable relationships of suprageneric groupings of Caenolestidae. Diagram shows only relative position of common ancestor. Numbers indicate character state distribution.

Key to Figure 36:

- 1, Plesiomorphic character states for Marsupialia—these are listed in Table 20, column 1.
- 2, Apomorphies for Caenolestidae: I_4^1 , C_1^1 , P_3^3 , M_4^1 ; palatal vacuities present; di-protodonty; most antemolar teeth greatly reduced in size; hypocone present on M^{1-3} ; no styler shelf; sharp size decrease of molars from M_1 to M_4 ; "intermediate conule" present at inner base of metacone in unworn M^{1-3} ; M^1 quadritubercular; talonids of M_{2-3} much larger in occlusal view than trigonids; teats 5 in number; sperm paired; sperm rectilinear with notch on one side from which mid-piece arises.
- 3, Apomorphies for Caenolestinae: I_{3-4}^1 , C_1^1 , P_3^3 , M_4^1 ; antorbital vacuity present between nasal, frontal, and maxillary.
- 4, Apomorphies for Caenolestini: None known—tribe retains only plesiomorphic states for subfamily.
- 5, Apomorphies for Pichipilini: paraconid very reduced on M_{2-3} ; trigonid cusps of M_{2-3} equal to or only slightly higher than talonid cusps; talonid basin broad and relatively shallow; cuspule present posterior to lingual trigonid cusp on M_{1-3} .
- 6, Apomorphies for immediate common ancestor of Palaeothentinae and Abderitinae: I_2^2 , C_1^1 , P_3^3 , M_4^1 ; mandibular ramus relatively shorter and deeper; molars brachyodont; protoconid-paraconid crest of M_1 trigonid elongated but not blade-like; sectorials P^3/M_1 trigonid; paraconid virtually lost on M_{2-3} ; trigonid and talonid regions of M_{2-3} subequal in size in occlusal view and in height in lateral view; and talonid basin shallow.
- 7, Apomorphies for Palaeothentinae: P_2 single rooted in some forms; P_3 in some forms small, single rooted, and less than $\frac{1}{2}$ the height of M_1 ; "intermediate conule" lost in some forms; P^3 large with posterolingual shear surface.
- 8, Apomorphies for Abderitinae: P_2 single rooted; molars bunolophodont; "intermediate conule" lost; trigonid of M_1 large, blade-like, and greatly elevated above rest of tooth row; loss of M_1 metaconid.
- 9, Apomorphies for Parabderitini: P_3 large, two rooted, and blade-like; sectorials $P^3(?) / P_3 - M_1$ trigonid; P_2 separated from P_3 by distinct diastema.
- 10, Apomorphies for Abderitini: mandibular ramus relatively shorter and deeper; P_3 very small, single rooted, styliiform, and set in notch in anterobasal edge of M_1 ; distinct accessory cuspule present anterior to paracone on M^{2-3} ; M^1 blade-like; trigonid of M_1 very large, blade-like with serrated edge, and talonid very reduced; sectorials M^1 / M_1 trigonid; trigonid and talonid regions on M_{2-3} typically difficult to differentiate.

DISCUSSION AND CONCLUSIONS

During the Cenozoic in South America, the ecological roles of small mammal niches were filled in part by members of the family Caenolestidae. Caenolestids reached their known evolutionary climax in the mid-Tertiary (*i.e.*, Santacrucian-Early Miocene time) when they were represented by three known subfamilies, seven genera, and 11 species. In beds of this age, caenolestids are the most abundant and the most taxonomically diverse of the small Marsupialia.

Factors influencing the times of origin, adaptive radiation, decline in diversity, and/or extinction of the various caenolestid groups are complex, but most of these events are correlated with the appearance and/or diversification of other mammalian groups. Thus, there occurred in South America successive replacement through time of (and by) different groups of animals stemming from different lineages but occupying the same adaptive zone. These "ecological replacements" or "evolutionary relays" may have resulted from *active* competition between the successive groups filling these roles or from *passive* replacement resulting from the disappearance of one group due to chance processes or as a result of concurrent environmental changes. Alternatively, such faunal changes were the result of a combination of these or of other possibilities.

The polydolopoids, a marsupial group with plagiaulacoid dental specializations, were taxonomically diverse in beds of early Tertiary age in South America. They declined in diversity after Casamayoran time and make their last appearance in the Deseadan of Bolivia (Patterson & Marshall, 1978, p. 95). It is either coincidental or significant that this group's last appearance coincides with the first documented appearance of caviomorph rodents in South America. It is generally agreed that polydolopoids were somewhat rodent-like in structure and ecology and may thus have been replaced by these rodents in the Early Oligocene.

Abderitines also make their first appearance in the Deseadan of Patagonia. They thus occur contemporaneously with polydolopoids.

but the two groups were allopatric in their geographic distribution; Deseadan abderitines are known only from Patagonia, southern Argentina, whereas Deseadan polydolopoids are known only from Bolivia. Abderitines and polydolopoids were very similar in dental morphology and presumably in ecology as well. It is tempting to speculate that abderitines rather than the caviomorph rodents were, at least in part, the ecological replacements of polydolopoids. The subfamily Palaeothentinae also appears in the Deseadan and may likewise have evolved to help fill part of the adaptive zone in the mid-Tertiary that was occupied by polydolopoids in the early Tertiary. Evolution of the Abderitinae and Palaeothentinae may thus have been triggered by the vacated or opening adaptive zone for small terrestrial omnivores-herbivores and may have been linked with the decline to extinction of the marsupial superfamily Polydolopoidea.

The appearance of caviomorph rodents in the Early Oligocene may or may not have been an influence on the decline to extinction of the polydolopoids. The appearance of these rodents certainly did not appear to hinder the evolutionary potential of abderitines and palaeothentines. Caviomorph rodents and these groups of caenolestids appear at the same time in the fossil record of South America and underwent successful concurrent and apparently sympatric adaptive radiations.

There is some suggestion that the abderitines and palaeothentines were at least in part competitively exclusive. The ratio of species of Abderitinae to Palaeothentinae in the Deseadan of Patagonia is 1:3, in the Colhuehuapian it is 4:1, and in the Santacrucian it is 2:5. Thus, in Patagonian faunas of a given Age one subfamily is dominant in species diversity over the other. These differences may be the result of some form of competitive interaction between members of these groups, or, alternatively, may simply be attributed to an artifact of sampling.

Causes of the post-Santacrucian decline to extinction of the Abderitinae and Palaeothentinae are obscure, but appear to be linked with major climatic and concomitant ecological changes. During the late Miocene and Pliocene, the Argentine sedimentation center shifted from Patagonia to the pampas and northwestern regions. The sediments changed from predominantly pyroclastic (*i.e.*, tuffs and bentonitic clays) that characterize pre-Chasican units, to predominantly clastic (*i.e.*, silts, sands, and clays) that predominate post-Friasian units of the pampean region. This change of sediment type coincided with a post-Friasian phase of Andean orogeny that was to result in elevation of the Andean Cordillera. A major period of orogenic activity occurred be-

tween 4.5 and 2.5 mybp and resulted in an increase in elevation of 2,000 to 4,000 meters. Elevation of the Andean Cordillera acted as a barrier to moisture-laden Pacific winds. The southern South American habitat changed from primarily savanna-woodland (which predominated during the early to middle Tertiary-Eocene through Miocene) to drier forests and pampas, ranging from forests in the northern parts of the continent to grasslands in the south. There was initiated the desertification of Patagonia, caused by the rain shadow effect of the newly elevated Andes. Pampas environments, predecessors of those prevailing today, probably came into prominence at this time. Many subtropical savanna-woodland forms retreated northward, and new opportunities arose for those mammals able to adapt to a plains environment (Marshall et al., In press and references therein). Those groups that neither moved nor adapted became extinct. Such was the apparent fate of the Abderitinae and Palaeotheninae.

One caenolestid group, the Pichipilini, did however adapt to these new conditions. A specimen of *Pliolestes* sp. is known from beds of Chasicoan age, and several specimens of *P. tripotamicus* are known from faunas of Montehermosan age from localities in the southwestern corner of Buenos Aires Province, Argentina. Pascual & Herrera (1973) have suggested that extinction of these marsupials may have been caused by competitive interaction with cricetine rodents that first appear in the South American fossil record in beds of Montehermosan age in the Province of Buenos Aires (Marshall, 1979a and references therein).

The only living caenolestids are members of the tribe Caenolestini. These are the most generalized of all known Caenolestidae, and they are carnivorous-insectivorous in their feeding habits. They are shrew-like in morphology and ecology and occur throughout the west coast of South America, from the Andes of Colombia and Venezuela in the north to southern Chile in the south. Caenolestini have apparently filled their present roles since the early Tertiary and have not been seriously challenged for them by invading ecologically similar groups during any time in their evolutionary history.

Their position may now be threatened. Members of the placental family Soricidae have recently invaded the northwestern corner of South America (Hershkovitz, 1972). They came from North America across the Panamanian Land Bridge that became established about 3 my ago (see Marshall, 1979a, and references therein). The family is represented by one genus, *Cryptotis*, which occurs sympatrically with species of *Caenolestes* over parts of its range. *Cryptotis* is significantly

smaller in size than *Caenolestes*, and this difference may explain or permit their sympatry. However, the biological consequences of potential competition between these groups is not yet fully understood or evident, but both are similar in structure and presumably in ecology as well. Thus, there may be an active "evolutionary relay" in progress, and the caenolestines may be in jeopardy. If so, the Caenolestini may well join the ranks as a fossil group along with their more specialized bygone relatives.

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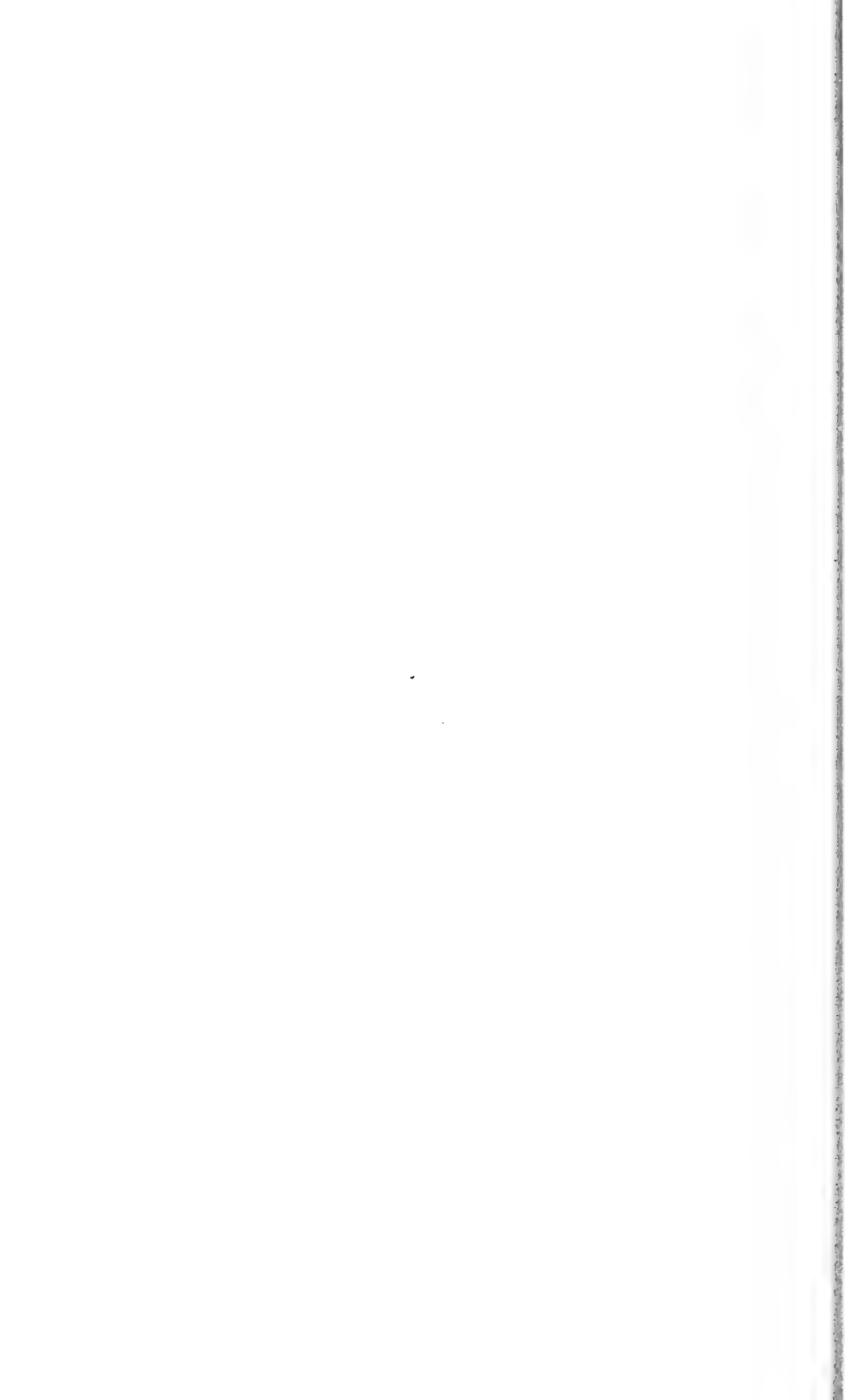
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