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New Series, No. 10

SYSTEMATICS OF THE SOUTH AMERICAN MARSUPIAL FAMILY MICROBIOTHERIIDAE

LARRY G. MARSHALL

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ABSTRACT

Members of the South American marsupial family Microbiotheriidae are known from Late Oligocene (Colhuehuapian) and Early Miocene (Santacrucian) age beds in Patagonia, southern Argentina, and in the Recent fauna from Chiloé Island, south central Chile, and from adjacent parts of Argentina. Two genera, *Microbiotherium* and *Dromiciops*, and seven species are recognized. *Microbiotherium divisum* (Ameghino, 1902e) is known only from the Colhuehuapian. *M. acicula* (Ameghino, 1891); *M. patagonicum* Ameghino, 1887; *M. tehuelchum* Ameghino, 1887; and *M. gallegosense* Sinclair, 1906 are known only from the Santacrucian. *M. praecursor* (Ameghino, 1898) is of unknown age and provenance, while *Dromiciops australis* (Philippi, 1893a) is known only from the Recent. These genera and species are distinguished primarily on the basis of absolute size, although relative size and minor structural differences in the canines, cheek teeth, and auditory bullae also have proven diagnostic.

The taxonomy of other didelphoid or supposed didelphoid taxa either referred to the Microbiotheriidae or implicated in the ancestry of this family are discussed. These include: *Ideodelphys microscopicus* Ameghino, 1902d (Casamayoran-Early Eocene); *Coona pattersoni* Simpson, 1938 (Casamayoran); *Eomicrobiotherium* [nov. gen.] *gaudryi* (Simpson, 1964) (Casamayoran); *E. gutierrezzi* (del Corro, 1977) (Casamayoran); and *Pachybiotherium acclinum* Ameghino, 1902e (Colhuehuapian). It is demonstrated that microbiotheres were among the syntypes of the caenolestid species *Stilotherium dissimile* Ameghino, 1887 (Santacrucian) and *Phonodromus gracilis* Ameghino, 1894 (Santacrucian).

INTRODUCTION

A major adaptive radiation of the marsupial superfamily Didelphoidea has been and continues to be documented for the South American Cenozoic. Aspects of this group's evolutionary history have been clarified in recent years, although many problems regarding the phylogenetic relationships of recognized taxa still remain. Existing problems are compounded by the fact that many of the taxa erected by the eminent Argentine paleontologist Florentino Ameghino some 80 to 90 years ago have not been adequately restudied since that time. The systematics of these taxa have yet to be stabilized at the generic and specific levels. Until this is done, the evolutionary history of South American didelphoids in particular and marsupials in general will remain more speculative than is really necessary.

One of the didelphoid groups most in need of such a review is the Microbiotheriidae. Nearly a score of species grouped in a dozen genera have been

referred by various workers to this family; many have been regarded in recent years as *nomina vana* or *nomina dubia*.

This paper presents a detailed systematic revision of living and fossil members of the South American marsupial family Microbiotheriidae. It reviews the taxonomic history of the Microbiotheriidae, discusses the possible phylogenetic relationships of the included taxa, stabilizes the group's taxonomy at the generic and specific levels, and represents an attempt to bring together in one place an updated and expanded systematic treatment of these animals. The systematics and phylogenetic positions of other didelphoid and caenolestoid taxa which 1) were formally assigned at one time or another to the Microbiotheriidae; 2) were implicated in the ancestry of the Microbiotheriidae; or 3) had specimens of microbiotheres included erroneously as syntypes in original descriptions, also are discussed and the systematic problems clarified. For all of these taxa, an attempt is made to give complete listings of generic and specific synonymies, complete literature citations, and hypodigms inclusive of all known specimens.

During the course of this study I was able to examine firsthand nearly all pertinent materials, including type and referred specimens. This work includes discussion and description of some new materials, but essentially is based on a reappraisal of previously known specimens and literature, and gives revised diagnoses for the family, genera, and species.

TECHNIQUES OF STUDY

Microbiotheres, as in living Didelphidae, have an adult dental formula of $I_1^{1-2-3-4-5}_0$, C_1^1 , $P_1^{1-2-3}_0$, $M_1^{1-2-3-4}_0$. The highest number of teeth known for any fossil or living marsupial, this formula is regarded as primitive (plesiomorphic) for Marsupialia (e.g., Marshall, 1979, p. 388). This conventional system for serial designation of the teeth is used in this study; it is intended to be descriptive and does not necessarily imply homology. The P3 of this system has a predecessor or "milk tooth" here referred to as dP3.

The Argentine fossil localities mentioned below are shown in Figure 1. The chronology and usage of South American land mammal ages follows Marshall et al. (in press).

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

ABBREVIATIONS

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

The following abbreviations are used for specimens from institutional collections: AMNH, American Museum of Natural History, New York; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires; 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; and PU, Princeton University, Princeton, New Jersey.

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

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HISTORICAL REVIEW

The family Microbiotheriidae¹ was created by Ameghino (1887, p. 6) and was diagnosed as:

Marsupiales sumamente pequeños con un gran incisivo en la mandíbula inferior y siete muelas en serie continua, que aumentan de tamaño desde la primera a la quinta y disminuyen desde la sexta a la séptima.²

Ameghino placed this family in the order Marsupialia and included within it two newly recognized genera and three species, all erected on the basis of partial lower dentitions: *Microbiotherium patagonicum*, *M. tehuelchum*, and *Stilotherium dissimile* (table 1). The major features uniting these taxa were their small size, supposed presence of a large procumbent incisor, overall similarity in structure of the molars, similarity in relative size of the molars to each other, and a small M_4 .

This same taxonomic arrangement was followed by Ameghino, who in 1889 (p. 263) (table 1) further included the family in a new order Microbiotheria diagnosed as:

No más de $\frac{5}{8}$ incisivos. Caninos $\frac{1}{2}$. Muelas no menos de $\frac{4}{8}$ a $\frac{7}{8}$ con tubérculos puntiagudos. Paladar con cavidades palatinas. Un interparietal. Arco cigomático delgado. Cráneo puntiagudo. Una rama externa del canal alveolar de la mandíbula inferior. Cola larga. Sacro de dos vértebras. Los cuatro miembros iguales o casi iguales. Un hueso intermedio del carpo. Dedos segundo y tercero del pie posterior, no reunidos por un tegumento externo. Plantígrados. Huesos marsupiales presentes.

Sólo existe en nuestro suelo como representante de este orden, la familia de los Microbiotheriidae.

It would appear from the diagnosis that relatively complete cranial and postcranial material were then known. If this were the case, however, then this material was subsequently never described nor figured by Ameghino.

In 1891, Ameghino removed *Stilotherium* from the Microbiotheriidae and redefined the family as:

Incisivos en número variable, un canino, tres premolares y cuatro molares, todos en serie continua, sin discontinuidad; incisivos pequeños; canino de tamaño variable y a menudo premolariforme; el tamaño de los tres premolares, pequeños y parecidos a los de *Didelphys*, aumenta del primero al último. Verdaderos molares inferiores parecidos a los de *Didelphys*, con dos conos externos y tres internos, pero cuyo tamaño disminuye constantemente del primero al último. M_7 con el talón posterior simple, no bipartido arriba como en *Didelphys*. Ramas mandibulares de borde inferior casi recto aumentando gradualmente el alto de adelante hacia atrás.

¹ Ameghino spelled the family-group name Microbiotheridae. This is a *lapsus*; according to Article 29 of the International Code of Zoological Nomenclature (see Stoll et al., 1961, 1964), the correct spelling is Microbiotheriidae. This emendation was made by many early workers and by Simpson (1929, p. 116) when he proposed the subfamily rank Microbiotheriinae.

² Ameghino numbered the premolars and molars as one series and called them all molars.

TABLE 1. Classification of Microbiotheriidae as proposed by various workers.

Ameghino, 1887	Ameghino, ca. 1904; Palmer, 1904; Trouessart, 1904	Ringuelet, 1953	This study
Marsupialia			
Microbiotheriidae	Microbiotheriidae	Microbiotheriinae	Microbiotheriidae
Microbiotherium patagonicum	<i>Clenia minuscula</i>	<i>Clenia minuscula</i>	<i>Microbiotherium acicula</i>
Microbiotherium tehuelchum	<i>Eodidelphys famula</i>	<i>Eodidelphys acicula</i>	<i>Microbiotherium patagonicum</i>
Stiloetherium dissimile	<i>Eodidelphys fortis</i>	<i>Eodidelphys famula</i>	<i>Microbiotherium praecursor</i>
Ameghino, 1889	<i>Hadroryhynchus conspicuus</i>	<i>Eodidelphys fortis</i>	<i>Microbiotherium divisum</i>
Microbiotheria	<i>Hadroryhynchus tortor</i>	<i>Eodidelphys obtusa</i>	<i>Microbiotherium tehuelchum</i>
Microbiotheriidae	<i>Hadroryhynchus torvus</i>	<i>Eodidelphys pavita</i>	<i>Microbiotherium gallegosense</i>
Microbiotherium patagonicum	<i>Ideodelphys microscopius</i>	<i>Eodidelphys praecursor</i>	<i>Dromiciops australis</i>
Microbiotherium tehuelchum	<i>Microbiotherium forticulum</i>	<i>Microbiotherium</i>	
Stiloetherium dissimile	<i>Microbiotherium patagonicum</i>	(<i>Microbiotherium</i>) <i>acclinum</i>	
Ameghino, 1891	<i>Microbiotherium tehuelchum</i>	<i>Microbiotherium</i>	
Microbiotheria	<i>Oligobiotherium divisum</i>	(<i>Microbiotherium</i>) <i>gallegosense</i>	
Microbiotheriidae	<i>Pachybiotherium acclinum</i>	<i>Microbiotherium</i>	
<i>Eodidelphys famula</i>	<i>Prodidelphys acicula</i>	(<i>Microbiotherium</i>) <i>patagonicum</i>	
<i>Eodidelphys fortis</i>	<i>Prodidelphys obtusa</i>	<i>Microbiotherium</i>	
<i>Hadroryhynchus conspicuus</i>	<i>Prodidelphys pavita</i>	(<i>Microbiotherium</i>) <i>tehuelchum</i>	
<i>Hadroryhynchus tortor</i>	<i>Proteodidelphys praecursor</i>	<i>Microbiotherium</i>	
<i>Hadroryhynchus torvus</i>	<i>Stylognathus diprotodontoides</i>	(<i>Hadroryhynchus</i>) <i>conspicuus</i>	
<i>Microbiotherium forticulum</i>		<i>Microbiotherium</i>	
<i>Microbiotherium patagonicum</i>		(<i>Hadroryhynchus</i>) <i>tortor</i>	
<i>Microbiotherium tehuelchum</i>		<i>Microbiotherium</i>	
<i>Prodidelphys acicula</i>		(<i>Hadroryhynchus</i>) <i>torvus</i>	
<i>Prodidelphys obtusa</i>		<i>Microbiotheridium hernandezii</i>	
<i>Prodidelphys pavita</i>		<i>Ideodelphys microscopius</i>	
<i>Stylognathus diprotodontoides</i>			

He further noted that microbiotheres share features with both the Diprotodonta (Garzonidae = Caenolestidae) and the Pedimana (Didelphyidae). As such he regarded microbiotheres as the basal stock ("tronco antecesor") of the diprotodont and polyprotodont marsupials. Within the Microbiotheriidae he included several new taxa (table 1): *Stylognathus diprotodontoides*, *Microbiotherium forticulum*, *Eodidelphys fortis*, *E. famula*, *Prodidelphys acicula*, *P. pavita*, *P. obtusa*, *Hadorrhynchus tortor*, *H. torvus*, and *H. conspicuus*.

This arrangement remained relatively unchanged for the next seven years. In 1898 Ameghino synoptically rediagnosed the group and the included genera as follows:

MICROBIOTHERIDAE. Parecidos a los *Didelphyidae*, pero con la bóveda del paladar sin prolongarse atrás de la última muela; cuarta a sexta muelas inferiores con dos tubérculos externos y tres internos, última inferior más pequeña y canino a menudo poco diferenciado de los incisivos. Aparecen en el Cretáceo inferior y adquieren su mayor desarrollo en el Eoceno superior, donde se extinguen. *Proteodidelphys praecursor* (n. gen., n. sp.) con algunos caracteres de ungulado, incisivos de corona ancha y excavada como en ciertos ungulados; canino vertical, pequeño y de raíz deprimida perpendicularmente en el centro; las tres primeras muelas inferiores simples sobre el lado externo y complicadas en el interno; tamaño muy pequeño; Cretáceo inferior (areniscas abigarradas) de Patagonia. *Microbiotherium* Ameghino, con el tubérculo anterior interno de las muelas inferiores atrofiado, tres especies: *Microbiotherium patagonicum*, *tehuelchum* y *forticulum* Ameghino, y restos indeterminados en la formación Guaranítica. *Stylognathus diprotodontoides* Ameghino, mandíbula muy grácil y con un solo incisivo a cada lado, formando una transición a los Diprotodontes. *Eodidelphys* Ameghino, se distingue por el tubérculo anterior interno bien desarrollado y el canino muy pequeño, vertical y apenas diferenciado de los incisivos y de la primera muela, dos especies: *Eodidelphys fortis* y *famula* Ameghino. El género *Prodidelphys* Ameghino, se distingue por el canino recto, vertical, muy pequeño, con un callo basal posterior y apenas un poco más elevado que el diente que le sigue; la primera, segunda y tercera muelas están formadas por un simple cono con un callo basal posterior, tres especies: *Prodidelphys acicula*, *pavita* y *obtusa* Ameghino, las tres de tamaño sumamente pequeño. *Hadorrhynchus* Ameghino, se distingue por la sínfisis muy fuerte, muy descendente hacia abajo y prolongada hacia adelante, canino muy robusto: *Hadorrhynchus tortor*, *torvus* y *conspicius* Ameghino (Ameghino, 1898, p. 187).

By 1904, faunas containing marsupials of Casamayoran (Early Eocene) and Colhuewapien (Late Oligocene) age were known in Patagonia. From the former, Ameghino (1902d, p. 43) described *Ideodelphys microscopicus*; from the latter, *Oligobiotherium divisum* (1902e, p. 124), *Pachybiotherium acclinum* (1902e, p. 123), and *Clenia minuscula* (1904c, p. 260). These four taxa he referred to the Microbiotheriidae.

At about that time other workers began either to study microbiotheres or at least to reach alternative conclusions based on Ameghino's published works. Bensley (1903, p. 208) suggested, for example, that

It is extremely probable that at least some of the Miocene Microbiotheriidae of South America were in reality Didelphyidae, and were the ancestors of the Epanorthidae [= Caenolestidae] and their allies and of the Sparassodonta [= Borhyaenidae].

Sinclair (1906) likewise concluded:

Although placed by Ameghino in a separate family, the Microbiotheridae, this genus [*Microbiotherium*] possesses so many important characters in common with the Didelphyidae that the propriety of its reference to the latter family seems beyond question (p. 408). Among living forms it approaches most closely some of the subspecies of *Caluromys laniger* (p. 412).

Winge (1923 [1941]) placed *Microbiotherium* in a new tribe Microbiotheriini in the family Epanorthidae (=Caenolestidae; see Marshall, 1980). He characterized the genus and tribe as having a typical didelphid dental formula of $\frac{2}{1}-\frac{1}{1}-\frac{3}{3}-\frac{1}{1}$. However, largely because of the reduction of the stylar shelf and cusps, relative enlargement of the protocone, reduction in size of the paraconid, and small size of the M_4 , he regarded *Microbiotherium* as a basal stock for the Epanorthidae and accordingly included it within that family. This classification was not followed by subsequent authors.

Simpson (1929, p. 116) regarded the microbiotheres as merely an aberrant group of didelphids, and formally recognized them as a subfamily, Microbiotheriinae, of Didelphidae. In 1935 (p. 136) he diagnosed the subfamily on the basis of dental characters:

Premolars trenchant. Metacone somewhat larger than paracone (except in M^4). No distinct metastylar spur. External cingulum moderate, of nearly equal width throughout, styles weak. M_4 reduced and with narrow, nearly unibasined, unicuspid heel unlike that of other subfamilies.

In his classification of 1945, Simpson (pp. 41–42) recognized the microbiotheres as a subfamily, Microbiotheriinae, of Didelphidae and included within it *Ideodelphys* and *Microbiotherium* (which included as junior synonyms *Proteodidelphys* and *Pachybiotherium*). He noted (p. 42, n. 1), however, that six or seven of Ameghino's other taxa may also belong here, although they are poorly characterized and were regarded by Simpson as *nomina vana*. Simpson clearly stated that until these taxa were revised their taxonomic position would remain uncertain.

Ringuelet (1953) was the first person since Ameghino to attempt a revision of fossil didelphoids of Argentina. She recognized a subfamily Microbiotheriinae and included within it the following taxa: *Clenia minuscula*, *Eodidelphys acicula*, *E. famula*, *E. fortis*, *E. obtusa*, *E. pavita*, *E. praecursor*, *Microbiotherium* (*Microbiotherium*) *acclinum*, *M. (M.) gallegosense*, *M. (M.) patagonicum*, *M. (M.) tehuelchum*, *M. (Hadorrhynchus) conspicuus*, *M. (H.) tortor*, *M. (H.) torvus*, *Microbiotheridion hernandezi*, and *Ideodelphys microscopius*. She created a new genus, *Microbiotheridion*, for the Colhuehuapian species *hernandezi* which Simpson (1932b, p. 2) earlier referred to *Microbiotherium*. Her recognition of two subgenera of *Microbiotherium* (*Microbiotherium* and *Hadorrhynchus*) was also a first in this paper.

At the time of Ringuelet's study it was believed that microbiotheres were an extinct group known only from fossil deposits in Argentina. It thus came as a surprise when O. A. Reig (1955a) convincingly demonstrated that the living opossum *Dromiciops australis* from south central Chile and adjacent parts of Argentina was a member of this group. Based on comparisons with the original description and illustrations of *Microbiotherium tehuelchum* by Sinclair (1906, p. 410, pl. 62, fig. 7), Reig placed *Dromiciops* in the Microbiotheriinae. He pointed out the similarity in the size and structure of the auditory bullae of these taxa and of the similarity in swelling of the periotic (=entotympanic of Segall, 1969b) and its participation in formation of the ossified bulla posteriorly. Reig also noted the similarity in development of the elongated premaxillaries and in the form and orientation of the incisors. He further gave detailed comparative descriptions of both upper and lower dentitions. He added that species of the living opossum genera *Caluromys*, *Caluromysiops*, and *Glironia* agree more closely in dental structure and in some particularities of the skull with *Dromiciops* and *Microbiotherium*.

than with other living opossums. Accordingly, Reig regarded these genera,³ albeit somewhat tentatively, as specialized microbiotheres and included them in the Microbiotheriinae.

In the same year, Reig (1955b) presented a brief but seminal synthetic review of fossil members of the marsupial family Caenolestidae. He demonstrated that many of these taxa were erected on specimens including microbiotheres. Realization of this fact presented another obfuscation to an already miasmatic problem with regard to taxonomic diversity and stability of microbiotheres.

This confusion was the result of similarities in lower molar morphology of fossil caenolestids here referred to the species *Stilotherium dissimile* and *Phonocdromus gracilis* and the microbiothere species *Microbiotherium patagonicum* and *M. tehuelchum* (see below). These similarities were responsible for Ameghino's (1887) initial referral of *Stilotherium dissimile* to the Microbiotheriidae, although he soon realized this error and in 1891 removed *Stilotherium* to the family Garzonidae (= Caenolestidae) where it clearly belongs (Marshall, 1980). A detailed comparison of the dentition of *Stilotherium dissimile* with microbiotheres is presented by Pascual & Herrera (1975), a study made with consideration of the didelphid-caenolestid dichotomy.

Segall (1969a,b) made detailed comparisons of the auditory region of *Dromiciops* with that of *Microbiotherium* and with a large number of living didelphids. He convincingly demonstrated the uniqueness of *Dromiciops* among living forms as well as its remarkable similarity with *Microbiotherium*. He also demonstrated that the auditory regions of the supposed microbiotheres *Caluromysiops*, *Caluromys*, and *Glironia* are very similar to each other and to *Didelphis*, and are notably different from those of *Dromiciops* and *Microbiotherium*. Segall (1969b, p. 497) concluded that

. . . in so far as the auditory region is concerned the similarities [of *Caluromysiops*, *Caluromys* and *Glironia*] with *Didelphis* are so close that I cannot agree with Reig (1955[a]) who considered them specialized *Microbiotherinae* (sic) rather than *Didelphinae*.

Furthermore, the tympanic region of *Caluromys*, while distinct from that of *Dromiciops*, shows little relationship to that of *Didelphis* (Reig & Simpson, 1972).

The chromosomes of *Dromiciops australis* have been studied by Hayman & Martin (1974, p. 7), Sharman (1973, p. 492), and Spotorno & Fernandez (1971, p. 40), and have been shown to have the primitive (plesiomorphic) marsupial number of $2n = 14$. *Dromiciops* alone of all didelphids studied has 22 autosomal arms, and all but one pair of its autosomes are metacentric or submetacentric. Chromosomes five and six are submetacentric as in *Caluromys* (Sharman, 1973, p. 492, fig. 4). The karyotypes of *Glironia* and *Caluromysiops* are unknown. As the karyotypes of species of *Marmosa* are very similar to those of *Caluromys* and *Dromiciops* (Hayman & Martin, 1974), cytology throws little conclusive light on the affinities of these forms.

Unfortunately, there is no comparative information yet available on the structure of the reproductive organs or on the morphology and behavior of sperm in *Dromiciops*. These characters clearly separate *Caluromys* from most other di-

³ As a further historical note it should be mentioned that Thomas (1894) originally suggested that, of the living opossums, *Dromiciops* is probably most closely related to *Caluromys*. In support of such a relationship Osgood (1943, p. 49) noted that, in both, the lining of the pouch is deep cinnamon rufous in color in sharp contrast to the surrounding parts.

delphids (Hill & Fraser, 1925; Biggers, 1966; Biggers & DeLamater, 1965; and Biggers et al., 1965).

Kirsch (1977) has recently used serological evidence to demonstrate that *Caluromys* is not a microbiothere, but instead represents a distinct line of didelphid evolution. He thus erected for it a new subfamily, *Caluromyinae*. Other evidence for separating *Caluromys* from the didelphines is their unique pairing of spermatozoa (Biggers & DeLamater, 1965) and structure of the urogenital tract (Hill & Fraser, 1925; Biggers, 1966). Structure of these features is unknown in *Caluromysiops* and *Glironia*.

The evidence from serology (Kirsch, 1977) is that *Dromiciops* is very distinct from all other didelphids. In addition, Reig (in press; and personal communication as cited in Kirsch & Calaby, 1977) has subsequently and independently concluded that the dental similarities between *Dromiciops* and the other putative microbiotheres (e.g., *Glironia*, *Caluromys*, *Caluromysiops*) are only convergently similar to *Dromiciops* and *Microbiotherium*, though undoubtedly distinct from typical didelphines. This view is more fully documented by Reig, Kirsch, and Marshall (in preparation).

In this study I follow recent workers and recognize a family Microbiotheriidae which includes only *Dromiciops australis* among the living opossums. Of the fossil taxa I recognize only one genus, *Microbiotherium*, and six species.

SYSTEMATICS

Order MARSUPIALIA Illiger, 1811, p. 75

Superfamily DIDELPHOIDEA (Gray, 1821, p. 308) Osborn, 1910, p. 515

Family MICROBIOTHERIIDAE Ameghino, 1887, p. 6

(= Microbiotheria Ameghino, 1889, p. 263;

Microbiotheriinae Simpson, 1929, p. 116)

(Including Clenialitidae Ameghino, 1909, p. 204)

Diagnosis.—Very small to medium sized opossums; I_4^1 , C_1^1 , P_3^1 , M_4^1 ; mandibular rami unfused along symphysis which extends posteriorly to position below C- P_1 contact; large mental foramen below P_{1-2} contact or below anterior root of P_2 ; depth of ramus relatively constant from back to front, part below C and incisors deep and splayed outward; angular process of dentary prominent and strongly inflected; upper and lower incisors broad and spatulate; lowers splayed outward; I 's separated from each other by small diastema; line of upper incisors semicircular (U-shaped); I^1 larger than I^{2-5} , I^{2-3} subequal in size and shape; I^4 smaller and I^5 smaller still; I_{1-4} subequal in size and shape; canines weakly to strongly developed; when well developed, canines set nearly perpendicular to jaw; when small, canines (especially lowers) incisiform-premolariform and tilted anteriorly; premolars increase sharply or gradually in length and breadth from P_1^1 to P_3^1 ; diastems may or may not separate lower premolars; P^1 set at slight oblique angle in jaw; P_3^1 has distinct posterobasal heel; P_3^1 shorter and narrower than M_1^1 ; in length $M_1 < M_2 > M_3 > M_4$; in width $M_1 < M_2 > M_3 > M_4$; on M_{1-3} trigonid cusps typically low, talonid broader than trigonid; talonid deeply basined; metaconid set directly linguad of protoconid; protoconid much larger than para- and metaconid, paraconid smaller than metaconid; hypoconulid extremely median in position; M_4 very reduced in size relative to M_{1-3} and with

talonid reduced to a nearly unbasined heel; in length $M^1 > M^2 > M^3 > M^4$; in width $M^1 < M^2 \geq M^3 > M^4$; on M^{1-3} styler shelf and cusps greatly reduced or absent, more so on M^1 than M^{2-3} ; no distinct metastylar spur; parastyle small but distinct on M^{1-3} ; protocone large and talon distinctly basined; paracone and metacone large, low, subequal in size and height; former slightly smaller than latter on M^{1-2} , subequal on M^3 ; M^4 extremely reduced in size; skull has large rounded braincase and short rostrum; interorbital region broad; broadest point of palate at anterior edge of M^3 ; posterior nares broad and mesial septum continues backward as narrow ridge along base of skull; palatal vacuities large and well-developed; premaxillaries greatly elongated resulting in notable development of precanine region of rostrum such that C is in relatively more posterior position in tooth row than occurs in other didelphoids; nasals expanded posteriorly; paroccipital process absent; postglenoid process of squamosal small, extremely short, and slightly concave anteriorly; ear region and ossicles highly specialized; auditory bullae large, ossified, much inflated, and occupy a relatively large area on base of skull; anterior one-third of bullar wall formed by large tympanic process of alisphenoid, and posterior two-thirds formed by inflated entotympanic (fide Segall, 1969b)⁴; ectotympanic does not participate in formation of bulla but is enclosed by bulla and forms a recess meatus only; ectotympanic thus hidden from lateral view; no open space on ventral side of bullae but a medial oval-shaped area is located in anteromedial part of entotympanic; tympanic cavity divided by two septa into three compartments, anterior, medial, and posterior; malleus differs greatly from other marsupials (Segall, 1969a,b); manubrial lever is elongated and lever ratio is greater than in other marsupials (Segall, 1969a, pp. 180–81); posterior carotid foramen appears lacking; pes didactylous; female with well-developed pouch or *marsupium* with four symmetrically placed mammae; ossified epipubic bones present; diploid chromosome number $2n = 14$.

Known range.—Microbiotheres are, and according to the known fossil record always have been, endemic to South America. Fossils are known from beds of Colhuehuapian and Santacrucian age in Patagonia, southern Argentina. Living forms occur on Chiloé Island, south central Chile, and adjacent parts of Argentina.

Microbiotherium Ameghino, 1887, p. 6.

Microbiotherium Ameghino, 1887, p. 6.

Stylognathus Ameghino, 1891, p. 309.

⁴ Reig and Simpson (1972, p. 525) believe that the identity of what Segall (1969 a,b, 1970) calls the entotympanic needs to be substantiated. Furthermore, Patterson (1965) believed that in addition to the alisphenoid and the inflated tympanic wing of the pars petrosa (=entotympanic of Segall) contributing to formation of the bulla, that an inflated wing of the pars mastoidea was involved posteriorly.

In support of his interpretation, Segall (1970, p. 197) noted that an entotympanic is found in several families of marsupials, as well as insectivores, and it increases in size with progressive specialization of the auditory region. *Didelphis*, he contends, has a small entotympanic and *Dromiciops*, a large one. The entotympanic in *Dromiciops* is, according to Segall (1969b, p. 500), separated on the outside from the tympanic process of the alisphenoid by a suture extending from the eustachian opening to the anterior part of the porus acusticus. This location, he believes, supports the assumption that the structure is an entotympanic and not a process of the periotic as Reig (1955a) and Patterson (1965) contend.

Eodidelphys Ameghino, 1891, p. 310.

Prodidelphys Ameghino, 1891, p. 310.

Hadorrhynchus Ameghino, 1891, p. 311; Ringuelet, 1953, p. 278 (as subgenus of *Microbiotherium*).

Phonocdromus Ameghino, 1894, p. 355.

Proteodidelphys Ameghino, 1898, p. 187.

Oligobiotherium Ameghino, 1902e, p. 124.

*Clenia*⁵ Ameghino, 1904c, p. 260.

*Clenialites*⁵ Ameghino, 1906, p. 422.

Microbiotheridion Ringuelet, 1953, p. 280.

Type of *Microbiotherium*.—*M. patagonicum* Ameghino, 1887, p. 6.

Type of *Stylognathus*.—*S. diprotodontoides* Ameghino, 1891, p. 309.

Type of *Eodidelphys*.—*E. fortis* Ameghino, 1891, p. 310.

Type of *Prodidelphys*.—*P. acicula* Ameghino, 1891, p. 310.

Type of *Hadorrhynchus*.—*H. tortor* Ameghino, 1891, p. 311.

Type of *Phonocdromus*.—*P. patagonicus* Ameghino, 1894, p. 355.

Type of *Proteodidelphys*.—*P. praecursor* Ameghino, 1898, p. 117, 187.

Type of *Oligobiotherium*.—*O. divisum* Ameghino, 1902e, p. 124.

Type of *Clenia*.—*C. minuscula* Ameghino, 1904c, p. 260.

Type of *Clenialites*.—*C. minusculus* (Ameghino, 1904c, p. 260).

Type of *Microbiotheridion*.—*M. hernandezii* (Simpson, 1932b, p. 2).

Diagnosis.—Very small to large-sized microbiotheres; lower canine small to large, and set at or near perpendicular angle in jaw; P_1 set at slight to sharp oblique angle in jaw; posterobasal heel on P_2 small but distinct; large mental foramina below P_{1-2} contact or below P_2 , and smaller foramen below M_1 ; supraorbital processes large and well-developed; para- and metaconules on M^{1-3} distinct but not large; middle cleft on M^3 shallow or absent; bulla larger and more elongated anteriorly than in *Dromiciops*.

Known Range.—Beds of Colhuehuapian and Santacrucian age, Chubut and Santa Cruz provinces, Patagonia, southern Argentina.

Comments.—Included here within Ameghino's genus *Microbiotherium* are nine other genera proposed by him (i.e., *Stylognathus*, *Eodidelphys*, *Prodidelphys*, *Hadorrhynchus*, *Phonocdromus*, *Proteodidelphys*, *Oligobiotherium*, *Clenia*, *Clenialites*) and a tenth (*Microbiotheridion*) proposed by Ringuelet. Ameghino's primary criteria for recognition of his genera included absolute overall size differences, relative size differences of the canine and paraconid, and structure of the mandibular symphysis. He also erroneously interpreted breakage patterns in the region of the lower canine and incisors as diagnostic features. The most extreme example of this was Ameghino's interpretation of the broken canine alveolus of the syntypes of *Stylognathus* as representing the alveolus of a large procumbent incisor. Ringuelet (1953) used the oblique orientation of P_1 and P_2 in the jaw to diagnose *Microbiotheridion*.

During the course of this study it became readily apparent that the characters used by Ameghino and Ringuelet to distinguish these taxa could, in many cases, be easily demonstrated to represent individual, age, or preservational differences among the various specimens which they studied. It became further apparent that, although many of these taxa could be readily relegated to synonymy, some

⁵ Ameghino (1906, p. 422; 1909, p. 206) substituted the name *Clenialites* for *Clenia*, which he said was preoccupied; however, *Clenia* is not preoccupied, and the name thus has priority by date of publication over *Clenialites*.

could not. A number of discrete morphological types among the relatively large sample size could be defined, and these I here choose to recognize as warranting specific recognition. It is granted and demonstrated that size and morphological differences exist between these specimens and species, although taken together the spectrum of differences does not, in my judgment, warrant generic recognition. Consequently, I here recognize but a single fossil genus of microbiothere, *Microbiotherium*. Six species of *Microbiotherium* are here recognized: one (*M. divisum*) is known from beds of Colhuehuapian age, four (*M. acicula*, *M. patagonicum*, *M. tehuelchum*, *M. gallegosense*) are known from the Santacrucian, and one (*M. praecursor*) is of uncertain age and provenance.

Microbiotherium acicula (Ameghino, 1891). Figure 2; Table 2.

Prodidelphys acicula Ameghino, 1891, p. 310; 1894, p. 361; 1898, p. 188.

Eodidelphys acicula Ringuelet, 1953, p. 285, pl. 2, fig. 2.

Prodidelphys pavita Ameghino, 1891, p. 310; 1894, p. 361; 1898, p. 188.

Eodidelphys pavita Ringuelet, 1953, p. 286, pl. 2, fig. 3.

Prodidelphys obtusa Ameghino, 1891, p. 311; 1894, p. 362; 1898, p. 188; 1906, p. 388, fig. 248.

Eodidelphys obtusa Ringuelet, 1953, p. 287, pl. 2, fig. 4.

Stylognathus diprotodontoides (*partim*, not lectotype) Ameghino, 1891, p. 309; 1894, p. 361.

Microbiotherium patagonicum Sinclair, 1906 (*partim*), p. 415, pl. 62, figs. 5, 5a.

Type of P. acicula.—MACN 5735, a fragment of a right mandibular ramus with alveoli of I_{1-4} and M_2 , and C– M_1 complete (listed as “tipo” in Ameghino’s catalog and figured by Ringuelet, 1953, pl. 2, fig. 2).

Type of P. pavita.—MACN 5736, a fragment of a left mandibular ramus with alveoli of I_1 –C and M_{1-2} , and with P_{1-3} complete (listed as “tipo” in Ameghino’s catalog and figured by Ringuelet, 1953, pl. 2, fig. 3).

Type of P. obtusa.—MACN 5737, a fragment of a left mandibular ramus with alveoli of I_1 – P_3 , and C complete (listed as “tipo” in Ameghino’s catalog and figured by Ameghino, 1906, fig. 248; and Ringuelet, 1953, pl. 2, fig. 4).

Hypodigm.—The three types and MACN 5727, a left mandibular ramus with P_3 – M_4 present and alveoli of rest of dentition (syntype of *S. diprotodontoides* and listed as “tipo” along with lectotype MACN 5728 of that species in Ameghino’s catalog); and AMNH 9121, a fragment of a right mandibular ramus with alveoli of C– P_2 , and with P_3 – M_2 present (figured by Sinclair, 1906, pl. 62, figs. 5, 5a).

Horizon and locality.—All MACN specimens were collected in 1890–91 by Carlos Ameghino from the Santa Cruz Formation at *Monte Observación* in Patagonia, southern Argentina; AMNH 9121 was collected by B. Brown in 1899 from near *Felton’s Estancia* along the north bank of the Río Gallegos.

Age.—Santacrucian.

Diagnosis.—Smallest known species of genus; averages 15% ($n = 10$, OR 0–30%) smaller in comparable linear tooth dimensions than *M. patagonicum*; lower C small, set nearly perpendicular in jaw, and about same height as M_1 ; P_1 set at slight oblique angle in jaw; small but distinct posterobasal heel on P_1 and P_2 ; P_2 set straight in jaw; sometimes large diastem between P_1 , P_2 and P_3 ; posterobasal heel on P_3 distinct but not large; slight size decrease from P_3 to P_1 ; P_3 less than height of M_1 ; M_4 smaller (relative to M_3) and talonid less well developed than in *M. patagonicum* and *Dromiciops australis*; P_1 averages slightly longer than in *M. patagonicum*.

FIG. 2. *Microbiotherium acicula* (Ameghino, 1891, p. 310) (Santacrucian). MACN 5727, a left mandibular ramus with P₃–M₄: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

TABLE 2. Measurements of lower cheek teeth of *Microbiotherium acicula*.

Specimen	P3		M1		M2		M3		M4		M1–4	P3–M4	P1–3
	L	W	L	W	L	W	L	W	L	W	L	L	L
AMNH 9121		0.5	1.3	0.9	1.4	1.0	...	...	...	...	...	...	ca 2.6
MACN 5727	1.0	0.5	1.3	1.0	1.4	1.0	1.2	1.0	1.0	0.6	4.9	5.7	...
MACN 5735	0.8	0.5	1.2	1.0	...	...	...	...	...	...	...	...	2.4
MACN 5736	1.0	0.6	...	...	...	...	...	...	...	...	...	...	...

Comments.—In 1891, Ameghino proposed the new microbiothere genus *Prodidelphys* and assigned to it three species. The genotype, *P. acicula*, was characterized by its small size compared with other known microbiotheres. The type, MACN 5735, is a fragment of a right mandibular ramus with alveoli of I_{1–4} and M₂, and with C–M₁ complete. The other two species, *P. pavita* and *P. obtusa*, are also of small size and were distinguished from *P. acicula*—and from each other—on the basis of relative size and proximity of the premolars and canine, and on the size and extent of the mandibular symphysis. The type of *P. pavita*, MACN 5736, is a fragment of a left mandibular ramus with alveoli of I₁–C and M_{1–2}, and

with P_{1-3} complete. The type of *P. obtusa*, MACN 5737, is a fragment of a left mandibular ramus with alveoli of I_1-P_3 , and with the C present. All three types are figured by Ringuelet (1953, pl. 2, figs. 2-4).

The differences which exist between these types and the features which Ameghino used to differentiate them may all be attributable to individual and/or age differences of the specimens; they clearly are referable to a single species for which the name *acicula* has priority by publication in a nominal list.

A syntype (but not the lectotype) of Ameghino's (1891) taxon *Stylognathus diprotodontoides* (see p. 12) is also referable to the species *acicula*. This specimen consists of a left ramus with P_3-M_4 present and with alveoli of rest of dentition. In addition, the specimen (AMNH 9121, a fragment of a right mandibular ramus with alveoli of $C-P_2$ and with P_3-M_2 present) referred by Sinclair (1906, p. 415) to *Microbiotherium patagonicum* is also assignable to *acicula*. These two specimens provide important knowledge of structure of the molars of this species.

Ringuelet (1953) recognized the species *acicula*, *pavita*, and *obtusa* as valid, and she placed them in the genus *Eodidelphys* (although she listed them in *Prodidelphys* in the caption to plate II). This assignment was made largely on the basis of the vertical orientation and small size of the canine, a feature shared with other taxa assigned to *Eodidelphys*. As discussed elsewhere (p. 11), I recognize *Eodidelphys* and *Prodidelphys* as junior synonyms of *Microbiotherium* and thus assign the species *acicula* to that taxon. *Microbiotherium acicula* is the name applied to this smallest known member of the genus.

Microbiotherium patagonicum Ameghino, 1887. Figures 3, 4; Table 3.

Microbiotherium patagonicum Ameghino, 1887, p. 6; 1889, p. 264; 1894, p. 361; Sinclair, 1906 (partim), p. 415; Ringuelet, 1953, p. 274, pl. 1, fig. 4.

Stylognathus diprotodontoides (partim) Ameghino, 1891, p. 309; 1894, p. 361.

Halmarhiphus didelpoides (sic) (partim, not lectotype) Ameghino, 1891, p. 308.

Parhalmarhiphus didelphoides (partim) Ameghino, 1903, pp. 157, 163, fig. 86.

Halmarhiphus didelphoides (partim) Ameghino, 1894, p. 357; 1899, fig. 4; 1903, p. 157, fig. 80; 1906, p. 357, fig. 195; Simpson, 1930, p. 56.

Garzonina annectens (partim, not type) Ameghino, 1891, p. 307.

Parhalmarhiphus annectens (partim) Ameghino, 1894, p. 357.

Halmarhiphus nanus (partim, not type) Ameghino, 1891, p. 308; 1894, p. 357.

Hadorhynchus conspicuus Ameghino, 1891, p. 311; 1894, p. 362.

Microbiotherium conspicuum Sinclair, 1906, p. 450.

Microbiotherium conspicuus Ringuelet, 1953, p. 279, pl. 1, fig. 6.

Type of *M. patagonicum*.—MLP 11-30, a partial right mandibular ramus with alveoli of P_{1-2} , part of anterior root of P_3 , and with M_{1-4} present (figured by Ringuelet, 1953, pl. 1, fig. 4).

Lectotype of *S. diprotodontoides*.—MACN 5728, a left mandibular ramus with alveoli of I_1-M_1 , and M_{2-4} present (listed as "tipo" in Ameghino's catalog along with MACN 5727, a syntype).

Type of *H. conspicuus*.—MACN 5740, a fragment of a left mandibular ramus with alveoli of I_1-P_1 , and with P_2-M_1 complete (listed as "tipo" in Ameghino's catalog and figured by Ringuelet, 1953, pl. 1, fig. 6).

Hypodigm.—The three types and MACN 1, a fragment of a right mandibular ramus with alveoli of I_1-C , and P_1-M_1 complete (listed as "tipo" of *M. tehuelchum* in Ameghino's catalog); MACN 5704, a fragment of a right mandibular ramus with M_{3-4} complete (possible syntype of *G. annectens*); MACN 5718, a fragment of a left mandibular ramus with M_{2-3} complete, and roots of M_4 (syntype of *H.*

FIG. 3. *Microbiotherium patagonicum* Ameghino, 1887, p. 6 (Santacrucian). MACN 5728 (lectotype of *Stylognathus diprotodontoides*), a left mandibular ramus with alveoli of C-M₁, and M₂₋₄ complete: a, occlusal; b, labial; c, lingual views. Scale = 5 mm.

FIG. 4. *Microbiotherium patagonicum* Ameghino, 1887, p. 6 (Santacrucian). MACN 8471, a right maxillary fragment with M¹⁻⁴: a, labial; b, occlusal; c, lingual views. Scale = 3 mm.

TABLE 3. Measurements of cheek teeth of *Microbiotherium patagonicum*.

Specimen	P3		M1		M2		M3		M4		M1-3 M1-4
	L	W	L	W	L	W	L	W	L	W	L
UPPER CHEEK TEETH											
MACN 8471	...	...	1.7	1.3	1.5	1.7	1.5	1.7	0.9	1.1	4.3
LOWER CHEEK TEETH											
MACN 1	0.8	0.8	1.5	1.1	...	...	...	...	...	...	...
MACN 5718	...	...	...	...	1.7	1.1	1.5	1.0	...	...	...
MACN 5719	...	...	...	...	...	...	...	...	1.2	0.7	...
MACN 5721	...	...	...	...	1.6	1.1	1.5	1.0	...	...	...
MACN 5728	...	...	...	...	1.7	1.1	1.5	1.0	1.3	0.6	ca 6.0
MACN 5740	0.9	0.7	1.5	1.2	...	...	...	...	...	...	...

didelphoides and figured under that name by Ameghino, 1903, figs. 80, 86; 1906, fig. 195, the M₄ was lost since it was figured by Ameghino); MACN 5719, a fragment of a left mandibular ramus with M₄ (syntype of *H. didelphoides*); MACN 5721, a fragment of a left mandibular ramus with M₂₋₃ complete, and alveoli of M₁ and M₄ (syntype of *H. nanus*); and MACN 8471, a right maxillary fragment with M¹⁻⁴ (figured by Reig, 1955a, fig. 1A).

Horizon and locality.—All specimens are from the Santa Cruz Formation, Santa Cruz Province, Patagonia, southern Argentina, and their localities and dates of collection are as follows: the type, MLP 11-30 was collected by Carlos Ameghino from "las barrancas del río Santa Cruz" (Ameghino, 1889, p. 264); *La Cueva* MACN 8471 (1892-93); *Sehuen* MACN 5718, 5719 (1890-91); *Santa Cruz* MACN 1 (probably 1887); *Monte Observación* MACN 5704, 5721, 5728, 5740 (1890-91); all MACN specimens were collected by Carlos Ameghino.

Age.—Santacrucian.

Diagnosis.—Small-sized microbiothere; averages 15% larger than *M. acicula* and averages 16% smaller than *M. tehuelchum*; lower canine small and set nearly perpendicular in jaw; P_1 set at slight oblique angle in jaw; P_2 set straight in jaw; posterobasal heel on P_3 distinct but not large; slight size decrease from P_3 to P_1 ; P_3 less than height of M_1 ; para- and metaconules on M^{1-3} distinct but not large; protocone on M^{1-3} narrower anteroposteriorly than in *M. tehuelchum*; labial ridge on styral shelf less distinct than in *M. tehuelchum*; middle cleft on M^2 very shallow; middle cleft on M^3 shallow; M^4 larger (relative to M^3) than in *D. australis* and smaller than in *M. tehuelchum*.

Comments.—Ameghino briefly diagnosed *Microbiotherium patagonicum* gen. y sp. n. in 1887 (p. 6), and in 1889 (p. 264) he presented an expanded diagnosis as follows:

Es éste, a buen seguro, uno de los mamíferos más pequeños que hasta ahora se conozcan; desgraciadamente me es conocido tan sólo por la mitad izquierda de la mandíbula inferior, en la que están implantados los últimos tres molares verdaderos [M_{2-4}], existiendo en la parte anterior los alvéolos de los demás dientes. El alvéolo del incisivo, aunque bastante destrozado, prueba que este diente era comprimido transversalmente como en los generos *Abderites*, *Acdestis* y *Epanorthus*; la protuberancia que forma el alvéolo sobre el lado interno, prueba que la base del diente llegaba hasta debajo del pm_7 [M_1]. Los dos primeros premolares [P_{1-2}] (de los que sólo se conservan los alvéolos), eran sumamente pequeños. El premolar cuatro [M_1], era de tamaño relativamente más considerable y con dos raíces distintas, como parece ser también el caso para los anteriores; todos estos dientes, a lo menos los posteriores, tienen la raíz posterior de tamaño considerablemente mayor que la anterior. Los cuatro premolares [P_1-M_1] ocupan un espacio longitudinal de 4 milímetros.

El m_7 [M_2] es el diente de tamaño más considerable de toda la mandíbula, alcanzando un diámetro anteroposterior de 0^m0015. La corona, bastante elevada, es más angosta adelante, más ancha atrás y con dos pares de tubérculos transversales, altos y puntiagudos, de los cuales los que constituyen el par anterior son de tamaño un poco menor que los del par posterior.

El m_7 [M_3] es de tamaño un poco menor, de ancho más igual adelante y atrás y también con los dos pares de tubérculos puntiagudos, uno adelante y otro atrás, formando casi dos crestas transversales separadas por un valle profundo.

El m_7 [M_4] es de tamaño mucho más pequeño que el precedente, pero también con dos pares de tubérculos, aunque más bajos y de cúspides más romas. Los tres verdaderos molares [M_{2-4}] ocupan un espacio longitudinal de cerca de 4 milímetros.

La rama horizontal de la mandíbula es casi derecha y de un alto casi uniforme de sólo dos milímetros.

Los agujeros mentonianos son en número de dos colocados: el anterior debajo de la parte posterior del pm_7 [P_3] y el posterior debajo de la parte anterior del m_7 [M_2]. La mandíbula, a la que le falta el incisivo y la parte posterior de la rama horizontal, cuando entera apenas debía tener unos 12 milímetros de largo.

In this publication, and elsewhere, Ameghino labeled the seven cheek teeth of marsupials as (from front to back) Pm_1 , Pm_2 , Pm_3 , Pm_4 , M_1 , M_2 , M_3 . These same teeth are referred to here as P_1 , P_2 , P_3 , M_1 , M_2 , M_3 , M_4 .

Based on her exhaustive study of fossil didelphoids in the MLP, Ringuelet

(1953, p. 274) deduced that MLP 11-30 was probably the specimen referred to by Ameghino and was thus the type of *M. patagonicum*. The only problem with this decision is that MLP 11-30 is a right mandibular ramus; Ameghino listed his specimen as a left. In all other respects the description and measurements presented by Ameghino accord with those of MLP 11-30 as published by Ringuelet.

It is almost certain that Ameghino's description of the type of *M. patagonicum* in his 1889 publication was made from either notes or memory, or a combination of these sources. F. Ameghino resigned from the MLP on 17 January 1888, the culmination of a progressive deterioration of relations with the director Alcedes Moreno, who thereupon barred Ameghino from the collections of that institution. Ameghino began work on his 1889 monograph in February 1888. Moreno did not allow him access to the specimens in the MLP, and Ameghino specifically stated (1889, p. xiii-xiv) that Moreno was indeed responsible for the fact that a number of specimens listed and described in the 1889 paper were not figured. Further details of these problems and of ensuing consequences with regard to the whereabouts of various specimens collected by Carlos Ameghino in 1887 and deposited in the MLP are discussed elsewhere (Marshall, 1980, p. 36n). The important point is that an explanation exists for the potential error in Ameghino's referral to the type as a left ramus when in fact it is a right. Realizing these developments and considering the agreement in structure and size of MLP 11-30 with Ameghino's description of the type, it appears permissible to follow Ringuelet and to regard MLP 11-30 as the type of *M. patagonicum*, despite the fact that it is not specifically labeled as such. I have not studied this specimen firsthand, although it is figured by Ringuelet (1953, pl. 1, fig. 4) in labial view. Ringuelet's measurements of MLP 11-30 are as follows:

Longitud del borde anterior del alvéolo del Pm_1 [P_1] al borde posterior del M_4	9.5 mm
Longitud ocupada por los alvéolos de los tres premolares	3.4 mm
Longitud ocupada por los M_1 - M_4	6.4 mm
Altura de la mandíbula debajo del alvéolo de Pm_3	2.5 mm
Altura de la mandíbula debajo de M_4	3.5 mm

In Ameghino's description of this species he records the presence of a large alveolus at the anterior end of the jaw which he regards as for an incisor and which he envisions further to be as large and procumbent as in species of the caenolestid genera *Abderites*, *Acdestis*, and *Epanorthus* (= *Palaeothentes*, see Marshall, 1980). As shown in Ringuelet's figure of this specimen (pl. 1, fig. 4), however, it is broken anterior to the P_1 and the partial alveolus retained at the anterior-most edge is that of the canine. The breakage pattern is such that it permits the interpretation reached by Ameghino, but knowledge of other specimens referable to this and related species clearly indicates the true identity of this alveolus.

Several of Ameghino's other species are in whole or in part referable to *M. patagonicum*. *Stylognathus diprotodontoides* was erected by Ameghino (1891, p. 309) on two relatively complete left mandibular rami: MACN 5727, with P_3 - M_4 present and alveoli of rest of dentition; and MACN 5728, with M_{2-4} present and alveoli of C - M_1 . These specimens are syntypes and both are listed as "tipo" in Ameghino's catalog. The first is here referred to *Microbiotherium acicula* (see p. 12), and the second is relegated to lectotype of *S. diprotodontoides*.

Ameghino (1891, p. 309) noted that *S. diprotodontoides* "[s]olo tiene dos incisivos inferiores muy pequeños, el canino es regularmente desarrollado; . . ." Both MACN 5727 and 5728 are missing the anterior-most edge of the mandibular rami such that, in the former, only two incisor alveoli are preserved and, in the latter, only one. Thus, the presence of only two incisors as noted by Ameghino is a feature attributable to this breakage. Judging from the canine alveolus in both specimens, the tooth was moderately developed and was either oriented perpendicular in the jaw or had only a slight anterior inclination. *Stylognathus* is here (see p. 11) recognized as a junior synonym of *Microbiotherium* and the species *diprotodontoides* is regarded as a junior synonym of *M. patagonicum*.

Halmarhiphus didelphoides Ameghino (1891, p. 308) was based on four specimens which can be regarded as syntypes (Reig, 1955b, p. 63). MACN 5716, a fragment of a right mandibular ramus with M_{1-2} present and roots of M_{3-4} (the M_2 is figured by Ameghino, 1899, fig. 4), is here selected lectotype and is referred to *Microbiotherium tehuelchum* (see p. 26). MACN 5717, a left mandibular ramus with P_3 and M_{2-3} present and roots of M_1 and M_4 , is referable to *Stilotherium dissimile* (see p. 67). MACN 5718, a fragment of a left mandibular ramus with M_{2-3} complete and roots of M_4 (figured by Ameghino, 1903, figs. 80, 86; 1906, fig. 195), and MACN 5719, a fragment of a left mandibular ramus with M_4 , are referable to *M. patagonicum*.

Reig (1955b, p. 63) noted that according to Ameghino's catalog and the original species description, *Garzonina annectens* Ameghino (1891, p. 307) is the genotype of *Parhalmarhiphus* Ameghino (1894, p. 356). The type, MACN 5703, is a fragment of a left mandibular ramus with M_{1-4} and is referable to *Stilotherium dissimile* (see p. 66). The generic diagnosis of *Parhalmarhiphus*, however, appears to have been based on two other specimens; MACN 5704, a fragment of a right mandibular ramus with M_{3-4} complete, is referable to *M. patagonicum*, and MACN 5705, a fragment of a left mandibular ramus with M_{3-4} missing paraconid of M_3 , is an indeterminate caenolestid.

Halmarhiphus nanus Ameghino (1891, p. 308) was based on three specimens (see Reig, 1955b, p. 63). The type, MACN 5720, a fragment of a right mandibular ramus with alveoli of M_1 , M_4 , and M_{2-3} present, is referable to *Stilotherium dissimile* (see p. 66). MACN 5721, a fragment of a left mandibular ramus with M_{2-3} complete and alveoli of M_1 and M_4 , is here referred to *M. patagonicum*. The third specimen, MACN 5722, a fragment of a left mandibular ramus with P_3 present and alveoli of P_{1-2} and M_{1-4} , is referable to *Phonocdromus gracilis* (see p. 69; Reig, 1955b, p. 63).

Hadorrhynchus conspicuus Ameghino (1891, p. 311) was based on MACN 5740, a fragment of a left mandibular ramus with alveoli of I_1-P_1 and with P_2-M_1 complete. This specimen, listed as "tipo" in Ameghino's catalog, is figured by Ringuelet (1953, pl. 1, fig. 6) and is here referred to *M. patagonicum*.

Microbiotherium praecursor (Ameghino, 1898). Figure 5.

Proteodidelphys praecursor Ameghino, 1898, p. 117, 187, fig. 52b; 1899, p. 557, figs. 1, 2, 15; 1900, p. 201, figs. 2-5; 1902a, pp. 6-7; 1902b, p. 21, figs. 1-3; 1902c, p. 421, figs. 1, 2, 15; 1903, p. 161, figs. 82, 84, 88; 1904a, p. 53, figs. 50-51; 1904b, p. 35, fig. 21; 1906, p. 288, fig. 69; Simpson, 1929, p. 130; 1932a, p. 4, fig. 1A; 1938, p. 3.

Eodidelphys praecursor Ringuelet, 1953, p. 284.

Type of P. praecursor.—MACN 10799, a right mandibular ramus with alveoli of I_{1-2} and I_3-M_4 complete (posterior edge of ramus and I_{1-2} have been lost since

FIG. 5. *Microbiotherium praecursor* (Ameghino, 1898, p. 117) (age unknown). MACN 10799 (type), a right mandibular ramus with alveoli of I_{1-2} , and I_3 - M_4 complete: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 8 mm.

specimen was figured by Ameghino, 1898, fig. 52b; 1899, figs. 1, 2, 15; 1900, figs. 2-5; 1902b, figs. 1-3; 1902c, figs. 1, 2, 15; 1903, figs. 82, 84, 88; 1904a, figs. 50, 51; 1904b, fig. 21; 1906, fig. 69); I_2 has been lost since specimen was figured by Simpson (1932a, p. 4, fig. 1A).

Hypodigm.—Type only.

Horizon and locality.—"Cretáceo inferior (areniscas abigarradas) de Patagonia" (fide Ameghino, 1898, p. 117). Collected by Nicolas Illin, an employee of the Museo de La Plata (Simpson, 1932a, p. 6).

Age.—Unknown (see below).

Measurements.— P_3 L=1.1 mm, W=0.8 mm; M_1 L=1.7 mm, W=1.2 mm; M_2 L=1.7 mm, W=1.2 mm; M_3 L=1.7 mm, W=1.1 mm; M_4 L=1.3 mm, W=0.8 mm; M_{1-4} =6.8 mm; P_3-M_4 =8.0 mm.

Diagnosis.—Indistinguishable in size and structure from smaller specimens of the Santacrucian species *Microbiotherium tehuelchum* (see below); C appears to be smaller than in those specimens.

Description.—Dental formula $I_{\overline{4}}, C_{\overline{1}}, P_{\overline{3}}, M_{\overline{4}}$. Incisors subequal, spaced, spatulate. Canine erect, root single but grooved, somewhat recurved crown, inner side excavated, very slight rudiment of internal heel. Premolars progressively larger, P_1 to P_3 . Molars of generalized didelphid pattern, trigonid little elevated above talonid. Protoconid larger than metaconid, metaconid larger than paraconid. Talonid typically didelphid on M_{1-3} . M_{1-2} subequal, M_3 somewhat smaller, and M_4 very small and with greatly reduced talonid, shorter and narrower than trigonid and with only one really distinct cusp. Horizontal ramus of moderate proportions, symphysis extending to between canine and P_1 , fused, mental foramina under P_{1-2} and anterior end of M_1 (Simpson, 1932a, p. 4).

Comments.—As demonstrated by Simpson (1932a), the location and age of the beds from which *Proteodidelphys praecursor* was collected are not known. This species was included by Ameghino (op. cit.), along with four isolated mammal teeth and "a small hard ball of doubtful nature" (Simpson, 1932a, p. 3), as part of his "*Proteodidelphys* Fauna." Ameghino (e.g., 1900 and elsewhere) noted that these specimens came from the "areniscas abigarradas" or from what is now called the Cretaceous dinosaur-bearing Chubutiano beds from the lower Chubut Valley in Patagonia. Simpson (1932a, p. 6) noted that Ameghino gave no data in support of this claim, despite the fact that he made frequent reference to these specimens. On the contrary, Simpson (ibid.) amassed considerable evidence, albeit some circumstantial, which suggests that these fossils are of Tertiary age and may have come from beds of Casamayoran, Mustersan, Deseadan, and/or Colhuehuapian age, all of which occur in or near the lower Chubut Valley and all of which may or do contain mammals. Most importantly, the specimens were not found by Carlos Ameghino, but by a collector whose field data is not reliable. Scott (1937) compromised the argument by assigning *P. praecursor* to the Riochican, but this is contrary to all the evidence and solves none of the unanswered problems (Simpson, 1948, p. 35, n. 1). Simpson further noted (ibid., p. 5):

There is no way in which *Proteodidelphys* can be distinguished generically from the common *Eodidelphys*. Certain specimens from the Santa Cruz formation referred by Ameghino to *Eodidelphys famula* cannot surely be distinguished specifically: size, structure, and position of each tooth, depth and form of mandible, position and size of mental foramina, even the non-essential characters of color and mode of preservation, are all nearly identical.

Technically it would perhaps be necessary to reduce the names of this genus and species to synonymy, as they cannot be defined in a diagnostic way, but in view of their history and the doubt that still clouds their true significance, it seems to be practical and permissible to retain them tentatively.

Based on Simpson's comments, Ringelet (1953, p. 284) referred the species *praecursor* to the genus *Eodidelphys*.

I have compared *praecursor* with most microbiotheres discussed or listed in this study and find that it is morphologically indistinguishable from specimens of the Colhuehuapian species *Microbiotherium divisum* and the Santacrucian species *M. tehuelchum* (in which *E. famula* is here included as a junior synonym). Furthermore, *praecursor* is slightly smaller than all of the known specimens of *M. divisum*, but does overlap in size with the smaller specimens of the *M. tehuelchum* sample. In this study I follow Simpson's caution and tentatively retain *praecursor* as a distinct species, although I do assign it to *Microbiotherium* (to include *Eodidelphys* as a junior synonym), as it is indistinguishable from members of that taxon.

Microbiotherium divisum (Ameghino, 1902e). Figures 6, 7; Table 4.

Oligobiotherium divisus (sic) Ameghino, 1902e, p. 124; Ringelet, 1953, p. 268.

Oligobiotherium divisum Simpson, 1930, p. 36; Reig, 1955a, p. 121.

?*Microbiotherium divisus* (sic) Pascual and Odreman Rivas, 1971, p. 387.

Clenia minuscula Ameghino, 1904c, p. 260; Ringelet, 1953, p. 281; Reig, 1955a, p. 121 (as junior synonym of *O. divisum*).

Clenialites minusculus Ameghino, 1906, p. 422n, fig. 315; 1907, fig. 1; Reig, 1955a, p. 122 (as junior synonym of *O. divisum*).

Microbiotherium hernandezi Simpson, 1932b, p. 2, fig. 1; Pascual and Odreman Rivas, 1971, p. 387.

Microbiotheridion hernandezi Ringelet, 1953, p. 280; Reig, 1955a, p. 122 (as junior synonym of *O. divisum*).

Type of Oligobiotherium divisus.—MACN 52-374, a fragment of a right mandibular ramus with posterior root of M_2 , M_3 missing metaconid, and roots of M_4 .

Type of Clenia minuscula.—MACN 52-381, a fragment of a left mandibular ramus with M_{1-2} (figured by Ameghino, 1906, fig. 315; 1907, fig. 1).

Type of Microbiotherium hernandezi.—AMNH 29664, a right mandibular ramus with crowns of P_2 - M_4 (protoconid, paraconid, and hypoconid of M_1 are partially broken), and alveoli of other teeth (figured by Simpson, 1932b, fig. 1).

Hypodigm.—The three types and AMNH 29684, a fragment of a right mandibular ramus with P_3 - M_2 complete; AMNH 29708, a fragment of a right mandibular ramus with alveoli of P_2 and M_3 , and with P_3 - M_2 complete; MMP M-217, a fragment of a right mandibular ramus with alveoli of P_{1-3} , M_1 complete, and roots of M_2 ; MMP M-942, a fragment of a left mandibular ramus with alveoli of I_1 -C, P_{1-3} complete, and alveoli of M_1 ; MMP M-943, a fragment of a left mandibular ramus with roots of C- P_2 , and P_3 - M_2 complete; MMP M-951a, a nearly complete edentulous left mandibular ramus; MMP M-951b, a fragment of a right mandibular ramus with alveoli of M_{1-4} (probably same individual as MMP M-951a).

Horizon and locality.—Colhué-Huapí beds at the Barranca south of Lago Colhué-Huapí, southern Argentina. The MACN specimens were collected by Carlos Ameghino; the AMNH specimens were collected by members of the Scarritt Expedition to Patagonia in 1930; MMP M-217 was collected by G. Scaglia in 1950;

FIG. 6. *Microbiotherium divisum* (Ameghino, 1902e, p. 124) (Colhuehuapian). MACN 52-381 (type of *Clenia minuscula*), a fragment of a left mandibular ramus with M_{1-2} : a, labial; b, occlusal; c, lingual views. Scale = 3 mm.

TABLE 4. Measurements of lower cheek teeth of *Microbiotherium divisum*.

Specimen	M1		M2		M3		M4		M1-4	P1-M4	P1-3
	L	W	L	W	L	W	L	W	L	L	L
MACN 52-374	...	...	...	...	2.0	ca 1.2	...	...	...	...	...
MACN 52-381	1.8	1.3	1.8	1.3	...	...	...	...	...	...	...
AMNH 29664*	2.0	1.3	2.0	1.4	2.1	1.3	1.5	0.9	7.8	ca 11.7	...
AMNH 29684	1.8	1.2	1.9	1.3	...	...	...	...	...	...	...
AMNH 29708	1.9	1.3	2.0	1.4	...	...	...	...	...	...	...
MMP M-217	1.8	1.3	...	...	...	...	...	...	...	...	...
MMP M-942	...	...	...	...	...	...	...	...	...	...	4.4
MMP M-943	1.8	1.3	1.9	1.4	...	...	...	...	...	...	...
MMP M-951a	...	...	...	...	...	...	...	...	ca 7.6	ca 11.7	...
MMP M-951b	...	...	...	...	...	...	...	...	7.8	...	...

* $P_3L = 1.4$ mm, $W = 0.9$ mm.

FIG. 7. *Microbiotherium divisum* (Ameghino, 1902e) (Colhuehuapian). AMNH 29664 (type of *M. hernandezii*), a right mandibular ramus with crowns of P_2 - M_4 (protoconid, paraconid, and hypoconid of M_1 are partially broken), and alveoli of other teeth: **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 10 mm.

the other MMP specimens were collected by G. Scaglia, Contreras and J. Hernandez in 1964 (MMP specimens are from "frente a Estacion La Parada").

Age.—Colhuehuapian.

Diagnosis.—Medium-sized microbiothere and only known microbiothere of Colhuehuapian age; similar in size and structure to larger specimens of Santacrucian species *M. tehuelchum*; lower canine medium to large size and set nearly perpendicular in jaw; P_1 set at slight oblique angle in jaw; P_2 set straight in jaw; posterobasal heel on P_2 small but distinct; posterobasal heel on P_3 distinct but not large; slight size decrease from P_3 to P_1 ; P_3 about same height as M_1 .

Comments.—Ameghino (1902e, p. 124) originally placed *Oligobiotherium divisum* in the family Microbiotheriidae, group Pedimana. He later (1904c, p. 260) named *Clenia minuscula* on the basis of a jaw fragment with two teeth from the same fauna and locality as *Oligobiotherium divisum*, and likewise placed it in the family Microbiotheriidae. In the original description of *C. minuscula*, Ameghino compared it only with *Pachybiotherium* and made no mention of *O. divisum*. In 1906, Ameghino (p. 422n) substituted the name *Clenialites* for *Clenia*, which he said was preoccupied, although he did not indicate where that name had earlier been used. I was unable to find an earlier usage of the name *Clenia*; in a nominal list, the name *Clenia* has priority over *Clenialites*.

Simpson (1932b, p. 2) erected another Colhuehuapian species of microbiothere, *Microbiotherium hernandezi*, on a nearly complete right mandibular ramus with most of the dentition, collected from the Barranca south of Lago Colhué-Huapí. He noted that *M. hernandezi* was much smaller than *Pachybiotherium acclinum*.

The only other possible didelphid yet described from the Colpodon Beds is *Oligobiotherium divisum*. This [species] nearly agrees with [*M. hernandezi*] . . . in size, but Ameghino describes . . . [*O. divisum*] as having only two trigonid cusps on M_3 and only one on M_4 , M_3 with the talonid cusps in a straight transverse series, and M_4 with a large basined talonid—characters so distinctive that it is doubtful whether *Oligobiotherium* belongs in this family at all.

Ringuelet (1953, p. 280) placed Simpson's species *hernandezi* in a new genus, *Microbiotheridion*. Her primary basis for doing so was

. . . la posición de los premolares: mientras en los microbiotherinos el Pm_1 [P_1] y el Pm_2 [P_2] están colocados transversalmente con relación al resto de la serie dentaria, en esta especie, dichos dientes están colocados en línea con relación a los restantes; siendo el único resto atribuido al género *Microbiotherium* que posee este carácter (Ringuelet, 1953, p. 281).

Based on an unpublished collaborative study with B. Patterson, Reig (1955a, p. 121) recognized these three species (*divisum*, *minuscula*, *hernandezi*) as synonymous. I have examined all three types and concur with Reig's conclusion.

The partial M_4 was lost from the type of *O. divisum* since that specimen was described by Ameghino. His reference to the presence of only two trigonid cusps on the M_3 (a feature commented upon by Simpson, 1932b) was based on the fact that the metaconid of that tooth was broken and missing. In all comparable size and structural features, the types and the referred specimens clearly are representative of a single species for which the name *divisum* has priority.

The species *divisum* is the only known microbiothere of Colhuehuapian age. In size and structure *divisum* is very similar to the Santacrucian species *Microbiotherium tehuelchum*, and *divisum* is here regarded as the direct Colhuehuapian

ancestor of that species (see p. 52). Accordingly, *divisum* is placed in the genus *Microbiotherium*.

***Microbiotherium tehuelchum* Ameghino, 1887. Figures 8–10; Tables 5–7.**

Microbiotherium tehuelchum Ameghino, 1887, p. 7; 1889, p. 265 (the specimen figured in pl. 1, fig. 17 as *M. tehuelchum* is a palaeoententine); 1891, p. 309; 1893, p. 78, fig. 2; 1894, p. 361, fig. 42; 1898, p. 187, fig. 52a; 1906, p. 386, fig. 245; Sinclair, 1906, p. 414, pl. 62, figs. 4, 4a, 6–12; Ringelet, 1953, p. 275, pl. 1, fig. 1; Segall, 1969b, p. 495, fig. 5.

Halmarhiphus didelphoides (sic) (partim) Ameghino, 1891, p. 308.

Parhalmarhiphus didelphoides (partim) Ameghino, 1903, pp. 157, 163, fig. 86.

Halmarhiphus didelphoides (partim) Ameghino, 1894, p. 357; 1899, fig. 4; 1903, p. 157, fig. 80; 1906, p. 357, fig. 195; Simpson, 1930, p. 56.

Microbiotherium forticulum Ameghino, 1891, p. 309; 1894, p. 361; Ringelet, 1953, p. 275, pl. 1, fig. 2 (as junior synonym of *M. tehuelchum*).

Eodidelphys fortis Ameghino, 1891, p. 310; 1894, p. 361; 1905, p. 11, fig. 10; Ringelet, 1953, p. 282, pl. 2, figs. 1, 5, 6; Reig, 1955a, p. 124, fig. 2A.

Eodidelphys famula Ameghino, 1891, p. 310; 1894, p. 361; 1898, p. 187; 1900, p. 201; 1905, p. 11, fig. 11; 1906, p. 387, fig. 246; Ringelet, 1953, p. 283.

Phonocdromys patagonicus Ameghino, 1894, p. 355 (partim); Reig, 1955b, p. 64 (invalid).

Hadrorthynchus tortor Ameghino, 1891, p. 311; 1894, p. 362.

Microbiotherium tortor Sinclair, 1906, p. 412, pl. 62, figs. 1, 2, 2a; Ringelet, 1953, p. 278, pl. 1, fig. 3.

Hadrorthynchus torvus Ameghino, 1891, p. 311; 1894, p. 361.

Microbiotherium torvus Sinclair, 1906, p. 412 (as junior synonym of *Microbiotherium tortor*); Ringelet, 1953, p. 280, pl. 1, fig. 5.

Neotype of *M. tehuelchum*.—MLP 11–36, a nearly complete right mandibular ramus with P_2 – M_4 complete (figured by Ringelet, 1953, pl. 1, fig. 1; Pascual & Herrera, 1975, pl. 1, fig. 1).

Lectotype of *H. didelphoides*.—MACN 5716, a fragment of a right mandibular ramus with M_{1-2} complete, and roots of M_{3-4} (listed as “tipo” in Ameghino’s catalog; figured by Ameghino, 1899, fig. 4).

Lectotype of *M. forticulum*.—MACN 5725, a fragment of a left mandibular ramus with alveoli of C and M_2 , and P_1 – M_1 complete (listed as “tipo” in Ameghino’s catalog; figured by Ringelet, 1953, pl. 1, fig. 2).

Lectotype of *E. fortis*.—MACN 5729, a left mandibular ramus with alveoli of I_1 –C, and P_1 – M_4 complete (listed as “tipo” in Ameghino’s catalog; figured by Reig, 1955a, fig. 2A).

Lectotype of *E. famula*.—MACN 5732, a right mandibular ramus with P_1 – M_4 and alveoli of all other teeth (listed as “tipo” in Ameghino’s catalog).

Lectotype of *P. patagonicus*.—MACN 5741, a left mandibular ramus with partial dentition.

Type of *H. tortor*.—MACN 5738, a fragment of a right mandibular ramus with alveoli of I_1 –C, roots of P_{1-2} , P_3 complete, and alveoli of M_{1-2} (listed as “tipo” in Ameghino’s catalog).

Type of *H. torvus*.—MACN 5739, a fragment of a right mandibular ramus with alveoli of C, roots of P_1 , P_{2-3} complete, and alveoli of M_1 (listed as “tipo” in Ameghino’s catalog; figured by Ringelet, 1953, pl. 1, fig. 51).

Hypodigm.—The eight types and MACN 5724, a fragment of a left mandibular ramus with I_3 – P_1 and P_3 present, and alveoli of I_{1-2} , P_2 and M_1 (labeled *M. tehuelchum* and figured under that name by Ameghino, 1893, fig. 2; 1894, fig. 42; 1898, fig. 52a; 1906, fig. 245; P_2 and M_1 have been lost since the specimen

FIG. 8. *Microbiotherium tehuelchum* Ameghino, 1887, p. 7 (Santacrucian). PU 15038, a nearly complete left mandibular ramus with alveoli of I_{1-4} , C-M₃ complete, and roots of M₄: a, labial; b, occlusal; c, lingual views. Scale = 10 mm.

was figured); MACN 5726, a fragment of a left mandibular ramus with alveoli of C and M₁, roots of P₁₋₂, and P₃ complete (labeled *M. forticulum*); MACN 5730, a left mandibular ramus with alveoli of C-P₂ and M₂, and P₃-M₁ and M₃₋₄ complete (probable syntype of *E. fortis*); MACN 5731, a left mandibular ramus with M₁ and M₃ complete, and alveoli of rest of dentition except M₄ (probable syntype of *E. fortis*); MACN 5733, a left mandibular ramus with P₂-M₃ complete (probable syntype of *E. famula* and the specimen measured in the original description of that species); MACN 5734, a fragment of a left mandibular ramus with alveoli of I_{1-4} and M₁, and C-P₃ present (probable syntype of *E. famula*); MACN 8472, a fragment of a right mandibular ramus with alveoli of I_{1-4} , and P₁₋₂ complete (labeled *M. tehuelchum*); MACN 8474, a right mandibular ramus with alveoli of I_{1-4} , and P₂₋₃ complete; MACN 8475, a left mandibular ramus with alveoli of P₁₋₂, and P₃₋₄ complete; MACN 8476, a fragment of a left mandibular ramus with alveoli of C, P₁₋₃ complete, anterior root of M₁, talonid of M₁ present, and roots of M₂ (labeled *Stylognathus crassus*); MACN 8477, a fragment of a right

FIG. 9. *Microbiotherium tehuelchum* Ameghino, 1887, p. 7 (Santacrucian). MLP 58-IX-3-4, a right upper jaw with base of C, P¹ complete, roots of P², and with P³-M⁴ complete: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

TABLE 5. Measurements of upper cheek teeth of *Microbiotherium tehuelchum*.

Specimen	M1		M2		M3		M4		M1-3
	L	W	L	W	L	W	L	W	L
MACN 8505	2.0	1.6	2.0	1.9	1.7	1.9	0.9	1.2	5.4
MLP 58-IX-3-4(l)	1.9	1.7	2.0	2.0	1.8	2.0	...	...	5.4
MLP 58-IX-3-4(r)	1.9	1.7	1.9	2.0	1.8	2.0	0.9	1.5	5.4
PU 15038	...	...	1.9	2.2	1.8	2.1	...	...	...
PU 15698(l)	2.2	2.2	2.2	2.3	2.0	...	...	...	6.1

TABLE 6. Measurements of lower cheek teeth of *Microbiotherium tehuelchum*.

Specimen	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	L
MACN 5716	...	...	2.0	1.3	2.0	1.3	...	...	...	...	ca 7.2	...
MACN 5724	1.1	0.7	...	...	...	...	...	...	...	...	...	...
MACN 5725	1.3	0.8	1.9	1.3	...	...	...	...	...	...	...	...
MACN 5726	1.2	0.8	...	...	...	...	...	...	...	...	...	...
MACN 5729	1.3	0.7	1.9	1.3	1.9	1.3	1.8	1.2	1.5	0.8	7.4	8.8
MACN 5730	1.3	0.8	1.9	1.2	...	...	1.9	1.3	1.4	0.8	7.6	9.0
MACN 5731	...	...	2.0	1.3	...	...	1.8	1.2	...	...	...	...
MACN 5732	1.3	0.7	1.8	1.2	1.8	1.3	1.7	1.1	1.3	0.8	7.5	8.8
MACN 5733	1.1	0.8	1.9	1.3	1.9	1.3	1.8	1.1	...	...	...	...
MACN 5734	1.3	0.8	...	...	...	...	...	...	...	...	...	...
MACN 5738	1.3	0.9	...	...	...	...	...	...	...	...	...	...
MACN 5739	1.3	0.9	...	...	...	...	...	...	...	...	...	...
MACN 8474	1.1	0.8	1.7	1.3	1.7	1.3	...	...	...	...	...	...
MACN 8475	1.1	0.7	1.7	1.2	1.7	1.3	1.7	1.1	1.3	0.8	6.8	7.8
MACN 8476	1.1	0.7	...	1.3	...	...	...	...	...	...	...	...
MACN 8477	1.1	0.8	1.7	1.2	1.7	1.2	...	...	...	...	...	...
MACN 8478	...	...	1.7	1.1	...	...	...	...	...	...	...	...
MACN 8479	1.3	0.9	1.8	1.2	1.8	1.3	...	...	...	...	...	...
MACN 8480	1.3	0.7	1.9	1.3	1.9	1.3	1.8	1.1	1.4	0.9	7.3	8.7
MACN 8481	1.3	0.8	...	...	1.8	1.4	1.8	1.3	1.4	1.0	...	...
MACN 8483	1.2	0.7	1.9	1.3	1.8	1.3	1.8	1.2	1.4	0.8	7.1	8.3
MACN 8503	...	...	...	...	...	...	1.9	1.1	...	...	...	...
MACN 8504	...	...	...	...	1.9	1.2	1.7	1.1	1.4	0.8	...	...
MACN 8506	1.1	0.7	1.7	1.1	1.7	1.2	1.6	1.1	1.1	0.8	6.4	7.6
MACN 8507	...	...	...	...	1.7	1.2	1.6	1.1	1.2	0.8	...	...
PU 15038	1.2	0.8	1.9	1.2	1.8	1.4	1.8	1.2	...	...	ca 7.0	ca 8.5
PU 15698(r)	1.3	0.9	2.0	1.4	2.0	1.5	1.9	1.3	1.5	1.1	7.7	9.2
PU 15698(l)	1.3	0.8	2.0	1.3	1.9	1.4	1.8	1.3	...	...	ca 7.6	9.2

mandibular ramus with P₂-M₂ complete; MACN 8478, a fragment of a left mandibular ramus with alveoli of P₁-M₁, and M₂ complete; MACN 8479, a right mandibular ramus with alveoli of I₁-C, and P₁-M₂ complete (labeled *E. fortis* and figured by Ringuelet, 1953, pl. 1, fig. 5); MACN 8480, a right mandibular ramus with P₃-M₄ complete (labeled *E. fortis* and figured by Ringuelet, 1953, pl. 1, fig. 1 erroneously as MACN 8479); MACN 8481, a left mandibular ramus with alveoli of I₁-C, P₁₋₃ and M₂₋₄ complete, and trigonid of M₁ missing (labeled *E. fortis* and figured by Ringuelet, 1953, pl. 1, fig. 6); MACN 8483, a left mandibular ramus with P₂-M₄ complete, and alveoli of rest of dentition (labeled *E. famula*); MACN 8493, a calcaneum (associated with MACN 8483 and figured as *E. famula* by Ameghino, 1905, fig. 11); MACN 8503, a left mandibular ramus with P₁ and M₃ complete, and alveoli of rest of dentition (labeled *E. famula*); MACN 8504, a

FIG. 10. *Microbiotherium tehuelchum* Ameghino, 1887, p. 7 (Santacrucian). PU 15038, ventral view of left auditory region (after Segall, 1969b, fig. 5).

fragment of a left mandibular ramus with M_{2-4} complete (labeled *E. famula* and figured by Ameghino, 1906, fig. 246e, o); MACN 8505, a very crushed skull with left M^1-4 complete (figured as *E. famula* by Ameghino, 1906, fig. 246a); MACN 8506, a right mandibular ramus with P_1-M_4 complete (labeled *E. famula*); MACN 8507, a right mandibular ramus with M_{2-4} complete (labeled *E. famula*); MACN 10248, an edentulous right mandibular ramus with alveoli of all teeth (labeled *E. famula*); MACN ?, an astragalus (figured as *E. fortis* by Ameghino, 1905, fig. 10); PU 15038, a left maxillary fragment with M^{2-3} complete; a nearly complete left mandibular ramus with alveoli of I_{1-4} , $C-M_3$ complete, and roots of M_4 ; part of a scapula, humerus, radius, ulna, cervical vertebrae, and the greater part of the left bullar region of skull (figured by Sinclair, 1906, pl. 62, figs. 4, 4a, 6-12; Segall, 1969b, fig. 5); PU 15698, a partial skull with alveoli or roots of right side; alveoli of $I^{1-2,4-5}$; complete I^3 , C , and M^1-2 ; and roots of P^1 and parts of crowns of M^{3-4} on right side; part of right mandibular ramus with P_3-M_4 present; and greater part of left mandibular ramus with I_{1-2} present, roots of I_{3-4} , $C-M_3$ present, roots of M_4 (figured by Sinclair, 1906, pl. 62, figs. 1, 2, 2a); MLP 11-35, a fragment of a left mandibular ramus with P_2-M_3 present (figured by Ringuelet, 1953, pl. 1, fig. 3); MLP 58-IX-3-4, rostral portion of skull with palate, roots of left $C-P^3$ and M^4 , and with M^{1-3} complete, and with base of right C , roots of P^2 ,

TABLE 7. Statistics for some cheek tooth dimensions of *Microbiotherium tehuelchum*.

Dimension	N	OR	x	s	CV
UPPER CHEEK TEETH					
M ¹ L	4	1.9-2.2	2.0	0.14	7.00
W	4	1.6-2.2	1.8	0.27	15.00
M ² L	5	1.9-2.2	2.0	0.12	6.00
W	5	1.9-2.3	2.08	0.16	7.70
M ³ L	5	1.7-2.0	1.82	0.11	6.04
W	4	1.9-2.1	2.0	0.08	4.00
M ⁴ L	2	...	0.9	...	...
W	2	1.2-1.5	1.35	0.21	15.56
M ¹⁻³	4	5.4-6.1	5.58	0.35	6.27
LOWER CHEEK TEETH					
P ₃ L	22	1.1-1.3	1.22	0.09	7.38
W	22	0.7-0.9	0.78	0.07	8.97
M ₁ L	18	1.7-2.0	1.86	0.11	5.91
W	19	1.1-1.4	1.25	0.08	6.40
M ₂ L	17	1.7-2.0	1.82	0.10	5.49
W	17	1.2-1.5	1.31	0.08	6.11
M ₃ L	17	1.6-1.9	1.77	0.09	5.08
W	17	1.1-1.3	1.17	0.08	6.84
M ₄ L	11	1.1-1.5	1.35	0.12	8.89
W	11	0.8-1.1	0.85	0.10	11.76
M ₁₋₄ L	11	6.4-7.7	7.24	0.39	5.39
P ₃ -M ₄ L	10	7.6-9.2	8.59	0.55	6.40

and with P¹ and P³-M⁴ complete (figured as *Microbiotherium* sp. by Sinclair, 1906, fig. 6, p. 409).

Horizon and locality.—All specimens are from the Santa Cruz Formation, Patagonia, southern Argentina. The specific localities and dates of collection are as follows: *Corriquen-Kaik* MACN 8504, 8505 (collected in 1892-93); *La Cueva* MACN 8474, 8481, 8483, 10248 (collected in 1892-93); *Quequa-Quemada* MACN 8472, 8479, 8480, 8503 (collected in 1892-93); *Monte Observación* MACN 5716, 5724, 5725, 5726, 5729, 5730, 5731, 5732, 5733, 5734, 5738, 5739, 5741 (collected in 1890-91); *Monte Observación* MACN 8477, 8478 (collected in 1891-92); *Monte Observación* MACN 8475, 8476, 8506, 8507 (collected in 1892-93); *Killik Aike Norte* (= *Felton's Estancia*) PU 15698 (collected by J. B. Hatcher and O. A. Peterson, 1896); PU 15038, MLP 11-35, MLP 11-36 and MLP 58-IX-3-4 are without specific locality data. The MACN specimens were collected by Carlos Ameghino.

Age.—Santacrucian.

Diagnosis.—Medium-sized microbiothere; averages 16% larger than *M. patagonicum*, and averages 29% smaller than *M. gallegosense*, and similar in size to larger specimens of *M. divisum*; lower canine medium to large and set nearly perpendicular in jaw; P₁ set at sharp oblique angle in jaw; lack of posterobasal heel on P₁; P₂ straight or set at slight oblique angle in jaw; posterobasal heel on P₂ small but distinct; posterobasal heel on P₃ large; very sharp size decrease from P₃ to P₁, P₃ usually proodont and much larger than P₂; bulla larger and more elongated anteriorly than in *D. australis*; supraorbital processes large and well developed; P¹ and P² set at slight oblique angle in jaw; P¹ single-rooted (or nearly so) with no trace of posterobasal heel; P³ with large, well-developed posterobasal heel; P₃ about same height as M₁, para- and metaconules on M¹⁻³ distinct but

not large; M^{1-3} protocone broader anteroposteriorly and more robust than in *M. patagonicum* or *D. australis*; styler shelf with low but distinct labial ridge which encloses shelf lingually; middle cleft on M^2 absent; middle cleft on M^3 very shallow or absent; size of M^4 (relative to M^3) larger than in *M. patagonicum*.

Comments.—*Microbiotherium tehuelchum* was diagnosed briefly by Ameghino in 1887 (p. 7), and an expanded description and characterization was presented by him in 1889 (p. 265) as follows:

Esta especie está fundada en algunos pequeños fragmentos de mandíbulas inferiores, el más completo de los cuales es una rama izquierda conteniendo implantados parte del pm_3 , el pm_4 y los tres molares siguientes. Este animal se distingue de la especie anterior [*M. patagonicum*] por su tamaño bastante más considerable, por sus molares uno y dos de tamaño más igual entre sí, y cada uno de ellos bastante más angosto adelante que atrás.

Las muelas desde el pm_3 al m_7 se presentan con una corona baja gastada por la masticación, pero todavía aparentemente dividida en dos lóbulos casi iguales y con las cúspides de los tubérculos casi completamente gastadas, menos las colocadas sobre el borde interno, que se conservan puntiagudas. Los dientes pm_3 y pm_4 , m_7 y m_2 parecen tener dos raíces distintas, una anterior y otra posterior, pero el m_3 , que es sumamente pequeño y de corona casi circular, no tiene probablemente más que una sola raíz.

Los dos últimos premolares y los tres verdaderos molares, todos muy apretados unos a otros, ocupan un espacio longitudinal de 8 milímetros.

La forma de la rama horizontal de la mandíbula es, como en la especie precedente, con un alto uniforme de cerca de 3 milímetros, mostrando también en el lado externo dos pequeños agujeritos mentonianos, colocados: el primero, debajo de la parte media del pm_3 el segundo, debajo de la parte media del m_7 ; este último agujerito se distingue del correspondiente en la especie precedente por su tamaño excesivamente pequeño, apenas visible a simple vista.

Ameghino further noted (ibid.) that the specimens were "[d]escubierta y coleccionada . . . en las barrancas del río Santa Cruz, en Patagonia austral." He clearly stated that this taxon was erected on the basis of several small fragments of mandibular rami, of which the most complete was a left mandibular ramus with part of P_3 [his pm_3] and M_{1-4} [his " pm_4 y los tres molares"] present. His description and measurements of *M. tehuelchum* are clearly based in large part, if not totally, on this specimen.

Unfortunately, no known specimens in the MLP collection agree perfectly with "the" specimen described by Ameghino. It would be appropriate to make this specimen the lectotype and this should be done when and if it is relocated. Several possibilities exist with regard to its whereabouts. Firstly, it may be misplaced in the MLP collections or it could be lost. Secondly, Ameghino may have taken it with him to the MACN when he resigned from his post at the MLP. This had been shown to be the case for other type and referred specimens described by Ameghino in 1887 (see Marshall, 1980, p. 36n), and it could well be the case with *M. tehuelchum*. There is one specimen in the Ameghino collection in the MACN (MACN 1) which is labeled "tipo" of *M. tehuelchum* and is listed as being collected from Santa Cruz. MACN 1 is, however, not "the" specimen described by Ameghino (it is a fragment of a right mandibular ramus with alveoli of I_1 – C , and with P_1 – M_1 complete), but it may well be, and it probably is, one of the "algunos pequeños fragmentos de mandíbulas inferiores" to which he called attention in his 1889 diagnosis. To further complicate matters, MACN 1 is here referred to *M. patagonicum* on the basis that length of P_3 (0.8 mm) and M_1 (1.5 mm) (see table 3) is smaller and outside the range of the large sample

of specimens referred to *M. tehuelchum* (see tables 6, 7; $L P_3 = 1.1-1.3$ mm, $N = 22$; $L M_1 = 1.7-2.0$ mm, $N = 18$). Accordingly, MACN 1 is referred to the smaller-sized species *M. patagonicum*. The probability thus exists that among the original syntypes of *M. tehuelchum* some, as MACN 1, are referable to *M. patagonicum*.

Despite these complications the measurements of *M. tehuelchum* presented by Ameghino do permit comparison with other specimens. Furthermore, as it is not possible to identify syntypes of *M. tehuelchum* in the MLP collection, it is necessary to select a neotype. I have thus chosen a specimen in the MLP, since that is the institutional collection where the original type was deposited. For neotype I select MLP 11-36, a nearly complete right mandibular ramus with P_2-M_4 complete (figured by Ringuet, 1953, pl. 1, fig. 1; Pascual & Herrera, 1975, pl. 1, fig. 1). Ringuet (1953, p. 275) believed MLP 11-36 to be a probable cotype of *M. tehuelchum*, and Pascual & Herrera (1975, pl. 1, fig. 1) figured it as type. This specimen, however, is more complete than the material described by Ameghino and it was therefore almost certainly not among the specimens referred to in his 1889 diagnosis of that species. Nevertheless, in size and structure MLP 11-36 agrees perfectly with Ameghino's diagnosis [I have not studied MLP 11-36 firsthand and its selection as neotype is based totally on my interpretation of the diagnosis given by Ameghino and Ringuet]: e.g., $L P_3-M_4 = 8.0$ mm in both, while the depth of the ramus was listed as 3.8 mm by Ameghino and in MLP 11-36 is listed by Ringuet as 3.5 mm below the P_1 and 4.0 mm below the M_1 and M_4 . Other measurements of MLP 11-36 given by Ringuet (1953, p. 276) include:

Longitud de la parte posterior del M_4 a la parte anterior de la sínfisis	14 mm
Longitud del espacio ocupado por Pm_1-M_4	10 mm
Longitud del espacio ocupado por Pm_1-Pm_3	3.5 mm
Longitud del espacio ocupado por M_1-M_4	7 mm
Longitud de sínfisis	4 mm

The specimen figured by Ameghino (1889, pl. 1, fig. 17) as *M. tehuelchum* is an unidentified member of the caenolestid subfamily Palaeothentinae. MACN 5724, a fragment of a left mandibular ramus with I_3-P_1 and P_3 present, and alveoli of I_{1-2} , P_2 and M_1 , is referable to *M. tehuelchum* and was figured under that name by Ameghino (1893, fig. 2; 1894, fig. 42; 1898, fig. 52a; 1906, fig. 245). All specimens figured by Sinclair (1906) as *M. tehuelchum* (and *M. tortor*) are indeed referable to this species.

As noted earlier (see p. 19), *Halmarhiphus didelphoides* Ameghino (1891, p. 308) was based on four specimens, of which MACN 5716 is here selected lectotype and is referred to *M. tehuelchum*. The M_2 of this specimen is figured by Ameghino (1899, fig. 4). The identity of the specimen from which the left M_2 figured in occlusal view by Ameghino (1903, fig. 86) as *Parhalmarhiphus didelphoides* is not surely known. The identities of the other three syntypes are discussed on p. 19.

Microbiotherium forficulum Ameghino (1891, p. 309) was erected on two specimens labeled "tipo" in Ameghino's catalog and which can be regarded as syntypes. The first, MACN 5725, is a fragment of a left mandibular ramus with alveoli of C and M_2 , and with P_1-M_1 complete. This is the more complete of the two specimens and clearly is the one measured by Ameghino. It is here selected lectotype and is figured by Ringuet (1953, pl. 1, fig. 2). The second, MACN

5726, is a fragment of a left mandibular ramus with alveoli of C and M_1 , roots of P_{1-2} , and P_3 complete. Both specimens are discussed by Ringelet (1953, p. 276) and referred by her to *M. tehuelchum*. I agree with this assignment.

Eodidelphys fortis Ameghino (1891, p. 310) was, according to Ameghino's catalog, erected on the basis of three specimens. MACN 5729, a left mandibular ramus with alveoli of I_1 -C and P_1 - M_4 complete, is listed as "tipo" in Ameghino's catalog; it is here selected lectotype and is figured by Reig (1955a, fig. 2A). Two additional specimens, MACN 5730, a left mandibular ramus with alveoli of C- P_2 and M_2 , and P_3 - M_1 and M_{3-4} complete; and MACN 5731, a left mandibular ramus with M_1 and M_3 complete, and alveoli of rest of dentition except M_4 , are both labeled *E. fortis*. All of these specimens are referred confidently here to *M. tehuelchum*. I could not locate the astragalus figured by Ameghino (1905, fig. 10) as *E. fortis*. Ringelet (1953, p. 282) described and figured three specimens as *E. fortis*: MACN 8479 (pl. 1, fig. 5), 8480 (pl. 1, fig. 1—listed erroneously as 8479), and 8481 (pl. 1, fig. 6); all are referable to *M. tehuelchum*.

Eodidelphys famula Ameghino (1891, p. 310) was apparently erected on the basis of three specimens. MACN 5732, a right mandibular ramus with P_1 - M_4 and alveoli of all other teeth is listed as "tipo" in Ameghino's catalog and is here selected lectotype. MACN 5733, a left mandibular ramus with P_2 - M_3 complete, is most probably the specimen measured by Ameghino in the original description and is labeled *E. famula* in Ameghino's catalog. The third specimen, MACN 5734, a fragment of a left mandibular ramus with alveoli of I_{1-4} and M_1 , and with C- P_3 present, is also labeled *E. famula*.

The calcaneum figured by Ameghino (1905, fig. 11) as *E. famula* is MACN 8493. Also figured by Ameghino as *E. famula* are MACN 8505, a left M^{1-4} complete (1906, fig. 246a), and MACN 8504, a fragment of a left mandibular ramus with M_{2-4} complete (1906, fig. 246e, o). All of these specimens are referable to *M. tehuelchum*.

Phonocdromus patagonicus Ameghino (1894, p. 355) was based on two specimens. MACN 5741, a left mandibular ramus with partial dentition is here selected lectotype. I could not locate this specimen in the MACN collection; although the box in which it was supposed to be was there, the specimen was not. Reig (1955b, p. 63) says that it is a microbiothere, however, and the measurements given by Ameghino suggest that it is referable to *M. tehuelchum*. The second specimen, MACN 8456, a fragment of a left mandibular ramus with alveoli of M_1 , and M_{2-4} complete, is referable to *Stilotherium dissimile*. This specimen is listed erroneously as 8450 by Reig (1955b, p. 64).

Hadorhynchus tortor Ameghino (1891, p. 311) was based on MACN 5738, a fragment of a right mandibular ramus with alveoli of I_1 -C, roots of P_{1-2} , P_3 complete, and alveoli of M_{1-2} , and is listed as "tipo" in Ameghino's catalog. To *Microbiotherium tortor* Sinclair (1906, p. 412, pl. 62, figs. 1, 2, 2a) referred PU 15698, and Ringelet (1953, p. 278, pl. 1, fig. 3) referred MLP 11-35. All of these specimens are referred to *M. tehuelchum*.

Hadorhynchus torvus Ameghino (1891, p. 311) was based on MACN 5739, a fragment of a right mandibular ramus with alveoli of C, roots of P_1 , P_{2-3} complete, and alveoli of M_1 . This specimen is listed as "tipo" of the species in Ameghino's catalog and is figured as *Microbiotherium torvus* by Ringelet (1953, pl. 1, fig. 5). Sinclair (1906, p. 412) regarded *H. torvus* as a junior synonym of *M. tortor*. In this study I regard both species as synonyms of *M. tehuelchum*.

In summary, seven of Ameghino's species are here included as junior synonyms in *Microbiotherium tehuelchum*. The points used by Ameghino to characterize these species are all here attributable to preservational, age and/or individual differences of the various specimens. Some linear tooth measurements of these and other specimens are given in Tables 5 and 6, and statistics for these dimensions are given in Table 7. Sample sizes for various lower tooth dimensions are quite large ($N=10-22$) and CV values range between five and nine with only one value ($M_4 W$) greater than 10. For upper tooth dimensions the sample sizes are smaller ($N=2-5$) with most CV values between four and eight, and with only two values ($M^1 W$ and $M^4 W$) greater than 10. Considering the generally large sample sizes these values are within the range expected within a population of a single species.

Microbiotherium gallegosense Sinclair, 1906. Figure 11.

Microbiotherium gallegosense Sinclair, 1906, p. 413, pl. 62, figs. 3, 3a; Ringuelet, 1953, p. 277.

Type of M. gallegosense.—AMNH 9591, a relatively complete right mandibular ramus with alveoli of $C-P_2$ and M_{3-4} , and with P_3-M_2 complete (figured by Sinclair, 1906, pl. 62, figs. 3, 3a).

Hypodigm.—Type only.

Horizon and locality.—Type is from the Santa Cruz Formation, Santa Cruz Province, Patagonia, southern Argentina, and was collected by Barnum Brown in 1899 from the north bank of the Río Gallegos near *Felton's Estancia*.

Age.—Santacrucian.

Diagnosis.—Largest known species of *Microbiotherium*; averages 29% larger than *M. tehuelchum*; lower canine large and set perpendicular in jaw; P_1 set at sharp oblique angle in jaw; P_2 set straight in jaw; posterobasal heel on P_3 large; very sharp decrease from P_3 to P_1 , P_3 proodont and much larger than P_2 ; P_3 same height as M_1 ; minute foramen pierces masseteric fossa anteriorly.

Measurements.— P_3 $L=1.9$ mm, $W=1.1$ mm; M_1 $L=2.5$ mm, $W=1.7$ mm; M_2 $L=2.6$ mm, $W=1.8$ mm; P_{1-3} $L=ca$ 5.9 mm; M_{1-4} $L=ca$ 9.5 mm; P_3-M_4 $L=ca$ 11.6 mm.

Comments.—This species is known only from its type and is easily distinguished from other members of the genus by its large size. *Microbiotherium gallegosense* differs from the large didelphid Colhuehuapian species *Pachybiotherium acclinum* in being slightly smaller in size and having an absolutely and relatively larger paraconid, a smaller protoconid, and large talonid basin on M_{1-2} .

Dromiciops Thomas, 1894, p. 186

Dromiciops Thomas, 1894, p. 186.

Type.—*Dromiciops australis* (Philippi, 1893a, p. 31).

Distribution.—As for type and only known species.

Diagnosis.—As for type and only known species.

Dromiciops australis (Philippi, 1893a). Figures 12–17; Tables 8, 9.

Didelphys australis Philippi, 1893a, p. 31; 1893b, p. 318.

Dromiciops gliroides Thomas, 1894, p. 187.

FIG. 11. *Microbiotherium gallegosense* Sinclair, 1906, p. 413 (Santacrucian). AMNH 9591 (type), a relatively complete right mandibular ramus with alveoli of C-P₂ and M₃₋₄ and with P₃-M₂ complete: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

Type of D. australis.—The type is in the Natural History Museum in Santiago, Chile and consists of a skin and skull (inside the skin) (see Osgood, 1943, p. 49), collected near Unión, Valdivia Province, Chile.

Type of D. gliroides.—British Museum (Natural History) 92.5.9.3, an aged male preserved as skin and skull, collected from Huite, near Ancud, Northeastern Chiloé Island, Chile. [This specimen was obtained by Dr. R. O. Cunningham in 1868, who referred to it (1871, p. 362) under the name *Didelphys elegans*.]

Distribution.—Known only from south central Chile, from Concepción south to Chiloé Island, and east to slightly beyond the Argentine border near Lago Nahuel Huapí. They occur in dense, cool, humid forested areas in the Cordillera de la Nahuelbuta and Cordillera de los Andes, above 360 meters in elevation and below tree line (fig. 12; see Marshall, 1978a, p. 2 for a summary list of some known collection localities).

Diagnosis.—Small sized microbiothere, closely resembling *Microbiotherium patagonicum* (Santacrucian) in size and structure; body fur silky, short, dense; ears short, rounded, covered with short hair, and anterior basal prominence little developed; backs of ears covered basally with thick fur similar to that of crown, and terminally with thin yellowish hairs.

Tail thick basally, tapering rapidly and evenly to tip; basal third of tail thickly clothed with shining fawn colored fur resembling that of body; terminal two-thirds of tail almost equally well clothed, but hairs straighter and nearly uniformly dark brown; below hairs are brownish white throughout; naked part of tail confined to a narrow strip 25 to 30 mm long on underside of tip.

Hands and feet are large and well developed, and limb bones are proportionately shorter, wider, and more robust than in species of *Marmosa*; digit four of hind foot is largest while two, three and five are shorter and one is shortest of all; soles of hind feet have five prominent transverse striated pads (plantar tubercles), one across base of hallux, three at bases of toes two through four, and a fifth (smallest) pad along posteroexternal border; large longitudinally striated terminal digital pads extend beyond claws.

Female has a small but well-developed abdominal pouch (Mann, 1958, p. 211, figs. 3, 4) with four mammae symmetrically placed in two pairs; a medial "pseudo" vagina is well developed (Osgood, 1943, p. 49; Mann, 1958, p. 209, figs. 1, 2). Scrotum of male is shortly pedunculate and covered with cinnamon rufous hairs, identical to those covering pouch area of females (Mann, 1958, p. 209).

No trace of distinct temporal ridges, supra- or postorbital processes, or a sagittal crest; auditory bullae smaller and not as elongated anteriorly as in *Microbiotherium tehuelchum*; no trace of para- and metaconules on M^{1-3} ; canines short, upper not exceeding line drawn from tip of P^3 to I^1 ; lower canine very small, incisivo-premolariform with broad posterobasal swelling and scarcely higher than P_3 ; P^{1-2} subequal in size, and smaller than P^3 ; P_{1-3} increase gradually and moderately in size from P_1 to P_3 ; P_1 not set obliquely in jaw; posterobasal heel on P_2 large and well-developed; no evidence of mental foramen below M_1 ; deep middle cleft on M^3 .

Description.—General body color above is generally a fawn gray; the dorsal area is decidedly darker than the sides. The face is a pale gray with distinct black rings around the eyes. Crown and nape of neck are rufous brown or cinnamon, the sides of the body where the hairs have prominent subterminal white rings are paler. Large whitish patches also occur on sides of body just behind shoulder,

FIG. 12. Map of south central Chile and western Argentina showing known geographic range of *Dromiciops australis* (after Marshall, 1978, fig. 4, and based on data in Osgood, 1943, map 3 and Gollan, 1946, pl. 3). Subspecies are: 1, *D. a. australis*; and 2, *D. a. gliroides*.

FIG. 13. *Dromiciops australis* (Philippi, 1893a, p. 31) (Recent). AMNH 92147, skull of a female from Lota, Concepción Province, Chile: **top**, dorsal; **middle**, lateral; **bottom**, ventral views. Scale = 5 mm. [After Marshall (1978, fig. 1).]

in front of shoulder, and just behind hips. The whole animal, when viewed from the side, presents an alternation of light and dark areas, with the whitish cheeks followed by a darker color below the ears, then paler on sides of the neck, and darker on the shoulder, center of the belly, and hips; each of these parts is separated from the others by paler areas. The dark of the shoulder is united above to that of the back, but that of the hips is separated by a narrow, longitudinal, light line passing approximately along the pelvic bones. These variations in color are in no case conspicuous or sharply defined. The appearance is suggestive, however, of the more distinctive color pattern of the water opossum *Chironectes*. The belly is a dirty yellowish white; the gray of the bases of the hairs shows through. The outer sides of the limbs and backs of the hands are

TABLE 8. Measurements of cheek teeth of *Dromiciops australis* (measurements are of dentition on right side).

Specimen	Sex	P3		M1		M2		M3		M4		M1-3	P3-M4
		L	W	L	W	L	W	L	W	L	W	M1-4	
UPPER CHEEK TEETH													
FMNH 22671	M	1.0	0.7	1.7	1.4	1.6	1.8	1.4	1.7	0.6	0.4	4.5	...
FMNH 22672	F	1.0	0.6	1.6	1.3	1.5	1.6	1.4	1.7	0.7	0.5	4.3	...
FMNH 22673	F	...	...	1.5	1.3	1.5	1.6	1.4	1.6	...	...	4.4	...
FMNH 22675	M	...	...	1.6	1.4	1.6	1.7	1.4	1.6	...	...	...	...
FMNH 50073	M	1.0	0.6	1.8	1.4	1.5	1.7	1.4	1.5	...	...	4.4	...
FMNH 50074	F	1.1	0.7	1.8	1.4	1.6	1.7	1.5	1.7	...	...	4.6	...
LOWER CHEEK TEETH													
FMNH 22671	M	1.1	0.6	1.5	1.0	1.5	1.1	1.4	0.9	1.0	0.6	5.5	6.5
FMNH 22672	F	1.0	0.6	1.4	0.9	1.5	1.0	1.4	0.8	1.2	0.5	5.5	6.5
FMNH 22673	F	...	...	1.4	0.9	1.5	1.0	1.4	1.0	...	...	...	...
FMNH 22675	M	...	...	1.4	0.9	1.5	1.1	1.4	1.0	...	...	...	...
FMNH 50073	M	1.0	0.5	1.5	0.9	1.5	1.0	1.3	0.8	1.0	0.6	5.3	6.2
FMNH 50074	F	1.1	0.6	1.4	0.9	1.6	1.1	1.5	1.0	1.2	0.7	5.7	6.7

TABLE 9. Statistics for some cheek tooth dimensions of *Dromiciops australis*.

Dimension		N	OR	x	s	CV
UPPER CHEEK TEETH						
P ³	L	4	1.0-1.1	1.03	0.05	4.85
	W	4	0.6-0.7	0.65	0.06	9.23
M ¹	L	6	1.5-1.8	1.67	0.12	7.19
	W	6	1.3-1.4	1.37	0.05	3.65
M ²	L	6	1.5-1.6	1.55	0.05	3.23
	W	6	1.6-1.8	1.68	0.08	4.76
M ³	L	6	1.4-1.5	1.42	0.04	2.82
	W	6	1.5-1.7	1.63	0.08	4.91
M ⁴	L	2	0.6-0.7	0.65	0.07	10.77
	W	2	0.4-0.5	0.45	0.07	15.56
M ¹⁻³	L	5	4.3-4.6	4.44	0.11	2.48
LOWER CHEEK TEETH						
P ₃	L	4	1.0-1.1	1.05	0.06	5.71
	W	4	0.5-0.6	0.58	0.05	8.62
M ₁	L	6	1.4-1.5	1.43	0.05	3.50
	W	6	0.9-1.0	0.92	0.04	4.35
M ₂	L	6	1.5-1.6	1.52	0.04	2.63
	W	6	1.0-1.1	1.05	0.05	4.76
M ₃	L	6	1.3-1.5	1.40	0.06	4.29
	W	6	0.8-1.0	0.92	0.10	10.87
M ₄	L	4	1.0-1.2	1.10	0.12	10.91
	W	4	0.5-0.7	0.60	0.08	13.33
M ₁₋₄	L	4	5.3-5.7	5.50	0.16	2.91
P ₃ -M ₄	L	4	6.2-6.7	6.48	0.21	3.24

brown; the inner sides of the limbs and backs of the hind feet are dull white. The tail is moderately prehensile and its pelage is denser than in species of *Marmosa* (Osgood, 1943, p. 49). The presence of fur on the tail of *Dromiciops* (and *Glironia*) is perhaps correlated with a decrease in the use of the tail as a prehensile organ (Tate, 1933, p. 15).

Adults caught in the Cordillera de Nahuelbuta average slightly larger in several

measurements, especially in length of head and body, than specimens of similar age taken in the Cordillera de los Andes (see table 8 in Greer, 1965). There are no significant color differences between skins from these areas (Greer, 1965, p. 103).

Osgood (1943) formally recognized two subspecies, the mainland *Dromiciops australis australis* and the Chiloé Island *D. a. gliroides*. He noted (p. 50) that a specimen of *D. a. gliroides* was "noticeably darker and shorter-tailed than specimens from the mainland, indicating at least subspecific distinction. The under parts especially are darker, and the tail, which in [*D. a.*] *australis* is usually somewhat lighter below, is wholly dark."

The following ranges of measurements (in mm, except weight) are from Mann (1955, p. 159, data for eight specimens), Gollan (1946, p. 192, data for six to seven specimens), and Greer (1965, p. 104, data for 23 to 26 specimens), and selected cheek tooth measurements of six specimens in the FMNH are given in table 8; all are referable to *D. a. australis*: weight 16.7–31.4 g; total length 195–246 mm; length of head and body 83–130 mm; length of tail 90–132 mm; length of hind foot 15–20 mm; length of forefoot 9–10 mm; height of ear at notch 17–20 mm; height of ear at crown 12–16 mm; condylobasal length of skull 23.6–27.9 mm; zygomatic breadth 14.4–16.4 mm; mastoid breadth 11.5–12.6 mm; least interorbital breadth 4.5–5.1 mm.

Measurements for type of *D. a. gliroides* given by Thomas (1894) are: combined head and body length 126 mm; length of tail 102 mm; length of hind foot 18 mm; ear (at notch) 14 mm; basal length of skull 26 mm; greatest breadth of skull 16.8 mm; nasal length 11.1 mm; greatest nasal breadth 4.4 mm; least nasal breadth 1.9 mm; interorbital constriction 5.3 mm; length of palate 14 mm; breadth of palate outside M^3 10 mm; length M^{1-3} 4.6 mm; length M_{1-4} 5.8 mm.

The summary of diagnostic and descriptive characters was compiled from Cabrera (1919, p. 30), Cabrera & Yepes (1960, p. 46), Fischer (1978), Mann (1955), Osgood (1943, p. 48), Thomas (1894, p. 187), Philippi (1893a,b), Walker et al. (1968, p. 17), and Wolffsohn (1913).

Behavior and ecology.—*Dromiciops australis* is almost entirely nocturnal and inhabits dense, cool, humid forests of the Chilean Andes. Osgood (1943, p. 48) considered *D. a. australis* restricted to the "Valdivian Forest District" from the highest parts of the Cordillera de la Nahuelbuta east to, and beyond, the Argentine-Chilean border. Moist, forested areas, at least in Malleco Province, appear to be the preferred habitat, although it is not confined to this habitat, being also found in *Araucaria-Nothofagus dombeyi* forests, *N. obliqua* woods, *N. obliqua-N. dombeyi* forests, and in localized wooded areas having evergreens, such as *Peumus boldus*, *Guevina avellana*, *Persea lingue*, *Myrcogenia* sp., and *Drimys winteri*, characteristic of southern forest. Cane (*Chusquea* sp.) thickets in these forested areas are likely places to trap *D. australis* (Greer, 1965, p. 103).

Mann (1955, p. 163) reported that these animals hibernate in winter when cold temperatures prevail and food is scarce. Hibernation is preceded by an accumulation of fat in the basal part of the tail (Fischer, 1978; Hunsaker, 1977). The heart rate drops from 230/minute to less than 30/minute (Mann, 1955, p. 161). Animals captured by Greer (1965, p. 105), kept alive in cages and exposed to the nighttime cold temperatures in the same region in which they were trapped, would assume a flexed position. If early morning temperatures dropped to 4.5° C or lower, the animals' bodies became stiff and cool to the touch. When placed in a warm place they soon emerged from their torpor and became quite

FIG. 14. *Dromiciops australis* (Philippi, 1893a, p. 31) (Recent). FMNH 22671, a right mandibular ramus with I₁–M₄ complete: a, labial; b, occlusal; c, lingual views. Scale = 6 mm.

FIG. 15. *Dromiciops australis* (Philippi, 1893a, p. 31) (Recent). FMNH 22673, a left dP_3 (stipple) and P_2 and M_1 (outline): a, labial; b, occlusal; c, lingual views. Scale = 3 mm.

active. Their dark dense fur and small ears appear to be additional adaptations to cold environments (Mann, 1955, p. 161).

Mann (1958, p. 210) reported finding nests of *Dromiciops* below fallen trunks, in hollow trees, and on branches. Nests in the bamboos *Chusquea coleu* and *C. cummingi* usually were about two meters above the ground. One nest (see Mann, 1958, p. 212, fig. 7), 200 mm in diameter, was spherical with an opening of 30 to 40 mm. A small wall, presumably affording some sort of protection, was found at the opening of two of the five nests observed. The nests are usually constructed of the water repellent leaves of *Chusquea* and are lined with grasses or moss. Four of the five nests were entirely covered with gray moss, which not only protected it against rains but closely resembled the substrate in form and color, thus concealing the nest admirably.

Greer (1965, p. 103) found no nests in trees as reported by Mann, but he did find a nest in a thicket of cane (*Chusquea* sp.) bent to the ground by a fallen tree. One animal was trapped in front of a burrow that opened onto a dry slope next to a stump of an old roble (*Nothofagus obliqua*). The burrow averaged 100 mm

FIG. 16. *Dromiciops australis* (Philippi, 1893a, p. 31) (Recent). FMNH 22671, a left maxillary and premaxillary with I¹-M¹ complete: a, labial; b, occlusal; c, lingual views. Scale = 6 mm.

FIG. 17. *Dromiciops australis* (Philippi, 1893a, p. 31) (Recent). FMNH 22673, a left dp^3 (stipple), and P^2 and M^1 (outline): a, labial; b, occlusal; c, lingual views. Scale = 3 mm.

in diameter and extended for 760 mm, sloping downward slightly before dividing into two separate smaller tunnels of undetermined length. No nests were found.

Both males and females become sexually mature during their second year. They reportedly live in pairs at least during the breeding season in spring (Mann, 1958).

Philippi (1893a) reported finding five young in a nest near Valdivia. Krieg (1924) observed a female with four young, but he did not specify the state of their development. Osgood (1943) found three young in the pouch of a female captured on 23 November at Peulla. In January and February 1958, Mann (1958) found two small young in an arboreal nest in the trees on the south slope of Osorno Volcano. He also reported capturing a female carrying a young male on her back. Greer (1965) trapped a female with two pouch young measuring 8.0 mm and 8.2 mm on 21 December 1960. Kirsch (in Collins, 1973, p. 60) reported having trapped a female during May, whose well-developed mammae were "[s]training against the pouch opening." From the appearance of the mammae, Kirsch surmised that the animal had large nest young at the time of capture.

Four stages have been described in the development of the young: 1) in the pouch attached to the teats; 2) in the nest; 3) on nocturnal trips on the mother's back; and 4) in loose association with other members of the family (Mann, 1958, p. 210).

In the wild, *D. australis* feeds largely on larvae and pupae of a variety of arthropods, especially insects, with preference for coleopterans (Mann, 1955, p. 164; Walker et al., 1968, p. 17). The intestine of *Dromiciops* is relatively shorter than that of *Marmosa*, reflecting the predominance of animal matter in the diet of *Dromiciops*, in contrast to the more omnivorous diet in species of *Marmosa* (Mann, 1955, p. 166).

Greer (1965, p. 105) maintained three specimens at Michigan State University on a diet consisting of oatmeal, potatoes, powdered milk mixed with canned peach syrup, plum, pear, watermelon, applesauce, blackberries, and hamburger. The hamburger was eaten ravenously.

According to Mann (1955, p. 166) *Dromiciops* has protection from predators in the form of strong and repugnant secretions from cutaneous glands. Greer (1965, p. 105) did not notice a disagreeable odor when the live animals were disturbed by handling as reported by Mann, nor did handling live-trapped animals provoke aggressive behavior.

The voice of *Dromiciops* has been recorded as a chirring trill with a slight coughing sound at the end (Walker et al., 1968, p. 17). The name colocolo is but an onomatopoeia of its distinctive cry: tzchí, tzchii, kod-kod (Cabrera & Yepes, 1960, p. 46). At night, or when left unmolested for a period of time, some individuals made soft buzzing noises (Greer, 1965, p. 105).

Greer (1965, p. 104) trapped *Dromiciops* in association with other small mammals, such as *Oryzomys longicaudatus*, *Akodon longipilis*, *A. olivaceus*, *Notiomys macronyx*, *N. valdivianus*, *Phyllotis micropus*, *Irenomys tarsalis*, and *Octodon bridgesi*.

In the Mapuche Indian language it is called "Kongoy-kongoy;" other indigenous names are "kunuuma" and "huenukiki" (Cabrera & Yepes, 1960, p. 46). In Chile the names "llaca" and "monito del monte" are in general use for this animal, although both names are sometimes also applied to *Marmosa elegans* (Osgood, 1943, p. 50).

SUMMARY OF EVOLUTION OF MICROBIOTHERIIDAE

Members of the South American marsupial family Microbiotheriidae are known from beds of Colhuehuapian and Santacrucian age in Patagonia, southern Argentina, in the Recent fauna from Chiloé Island and south central Chile, and from adjacent parts of Argentina. As yet, they are the only known didelphoids of Santacrucian age in all of South America. Two genera, *Microbiotherium* and *Dromiciops*, and seven species are recognized. These species are distinguished primarily on the basis of absolute size (figs. 18–21). For example, in length of M_{1-4} (fig. 20), all species for a known given age are readily separable one from the other. The same is true for plots of $L M_1$ versus $L M_4$ (fig. 21A), $L P_3$ versus $W P_3$ (fig. 21B), and $L M_1$ versus $W M_1$ (fig. 21C). Relative size and minor structural differences in the canines and cheek teeth have also proven diagnostic (table 10).

Microbiotherium is known from six fossil species while *Dromiciops* is known from one living species. *Dromiciops* differs from *Microbiotherium* as follows: 1) has a more reduced lower canine which is incisiform-premolariform in shape and

FIG. 18. Comparison of upper dentitions of various species of Microbiotheriidae and a caenolestid, showing relative size and proportions of teeth. All illustrations are drawn to same scale. A, labial; B, occlusal; C, lingual views. 1, *Microbiotherium tehuelchum*; 2, *Microbiotherium patagonicum*; 3, *Dromiciops australis*; 4, *Stilotherium dissimile*.

FIG. 19. Comparison of lower dentitions of various species of Microbiotheriidae and some Didelphidae and Caenolestidae showing relative size and proportions of teeth. All illustrations are drawn to same scale. A, labial; B, occlusal; C, lingual views. 1, *Microbiotherium gallegosense*; 2, *Microbiotherium tehuelchum*; 3, 4, *Microbiotherium divisum*; 5, *Microbiotherium praecursor*; 6, *Dromiciops australis*; 7, *Microbiotherium patagonicum*; 8, *Microbiotherium acicula*; 9, *Pachybiotherium acclinum*; 10, *Patene pattersoni*; 11, 12, *Eomicrobiotherium gaudryi*; 13, *Stilotherium dissimile*; 14, *Phonocromus gracilis*.

FIG. 20. Size distribution of the species of *Microbiotherium* as indicated by length of M_{1-4} . Symbols are: Colhuehupian (triangles), Santacrucian (circles), unknown (square).

is set at an anterior inclination in the jaw (in *Microbiotherium* the canine is larger and is set nearly perpendicular in the jaw); 2) P_1 is set straight in jaw relative to rest of tooth row (not obliquely as in *Microbiotherium*); 3) posterobasal heel on P_2 is large and well-developed (it is small but distinct in *Microbiotherium*); 4) a small mental foramen below M_1 is absent (one is present in *Microbiotherium*); 5) auditory bulla is relatively smaller and not as elongated anteriorly as in *Microbiotherium*; 6) a supraorbital process is absent (a large one is present in *Microbiotherium*); 7) para- and metaconules are absent on M^{1-3} (small ones are present in *Microbiotherium*); 8) middle cleft on M^3 is deep (not shallow or absent as in *Microbiotherium*); and 9) M^4 is smaller relative to M^3 than in species of *Microbiotherium*.

Microbiotherium acicula is the smallest and most generalized of known microbiotheres. In comparable linear tooth dimensions it averages 15% ($n=10$, OR 0–30%) smaller than the contemporaneous Santacrucian species *M. patagonicum*. P_1 , however, averages slightly larger and M_4 is smaller relative to M_3 —with a smaller talonid in *M. acicula* than in *M. patagonicum*—but in morphological features these species are similar point for point. In other respects *M. acicula* serves as a proto- or morphotype from which may be derived all other known species of Microbiotheriidae.

Microbiotherium patagonicum is intermediate in size between the contemporaneous, smaller *M. acicula* and the contemporaneous, larger *M. tehuelchum*, and differs in average size from each by about 15% in linear tooth dimensions. *M. patagonicum* differs structurally from *M. tehuelchum* as follows: an absolutely and relatively smaller lower canine; a smaller posterobasal heel on P_3 ; but a slight size decrease in P_3 to P_1 (not a sharp one as in *M. tehuelchum*); P_3 less than height of M_1 ; protocone on M^{1-3} narrower anteroposteriorly; labial ridge of stylar shelf on M^{1-3} less distinct; a very shallow middle cleft on M^2 (absent in *M. tehuelchum*); and M^4 smaller relative to M^3 than in *M. tehuelchum*.

Microbiotherium patagonicum is extremely similar in size and molar morphology

FIG. 21. Size distribution of the species of *Microbiotherium* as indicated by relationship of: A, length of M_1 and M_4 ; B, length and width of P_3 ; C, length and width of M_1 .

TABLE 10. Summary of some diagnostic characters of known species of Microbiotheriidae.

Character	<i>Microbiotherium acicula</i>	<i>Microbiotherium patagonicum</i>	<i>Dromiciops australis</i>	<i>Microbiotherium divisum</i>	<i>Microbiotherium tehuelchum</i>	<i>Microbiotherium gallegosense</i>
1. Relative average over-all size	very small	small	small	medium	medium	large
2. Size and structure of lower canine	small and set nearly perpendicular in jaw	small and set nearly perpendicular in jaw	very small, incisiform-premolariform with broad posterobasal swelling	medium to large and set nearly perpendicular in jaw	medium to large and set nearly perpendicular in jaw	large and set perpendicular in jaw
3. Orientation of P_1 relative to rest of tooth row	set at slight oblique angle	set at slight oblique angle	straight	set at slight oblique angle	set at sharp oblique angle	set at sharp oblique angle
4. Posterobasal heel on P_1	small but distinct	unknown	small but distinct	unknown	absent	unknown
5. Orientation of P_2 relative to rest of tooth row	straight	straight	straight	straight	straight or set at slight oblique angle	straight
6. Posterobasal heel on P_2	small but distinct	unknown	large and well developed	small but distinct	small but distinct	unknown
7. Spacing between P_{1-3}	sometimes none, sometimes large diastems	sometimes none, sometimes large diastems	sometimes none, sometimes large diastems	none	sometimes none, sometimes large diastems	small diastems present
8. Posterobasal heel on P_3	distinct but not large	distinct but not large	large	distinct but not large	large	large
9. Relative size of P_{1-3}	slight size decrease from P_3 to P_1	slight size decrease from P_3 to P_1	moderate size decrease from P_3 to P_1	slight size decrease from P_3 to P_1	very sharp size decrease from P_3 to P_1 ; P_3 usually proodont and much larger than P_2	very sharp size decrease from P_3 to P_1 ; P_3 proodont and much larger than P_2
10. Relative height of P_3 and M_1	P_3 less than height of M_1	P_3 less than height of M_1	P_3 slightly less than height of M_1	P_3 about same height as M_1	P_3 about same height as M_1	P_3 same height as M_1
11. Mental foramina	large foramen below P_{1-2} contact; small foramen below anterior root of M_1	large foramen below P_{1-2} contact; small foramen below anterior root of M_1	only large foramen below posterior root of P_{1-2} contact or below anterior root of P_2	large foramen below posterior root of P_{1-2} contact; small foramen below posterior root of M_1	large foramen below posterior root of P_{1-2} contact; small foramen below anterior root of M_1	large foramen below P_{1-2} contact; small foramen below anterior root of M_1
12. Auditory bulla	unknown	unknown	smaller and not as elongated anteriorly as in <i>M. tehuelchum</i>	unknown	larger and more elongated anteriorly than in <i>D. australis</i>	unknown

TABLE 10. Continued.

Character	<i>Microbiotherium actula</i>	<i>Microbiotherium patagonicum</i>	<i>Dromiciops australis</i>	<i>Microbiotherium divisum</i>	<i>Microbiotherium tehuelchum</i>	<i>Microbiotherium gallegosense</i>
13. Supraorbital processes	unknown	unknown	absent	unknown	large and well developed	unknown
14. Orientation of P ¹ relative to rest of tooth row	unknown	unknown	set at slight oblique angle	unknown	set at slight oblique angle	unknown
15. Structure of P ¹	unknown	unknown	two rooted with small but distinct postobasal heel	unknown	single rooted (or nearly so) with no trace of postobasal heel	unknown
16. Orientation of P ² relative to rest of tooth row	unknown	unknown	straight	unknown	set at slight oblique angle	unknown
17. Structure of P ³	unknown	unknown	postero basal heel large and well developed	unknown	postero basal heel large and well developed	unknown
18. Para- and metaconules on M ¹⁻³	unknown	distinct but not large	absent	unknown	distinct but not large	unknown
19. Protocone on M ¹⁻³	unknown	narrower antero-posteriorly than in <i>M. tehuelchum</i>	narrower antero-posteriorly than in <i>M. tehuelchum</i>	unknown	broader antero-posteriorly and more robust than in <i>M. patagonicum</i> or <i>D. australis</i> .	unknown
20. Styral shelf	unknown	labial ridge less distinct than in <i>M. tehuelchum</i>	labial ridge less distinct than in <i>M. tehuelchum</i>	unknown	with low but distinct labial ridge which encloses shelf lingually	unknown
21. Middle cleft on M ²	unknown	very shallow	shallow	unknown	absent	unknown
22. Middle cleft on M ³	unknown	shallow	deep	unknown	very shallow or absent	unknown
23. Size of M ⁴ relative to M ³	unknown	M ⁴ larger than in <i>D. australis</i> ; smaller than in <i>M. tehuelchum</i>	M ⁴ smaller than in <i>M. patagonicum</i>	unknown	larger than in <i>M. patagonicum</i>	unknown
24. Minute foramen piercing masseteric fossa anteriorly	absent	absent	absent	absent	absent	present

to the living species *Dromiciops australis*. In the known comparable characters these species differ as follows: *D. australis* 1) has a more reduced lower canine which is incisiform-premolariform and set with an anterior inclination in the jaw (the canine is larger and set more perpendicular in *M. patagonicum*); 2) P_1 set straight relative to rest of tooth row and not at slight oblique angle as in *M. patagonicum*; 3) has a large posterobasal heel on P_3 ; 4) shows a moderate, not slight, size decrease from P_3 to P_1 ; 5) lacks a small mental foramen below M_1 ; 6) lacks para- and metaconules on M^{1-3} ; 7) has deep, not shallow, middle cleft on M^3 ; and 8) has a smaller M^4 relative to M^3 than in *M. patagonicum*. These differences are minor and I here recognize *M. patagonicum* as the probable Santacrucian ancestor of *D. australis*. The major changes involved in such a lineage involve either loss or size reduction in some features (e.g., mental foramen below M_1 , canine, conules, M^4) or relative and absolute size increase in others (e.g., posterobasal heel on P_3).

Microbiotherium praecursor is known only from its type, which is of uncertain age and provenance. It is of medium size and is indistinguishable in size and structure from smaller specimens of the Santacrucian species *M. tehuelchum*, and is slightly smaller than known specimens of the Colhuehuapian species *M. divisum*. Because of the uncertain age and locality data, *M. praecursor* is tentatively retained here as a valid species.

Microbiotherium divisum is the only known microbiothere of Colhuehuapian age. It is of medium size and is similar in size and structure to larger specimens of the Santacrucian species *M. tehuelchum*, and differs from the latter as follows: 1) P_1 is set at only a slight oblique angle in jaw; 2) posterobasal heel on P_3 is distinct but not large; and 3) a more gradual size decrease occurs from P_3 to P_1 . These differences are minor and I have recognized *M. divisum* as the probable Colhuehuapian ancestor of *M. tehuelchum*. In the evolution of this lineage there occurred a slight reduction in size of the premolar region of the jaw, resulting in a crowding of the premolars such that 1) P_1 is set at a sharp oblique angle in the jaw and 2) a sharp decrease occurs in size from P_3 to P_1 .

The Santacrucian species *Microbiotherium tehuelchum* is the most abundant microbiothere known in the fossil record. It is of medium size and averages 16% larger in linear tooth dimensions than the contemporaneous *M. patagonicum* and 29% smaller than the contemporaneous *M. gallegosense*. *M. tehuelchum* differs from all other microbiotheres where comparable features are preserved, as follows: 1) P_2^1 (in some specimens) set at slight oblique angle in jaw; 2) P^1 single rooted (or nearly so) with no trace of a posterobasal heel; 3) protocone on M^{1-3} broader anteroposteriorly and more robust, and labial ridge on stylar shelf better developed; and 4) a middle cleft on M^2 absent. As noted above, *M. tehuelchum* is here regarded as the direct Santacrucian descendant of *M. divisum*.

The largest known species of microbiothere is *M. gallegosense* which is known only from its type, collected from beds of Santacrucian age of southernmost Patagonia. Apart from averaging 29% larger than the contemporaneous *M. tehuelchum*, it differs from that and other microbiotheres in having a minute foramen which pierces the masseteric fossa anteriorly.

The only living microbiothere is *Dromiciops australis*. This small microbiothere is restricted to a Chiloé island and a small area of south central Chile and adjacent Argentina. It is, as noted above, regarded as the living descendant of the Santacrucian species *Microbiotherium patagonicum*. These species are extremely similar

FIG. 22. Dendrogram showing probable phylogenetic relationships of the genera and species of Microbiotheriidae. Only relative positions of pre-Colhuehuapian common ancestors are indicated.

in their dental structure, suggesting that this lineage has been little changed during the last 20 million years of its evolutionary history.

The seven recognized species of microbiothere are listed in Figure 22 in the order of their chronostratigraphic occurrence and with indication of their probable phylogenetic relationship. The proposed phylogeny is based largely on the data set summarized in Table 10, although it includes consideration of other features discussed in the text.

REVIEW OF SUPPOSED MICROBIOTHERES

In the following section the taxonomic history of genera and species 1) formally assigned at one time or another to the Microbiotheriidae; 2) implicated in the ancestry of this family; or, 3) in which specimens of microbiotheres were included erroneously as syntypes in the original descriptions, are discussed and the systematic problems clarified. For all of these taxa an attempt is made to give complete listings of generic and specific synonymies, complete literature citations, and hypodigms which include all known specimens. In cases where microbiotheres were among syntypes, as in the caenolestid species *Stilotherium dissimile* and *Phonocdromus gracilis*, the taxonomic history of each of the disputed specimens is discussed in the Systematic Section of the relevant microbiothere species (see above).

Superfamily INDETERMINATE

Ideodelphys Ameghino, 1902d, p. 43

Ideodelphys Ameghino, 1902d, p. 43.

Ideodidelphys Schlosser, 1923, p. 442.

Type.—*Ideodelphys microscopicus* Ameghino, 1902d, p. 43.

Distribution.—As for type and only known species.

Diagnosis.—As for type and only known species.

Ideodelphys microscopicus Ameghino, 1902d. Figure 23.

Ideodelphys microscopicus Ameghino, 1902d, p. 43; Simpson, 1938, p. 3; 1948, p. 34 (*nomen vanum*); Ringuelet, 1953, p. 287.

Ideodelphys microscopica Reig, 1955a, p. 122 (*nomen vanum*).

Type.—MACN 10344, an edentulous right mandibular ramus with eight complete alveoli.

Hypodigm.—Type and possibly AMNH 28423, an edentulous mandibular ramus with eight complete alveoli.

Horizon and locality.—Type is from the barranca south of Lago Colhué-Huapi and was collected by Carlos Ameghino; AMNH 28423 is from Cañadón Vaca and was collected by members of the Scarritt Expedition to Patagonia in 1930; both localities are in Chubut Province, Patagonia, southern Argentina.

Age.—Casamayoran.

Diagnosis.—Indeterminate.

Comments.—The eight complete alveoli in the type measure 5.4 mm in length and those in AMNH 28423 are 5.8 mm. It appears that the alveoli in the type represent P_2-M_2 and in the referred specimen they are P_3-M_3 , although this is

FIG. 23. *Ideodelphys microscopica* Ameghino, 1902d, p. 43 (Casamayoran). MACN 10344 (type), an edentulous right mandibular ramus with eight complete alveoli: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

not certain. In both, the alveoli increase gradually in size from front to back. In AMNH 28423 a large mental foramen occurs below the 5th complete alveolus.

Ideodelphys microscopica thus is virtually indeterminate and the genus and species are, for all practical purposes, nomina vana (Simpson, 1948, p. 34; Reig, 1955a, p. 122). Ringelet (1953, p. 287) provisionally included this species in the subfamily Microbiotheriinae. Alternatively, the specimens assigned to this species possibly could be referable to a species of *Eomicrobiotherium* (see below), but this too is only speculative.

Superfamily DIDELPHOIDEA (Gray, 1821, p. 308) Osborn, 1910, p. 515

Family DIDELPHIDAE (s.l.) Gray, 1821, p. 308

Coona⁶ Simpson, 1938, p. 1

*Coona*⁶ Simpson, 1938, p. 1.

Type.—*Coona pattersoni* Simpson, 1938, p. 2.

Distribution.—As for type and only known species.

Diagnosis.—As for type and only known species.

***Coona pattersoni* Simpson, 1938. Figure 24.**

Coona pattersoni Simpson, 1938, p. 2, fig. 1; 1948, p. 34, fig. 3; Ringelet, 1953, p. 301.

⁶ 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 name originally spelled *Coöna*.

FIG. 24. *Patene pattersoni* Simpson, 1938, p. 2 (Casamayoran). AMNH 28907 (type), a left mandibular ramus with alveoli of P_3 - M_2 , M_3 complete, and M_4 with talonid complete and with crown of trigonid broken: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

Type.—AMNH 28907, a left mandibular ramus with alveoli of P_3 – M_2 , M_3 complete, and M_4 with talonid complete and with crown of trigonid broken (figured by Simpson, 1938, fig. 1; 1948, fig. 3).

Hypodigm.—Type only.

Horizon and locality.—Casamayor beds, green bentonite series ("bird clay") at Cañadón Hondo, Chubut Province, Patagonia, southern Argentina. Collected by C. S. Williams and G. G. Simpson as members of the Scarritt Expedition to Patagonia, March 1931 (locality is shown as "E" in fig. 1 in Schaeffer, 1947, p. 3).

Age.—Casamayoran.

Diagnosis.—Didelphoids of small size; P_3 (alveoli) about as large as M_1 ; M_3 (and probably also M_{1-2}) with talonid markedly wider than trigonid, paraconid slightly higher than entoconid, metaconid intermediate between paraconid and protoconid, trigonid moderately elevated and not compressed, hypoconulid very small, nearly internal, and near entoconid; M_4 talonid as wide as trigonid or slightly wider and of about same area, fully basined and similar to that of M_3 with three distinct cusps, hypoconulid not enlarged and similar to that in M_3 ; M_4 well developed, but smaller than M_3 (after Simpson, 1938, p. 1).

Measurements.— M_3 L=2.6 mm, W=1.8 mm; M_4 talonid W=1.4 mm; M_{1-4} L=ca 10.0 mm.

Comments.—Simpson (1938; 1948, p. 36) emphatically stated that the most important characteristic of *Coona pattersoni* is that it is definitely not a microbiothere. However, he did entertain the possibility that it was an ancestral microbiothere.

In defense of this view he noted that the M_4 in microbiotheres is very reduced in size with a narrow, nearly unbasined heel with one distinct posteromedian cusp. *Coona* on the other hand has a large talonid, and the M_4 is only slightly smaller than the M_3 . In addition, he noted that microbiotheres typically have the hypoconulid of M_{1-3} more median in position than in *Coona* and more co-ordinate with the hypoconid and entoconid as an element of the talonid rim. I concur with Simpson's views and support the nonmicrobiothere position of *Coona*.

Simpson (1964, p. 7) questionably referred a second species to *Coona*, ?*C. gaudryi*. This species is here made the type of a new genus (see p. 58) and is shown to share features with typical microbiotheres of the genus *Microbiotherium*, although it is not itself regarded a microbiothere.

Eomicrobiotherium nov. gen.

Etymology.—*Eos* Gr. dawn, morning, early, east; *micro-* Gr. small, little; *bios* Gr. life; *thēr* Gr. a wild beast; *-ium* Gr. suffix added to noun and verb stems denoting groups. Name given in reference of this Eocene age taxon and the similarity of its members with species of the mid-Tertiary genus *Microbiotherium*.

Type.—*Eomicrobiotherium gaudryi* (Simpson, 1964, p. 7).

Distribution.—Casamayor beds, Patagonia, southern Argentina.

Diagnosis.—Small size; P_3 about subequal in height to but slightly shorter than M_1 , and with a large and distinct posterobasal heel; M_1 slightly shorter than M_{2-3} which are subequal in length; M_{1-3} subequal in breadth, and with talonids broader than trigonids; M_4 smaller than M_3 but not to degree that occurs in species of *Microbiotherium*; protoconid much larger than para- and metaconids

on M_{1-3} ; paraconid much smaller than metaconid on M_1 , relatively larger on M_2 , and subequal in size to metaconid on M_3 ; metaconid set slightly posteriad of protoconid; anterobasal cingulum absent on M_{1-2} , and only weakly developed on M_3 .

Eomicrobiotherium gaudryi (Simpson, 1964). Figures 25–26; Table 11.

?*Coona gaudryi* Simpson, 1964, p. 7, fig. 1; 1967, p. 7, fig. 1.

Type.—MNHN Tournouër Collection No. 1, two fragments of mandibular rami, probably of same individual. No. 1a, a fragment of a right mandibular ramus with roots of P_3 , and M_{1-2} complete; and No. 1b, a fragment of a left mandibular ramus with roots of P_{1-2} and M_{1-2} , and with P_3 and M_3 complete. If these fragments prove to be of different individuals, the right side is to be taken as lectotype (Simpson, 1967, p. 7). The teeth of both specimens are figured by Simpson (1964, fig. 1; 1967, fig. 1).

Hypodigm.—Types only.

Horizon and locality.—Casamayor beds at the Barranca south of Lago Colhué-Huapí, Chubut Province, Patagonia, southern Argentina. Collected by A. Tournouër from his "Coli-Huapi" locality (see Tournouër, 1903, p. 472).

Age.—Casamayoran.

Diagnosis.—Molars relatively and absolutely longer, and trigonids relatively and absolutely lower than in *E. gutierrezii*.

Comments.—Simpson (1964, p. 7; 1967, p. 7) questionably assigned this species to the genus *Coona*, noting (1967, pp. 7–8) that, in both,

the talonid is distinctly wider than the trigonid, the trigonid is moderately elevated and not definitely compressed, the paraconid is slightly higher than the entoconid, the metaconid is between the paraconid and protoconid in height, and the hypoconulid is small and near the entoconid.

FIG. 25. *Eomicrobiotherium gaudryi* (Simpson, 1964, p. 7) (Casamayoran). MNHN Tournouër Collection no. 1a (type), a fragment of a right mandibular ramus with M_{1-2} complete: a, labial; b, occlusal; c, lingual views. Scale = 2 mm.

FIG. 26. *Eomicrobiotherium gaudryi* (Simpson, 1964, p. 7) (Casamayoran). MNHN Tournouër Collection no. 1b (type), a fragment of a left mandibular ramus with roots of P_{1-2} and M_{1-2} , and with P_3 and M_3 complete: a, labial; b, occlusal; c, lingual views. Scale = 4 mm.

However, there are important features in which these species differ and for which I feel they warrant generic separation. The species *gaudryi* differs from *pattersoni* in that it is smaller in size (it averages 45% smaller in comparable linear tooth dimensions), lacks a prominent anterobasal cingulum on the M_3 , in the M_3 para- and metaconid being about subequal in size (in *pattersoni* the paraconid is much smaller than the metaconid), and has metaconid set posteriad of the protoconid in *gaudryi* but directly linguad of the protoconid in *pattersoni*. On the basis of these features I place *gaudryi* along with the species *gutierrezzi* del Corro (1977) (see below) in a new genus, *Eomicrobiotherium*.

Of the mid-Tertiary members of the genus *Microbiotherium*, *E. gaudryi* compares more closely with *M. patagonicum*: i.e., both are of similar size and lack a distinct anterobasal cingulum on M_{1-2} but have a small one on M_3 . These species differ in that *E. gaudryi* has a much narrower M_1 trigonid and a more reduced paraconid; the metaconid is set posteriad of the protoconid (not labiad as in species of *Microbiotherium*); and the talonid basin is relatively smaller. The former two features are here regarded as derived, and their presence in *E. gaudryi* suggests that the species is too specialized to be ancestral to any later member of the

TABLE 11. Measurements of lower cheek teeth of *Eomicrobiotherium gaudryi*.

Specimen	P_3		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W
MNHN (TC #1a)	...	...	1.4	1.0	1.6	1.0	...	...
MNHN (TC #1b)	1.3	0.8	...	...	...	...	1.6	0.9

genus *Microbiotherium*. For this reason, *E. gaudryi* (and *E. gutierrezzi*) are not included in the Microbiotheriidae.

However, *E. gaudryi* shares these same derived features with the large Colhuehuapian species *Pachybiotherium acclinum*. In *P. acclinum* these features are more pronounced (i.e., there is a greater reduction of the paraconid; more posteriad position of metaconid relative to protoconid). It is conceivable to envision an ancestral-descendant relationship for these species if it is granted that in the evolution of this lineage there occurred an elaboration of these features, along with size increase and a reduction in breadth of the talonid and increase in importance of the trigonid. This view is followed here.

***Eomicrobiotherium gutierrezzi* (del Corro, 1977). Figure 27.**

Microbiotherium gutierrezzi del Corro, 1977, p. 32, fig. on p. 32.

Type.—MACN 18288, a fragment of a left mandibular ramus with roots of P_1 , P_3 , M_2 , M_4 ; and with P_2 , M_1 , and M_3 present, latter is missing para- and metaconid (figured by del Corro, 1977, fig. on p. 32).

Hypodigm.—Type only.

Horizon and locality.—Collected from the green bentonite series ("bird clay") at Cañadón Hondo, Chubut Province, Patagonia, southern Argentina, by Orlando Gutiérrez in February 1975 (locality is shown as "E" in fig. 1 in Schaeffer, 1947, p. 3).

Age.—Casamayoran.

Diagnosis.—Molars relatively and absolutely shorter, and trigonids relatively and absolutely lower than in *E. gaudryi*.

Comments.—I attempted to study the type during a visit to the MACN in November 1979, although the specimen could not be located and its whereabouts is still unknown. Comparison of this species with other taxa thus is based solely on del Corro's (1977) comments and on the two line drawings of the type which he included as figures on page 32 of his publication. Del Corro (1977, p. 32) described the type as follows:

El alvéolo del tercer premolar tapado aunque por lo que se distingue es algo más grande que el anterior, el alvéolo del cuarto molar también está tapado, aparentemente

FIG. 27. *Eomicrobiotherium gutierrezzi* (del Corro, 1977, p. 32) (Casamayoran). MACN 18288 (type), a fragment of a left mandibular ramus with roots of P_1 , P_3 , M_2 , M_4 ; and with P_2 , M_1 , and M_3 present (redrafted after del Corro, 1977, fig. on p. 32): a, labial; b, occlusal views. Scale = about 5 mm.

casi del mismo tamaño que el molar anterior aunque, ligeramente más angosto hacia el extremo posterior.

El área del primer molar correspondiente al trigónido y talónido casi iguales, tanto en largo como en ancho, con una profunda cubeta. El segundo premolar, ligeramente alabeado de adelante hacia atrás, un poco después del ápice y angosto. Los molares con la corona alta. No se observa cingulo.

Del Corro (p. 32) also gave the length and breadth of "molar 2°" as 1.0 and 0.99 mm, respectively. However, as there is no M_2 preserved in this specimen it is not clear to which tooth these measurements belong.

Nevertheless, the measurements and figures given by del Corro do indicate that the molars in *Eomicrobiotherium gutierrezzi* are relatively shorter than but are of approximately the same breadth as those in *E. gaudryi* in which the M_1 $L=1.4$ mm and $W=1.0$ mm, and M_3 $L=1.6$ mm and $W=0.9$ mm (see table 11). Furthermore, in *E. gaudryi* there is no anterior cingulum on the M_1 as in *E. gutierrezzi*, but there is a small cingulum on the M_3 in *E. gaudryi*, a feature which del Corro did not observe in *E. gutierrezzi*. However, the anterior part of the M_3 is broken in *E. gutierrezzi* (see fig. 47) and the absence of a cingulum in this area may be due to this breakage. Use of this feature as a specific character to separate these species must thus remain tentative. The trigonid is only slightly higher than the talonid on both M_1 and M_3 in *E. gutierrezzi*, while in *E. gaudryi* the trigonid is much higher than the talonid (compare figs. 43 and 45 with 47). These features may represent specific differences, but they also could be attributable to more advanced occlusal wear in *E. gutierrezzi*, a feature which I observed when the specimen was collected but which del Corro did not mention in the description of the species. Tentatively, these observed differences, for want of others, are here used to distinguish *E. gaudryi* from *E. gutierrezzi*. It is cautioned, however, that direct comparison of the types of these species may prove them to be synonymous; their specific separation has yet to be adequately demonstrated.

Del Corro compared his new species *gutierrezzi* only with the Santacrucian species *Microbiotherium conspicuus* (Ameghino, 1891) as that species was defined by Ringuelet (1953). He noted that these species were very similar and accordingly assigned *gutierrezzi* to the genus *Microbiotherium*. The species *gutierrezzi* differs from species of *Microbiotherium* in the same features as does *Eomicrobiotherium gaudryi* (see above), and for this reason I here refer *gutierrezzi* to the genus *Eomicrobiotherium*. *E. gutierrezzi*, as is *E. gaudryi*, is here regarded as too specialized to be ancestral to any later known microbiothere.

***Pachybiotherium* Ameghino, 1902e, p. 123**

Pachybiotherium Ameghino, 1902e, p. 123; Simpson, 1932b, p. 3 (as probable synonym of *Microbiotherium*); Ringuelet, 1953, p. 277 (as synonym of *Microbiotherium*).

Type.—*Pachybiotherium acclinum* Ameghino, 1902e, p. 123.

Distribution.—As for type and only known species.

Diagnosis.—As for type and only known species.

***Pachybiotherium acclinum* Ameghino, 1902e. Figure 28; Table 12.**

Pachybiotherium acclinum Ameghino, 1902e, p. 123; Reig, 1955a, p. 121.

Microbiotherium acclinum Ringuelet, 1953, p. 277.

Type.—MACN 52-370a, a fragment of a left mandibular ramus with alveolus of C; roots of P_1 , and M_2 ; anterior root and portion of posterior alveolus of M_4 ; and P_2 - M_1 and M_3 complete.

FIG. 28. *Pachybiotherium acclinum* Ameghino, 1902e, p. 123 (Collhuehupian). MACN 52-370a (type), a fragment of a left mandibular ramus with alveoli of C, roots of P_1 and M_2 , anterior root and portion of posterior alveoli of M_4 , and P_2 - M_1 and M_3 complete: a, labial; b, occlusal; c, lingual views. Scale (for a + c) = 10 mm.

TABLE 12. Measurements of lower cheek teeth of *Pachybiotherium acclinum*.

Specimen	P ₂		P ₃		M ₁		M ₂	M ₃		P ₁₋₃	M ₁₋₃
	L	W	L	W	L	W	L	L	W	L	L
MACN 52-370a	2.0	1.2	2.9	1.7	3.3	2.0	ca 3.4	3.1	2.0	ca 7.0	9.7
MACN 52-370b	...	...	2.8	1.7	...	...	...	...	...	ca 8.0	...

Hypodigm.—Type and MACN 52-370b, a fragment of a right mandibular ramus with alveoli of C-P₁, roots of P₂, P₃ complete and anterior alveolus of M₁.

Horizon and locality.—Both specimens were collected by Carlos Ameghino from Colhué-Huapi beds, probably from the Barranca south of Lago Colhué-Huapi, Chubut Province, southern Argentina.

Age.—Colhuehuapian.

Diagnosis.—Largest known species of Colhuehuapian didelphoid; mandibular ramus very deep throughout its length and bowed or curved labially; mandibular symphysis extends posteriorly to point below anterior root of P₁; a large mental foramen occurs below P₁; C, judging from its alveolus, was very large and set perpendicular to jaw; P₁₋₂ are much smaller than P₃; P₁, judging from its roots, was slightly smaller than P₂ and was set at slight angle in jaw relative to rest of tooth row with anterior root located labial of posterior root; P₂ is broad for its length and is bulbous basally, with a small posterobasal heel and a small posterobasal cuspule; P₃ with large pointed cusp anteriorly and low, broad heel with a posterolingual cusp posteriorly; M₁ is equal in breadth but is slightly longer than M₃; trigonid and talonid of M₁ are of about equal width; trigonid of M₃ is slightly broader than talonid; paraconid is very reduced on M₁ and M₃ (more so on M₁); metaconid well-developed but relatively smaller, compared with protoconid on M₁, than M₃; talonid basin is broad with a very shallow basin; hypoconid and entoconid are subequal in size on M₁ and M₃; hypoconulid is about half size of entoconid on M₁ and separated from it by a distinct space, while on M₃ these cusps are subequal in size and united basally; M₄, judging from the size of its anterior root and part of the posterior alveolus, was large and apparently subequal to M₃ in size.

Comments.—Ameghino (1902e, p. 123) originally placed *Pachybiotherium acclinum* in the family Microbiotheriidae, within his group Pedimana. Simpson (1932b, p. 3) suggested that *Pachybiotherium* "is probably synonymous with *Microbiotherium*" and formally recognized this synonymy in his classification of 1945 (Simpson, 1945, p. 42). This synonymy was followed by Ringuelet (1953, p. 277), who concluded

... estoy de acuerdo con Simpson en considerar que el hecho de poseer la rama mandibular arqueada, y siendo único carácter distintivo, no tiene valor suficiente como para constituir con él un género distinto.

Reig (1955a, p. 121), based on an unpublished collaborative study with Bryan Patterson, recognized *Pachybiotherium* as distinct from *Microbiotherium* and reaffirmed its microbiothere affinities. Recently, Reig (in press) proposed that *Pachybiotherium* is not a microbiothere but is the earliest known member of the didelphid subfamily Caluromyinae.

It is my opinion that *Pachybiotherium acclinum* is not a microbiothere (s.s.), but that it did parallel the microbiotheres in many of its specializations (e.g., bowed mandibular ramus; large canine oriented perpendicular in jaw; loss of anterior basal cingula on molars; P₃ proodont with large posterobasal heel; reduction in

size of paraconid). *P. acclinum* is not a microbiothere in the strict sense because it has a large M_4 (judging from its anterior root); the talonid on M_3 is narrower (not wider) than the trigonid; and the paraconid is much more reduced, especially on the M_1 . In addition, *P. acclinum* appears too specialized in the same feature (as well as in the size and structure of the canine, great reduction in size of P_1 and P_2 , and posterior position of the metaconid) to be ancestral to any known living Caluromyinae. For these reasons I recognize *P. acclinum* and the Casamayoran species *Eomicrobiotherium gaudryi* and *E. gutierrezi* as members of the family Didelphidae (*s.l.*) which parallel microbiotheres in aspects of dental and mandibular evolution.

Superfamily CAENOLESTOIDEA (Trouessart, 1898, p. 1205)

Osborn, 1910, p. 517

Family CAENOLESTIDAE Trouessart, 1898, p. 1205

Stilotherium Ameghino, 1887

Stilotherium Ameghino, 1887, p. 7.

Garzonía Ameghino, 1891, p. 307.

Parhalmarhiphus Ameghino, 1894, p. 356.

Halmarhiphus Ameghino, 1891, p. 308.

Type of *Stilotherium*.—*S. dissimile* Ameghino, 1887, p. 7.

Type of *Garzonía*.—*G. typica* Ameghino, 1891, p. 307.

Type of *Parhalmarhiphus*.—*P. annectens* (Ameghino, 1891, p. 307).

Type of *Halmarhiphus*.⁷—*H. nanus* Ameghino, 1891, p. 308.

Diagnosis.—As for type and only known species.

Known range.—As for type and only known species.

Stilotherium dissimile Ameghino, 1887. Figures 29–31; tables 13, 14.

Stilotherium dissimile Ameghino, 1887, p. 7; 1889, p. 265; 1894, p. 358; 1897, p. 499, fig. 75; 1903, pp. 115, 167, figs. 33, 92; 1904b, p. 45, fig. 32; 1906, p. 357, fig. 196; Schlosser, 1923, p. 27, fig. 390; Rusconi, 1933, p. 248, fig. 8; Reig, 1955b, p. 62, fig. 1; Marshall, 1980, p. 35, figs. 4–6.

Pichipilus exilis Ameghino, 1891, p. 307; 1894, p. 351.

Garzonía captiva Ameghino, 1891, p. 308; 1894, p. 355.

Garzonía minima Ameghino, 1891, p. 308; 1894, p. 355; 1903, pp. 157, 186, figs. 81, 121; 1904b, p. 45, fig. 31; 1906, p. 357, fig. 197.

Halmarhiphus didelphoides (sic) (*partim*, not lectotype), Ameghino, 1891, p. 308.

Parhalmarhiphus didelphoides (*partim*) Ameghino, 1903, pp. 157, 163, fig. 86.

Halmarhiphus didelphoides (*partim*) Ameghino, 1894, p. 357; 1899, fig. 4; 1903, p. 157, fig. 80; 1906, p. 357, fig. 195; Simpson, 1930, p. 56.

Garzonía typica Ameghino, 1891, p. 307; 1893, p. 80, fig. 5; 1894, p. 354, fig. 41; 1898, p. 186, fig. 51; 1903, p. 168, fig. 93; Schlosser, 1925, p. 27, fig. 39A.

Garzonía tipica (sic) Ameghino, 1903, p. 167, fig. 91.

Stilotherium typica Reig, 1955b, p. 62.

Stilotherium typicum Reig, 1955b, p. 63; Pascual & Odreman Rivas, 1971, p. 392.

Garzonía annectens (*partim*) Ameghino, 1891, p. 307.

Parhalmarhiphus annectens (*partim*) Ameghino, 1894, p. 357.

Halmarhiphus nanus (*partim*) Ameghino, 1891, p. 308; 1894, p. 357; Sinclair, 1906, p. 421, fig. 7, pl. 63, figs. 9, 9a.

⁷ "*H. didelphoides* has been considered the type of this genus, but as Ameghino later suggested its removal to a distinct genus he cannot so have considered it" (Simpson, 1930, p. 56).

Phonocdromus patagonicus Ameghino, 1894, p. 355 (*partim*, not lectotype); Reig, 1955b, p. 64 (invalid).

Garzonia patagonica Sinclair, 1906, p. 424, pl. 63, figs. 8, 8a, 10–13.

Neotype of *S. dissimile*.—MACN 8464, a fragment of a right mandibular ramus with complete dentition, missing only tip of large incisor (figured by Reig, 1955b, fig. 1; Pascual & Herrera, 1975, pl. 1, fig. 2; Marshall, 1980, fig. 6) (selected neotype by Reig, 1955b, p. 62).

Type of *P. exilis*.—MACN 5698, a fragment of a left mandibular ramus with alveoli of M_2 , M_3 present but very worn, and alveoli of M_4 (listed as "tipo" in Ameghino's catalog).

Type of *G. captiva*.—MACN 5706, a right mandibular ramus with P_3 – M_2 complete, and alveoli of M_{3-4} (listed as "tipo" in Ameghino's catalog).

Type of *G. minima*.—MACN 5709, a fragment of a right mandibular ramus with alveoli of M_1 , and M_{2-4} complete (listed as "tipo" in Ameghino's catalog).

Type of *G. typica*.—MACN 5700, a fragment of a right mandibular ramus with

FIG. 29. *Stilotherium dissimile* Ameghino, 1887, p. 7 (Santacrucian). MACN 8427, a fragment of a rostrum with left C , P^2 and P^3 (same individual as in fig. 30): a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

FIG. 30. *Stilotherium dissimile* Ameghino, 1887, p. 7 (Santacrucian). MACN 8426, a fragment of a right maxillary with M_2^{-3} ; and MACN 8431, an isolated right M_1 (same individual as in fig. 29): **a**, labial; **b**, occlusal; **c**, lingual views. Scale = 5 mm. Abbreviations are: **pr**, protocone; **pa**, paracone; **me**, metacone; **hy**, hypocone; **ic**, intermediate conule.

P_{2-3} and M_{1-2} complete (listed as "tipo" in Ameghino's catalog; posterior part of ramus with M_{3-4} has been lost since specimen was figured by Ameghino, 1893, fig. 5; 1894, fig. 41; 1898, fig. 51).

Type of G. annectens.—MACN 5703, a fragment of a left mandibular ramus with M_{1-4} complete but worn (listed as "tipo" in Ameghino's catalog).

Type of H. nanus.—MACN 5720, a fragment of a right mandibular ramus with alveoli of M_1 and M_4 , and M_{2-3} complete but worn (listed as "tipo" in Ameghino's catalog).

Hypodigm.—The seven types and MACN 5701, a fragment of a left mandibular ramus with P_2 complete, alveoli of P_3 and anterior root of M_1 , talonid of M_1 , M_2 and trigonid of M_3 complete but very worn; MACN 5702, a fragment of a right mandibular ramus with P_{1-2} complete, roots of P_3 , M_{1-2} complete, and alveoli of M_{3-4} ; MACN 5708, a fragment of a right mandibular ramus with alveoli of M_{1-2} and M_4 , and M_3 complete (labeled *G. captiva*); MACN 5710, a fragment of a right mandibular ramus with M_{1-3} complete, and roots of M_4 (labeled *G. minima*). The jaw figured by Ameghino (1903, figs. 81, 121; 1904b, fig. 31; 1906, fig. 197) as *G. minima* is apparently based, at least in part, on this specimen. The part of the jaw from M_1 back is probably based on MACN 5710, as this specimen lacks

TABLE 13. Measurements of cheek teeth of *Stilotherium dissimile*.

Specimen	M1		M2		M3		M4		M1-4
	L	W	L	W	L	W	L	W	L
UPPER CHEEK TEETH									
MACN 8426	...	...	1.6	1.8	1.0	1.4	...	...	...
MACN 8431	1.9	1.8	...	...	...	...	...	...	...
LOWER CHEEK TEETH									
MACN 5700	1.8	1.2	1.5	1.2	...	...	...	...	...
MACN 5701	...	1.2	1.5	1.1	...	...	...	...	...
MACN 5702	1.7	1.2	1.5	1.2	...	...	...	...	...
MACN 5703	1.8	1.1	1.5	1.2	1.3	1.0	0.4	0.6	5.6
MACN 5706	1.9	1.1	1.5	1.1	...	...	...	...	...
MACN 5708	...	...	...	...	1.3	1.0	...	...	...
MACN 5709	...	...	1.7	1.2	1.2	1.0	0.5	0.4	...
MACN 5710	1.8	1.2	1.5	1.1	1.1	1.0	...	...	...
MACN 5717	...	...	1.8	1.2	1.3	1.0	...	...	...
MACN 5720	...	...	1.6	1.3	1.3	1.0	...	...	...
MACN 8428	...	...	...	...	1.3	1.0	...	...	...
MACN 8429	...	...	1.6	1.2	1.3	1.0	0.6	0.5	...
MACN 8447	...	...	...	...	1.2	1.0	...	...	...
MACN 8448	1.8	1.2	1.6	1.2	1.3	0.9	...	...	ca 5.7
MACN 8456	...	...	1.5	1.1	1.2	1.0	0.4	0.6	...
MACN 8464	1.9	1.2	1.6	1.2	1.2	1.0	0.4	0.4	5.7
MACN 8465	2.0	1.2	1.6	1.1	1.2	1.0	0.4	0.4	5.8
MACN 8466-7	2.0	1.2	1.8	1.2	1.3	1.0	0.5	0.5	5.8

TABLE 14. Statistics for some lower cheek tooth dimensions of *Stilotherium dissimile*.

Dimension		N	OR	x	s	CV
M ₁	L	9	1.7-2.0	1.86	0.10	5.38
	W	10	1.1-1.2	1.18	0.04	3.39
M ₂	L	15	1.5-1.8	1.57	0.09	5.73
	W	15	1.1-1.3	1.17	0.06	5.13
M ₃	L	14	1.1-1.3	1.25	0.07	5.60
	W	14	0.9-1.0	0.99	0.03	3.03
M ₄	L	7	0.4-0.6	0.46	0.08	17.39
	W	7	0.4-0.6	0.49	0.09	18.37
M1-4	W	5	5.6-5.8	5.72	0.08	1.40

an M₄ and the breakage of the ascending portion of the ramus is similar, but not identical. The part of the figured jaw from P₃ forward has no counterpart in the MACN collection.]; MACN 5717, a left mandibular ramus with P₃ and M₂₋₃ complete, roots of M₁ and M₄ (syntype of *H. didelphoides*); MACN 5723, a fragment of a right mandibular ramus with P₂₋₃ complete, base of M₁ and base of M₂ trigonid (listed as "tipo" of *S. dissimile* in Ameghino's catalog); MACN 8426-29 and 8431 (all of a single, associated individual, labeled *G. captiva*) [8426, a fragment of a right maxillary with M²⁻³ (figured by Marshall, 1980, fig. 5); 8427, a fragment of a rostrum with left C-P² and right P¹⁻² complete (figured by Marshall, 1980, fig. 4); 8428, a fragment of a right ramus with M₃ complete and alveoli of M₄; 8429, a left mandibular ramus with large incisor and M₂₋₄ complete and alveoli of rest of dentition; and 8431, an isolated right M¹ (figured by Marshall, 1980, fig. 5, erroneously as 8231)]; MACN 8447, a fragment of a right mandibular ramus with M₃ complete, and alveoli of M₄ (labeled *G. minima*); MACN 8448, a right mandibular ramus with large incisor, M₁₋₃ complete, and alveoli of rest of

FIG. 31. *Stiloitherium dissimile* Ameghino, 1887, p. 7 (Santacrucian). MACN 8464 (neotype), a right mandibular ramus with complete dentition, missing only tip of I₁: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

dentition (labeled *G. minima*); MACN 8456, a fragment of a left mandibular ramus with alveoli of M_1 , and M_{2-4} complete (labeled *P. patagonicus* and probably a cotype of that species, see Reig, 1955b, p. 64; he lists this specimen erroneously as 8450); MACN 8465, a fragment of a right mandibular ramus with P_3 – M_4 complete [Part of the jaw figured by Ameghino (1897, fig. 75; 1903, figs. 33, 92; 1904b, fig. 32; 1906, fig. 196), the part from P_3 posteriorly clearly was based on this specimen, as the breakage of the coronoid process is identical in the specimen and the illustration. The antemolar region and incisor may have been based on MACN 8464, but this is less certain.]; MACN 8466–67, a nearly complete left mandibular ramus with dentition; PU 15238, greater part of a left mandibular ramus with most of dentition, very worn, and various postcranial fragments (figured by Sinclair, 1906, pl. 63, figs. 8, 8a, 10–13).

Horizon and locality.—All specimens are from the Santa Cruz Formation, Santa Cruz Province, Patagonia, southern Argentina and their localities and dates of collection are as follows: *Sehuen* MACN 5706, 5708, 5717 (collected by C. Ameghino, 1890–91); *La Cueva* MACN 8426–29, 8431, 8447, 8448, 8464, 8465, 8566–67 (collected by C. Ameghino, 1892–93); *Monte Observación* MACN 5698, 5700, 5701, 5702, 5703, 5709, 5710, 5720, 5723 (collected by C. Ameghino, 1890–91), MACN 8456 (collected by C. Ameghino, 1891–92); PU 15238 was collected by O. A. Peterson in 1896, five miles south of *Coy Inlet*.

Age.—Santacrucian.

Comments.—Among the syntypes of *Halmarhiphus didelphoides*, *Garzonía annectens*, *Halmarhiphus nanus*, and *Phonocdromus patagonicus* were included specimens referable to *Stilotherium dissimile* and *Microbiotherium patagonicum* and/or *M. tehuelchum*. The taxonomic position of each of the syntypes of these species are discussed and clarified in the Systematic Section of the relevant microbiothere species.

Phonocdromus Ameghino, 1894

Phonocdromus Ameghino, 1894, p. 355.

*Lectogenotype*⁸ of *Phonocdromus*.—*P. gracilis*⁸ Ameghino, 1894, p. 356.

Diagnosis.—As for type and only known species.

Known range.—As for type and only known species.

Phonocdromus gracilis Ameghino, 1894. Figures 32, 33; Table 15.

Phonocdromus gracilis Ameghino, 1894, p. 356; Reig, 1955b, p. 64, fig. 2; Marshall, 1980, p. 40, fig. 7.

Garzonía gracilis Sinclair, 1906, p. 457.

Halmarhiphus nanus Sinclair, 1906 (*partim*), p. 421, text fig. 7, pl. 63, figs. 9, 9a.

Lectotype of *P. gracilis*.—MACN 8457, a fragment of a left mandibular ramus with P_3 – M_3 complete (selected lectotype and figured by Reig, 1955b, p. 64, fig. 2; and Marshall, 1980, fig. 7).

Hypodigm.—The type and MACN 5707, a fragment of a right mandibular ramus with M_{2-4} complete (a possible syntype of *G. captiva*); MACN 5722, a fragment of a left mandibular ramus with P_3 complete, alveoli of P_{1-2} and M_{1-4} (possible syntype of *H. nanus*); MACN 8458, a fragment of a right mandibular ramus with

⁸ *Phonocdromus patagonicus* was original genotype, but has been shown to be invalid by Reig (1955b, p. 64).

FIG. 32. *Phonocdromus gracilis* Ameghino, 1894, p. 356 (Santacrucian). MACN 8457 (lectotype), a fragment of a left mandibular ramus with P_3 - M_3 complete, and alveoli of M_4 : a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

TABLE 15. Measurements of lower cheek teeth of *Phonocdromus gracilis*.

Specimen	M_1		M_2		M_3		M_4		M_{1-4}
	L	W	L	W	L	W	L	W	L
AMNH 9123	1.3	0.9	1.4	1.0	1.3	0.9	...	...	ca 4.9
AMNH 9593	1.2	1.0	1.4	1.1	1.3	1.0	0.9	0.6	5.0
MACN 5707	...	...	1.5	1.0	1.2	0.8	0.6	0.5	...
MACN 8457	1.4	0.9	1.6	1.0	1.3	0.9	...	...	...
MACN 8458	...	...	1.5	1.0	1.3	0.9	...	...	4.7

M_{2-3} complete and roots of M_4 (labeled *P. gracilis*); MACN 8461, a fragment of a right mandibular ramus with alveoli of P_3 - M_4 (labeled *P. gracilis*); MACN 8462, a fragment of a right mandibular ramus with M_{2-4} complete (labeled *P. gracilis*); AMNH 9123, a fragment of a left mandibular ramus with M_{1-3} complete and with alveoli of M_4 ; AMNH 9593, a nearly complete right mandibular ramus with base of large incisor and with most of rest of dentition (figured by Sinclair, 1906, text fig. 7, pl. 63, figs. 9, 9a).

Horizon and locality.—All specimens are from the Santa Cruz Formation, Santa

FIG. 33. *Phonocdromus gracilis* Ameghino, 1894, p. 356 (Santacrucian). AMNH 9593, a nearly complete right mandibular ramus with base of large incisor and with most of rest of dentition: a, labial; b, occlusal; c, lingual views. Scale = 5 mm.

Cruz Province, Patagonia, southern Argentina and their localities and dates of collection are as follows: *La Cueva* MACN 8457, 8458, 8461, 8462 (collected in 1892–93); *Sehuen* MACN 5707 (collected in 1890–91); *Monte Observación* MACN 5722 (collected in 1890–91); all MACN specimens were collected by Carlos Ameghino. AMNH specimens were collected in 1899 by Barnum Brown along the north bank of the Río Gallegos near *Felton's Estancia*.

Age.—Santacrucian.

Comments.—Among the syntypes of *Halmarhiphus nanus* were three specimens of which one is referable to *Stilotherium dissimile*, one to *Microbiotherium patagonicum*, and one to *Phonocdromus gracilis* (see p. 19).

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