THE BEGINNING OF THE AGE OF MAMMALS IN SOUTH AMERICA

GEORGE GAYLORD SIMPSON

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PART 1. INTRODUCTION. SYSTEMATICS: MARSUPIALIA, EDENTATA, CONDYLARTHRA, LITOPTERNA AND NOTIOPROGONIA

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PREFACE

THIS PUBLICATION begins what is planned as an essentially complete survey of present knowledge of the strata and faunas of the early Tertiary in Patagonia, together with the many problems of phylogeny, paleogeography, correlations, etc., in which they are involved. Part 1, presented herewith, includes the general introduction and the beginning of the systematic descriptions of the known fossils, covering the four mammalian orders Marsupialia, Edentata, Condylarthra, and Litopterna and the first suborder, Notioprogonia, of the great order Notoungulata. Later parts will conclude the systematic descriptions, then will list the local and stage faunas and discuss faunal succession and relationships and the detailed and general stratigraphy of the early Tertiary of Patagonia. A brief account of the Scarritt Patagonian Expeditions and of the geography of central Patagonia will also be given in a later section.

This work was originally proposed by F. von Huene of Tübingen, Germany. Because of his interest in South American stratigraphy, paleogeography, and faunal relationships and my interest in early Tertiary mammals in general, he suggested that Tübingen University and the American Museum of Natural History undertake a joint expedition to Patagonia, the University's representatives to devote themselves mainly to stratigraphy and areal geology and the Museum's mainly to collecting vertebrate fossils. Tübingen University was unable to carry out its part of the plan, but the American Museum sent two expeditions to Patagonia, under my leadership, in 1930–1931 and 1933–1934. In 1931 I also spent some months in Buenos Aires and La Plata studying all the pertinent materials in the Museo Argentino de Ciencias Naturales and in the Museo de La Plata. Our own collections have been prepared and studied in New York.

Although attention was concentrated on the earliest defined stages with mammalian faunas, the Riochican, Casamayoran, and Mustersan, we also obtained large collections from the Deseadan and Colhuehuapian and a few scattered specimens from other stages. By a later arrangement with the Chicago Natural History Museum (formerly the Field Museum of Natural History), it was agreed that Bryan Patterson, of that institution, would monograph the Deseadan and Colhuehuapian faunas. The present memoir includes only the three earlier stages. Merely preparing our new materials for study took several years. The study itself is still not complete, although more than 15 years have elapsed since I first embarked for Patagonia. The delay has been in large part caused by the necessity for doing other work in the meantime, including several expeditions only indirectly if at all related to this memoir and also including a period of service in the army. Another great factor in my slowness has, however, been the enormous complexity of the problems faced, a complexity that was not fully realized when the work was undertaken. Some idea of the difficulty can be obtained from the fact that Ameghino and Roth named 208 genera and 386 species of mammals in the Casamayoran and Mustersan faunas. To this must be added the smaller but important Riochican fauna, scarcely known to Ameghino or Roth, and additional Casamayoran and Mustersan genera and species discovered after Ameghino and Roth by the American Museum, Chicago Museum, and others. The redefinition or reduction to synonymy of many more than 400 specific names, well over 200 generic names, and dozens of names of higher rank is in itself a really herculean task, not to mention consideration of the many other problems involved. In view of this, the long delay in starting publication and the decision to publish in parts, as each is completed, probably need no defense.

The field and musem work in Patagonia and a considerable part of the work in New York were supported by Horace S. Scarritt. I cannot too warmly thank Mr. Scarritt for his generous, disinterested, and continued support of this long project. Some financial assistance during the early phases was also received from Walter W. Holmes and Childs Frick. Most of the routine work throughout has been carried by the American Museum of Natural History, the authorities of which have been constantly encouraging and patient.

Special acknowledgments are also due to

Coleman S. Williams, who accompanied me in the field on both expeditions. He not only found and collected many important specimens but also gave invaluable and indispensable assistance in many other ways. In addition to his field work, he carried out much of the preparation and preliminary sorting of the collections in New York in 1931–1933 and 1934–1935.

Among a number of local men who worked with us in the field, Justino Hernández was outstanding. He carried most of the responsibility for the camp on both expeditions and also found many specimens. Aside from those who were our employees, it is a pleasure to pay tribute to the generous and friendly spirit of the *pobladores* of Patagonia, its humble inhabitants who received us, strange apparitions from another world, with uniform courtesy. We benefited by the essential and freely granted assistance and tolerance of persons too numerous to name and, indeed, of many whose names were never made known to us.

In Buenos Aires, M. Doello-Jurado, former director of the Museo Argentino de Ciencias Naturales, assisted us almost beyond my power to acknowledge. He helped us to obtain permits for exploration and exportation and to secure cooperation from other governmental organizations and various individuals. He also placed the great Ameghino Collection and all facilities for its study at my full disposal. Without his aid, this work would have been quite impossible from the outset.

Alejandro Bordas also aided us very materially in Buenos Aires, in connection with my work in the museum there and in other ways, and he accompanied us in the field for a time during the second expedition. The late Lucas Kraglievich greeted us cordially when we first arrived in Buenos Aires and assisted my studies during the relatively short stay at the museum before we first went to Patagonia. After our return, it was my good fortune to have several long talks with the late Carlos Ameghino, during a remission in the tragic illness that clouded his last years. He shared with me his memories of the great days of Patagonian exploration and gave me important unpublished data on several crucial points.

At the Museo de La Plata, L. M. Torres, then director of that institution, extended the fullest hospitality, and Angel Cabrera assisted my research there in every possible way and proved himself both a steadfast friend and a disinterested scientist in many other respects.

The Dirección General de los Yacimientos Petrolíferos Fiscales aided us very materially both as an organization and through its various officials and employees, granting us transportation in various instances, supplying gasoline cheaply or gratis, and making available unpublished maps and reports. The geological staff cooperated closely with us in the field and elsewhere and greatly assisted us, especially Egidio Feruglio and A. Piatnitzky, to both of whom we are also indebted for many personal kindnesses, and also E. Fossa-Mancini, I. Conci, J. Brandmayr, and L. von Platen.

Among many others who aided us in the field were William A. Watkins, then of Plaza Huincul, Marcelo Lemonnier, then of Roca, M. J. Deckers, then of Bahia Solano, Kenneth Watts and W. R. Smellie, both then of Comodoro Rivadavia, and the late T. N. Tappen, then of Gaiman.

In Buenos Aires, the Dirección General de Minas, Geología e Hidrología provided stratigraphic and other data, as did a number of individuals, among them P. Groeber, A. Tapia, and J. J. Nágera.

The Munson Line and the Grace Line both assisted us generously in obtaining transportation for ourselves, our equipment, and our collections.

In New York, virtually the whole paleontological staff of the American Museum has been involved in this work at one time or another. As already noted, C. S. Williams had charge of the preparation of our collections, and did much of this work himself until he left the museum in 1935. Among others who did much laboratory work on the collection were Albert Thomson, Carl Sorensen, and the late George Olsen.

The collection was catalogued by Rachel H. Nichols. Mrs. Nichols has also contributed very materially in checking the present manuscript and in preparation of the bibliography which is mainly her work.

The text illustrations have been drawn mostly by Mildred Clemens and John C. Germann, and the maps and diagrams by

Marie Bohrn. Miss Bohrn also assisted my research materially in many other ways, compiling faunal records, checking manuscript, mounting illustrations, etc. The photographs of specimens in the Ameghino Collection were provided by the Museo Argentino de Ciencias Naturales, through M. Doello-Jurado, and those of specimens in the Roth Collection were provided by the Museo de La Plata, through A. Cabrera.

The Chicago Natural History Museum, through E. S. Riggs and B. Patterson, placed all its fossils of these faunas at my disposal, and their collection is here described along with ours. Mr. Patterson has also offered many useful suggestions and has discussed many of the general problems of the Patagonian Tertiary with me.

Numerous as they are, these acknowledgments by no means list all the persons who have been of assistance at one phase or another of this long project. Some may have been omitted through inadvertance, and to them I can only offer an apology and the hope that the publication of this work is nevertheless some recompense. In the case of others, they have stated, or I have felt, that they would prefer not to be explicitly named but only to be included in general thanks to all who have helped and encouraged me over the long years during which this memoir has been in preparation. Such thanks are hereby tendered in the most heartfelt way.

GEORGE GAYLORD SIMPSON
The American Museum of Natural History
April 1, 1946

CONTENTS

"En los libros que han sido escritos sólo encontramos las verdades adquiridas. Sólo en el libro de la Naturaleza, en la observación e interpretación de lo que nos rodea, es donde podemos adquirir nuevas verdades con que enriquecer nuestros conocimientos y los de la Humanidad."

FLORENTINO AMEGHINO

"In written books we find only the truths that are already known. It is only in the Book of Nature, in the observation and interpretation of our surroundings, that we can win new truths with which to enrich our knowledge and that of the human race."

INTRODUCTION

SCOPE AND PURPOSE

THIS WORK is primarily devoted to the description of the three oldest known mammalian faunas of South America, those of the Riochican, Casamayoran, and Mustersan stages of Patagonia, each including a number of faunules of different ages, facies, or both. Stratigraphic data relating to their field occurrence will also be given, and the general stratigraphic problems involved will be discussed. The classification and relationships of the members of these faunas are considered in detail, and their crucial bearing on many broader problems of the taxonomy and phylogeny of later South American mammals is considered.

It would be impossible to overemphasize the importance of these faunas for an understanding of the history of life, particularly in South America but also in general. As far as such a key is yet available, they are the key to the origin of South American mammals, and they lead into the richest and most characteristic development of these. They also illustrate in the most interesting way and on the most magnificent scale the deployment and evolution of a fauna developing in isolation but on a continental scale. They display an experiment in evolutionary principles conducted for us by nature in a space and over a period of time far greater than any laboratory research can encompass.

This importance has been partly but not fully realized. The work of the Ameghinos, to be discussed at length in this memoir, whetted but did not satisfy curiosity. Relatively few of their specimens were figured, and Florentino Ameghino's publications on these faunas, excellent and numerous as they were, were mostly preliminary notes and gave brief diagnoses rather than descriptions. It has hitherto been almost impossible for students of mammalian morphology and evolution to get a clear idea of the faunas as a whole or of most of their many members. The revision of these faunas, with the addition of as much new material as could soon be accumulated, has been one of the greatest desiderata of vertebrate paleontology. This memoir attempts to provide this desideratum, as far as is possible to me and at the present time.

It need hardly be added that this is not the last word on the subject and that it is written with the hope that it will only be an interim report and an aid for better future work. There are still vast areas in Patagonia that have not even been scratched by the collector. One of these faunas, the Casamayoran, is already among the largest, most varied mammalian faunas known from any one stage and region in the history of the earth. It will, nevertheless, be greatly increased by further and more extensive collecting. Regarding the other faunas, only the main outlines can now be sketched.

HISTORY

In a broad sense the history of this study goes back to Magellan and Drake, for these and others of the earliest explorers and adventurers revealed to the modern world that Patagonia exists. They learned little more than this bare fact. The extent of knowledge by the seventeenth century is exemplified by a map of South America by Henricus Hondy, Amsterdam, 1632, on which Puerto Deseado, Cabo Blanco, and Camarones are already indicated in central Patagonia, but on which the whole interior region is blank and the coast line is almost completely erroneous. Even the great Golfo de San Jorge, a primary feature of South American geomorphology, is not distinctly indicated. It was not until two centuries later that any detailed and accurate knowledge of central Patagonia was attained.

Inland features began to be known, or, at least, suspected, towards the beginning of the nineteenth century. F. de Azara in 1809 showed a lake "Coluguape" as the source of the Rio Gallegos, and in De Moussy's atlas of 1865 there is indicated a lake "Colu-Suapo."

These undoubtedly derive from reports of Lago Colhué-Huapí,[1] which is a focal point for the Patagonian early Tertiary. These indications were, however, evidently based on rumor or reports of the natives and not on European visits to the lake, because its position and hydrography are grossly erroneous on both these maps, and the other interior features shown are altogether unrecognizable on the actual terrain.

The first map to show much of the interior from first-hand data was that of George Chaworth Musters, an Englishman, who in 1869 made a remarkable overland trip along the entire length of Argentine Patagonia. He scarcely entered the area important for the present study, his route lying near the Andes to the west, and he never saw the lake that now bears his name. His map shows, however, a lake "Coluguape" and a river "Sengel," which are undoubtedly intended for Lago Colhué-Huapí and the Río Senguer or Senguerr of modern maps. Neither was correctly shown by Musters, but his map approximates the truth more closely than previous maps and doubtless represents information from the Indians obtained when Musters was near this area. It is curious that his informants did not point out that there are two large lakes here, not one alone.

In the meantime the coast had become well known, indeed almost as well as today, particularly by the voyages of D'Orbigny (1828–1829), King (1826–1830), and Fitz-Roy (1831–1836), Darwin accompanied Fitz-Roy, as all students of evolution know, and he made the beginning of geological and paleontological work in Patagonia, a meager beginning, indeed, but one of the greatest historical significance. The few fossil mammals collected by him were Pleistocene.

Following Musters, the essential inland features were made known by, among others, C. M. Moyano, L. J. Fontana, R. Lista, and F. P. Moreno. It was Moreno who first recognized the presence of two large lakes in the meseta region of central Patagonia. He believed the western lake to be the Colhué-Huapí or "Coolu-Huape" of older authors, but renamed it Lago Musters and called the eastern lake "Dillon."[2]

In 1884 the Territorio del Chubut was created, and white colonization dates from that era. In 1885 the first governor of the territory, Fontana, followed the Río Senguer from the Andes to the lakes, went out to the coast near the site of Comodoro Rivadavia, then returned to the lakes and followed the Río Chico del Chubut to the Río Chubut. He thus finally determined the essential hydrographic and other features of the region, previously so wrongly understood.

In the early 1890's there were already wagon tracks from the site of Comodoro Rivadavia westward to the cordillera and northward to Camarones by way of the Río Chico valley. Colonia Sarmiento, the chief and almost the only inland settlement in central Patagonia, was founded by Pietrobelli in 1897. Comodoro Rivadavia, now the principal coastal town, was settled in 1898, although its official establishment was dated June 26, 1900. In the 1910's a government railroad was built from Comodoro Rivadavia to Colonia Sarmiento, and the later oil development led to the construction of a coarse network of roads passable by motor car. In spite of these developments, when we did our work in the

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[1] This has become the accepted orthography and is retained throughout this memoir, but it does not correctly represent the word as spoken by all the present inhabitants of the region. They call the lake "Coluuapi," or some variant near that Spanish phonetic spelling, such as "Colu-huapi" or "Coluapi."

[2] There has been considerable argument and confusion as to which lake is which. Fontana transferred the name "Musters" to the eastern lake, although Moreno explicitly proposed it for the other lake. Roth perpetuated Fontana's error and further considered that the same eastern lake was also "Colhuapi," i.e., Colhué-Huapí in the official orthography. He called the western lake Colhué, obviously merely the first half of the usual name for one lake or the other, or both, an aberration for which I have found no reason or precedent. Even some recent maps, e.g., that published by the Oficina Cartográfica Ludwig in 1930, call the eastern lake "Musters" and the western "Colhué-Huapí." It is rather futile at this date to discuss which lake was the "original" Colhué-Huapí, as the name was originally applied when there was believed to be only one lake rather than the two that really exist. The fact is that all the local inhabitants understand Colhué-Huapí ("Coliuapi," "Colu-huapi," "Coluapi," etc., as actually pronounced) to be the eastern lake and Musters the western. Moreno's name "Dillon," first applied to the eastern lake, is now sometimes given to a small laguna still farther east. The Oficina de Tierras and Colonias and other official Argentine agencies confirm and legalize the local usage, "Musters" for the western and "Colhué-Huapí" for the eastern lake.

1930's life continued to be extremely primitive outside the few towns, and large areas away from the few routes of traffic were unmapped (or, what is worse, mapped by guesswork with extreme inaccuracy) and virtually unknown except to the sparse and hardy *pobladores*.

The opening up of the interior to colonization in the 1890's coincided with the first serious geological study and fossil collecting in this region. The history of discovery and study of the early Tertiary faunas begins at this point, except as the previous explorations may be considered necessary preliminaries for this.

The occurrence of abundant fossil mammals in what is now classed as the later Tertiary of southern Patagonia had been known for some time. The history of knowledge of the Santa Cruz and later faunas will not be followed here, except as it bears on knowledge of the earlier faunas and strata. An incident that most decidedly had such a bearing occurred in 1887, when the brothers Ameghino began work in Patagonia and on its fossils. The older brother, Florentino, was then in his thirty-third year and had been studying and publishing on Argentine fossil mammals since he was 20. Carlos, one year younger, had already devoted himself to collecting fossils for Florentino's studies and had acquired considerable skill in finding specimens and in field interpretation of their occurrence and stratigraphy. In January of 1887 he set out for the first of what were to be many sensationally successful collecting trips to Patagonia.

Carlos Ameghino's early expeditions were mostly devoted to the rich Santa Cruz fauna of southern Patagonia, but he soon began some collecting in the pre-Santa Cruz beds that concern us more immediately here and these eventually became his main aim. A pre-Santa Cruz mammal had been found under somewhat mysterious circumstances before 1880. This first early Tertiary mammal find in South America consisted of a cheek tooth and a tusk given to Florentino Ameghino by Captain D. Antonio Romero, who said they came from Neuquen Territory. (If this vague locality record is correct, the deposit in question has yet to be rediscovered.) Ameghino applied the name *Pyrotherium romeri* to these remains in 1888. In the same year and on his next three annual expeditions to Patagonia, Carlos Ameghino found scattered remains supposedly of the *Pyrotherium* fauna, but only in passing, without being able to investigate the beds with care or collect extensively. (Later, when the fauna was better known, Carlos found that he had been mistaken in at least one case and that the fauna was younger than *Pyrotherium*.) In 1893–1894 he worked northward from his main (Santacrucian) collecting grounds to the Río Deseado, where he found *Pyrotherium* and a considerable associated fauna. At this time he also made the crucial observation that this fauna is definitely older than the Santa Cruz formation, the beds in which it occurs lying below the marine Patagonian formation which, in turn, underlies the Santa Cruz.

This geological observation and the description of the fossils were published by Ameghino in 1895 in a classic paper in which appeared the first diagnoses of *Parastrapotherium*, *Leontinia*,[1] and others among the most striking and important of South American fossil mammals.

During his next campaign, in 1894–1895, Carlos Ameghino again worked northward in search of pre-Santa Cruz mammals and again found them, this time in the coastal region of southern Chubut, between Bahia Sanguinetti and Punta Casamayor. The succeeding expedition, 1895–1896, was especially devoted to these earlier fossils, and Carlos spent about six months exploring the whole coastal region nearly to the Chubut River in northern Chubut Territory.[2]

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[1] This may be as good a place as any to correct an injustice which has, as far as I know, been left without comment for more than 40 years. In his "Index generum mammalium" (1904), Palmer gives the origin of the name *Leontinia* as, "In honor of Leontina—, a friend of Dr. Florentino Ameghino," an expression open to possible misunderstanding. The lady in question was Léontine (Hispanicized as Leontina) Ameghino, née Poirier, a French girl whom Ameghino married during his stay in Europe in 1878–1881. Señora Ameghino deserves to be honored as an anonymous literary collaborator in Ameghino's many publications in French, and she was a great deal more than a friend to her famous husband. The marriage was without other than literary issue. She died in 1908, three years before her husband.

[2] In the collected letters of the Ameghinos ("Obras completas," vols. 20–23), which are a priceless source of otherwise unavailable information about these dis-

The collections of these two years, 1894–1895 and 1895–1896, with added notes on earlier collections, were published by Florentino Ameghino in 1897a as the "Deuxième contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium*." As the Ameghinos later established, the mammals then described were not, in fact, all contemporaneous with *Pyrotherium*. A considerable number of them are decidedly older than *Pyrotherium* and belong to what the Ameghinos later called the *Notostylops* beds and fauna, now designated as Casamayoran. Among these older fossils was *Notostylops* itself, along with *Polydolops*, *Trigonostylops*, and others of the most characteristic Casamayoran genera. This was the first discovery and description of pre-*Pyrotherium* (i.e., pre-Deseadan) mammals from South America.

Carlos was again in Patagonia for the season 1896–1897, wintered there in 1897, and continued in the field in the summer of 1897–1898. This long campaign involved a series of mishaps and disappointments and was fruitless as far as the now eagerly sought pre-Santacrucian fossils were concerned. Nothing daunted, he returned to Patagonia later in 1898 and in 1898–1899 again worked in Chubut. It was then that he discovered that the publication of 1897 was based on a mixture of two faunas. He wrote Florentino from Camarones on February 15, 1899, saying; "It turns out that what we have been accustomed to call the *Pyrotherium* fauna is, according to new observations, really a succession of two different faunas separated by an enormous interval of time . . . the older of these two faunas, which might well be called the *Notostylops* fauna after its most abundant and characteristic genus, is doubtless Cretaceous . . . "[1] It is illuminating that Florentino was reluctant to believe that two faunas were involved or that, if so, they were of very different ages, but he soon abandoned his skepticism. In a later letter, October 9, 1899, Carlos noted the superposition of not only two but three pre-Santacrucian and pre-Patagonian faunas in the barranca south of Colhué-Huapí and proposed (with a different spelling) the name now current, Colhuehuapian, for the third and youngest of these. From locality records preserved with some of the fossils described in 1897 and from Carlos Ameghino's recollection in 1931, there is little doubt that the expedition of 1895–1896 was not confined to the coastal region but also included the great barranca south of Lake Colhué-Huapí, the most important single locality for early Tertiary mammals and stratigraphy.

Carlos Ameghino worked near Punta Casamayor in 1894–1895 and the *Notostylops* fauna, now named Casamayoran after that locality, occurs there. It might, then, seem probable that this fauna was discovered on this occasion, but I think this incorrect. Carlos Ameghino told me that he first found this fauna in 1895–1896 south of Lake Colhué-Huapí, and this agrees with what other evidence is available. It is true that his memory of the Punta Casamayor occurrences was vague and partly incorrect when I discussed them with him, which is not surprising after the lapse of 35 years and during a brief remission in a serious illness, but I feel sure that he correctly remembered the original discovery of the fauna. In fact, in the Ameghino Collection there is only one (unidentified) specimen labeled as from Punta Casamayor.

It may be interpolated here that all this collecting was undertaken at the Ameghinos' own expense and that they labored under constant financial difficulties. Much of the early work was supported by a small stationery store run by the family in La Plata. Florentino held various unremunerative posts until in 1902 he became director of the National Museum in Buenos Aires. In 1903 Carlos also was employed by that museum (of which he also was for a time director after Florentino's death). Thereafter their financial difficulties were relatively, but not absolutely, relieved, but their Patagonian collecting was then ended. During these collecting campaigns Carlos had no personal income, and the funds that Florentino could send him were so small that the physical difficulties of the field work were heightened by his usual condition of dire poverty. In 1899 in order to

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coveries, there is an error of compilation that is puzzling for the unwary. The letter inserted as No. 177 with date given as June 20, 1890, refers to this expedition. The correct date is June 20, 1896. The letter is again inserted, without comment, in the correct position as No. 694.

[1] Original in Spanish. "Obras completas," vol. 21, p. 105.

increase the means available for Carlos' work, Florentino entered into an arrangement with Karl von Zittel of Munich, Germany, under which the University of Munich agreed to contribute to the field expenses for four years and was to receive in return all specimens except those new to the Ameghino Collection. This arrangement remained in effect for the stated term, until 1903, when Carlos ceased to collect in Patagonia. A relatively large Patagonian collection, probably to this day the most extensive to be sent to Europe, was accumulated in Munich. As regards the Casamayoran and Mustersan faunas, those of special interest here, it was, however, found somewhat disappointing by Zittel's successors in Munich. A very high proportion of these specimens were considered by Ameghino to represent new species and so were retained by him in accordance with the agreement. Some important specimens were nevertheless sent to Munich and several of these were figured in Schlosser's revision of Zittel's "Grundzüge."[1] It is now (1946) reported that the collection was destroyed during the recent war. As far as I know, the only surviving European collection of pre-Deseado Patagonian fossils of any importance is the relatively small collection made by Tournouër and sent to Paris.

Carlos again wintered in Patagonia in 1899 and took the field in 1899–1900 with somewhat disappointing results as regards collections. The next three years were also devoted mainly to pre-Patagonian mammals. Few details of this field work seem to be recorded, but for the Casamayor, especially, the 1901–1902 season was apparently one of the most successful of the whole campaign. Later in 1902 Carlos' health broke down and in January, 1903, this induced Florentino to make his one trip to Patagonia. At Cabo Blanco he met Carlos, who was sufficiently recovered to spend several weeks showing Florentino key stratigraphic sequences in northeastern Santa Cruz territory, including Punta Casamayor, which became the type locality for the Casamayor formation. In April, 1903, the two brothers returned together to Buenos Aires, and their long Patagonian campaign, which had kept Carlos almost continuously in that desolate region for more than 16 years, was over.

Florentino Ameghino continued the description of the early mammals, especially in three large papers between 1901 and 1904 (1901, 1902a, and 1904a of the appended bibliography). In the first of these (1901) he first announced Carlos' discovery of another fauna, named the *Astraponotus* fauna (now called Mustersan) between those of *Notostylops* (Casamayoran) and *Pyrotherium* (Deseadan), completing the roster of pre-Patagonian mammalian faunas definitely established by the Ameghinos. The descriptions and definitions were completed, as far as Ameghino lived to do so, in scattered observations in papers on special subjects, of which his large work on molar evolution (1904b) is especially important and contains the only previous figures of many species of these earliest faunas.

In 1900–1903 Ameghino also published at length on the stratigraphy and correlation of the Patagonian deposits. This was expanded and revised in a still larger work, the famous "Formations sédimentaires du crétacé supérieur et du tertiaire de Patagonie," published in 1906. In this for the first time locality maps (still necessarily rather generalized), sections, and other geological data gathered by Carlos were clearly set forth. The affinities of the various groups of mammals were also discussed, and full generic faunal lists were given for the whole Patagonian sequence as then known. This proved to be the Ameghinos' definitive work on the subject. During the five years that remained of his life, Florentino's interest turned in other directions, especially the antiquity of man in the Argentine, and Carlos, never very articulate, made only one addition, when he replied to some of Loomis' criticisms of his work (C. Ameghino, 1914).

It is unnecessary at this point to go further into Ameghino's opinions as to the classification and affinities of the animals of these faunas and the stratigraphy and correlation of the beds that contain them. Points of detail are constantly discussed throughout the present memoir, and a critical evaluation of the Ameghinos' work in general is given in a later section of this introduction.

The work of the Ameghinos is so much the

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[1] I examined most of these specimens in Munich in 1927.

most important previously done on the subject of this memoir that it has been discussed in sequence, but it was not the only work done in the period already spanned in review. The discovery of pre-Patagonian mammals by Carlos Ameghino awakened lively interest especially in the Argentine but also all over the world. The keen rivalry (to avoid using less pleasant and perhaps more accurate words) then existing in Argentine paleontology led to a scramble to try to catch up with or forestall the Ameghinos' discoveries. Lacking Carlos Ameghino's skill and knowledge of the field, and lacking also precise data as to his localities, most of these explorations came to little or nothing as regards these early faunas. Thus a Dr. Valentin went to Chubut in the summer of 1897–1898 especially to collect the *Pyrotherium* fauna, but he had barely reached the field when he fell off a cliff and was instantly killed. Others survived to pursue their investigations but could not find the faunas or recognize the beds.

The most nearly successful of these rivals of the Ameghinos was Santiago Roth, a Swiss naturalized in the Argentine and then working at the Museo de La Plata. Roth made several expeditions to Patagonia and in 1896–1897, 1898–1899, and 1902 he worked in the Chubut Valley and between there and Lago Colhué-Huapí, looking for the so-called Cretaceous mammals (now considered early Tertiary) of the Ameghinos. In this he was successful, amassing a collection much smaller than that of the Ameghinos, to be sure, but containing some exceptional specimens and important because the localities found by him were new, for the most part, and yielded some mammals different from those known to the Ameghinos. Although Roth himself was not aware of this, his collections are particularly interesting for their additions to the poorly known "*Astraponotus*" (Mustersan) fauna. Roth published three brief papers on his fossil mammals from this general part of the sequence (1899, 1901, 1903a) and later gave a discussion of the stratigraphy (1908). In a posthumous work (1927) he also discussed molar evolution on the basis of these early mammals. Details of his observations and opinions are considered in pertinent later parts of this memoir. It may fairly be said here that his brief and somewhat confused published contributions did not particularly advance knowledge at the time, as regards these particular strata and faunas. It will, however, be remembered that he was the first to recognize the essential unity of the Notoungulata and to apply that name to them.

Another relatively successful collector was A. Tournouër, who made several trips to Patagonia during the later years of Carlos Ameghino's work there and sent his collections to the Muséum d'Histoire Naturelle in Paris. It is pleasant to record, as an exception to the rule during that period of Patagonian exploration, that Tournouër and the Ameghinos cooperated amicably and that the key sites for this part of the sequence were pointed out to Tournouër by Carlos Ameghino. He published a short stratigraphic note (Tournouër, 1903), important because he gave the first published locality data and geological sections of these deposits and gave a reasoned opinion as to their age much more conservative than that of the Ameghinos and nearly agreeing with the views now generally accepted. In Paris, Gaudry (1904–1909) published some discussions and figures of fossils collected by Tournouër, without attempting any full consideration of the faunas, for which, indeed, the collections would not have sufficed. Basing himself on Tournouër's field observations, Gaudry applied the first geographic names to these beds and faunas, Casamayor for the *Notostylops* beds of Ameghino and Deseado for the *Pyrotherium* and *Colpodon* beds. (The full use of such terms for the sequence now recognized was developed on the basis laid by Gaudry in successive steps, especially by Kraglievich, 1930, Frenguelli, 1930, and me, 1933h.)

Also contemporaneous with the Ameghinos' Patagonian work was that of Hatcher, fully reported by him, Scott, Sinclair, and others and only indirectly of interest for the present subject. Hatcher's fossil mammal collections were almost entirely of Santacrucian age, and he did not work on the earlier mammal-bearing beds. In spite of this fact, he concluded that the Ameghinos were wrong regarding the sequence and stratigraphic relationships involved and published some severe strictures on their work. Many of the observations that Hatcher "corrected" or questioned were basically correct, and it is no detraction from his wonderful success in the Santacrucian or his whole great career as a collector to deprecate his rashness in making such criticisms without real knowledge of the facts in the field. Historically, this had at least two very unfortunate effects: it retarded real appreciation and comprehension outside the Argentine of the permanently sound parts of the Ameghinos' work, and it had a psychological effect on Florentino Ameghino reflected in an unfortunate way in his subsequent work as will be mentioned again later.

In 1911–1912 another North American, F. B. Loomis, worked in Patagonia, and this time on the pre-Santacrucian formations. His party obtained a remarkably large and fine Deseadan collection from a single locality (Cabeza Blanca) on the Río Chico del Chubut, which was (as Loomis suspected) one of Carlos Ameghino's main localities for this fauna. Loomis later (1914) published an extended account of this collection and a survey, rather than a revision, of the Deseadan fauna as a whole. Loomis thus made a noteworthy contribution to knowledge of the Deseado fauna. More exactly within the scope of the present study, he also made a few very positive statements regarding the pre-Deseado beds. It is not necessary to go into these in detail here, but it is necessary to place on record the warning that almost all of these statements are incorrect.

In 1922–1924 an expedition from the Chicago Natural History Museum (then the Field Museum of Natural History), under the leadership of E. S. Riggs, worked in Patagonia. Attention was mostly devoted to the Deseadan and later faunas, but some Casamayoran specimens were also collected. The best of these were described by Riggs and Patterson (1935), and all were then lent to the American Museum for this study, under the arrangement mentioned in the preface to this memoir. These specimens are described along with ours in the following pages.

Since the discovery of oil in 1907 near Comodoro Rivadavia, and more particularly in the 1930's, a great deal of regional geological field work has been done in central Patagonia by the Argentine government geologists and by other Argentine and foreign geologists. These studies have often included the early Tertiary, but usually only in a generalized way. As a rule, the four formations and mammalian faunas distinguished by the Ameghinos below the marine Patagonian formation have been treated in these studies as a single unit, now called the Sarmiento group, without attempting to subdivide them in practice or to collect their faunas. For this reason, no attempt will be made here to summarize all these explorations and studies, although their bearing on some stratigraphic problems will be discussed in due course in the pertinent section of this memoir. A few studies of more general nature or more immediate bearing on the present study may, however, be briefly noted here.

A pioneer in this series of modern areal studies was Stappenbeck, who in 1908 and 1909 published observations on the geology of the region of the central Patagonian lakes and southeastern Chubut. Schiller, Keidel, Wichmann and others followed in the 1910's. This phase of investigation may be said to have culminated in the work of Windhausen, who in 1924 published a general work on the regional geology of central Patagonia, or more particularly that part west of the Golfo de San Jorge, precisely the region crucial for the present memoir. Subsequent work by Tapia, Frenguelli, Groeber, and others is, except for certain details or indirect references, less pertinent to this study.

Special reference may be made to the work of Egidio Feruglio in the late 1920's and the 1930's, because, more than most of the regional and petroleum geologists, he was interested in the earlier mammalian faunal horizons and has contributed some specific and detailed, although brief, comments on them. For instance in his "Apuntes sobre la constitución geológica de la región de Golfo del San Jorge" (1929) he confirmed the often debated sequence of the Ameghinos' four terrestrial pre-Patagonian stages and gave some important new stratigraphic data on them. He also made small but important collections of the mammals of all four stages, most of which he kindly submitted to me for use in this study. His great "Palaeontographia Patagonica" (1937), although primarily devoted to the marine fossils, also contains a useful discussion of the terrestrial beds. He also published in 1939 a geological map of the whole of

Patagonia on the scale of 1:2,000,000, which supersedes other much more sketchy and incomplete geological maps of that still imperfectly known region and is indispensable for general orientation of geological studies in it.

The most recent important development directly pertinent to this memoir has been the addition of a fifth to the Ameghinos' four pre-Patagonian mammal-bearing stages and the related clear separation of pre- from post-Salamancan beds and of dinosaur- from mammal-bearing horizons. Details, again, are deferred to the stratigraphic part of this memoir, but the essential discovery is here briefly reviewed. As is well known, Florentino Ameghino believed that his earlier mammalian faunas (through the Deseado) were of the same age as dinosaur-bearing beds and had, indeed, been found associated with dinosaurs. Carlos Ameghino agreed as to the general age relationships, although with his usual care and honesty in field observations he was aware that in the field he had never found dinosaurs with mammals but always below them, when the sequence could be surely established.

Little as he agreed with the Ameghinos on many points, Roth did agree that the early mammals were associated with dinosaurs. In 1899 and again in more detail in 1908 he reported the discovery of mammals, which he believed to be those of the *Notostylops* fauna, in what he called a "Dinosauriersandstein" at Gaiman Nuevo in the Chubut Valley. In his major stratigraphic publication of 1906, Ameghino stressed this occurrence as proof of the Cretaceous age of the *Notostylops* fauna. Neither of the Ameghinos ever visited the locality, and Florentino's remarks of 1906 must have been based on personal communication from Roth. However the misunderstanding may have arisen, the fact is that the data given by Ameghino, although quite surely derived from Roth, disagree radically with those later (1908) published by Roth himself. Although he used the misleading name "Dinosauriersandstein," Roth did not find dinosaurs in these beds and did not have any good evidence of their contemporaneity with dinosaur-bearing beds, a correlation that was, as it turns out, merely an incorrect assumption. He did find a very small number of mammalian remains which resemble but are not, as he thought or implied, the same as those of the *Notostylops* fauna.

Neither Roth nor the Ameghinos were in a position to appreciate the real significance of this discovery, which required collation with other discoveries made much later before anyone could have seen it clearly. This significance is that the mammals described by Roth in 1899 were, in fact, pre-Casamayor (pre-*Notostylops*), and the oldest known from South America up to that time.

Farther south in the region of the Golfo de San Jorge, the existence of a lithologically distinct formation later than the marine Salamanca formation and earlier than the mammal-bearing Casamayor was recognized by the government geologists and others in the 1920's. By a rather complicated series of misunderstandings not necessary to recount here, they at first considered these to be dinosaur bearing and called them Pehuenche, a name implying a double correlation with poorly distinguished, mainly earlier beds so called by Ameghino in this region and with a definitely older series far away in Neuquen. (Feruglio, 1929, exemplifies the state of knowledge at this point.) In the summer of 1930–1931, however, Feruglio and his associates began to suspect that reports of dinosaurs in these beds were erroneous and during that season they found mammals in them at two localities: A. Piatnitzky made this discovery in Cañadón Hondo and J. Brandmayr near Pico Salamanca. Feruglio visited both localities and made additional discoveries. These gentlemen guided me to the localities in 1931, and then and later our party made considerable collections of the mammals of these beds. The discovery was announced in 1931 by Piatnitzky, who was still inclined to consider these beds as Cretaceous in age. In a series of papers (1932c, 1933h, 1935a, 1935b, 1935c) I pointed out that there is no valid evidence for the occurrence of dinosaurs in these beds or for their pre-Tertiary age, described the specimens available to me, and applied the name Río Chico to this formation and Riochican to the corresponding pre-Casamayoran stage. In 1935 Cabrera described a collection from the locality discovered by Brandmayr. Bordas (1935, 1939) has also contributed notes on these and other early

Tertiary horizons, which he visited with us or independently in 1933–1934.

The other work of the Scarritt expeditions of the American Museum in 1930–1931 and 1933–1934 is summarized in a later narrative section of this memoir, and previous publications based on these collections will be fully listed in the final bibliography and referred to where pertinent throughout the memoir.

THE WORK OF THE AMEGHINOS

Any work on Patagonian fossils must in a sense be a monument to Florentino and Carlos Ameghino. This is particularly true of the present memoir, which revises large faunas discovered and described by the Ameghinos in the first instance and which has the name "Ameghino" on almost every page. This is an exceptional opportunity for an evaluation of a large part of their work. Such an evaluation is interesting and helpful in itself, but it may particularly serve to clear away many of the false ideas about the Ameghinos generated on one hand by unreasoning adoration and on the other by equally unreasoning criticism. The fact that many of the theoretical and taxonomic conclusions and some of the morphological data in the following pages disagree markedly from Florentino Ameghino's results might make this memoir appear to be another such criticism. I am therefore all the more anxious to give here an appraisal that will show that such disagreement is not destructive criticism but is consistent with the liveliest appreciation of his labors and the most sincere admiration for his ability. So much that is false, emotional, and biased has been said and written about him, that an honest attempt at dispassionate judgment can only be a service to his memory.

The partnership of the Ameghino brothers was an outstanding example of teamwork, and their achievement was one of the most remarkable in scientific history. When they began their career, one was an obscure provincial school teacher, without formal scientific training or higher education, and the other was his almost unlettered younger brother.[1] Between them, the older brother in the study and the younger in the field, they revolutionized South American geology and rewrote one of the most important chapters in the history of the earth.

The contribution of Carlos to this achievement is probably less appreciated and understood, even today. Florentino never failed to acknowledge and emphasize what he owed to Carlos, but it was Florentino who published almost all the results and who became recognized as a great scientist. "Ameghino" has come to mean Florentino, but I think that the ultimate judgment of history may rank Carlos as high. He was certainly a genius as a field geologist and collector. That he remained to the end relatively inarticulate, a hearty, gaucho-like man without the graces of academic circles, is only additional evidence that he spent most of his active years in the wilderness, at the real frontier of his science.

He correctly deciphered almost the whole sequence of the early and middle Tertiary in Patagonia. The sheer physical difficulties and privations involved cannot be appreciated by anyone who has not worked in Patagonia, and can be only imperfectly appreciated by anyone who has traveled there on roads and in motor cars, where Ameghino had to make his own trail and travel on foot or horseback. The geology is exceptionally confusing. The best evidence of this is that so many geologists, academically trained as Ameghino was not, with his pioneering work to help them, and with much better facilities than he ever enjoyed, failed to straighten out the sequence—and often blamed the failure on him! Of course his observations usually lacked detail and of course he overlooked some things, but he had the sequence right long before anyone else could confirm or would even believe this.

I have gone over most of the ground that Carlos Ameghino covered in central Patagonia and have checked everything that he said about it, either directly or through his brother's publication. I failed to find an important positive error in any of his field ob-

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[1] A third brother, Juan, assisted in the support of the family but was not more directly concerned in the scientific work of Florentino and Carlos.

servations—something that I cannot say for any other geologist who has worked in that region and, for that matter, that I feel quite sure will never be said of me.

There are errors in the published data, and there is one important systematic error running all through them: the statement that the terrestrial formations from the Casamayor through the Deseado (in modern terminology) contain dinosaurs or are contemporaneous with beds that do. Related to this is the claimed interdigitating and contemporaneity of the Casamayor and Salamanca. There is now really no question at all that these are definite and fundamental errors, and Carlos accepted them as established. This was a very natural mistaken judgment on his part, but these were not errors in his field observations. The errors arose from uncritical acceptance of erroneous observations by others, from faulty identification of a few specimens, and from unjustified inferences based on, but not logically demanded by, Carlos' observations. He knew and indicated that as far as he had seen in the field, the Casamayor overlay the Salamanca, where both occurred, and that he had found dinosaurs only at still lower levels, when the relative level could be determined objectively.

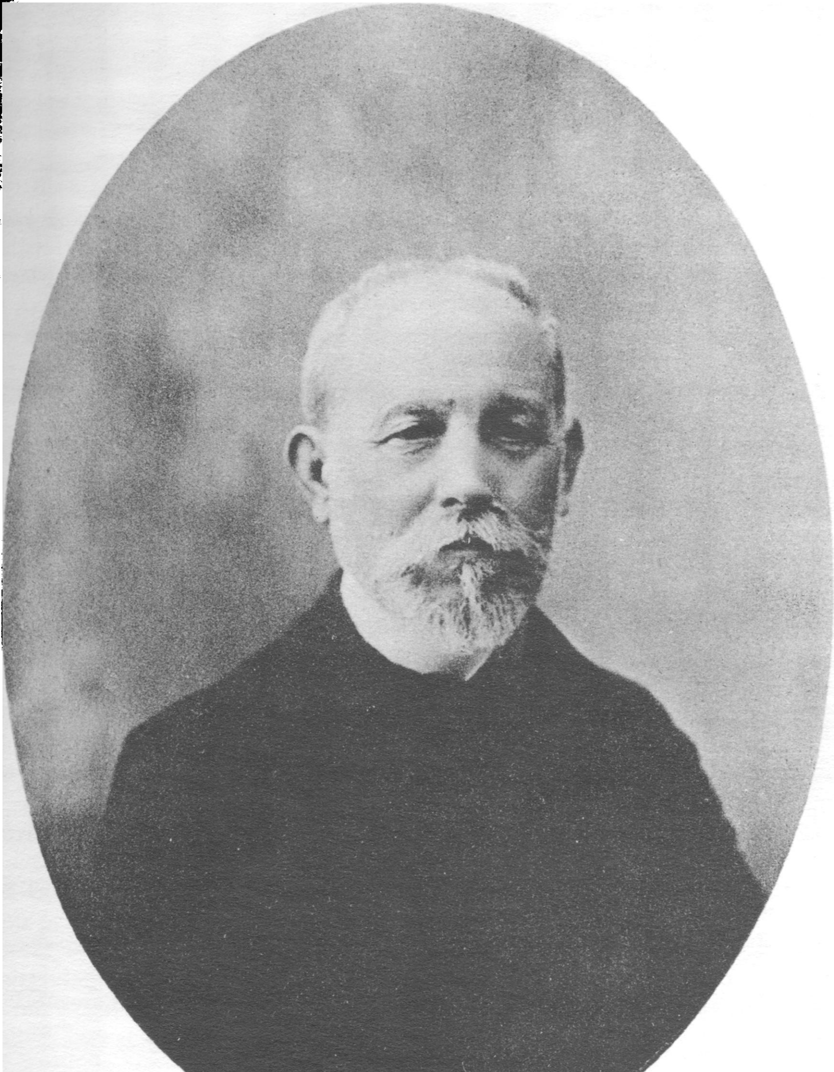
Carlos was very much, and quite properly, swayed and overawed by the dazzling intellectual achievements of his older brother. His own intellectual achievement in forming a clear and correct picture of Patagonian stratigraphy was also of the highest order and has permanent value.

As a collector, Carlos must be ranked high. He was unfamiliar with modern methods of excavation, bandaging, etc., just coming into use in his Patagonian field days, and his lack of adequate transportation would have made these difficult or impossible for him in any case. As a rule, he picked up what he could find and carried it off just so. Nevertheless he obtained a great number of specimens, many of them fine skulls that were collected entire or that could later be pieced together. He obviously had a remarkable eye and flair for collecting, as witnessed for instance by his large collection of very small Casamayor mammals, which are extraordinarily difficult to find on these usually rather barren exposures. A fair and illuminating comparison is provided by the fact that a whole collecting party later camped for three weeks on one of Carlos' Casamayor localities, failed to find any mammals in these beds, and so reported in the most positive terms that Carlos was mistaken in calling these beds Casamayor. Still later we were able to confirm that Carlos was right, and there are Casamayor specimens from this locality in the Ameghino Collection.

The one general adverse criticism of Carlos Ameghino's work can be made only as an abstraction and not in the framework of the actual conditions of his life and labors. He kept almost no field notes and recorded almost none of the myriad detailed observations that he made. Even in his letters to his brother he seldom gave any of these details but usually confined himself to important conclusions. What data were saved were usually transmitted orally to Florentino. Locality data with the specimens are often wholly lacking and never more than a vague mnemonic like "Coluapi" or "Río Chico." Like the gauchos with whom he was spiritually kin, Carlos kept his records in his head and most of them were lost to science. If Carlos had only had the opportunity and inclination to become as articulate as Florentino, his geological studies would have been as important as Florentino's paleontological studies, but then Carlos would have been a different man and probably would not have spent 16 years in Patagonia.

The more famous older brother, Florentino Ameghino (pl. 1), was a more subtle and complex character. Appraisal of him and of his voluminous publications requires more psychological insight, a closer weighing of conflicting tendencies, and a more carefully balanced statement.

As a research worker, Florentino Ameghino was enormously productive. He was as articulate as Carlos was inarticulate. He was not yet 57 when he died, but he wrote nearly 200 memoirs and monographs, some of them of great length. His collected works fill 18 very bulky tomes, and his correspondence fills four more. His earliest work, 1875–1882, and his latest, 1907–1911, were mainly devoted to studies of fossil man, artifacts, stratigraphy as related to human antiquity, and related



Florentino Ameghino
1854–1911

anthropological subjects. This work, mostly bearing on his claims that man arose in the Tertiary in Argentina, has been most extensively noticed and seems to be the main basis for his popular reputation in South America. It is, however, already fairly clear that his permanent place in the history of science will be due not so much to this anthropological work as to his less sensational studies carried out in the middle quarter century of his career, 1883–1906, when almost all his efforts were devoted to the non-human fossil vertebrates of Argentina, especially the mammals.

A few had worked on Argentine fossil mammals before 1883 and many besides Ameghino have worked on them since, but it remains true that he, single-handed, in 25 years made known to science more new South American fossil mammals than all other students together, before or since. Even without considering the economic and other difficulties that beset him during those years, this is an accomplishment of almost superhuman magnitude. Few in the Argentine or elsewhere paid much attention to Ameghino's earliest work. As its magnitude increased, however, it became widely known among paleontologists. Other paleontologists in the Argentine were often hostile, and the local scientific scene sometimes was one of internecine warfare. (This unfortunate situation was by no means confined to the Argentine: the Marsh-Cope war in North America overlapped this period.) Outside the Argentine, some aspects of Ameghino's work aroused certain misgivings, still not wholly allayed. His fame increased and his discoveries were widely hailed, but it has been usual to take many of his conclusions with a grain of salt.

Not unnaturally, the lay public in the Argentine was long completely indifferent to Ameghino's work, which they did not at all understand. As his scientific fame increased, popular acclaim also came to him, with only a limited measure of understanding of his aims. In fact the greatest acclaim was and is given to the least important and least sound parts of his work. By the time he died, he was a great man and recognized as such by his colleagues and countrymen. Thereafter, his popular reputation in the Argentine has resulted in what may almost be called deification. Any suggestion that he was mistaken on any point or that part of his work has been superseded is to this day considered personally insulting, if not downright blasphemous, by a considerable section of the public in Argentina. At one extreme any statement by Ameghino has been *ipso facto* suspect, and at the other his utterances have been considered completely infallible. It will not be too surprising to find that the truth lies between these two extremes. Most aspects of his work stand up at least as well as could be true of so large a body of research after 40 years of rapid progress. Other aspects are now entirely disproved.

This is really the first time that any considerable part of Ameghino's faunal studies has been thoroughly restudied and revised, on the basis of all his materials as well as those subsequently gathered. This has been an unparalleled opportunity to see how he worked and to judge his strength and weakness, free of blinding personalities. The strength is enormous and amounts to great genius. The weakness exists also, as it does in every mortal, and is partly that of the science of his time, weak only in retrospect, and is partly involved in his personality and history. The ambivalent mixture of reverence and distrust with which he was regarded in life and which still affects his reputation is rooted in a deep-seated duality in his own character, a complex antithesis that runs through all his work.

With particular reference to that part of his work to be revised here, the outstanding features of Ameghino's studies seem to me to be three: keenness and accuracy of morphological observation, breadth and insight in generalizing on the basis of the resemblances and differences detected, and a remarkable sense of sequence and ability for historical inference. These fine qualities make his work of lasting value, but each has a negative side that must also be honestly appraised: his detection of minute morphological differences was translated into an inflated taxonomy, his study of broad resemblances led to a strange dual phylogenetic scheme, half right and half wrong, and his sense of sequence was betrayed by a basic, subconscious fallacy into a consistent bias as to the age of each member of the sequence.

When Ameghino's specimens are compared

with his descriptions of them, the latter are usually found to be models of brevity, accuracy, and acuity. Most of his specimens are very fragmentary, his time and means did not permit their complete preparation, optical aids available were primitive, at best, from our present point of view, and many of the descriptions were written in a language foreign to him. In spite of these disadvantages, against which few today would even attempt to struggle, he saw and recorded all the essential characters of his materials, often including the most minute variations. Descriptive statements of fact in Ameghino's studies are usually completely correct, and I know of no student in this field who has maintained a higher standard of accuracy in combination with such an enormous output.

The reverse side of this medal is that he interpreted the slightest structural distinction as a taxonomic difference. There can be no serious question that he consistently exaggerated the taxonomic value of the real differences that he observed in his specimens. In the Casamayoran fauna, 16 specimens from a single locality, all surely of one genus (*Trigonostylops*), all of about the same size, and all closely similar in structure, were referred to 13 different species. A larger number of specimens which now appear to represent a single variable species (*Henricosbornia lophodonta*), and surely do not belong to more than a few very closely related species, were placed by Ameghino in three orders, four families, seven genera, and 16 species. The definitions given for these taxonomic units are correct descriptions of the specimens, but they cannot now be accepted as corresponding with real populations in nature.

This lack of a controlled and valid criterion for group as against individual characters was typical of Ameghino's day and is by no means unknown in ours. If he tended to inflate taxonomy more than was then usual, this, too, had understandable causes. Even when he later acquired excellent materials (e.g., in the Notopithecidae), the first descriptions were usually based on isolated teeth or small jaw fragments. Hence different names were applied to different parts of the dentition, to different stages of wear, or to specimens broken in different ways. Correction could only come from revision with larger collections and more complete specimens, but Ameghino never was able to revise his own work. He intended to do so, and the published descriptions are in almost all cases manifestly and explicitly preliminary, hastily written notes. The very magnitude of his discoveries and the shortness of his life prevented his going beyond these preliminary observations in most cases. This necessary haste, to which we owe the fact that he did accomplish so much, also meant that he did not always make all the necessary comparisons. Occasionally a specimen would be placed by first, rough sorting in the wrong genus and hence designated as a new species, although it belonged to a known species in its own genus. Ameghino ascribed 131 genera to the Casamayoran fauna alone, and not even that phenomenal mind sufficed to place every specimen without failure in its proper genus at first sight.

In the Casamayoran Ameghino's tendency to make little or no allowance for individual variation and his inevitable lack of modern biometric criteria were especially unfortunate. This fauna represents an "explosive" phase of mammalian expansion, when there were many very closely related lines and each line showed much variability: exactly the situation in which the criteria unavailable to Ameghino now appear most necessary.

These are the reasons why so many of Ameghino's names are reduced to synonymy in this memoir. The opinion has already been expressed to me that this "destruction of species and genera created by Ameghino" is unwarranted if not downright irreverent. It is unnecessary for most readers, but may help to placate these critics, to point out that Ameghino created no species. He only tried to recognize them. With many years' further accumulation of knowledge, with larger collections available as a unit and not coming in from the field piecemeal, and with modern facilities and concepts, I am sure that Ameghino himself would have come nearer to the present arrangement than to that he published so long ago.

It is probably Ameghino's views on phylogeny and broader relationships that have been most severely censured by his critics and most emotionally upheld by his supporters. Again, knowledge has increased enormously since 1906, when Ameghino published his essentially definitive views on this subject, and this has inevitably made possible and necessary many differences in detail. Nevertheless, in most cases Ameghino indicated in a general way what are still believed to be the correct relationships and approximate phylogenetic connections of most of the groups involved in this revision. Many of the criticisms of Ameghino's work in this field now appear to be unjustified, and insufficient tribute has been paid to his insight in inferring the affinities of his fossils.

Here the reverse of the picture is that in almost all cases he indicated two lines of relationship for his groups and that the two, believed consistent by him, must now be considered contradictory. For almost every group he indicated on one hand a true relationship and on the other what is quite surely a false relationship. The ancestral relationships indicated for the various lines and those within the lines themselves, as far as these concern Argentine fossils only, stand up very well, on the whole, in the light of modern knowledge. But in most cases he also indicated mainly or solely non-Argentine groups as derived from those of the Argentine, and these indicated relationships must now be considered incorrect, perhaps without exception.

Of course the resemblances on which Ameghino based these inferred phylogenies really exist. They were well observed and correctly reported. The difficulty is that all these groups have two sets of resemblances, and in some cases there is little to choose between the two as to quantity of resemblance although the quality is always different. Ameghino assumed that both sorts of similarities were homologies. Other students inferred that only one sort is homologous and that the other is homoplastic: one indicates phylogenetic relationship and the other indicates convergence or parallelism between unrelated or only distantly related groups. There can now be no serious doubt that this interpretation is usually if not always correct. Ameghino's almost complete rejection of the principle of homoplasy is as pervading in his work as his almost complete rejection of the reality of nontaxonomic variability.

Here again, and even more strikingly, Ameghino was unfortunate in his materials. It happens that the Tertiary mammals of South America exemplify homoplasy on probably the grandest scale of any known faunas. They underwent an independent adaptive radiation that resulted in most of these groups' resembling, sometimes very closely, an unrelated holarctic group of similar ecological status. The only key to this great, complex puzzle is homoplasy, and Ameghino did not use this key.

It is a peculiar, indeed ironic, fact that contemporary students of Ameghino's work frequently ignored the correct, or at least more probable, views as to affinity that he advanced and stressed the less probable in the many cases in which he indicated the two sorts of affinities noted above. For instance, Ameghino held that the Polydolopidae were related on one hand to the caenolestids and on the other to the multituberculates. Other students felt that both relationships cannot be phylogenetic and that one must be homoplastic. Until relatively recently it was generally considered that the phylogenetic relationships were with the multituberculates. There is now no doubt that this relationship is purely convergent and that the phylogenetic affinity is with the caenolestids. In accepting the wrong alternative, other students fell into more serious error than Ameghino, whose work they were seeking to correct but who did, at least, give the correct view along with the other.

The third outstanding characteristic and achievement of Ameghino's work, the correct establishment of a long, complex faunal sequence has already been stressed in connection with Carlos Ameghino, to whom, more than to Florentino, this achievement is due. It was, however, Florentino who systematized and published their stratigraphic system and it was he who established, with great skill, the local correlations necessary when the sequence could not be compiled from field observations alone. Thus the stressing of Carlos' contribution, which has sometimes been overlooked and usually undervalued, should not obscure the fact that Florentino's role in this, too, was far from negligible and that neither brother could have accomplished this part of the work alone.

As with his phylogenies, Ameghino's stratigraphic conclusions within his own field, that is, as far as they were confined to the Argentine, were generally correct. They were, in fact, surprisingly good for the time and far ahead of the work of any contemporaneous student. The few definite errors since detected, such as the correlation of the Casamayor with the Salamanca formation, were of the sort hardly avoidable in reconnaissance of an unknown and difficult field, to be corrected only after many years of additional study.

But, also as in the phylogenies, Ameghino went consistently astray when he compared his Argentine sequence with that of the rest of the world. It is now universally agreed, by the Argentine successors of Ameghino as well as non-Argentine geologists, that he claimed too great an age for all the Argentine stages and faunas in terms of the world sequence. For instance, he considered the Casamayoran and Mustersan as Cretaceous, and not latest Cretaceous (Cenomanian to Senonian). It is now recognized by everyone that they are Tertiary, and not earliest Tertiary.

Ameghino marshalled a great body of evidence in favor of his intercontinental correlations, and he argued his case carefully and cogently. It would be possible to take up again each item of the evidence and to show that in the light of present knowledge, at least, the stated conclusion does not really follow. I have, in fact, done this and so, on various points, have other students, but it is unnecessary to give these details here. The evidence available to Ameghino was both incomplete and equivocal. He happened to be dealing, as in his phylogenetic studies, with one of the most difficult problems in this field, one that is still not solved with sufficient precision and certainty. It is not adverse criticism to say that the evidence did lead him astray, but it must be frankly recognized that he showed strong personal bias in his evaluation of it and that he considered it sufficient and conclusive when it was not.

Injustice was also done to Ameghino in stratigraphy as in phylogeny, and the progress of knowledge has been delayed by some tendency to reject what was correct in his work and, at times, to accept what was incorrect. Thus until rather recently it was accepted that the beds now called Riochican were Cretaceous and dinosaur bearing, as Ameghino incorrectly believed, but that they were not closely related in time and fauna to the Casamayor, as he correctly inferred. There has been a general tendency to ignore or even to deny the existence of the *Astraponotus* (Mustersan) fauna, but it exists and has the characteristics assigned to it by Ameghino. Numerous examples of this curious failure to distinguish the sound and the unsound in Ameghino's work will appear in the course of the present memoir. General and, it must be admitted, justified recognition of bias in one part of his work has infected judgment of the whole. It has not been sufficiently recognized that most of his work was perfectly sound and that there is a consistent, definable difference between the fields in which he was sound and those in which he was not.

The particulars in which Ameghino's work was unsound or, more fairly, in which it has proved not to be definitive, are all parts of a larger picture. His taxonomic inflation is a partial exception, but even this, to the extent to which it went beyond that usual in his day and in work on such materials, has some relationship. As far as his work was purely observational, it was usually sound and has high permanent value. Beyond this, his interpretive work was orthodox in his day and still stands up very well in ours as far as it was confined to the local scene. It was in fitting this Argentine material, taxonomic, phylogenetic, and stratigraphic, into the broader framework of world history that Ameghino became an extreme non-conformist and that he produced theories that have not stood the test of time.

It would be a facile explanation to suppose that the source of this non-conformism was Ameghino's isolation, but this could be and sometimes has been overstressed. Early in his career (1878–1881) he spent three years in Europe where he collaborated with Gervais and met many other leading scientists. He later corresponded continually with almost all the vertebrate paleontologists of his time, and he kept well abreast of all the pertinent current literature. Paleontological work was quite active in the Argentine during his lifetime, perhaps even more so than now, and several distinguished foreign paleontologists made long visits there. It is true that he was not on good terms with all his compatriots or all foreign visitors, but he certainly came in contact with their knowledge and ideas and he cooperated liberally with those, like Ihering, Tournouër, and Scott, who approached him in a courteous and cooperative spirit.

Ameghino was intellectually isolated in his formative earliest few years of research, but during much the greater part of his career this cannot be considered a simple or sufficient explanation of the eccentricity of certain of his basic theories. In later years, too, there was an element of isolation, but this was much more subtle than a mere lack of contact with the general currents of scientific opinion and can be viewed as an effect rather than as a cause of his tendency to go against these currents. Then, too, isolation would hardly explain why within the limits of his immediate field his work was orthodox and, for the time, completely modern if not ahead of his contemporaries and that it became unorthodox or really eccentric only where it touched on certain broader problems.

The peculiarities of these phases of Ameghino's work can only be ascribed to a fundamental intellectual orientation, an orientation with a deeply rooted emotional basis. This eventually became so ineradicably a part of his scientific outlook that it blinded his otherwise excellent critical faculties whenever this part of the subject arose. He never put this growing obsession into quite such blunt words, but it can be expressed thus: "My country is the center of origin of all groups of mammals and of man, and I am the discoverer of their ancestors." Some degree of egocentricity and of nationalism is inevitable, even in scientists, but in Ameghino's case this orientation became so complete and was so emotionally sustained as to be more than normal. The irrational element was evidently subconscious, and no trace of intellectual dishonesty exists, but I think no one can follow Ameghino's work as it developed year after year without agreeing that this unscientific *parti pris* did come to influence all his mature work.

Perhaps the ultimate origin of this subconscious bias can never be fixed, but there are some hints. Ameghino was the son of poor Italian immigrants. In later polemics against him by some of his unfriendly colleagues, it was claimed that he was born in Italy. Objectively it is hard to see what possible difference it would make whether he was born in Italy just before his parents emigrated to the Argentine or in the Argentine just after they arrived there. In either case his earliest memories and all his formative influences were Argentine, and in either case his parents were immigrants. But the fact that by Ameghino himself this suggestion was taken as a serious accusation is enlightening as to the emotional effect on him of the family history.

When he was only 20 and was in fact an isolated and unappreciated masterless apprentice in science, his first publications were on the great antiquity of man in the Argentine. In 1876 he said (in a memoir unpublished until after his death) that he had then been making geological and paleontological investigations for seven years (i.e., since the age of 15!) with "the principal aim of ascertaining the true geological age of man on the pampa." These early and necessarily amateurish investigations brought him his first fame, definitely committed him to his career, and incidentally established a position from which he never retreated.

His fiery determination and tremendous drive towards accomplishment were accentuated by struggles throughout his life. Poverty, hardship, and hostility were usual companions, and the natural reaction was intense determination to maintain and prove that he was right. It is only necessary to read some of the almost indecent and wholly disgraceful printed attacks on Ameghino by Burmeister, who seems simply to have been jealous of an able junior colleague, to see what an effect they would have on a sensitive, proud man who had always had to make his own way in the world.

Even so, there is reason to believe that he might have abandoned his great, mistaken, underlying thesis before it became an *idée fixe* if his critics, however violent, had been more judicious. I have repeatedly referred to the dualism of his work: sound and excellent in the main, but unsound when it bordered on this central obsession. His contemporaneous critics made no such distinction. They attacked his sound views as much as his unsound. Much of what they said was flatly wrong, and Ameghino knew beyond any doubt that it was wrong. He can, then, hardly be blamed for becoming confirmed in all his own opinions.

An exemplification of this is provided by an important incident that may finally and immutably have fixed Ameghino in his ways. Hatcher attacked Ameghino's ideas of faunal sequence in Patagonia, a field in which Ameghino made very few mistakes indeed. Hatcher was quite wrong on this point, as Ameghino knew without question. Ameghino (1898) concluded that, "This is not a personal error: it is rather the collapse of a very vast structure, built on foundations that seemed solid but that are seen today to be quite fragile." For Ameghino, the whole body of theory upheld by European and North American paleontologists was tested by this incident, and it failed. Therefore, he concluded, he must also be right and the Europeans and North Americans wrong in theories of molar evolution, of world-wide phylogeny and correlation, and the rest. In fact Hatcher's mistake was entirely personal. It was not that he applied the "preconceived ideas," as Ameghino called them, of the orthodox school and came up with the wrong answer, but just that he failed to apply them. Not to put too fine a point on it, he did not know what he was talking about. The orthodox theories, as Hatcher later recognized when he did become acquainted with the facts, show well enough that Ameghino was right on this particular point, just as they prove him wrong on others. This incident and others like it are tragic, because they effectively prevented Ameghino's wider progress as a theoretician, progress which would greatly have benefited him and the world.

So Ameghino proceeded to build up a complex, rigidly interwoven body of theory that has had to be almost wholly discarded. Early Patagonian mammals were ancestral to those of Holarctica because they were similar but older and more primitive. Their being more primitive confirmed the greater age of the beds in which they occurred. Characters of mammals found in beds of such great age must be primitive. Morphogenetic theories, like that of trituberculy, indicated that they were less, not more, primitive. Hence the theories were wrong and new diametrically opposed theories must be produced. These new theories do not agree with the usual concepts of phylogeny and correlation, so those concepts are wrong and must be replaced. And so the structure grew, each step dependent on the last, each in turn taken as confirming the last, and underlying all, a deep emotional conviction which no evidence really supported but no opposing evidence could shake.

Insight into these and other factors of Ameghino's personality and life serves only to strengthen sympathy for him and admiration for his achievements. He had no peace or rest, but he labored endlessly, and the results of those labors are truly great. He suffered and some aspects of his work suffered but his fundamental emotional compulsions also sustained him. His enormous productivity was largely brought about by the drive thus originated and strengthened. It is noteworthy that many of his longer and more valuable works, such as the "Formations sédimentaires" and the "Recherches de morphologie phylogénétique," were inspired by criticism and written in polemic mood. He complained that his critics kept him so busy answering them that he had no time for more serious work, but it is clear that these answers contain much of his most serious work and that he would never have gotten around to publishing some of his most important data without the spur of criticism. Much of his work—it might not go too far to say all of it—was his answer to a world that he found hostile. Appreciation and revaluation of all that can be approved in his work—and how much this is!—and an attempt at understanding whatever cannot now be approved, these are the most sincere tribute that I can pay to the memory of my great predecessor in the study of the beginning of the Age of Mammals in South America.

ORIENTATION: LOCALITIES

Precise and full data as to collecting localities, local faunas, faunal succession, and stratigraphy will be given in a later section of the memoir. It is, however, necessary from the start to give the general geographical and geological framework into which the systematics parts of the memoir fit.

The accompanying map (fig. 1) shows, in a somewhat general way, most of the localities worked by the Scarritt expeditions. These include or are near all of the Ameghinos' localities for the faunas here in question. After our first expedition I was able to check this with Carlos Ameghino himself, and he confirmed that virtually all of his specimens of these faunas came from one or the other of the localities here indicated, at least from the general areas shown if not from the exact spots. Two other rather large areas of Casamayoran exposures are indicated in Ameghino, 1906 (fig. 22), one on the Río Deseado and one on the upper Río Senguerr. The identification of Casamayoran strata in these areas is believed to be correct, but no identifiable fossil mammals were found in them, either by Carlos Ameghino or by us.

The localities shown and the principal faunas collected at each are as follows:

1. Barranca (cliff) south of Lago Colhué-Huapí: Casamayoran and Mustersan (also the later Deseadan and Colhuehuapian), all relatively rich. The most important single locality both faunally and stratigraphically. This was Carlos Ameghino's discovery local-

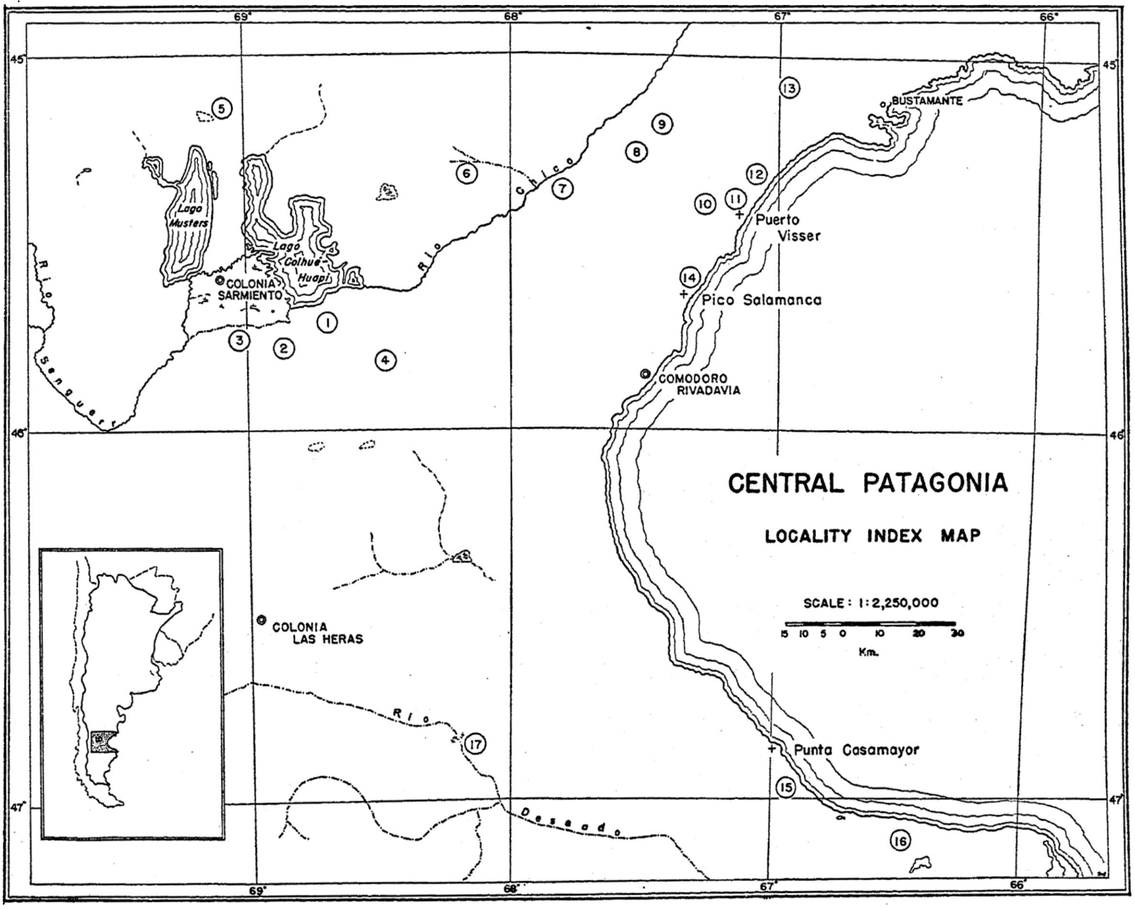


FIG. 1. Locality index map of central Patagonia. The numbered localities are specified in the accompanying text.

ity for both the Casamayor and the Musters and most of his specimens of both faunas are from here.

2. Kilometer 170 (of the railroad from Comodoro Rivadavia to Colonia Sarmiento): Relatively unimportant Casamayoran locality, section similar to part of locality 1.

3. Cerro Blanco: Essentially a continuation of locality 1.

4. Valle Hermoso: Small Casamayoran collection.

5. Cerro del Humo: A major locality for the Mustersan, also some Casamayoran (and Deseadan). This is probably Roth's "Lago Musters" locality. A locality called by the Ameghinos "Colhué-Huapí Norte" was in the vicinity, but probably not exactly the same.

6. Cañadón Vaca: One of the richest Casamayoran localities. Carlos Ameghino also collected extensively in this region, although he did not think, in 1931, that he had been at the exact spot where we found most of our specimens.

7. Cañadón Hondo: A major locality for the Riochican fauna and also includes an unusual variety of Casamayoran facies.

8. Cabeza Blanca: Mainly a Deseadan locality, source of a great part of the Ameghino collection of that age and all the Loomis collection, but with large Casamayoran exposures around it, nearly barren but some identifiable specimens. Carlos Ameghino found a few of his Casamayoran fossils at and near this locality.

9. Near Cabeza Blanca: Extensive but not very rich Casamayoran exposures. Carlos Ameghino told me that he, too, had collected at this locality, with poor results.

10. Lomas Blancas: Faunally unimportant Casamayoran locality.

11. Cerro Redondo: Riochican (and Salamancan).

12. Las Tortugas: (Salamancan and transitional to Riochican, no mammals).

13. Las Violetas: Salamancan and Riochican, possibly some Casamayoran but fossils not found in latter. Unimportant for mammals.

14. Pico Salamanca: The region around the peak is one of the most important for Riochican stratigraphy and mammals. Rather sparsely fossiliferous Casamayoran is also widely exposed. (Also type Salamancan, which, however, does not form the peak itself.) Three of Ameghino's Casamayoran types, and some other fragments, were found in this general region.

15. Cañadón Lobo: This (Cañadón Tournouër of Ameghino) is essentially the type locality of the Casamayor, but it is only sparsely fossiliferous and is of little importance for this fauna.

16. Punta Nava: (A Deseadan locality).

17. Pico Truncado: Very sparsely fossiliferous, probable Casamayoran. (Also Deseadan in the general vicinity.) The Ameghinos indicated Casamayoran in this region, but the collection contains no specimens so labeled, and Carlos Ameghino told me he had found none here.

Scattered specimens have been found in this region aside from these key localities for stratigraphy, faunas, or both. There are also a few localities to the north, beyond the limits of the index map now published. They will be included on a map on a larger scale and in greater detail being prepared for the stratigraphic section of the memoir. Most pertinent at the present point are the following:

A. Trelew-Gaiman region on the Río Chubut: Sparsely fossiliferous Riochican and probably Casamayoran, without known identifiable fossils (also important Coluehuapian mammals). This was one of Roth's localities but was not visited by Carlos Ameghino.

B. Rinconada de los Lopez, on the west side of the Meseta Canquel, between the Chubut Valley and the Colhué-Huapí basin. Some Casamayoran mammals (also an unusual and rich Deseadan fauna).

C. "Cañadón Colorado" of Roth: A small but important Mustersan collection made by Roth is so labeled. On an unpublished map based on Roth's notes, the locality is shown at approximately 68° 30′ W., 44° 30′ S. The deposit has not been relocated.

Roth also said that he had found Casamayoran mammals in another locality, apparently somewhere around 70° W., 44° 30′ S. The specimens were not described and have apparently been lost. The significance is nil at present, except as a possible lead for future exploration.

ORIENTATION: STAGES

One to 15 sections were measured by me at each of the localities listed above (and a few others), except "C," one of Roth's localities not yet rediscovered. Almost all of our specimens are exactly located on one of these measured sections, and these data will be given *in extenso* in the stratigraphic part of this memoir. In the systematic part of the memoir, stratigraphic occurrence will be defined by locality and stage, with supplementary comment when there is more than one faunally separable occurrence at one general locality within one stage. Similar data are available and are given here for the Chicago Museum specimens.

Because of the early date and pioneering nature of Carlos Ameghino's work, the primitive conditions under which it was done, and his tendency to keep notes in his head rather than on paper, there are no exact data for any specimens in the Ameghino Collection. All the specimens are labeled as to stage or general fauna ("*Notostylops*" or "*Astraponotus*"), and in a very few scattered cases there is some indication as to position within the stage, upper or lower. A general locality is recorded for perhaps half the specimens. As far as they exist, these data are given for the Ameghino specimens throughout the systematic part of this memoir.

The age or stage data given by Roth all appear to be incorrect, but in all but a few cases the stage can now be identified without serious doubt. General localities were recorded by Roth and are here given for his specimens.

The early Tertiary mammals of Patagonia, as here understood, are those that occur between two major marine incursions, the Salamancan below and the Patagonian above. In previous literature, the Salamancan is usually designated as late Cretaceous, but there is some probability that it is Paleocene. The Patagonian is now generally considered mid-Tertiary, latest Oligocene, or earliest Miocene as to its basal part. Between these (usually) easily recognizable marine formations there is a thick and widespread sequence of terrestrial deposits grossly divisible into two lithologic groups, a lower complex of sandstones and clays, now called the Río Chico group, and an upper complex almost entirely composed of tuffs (often or usually reworked) and bentonites, now called the Sarmiento group.

As will appear in detail later, there is evidence that the Río Chico group contains different successive faunas so distinctive that separate designations and stage names will probably be necessary for them. At present, however, few of these successive phases are known, and each is represented only by a scanty local fauna. It would be premature to attempt definite stratigraphic or temporal subdivision. All fossils from this group are therefore now considered as representing a broad Riochican stage, although, of course, the local faunas are separately designated as such, by locality and horizon.

In what is now called the Sarmiento group, Ameghino distinguished four successive beds ("couches" in the French of Ameghino, 1906) and four corresponding faunas. He named these for characteristic (but not the most abundant) mammalian genera in each, in sequence from oldest to youngest Notostylopéen (for *Notostylops*), Astraponotéen (*Astraponotus*), Pyrotheréen (*Pyrotherium*), and Colpodonéen (*Colpodon*). At any one locality it is almost always possible to determine which beds occur and to draw a line between them if more than one is present, so that in theory these could and should be mapped as separate formations. As far as I know, however, this has yet to be done in practice, even for very small areas.[1] The whole group is lithologically fairly similar throughout, and horizontal differences of lithology in beds of the same age are likely to be considerably greater than vertical differences between beds of different ages. The mapping unit is thus the Sarmiento group as a whole, although it is proper to speak of it as including (at least) four distinct and distinguishable but as yet unmapped formations.

The successive faunas of Ameghino corre-

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[1] Ameghino (1906) gave separate maps showing the distribution of each of these formations, but on a very small scale and in a general way. The maps cannot be put together to give a real areal geological map, properly speaking.

spond with sufficiently clear-cut temporal units approximately equivalent in status to North American or European Tertiary provincial ages and stages and well definable as such. In accordance with modern practice, names of geographic rather than generic origin are now applied to these: Casamayoran, Mustersan, Deseadan, and Colhuehuapian. The corresponding names in substantive rather than adjectival form are applied to the formations, when reference is to these rather than to stages: Casamayor, Musters, Deseado, and Colhué-Huapí. As a matter of fact, because of the great horizontal variation and the occurrence of strikingly distinctive local or regional lithologic units within a given stage, a considerably larger number of names will be required for rock units when these come to be distinguished consistently as such in the areal geology.

The early Tertiary sequence as here used is summarized in the accompanying table (table 1). As previously stated, the systematic part of this memoir is confined to the faunas of the Riochican, Casamayoran, and Mustersan stages.

TABLE 1

SUMMARY OF EARLY TERTIARY STRATA AND STAGES IN PATAGONIA

Ameghino, 1906		Current Map Units	Current Stages	Approximate Ages
"Formations"	"Couches" and "Faunes"			
Patagonienne	Patagonien[a]	Patagonia group[a]	[Patagonian]	Miocene
	Colpodonéen	Sarmiento group	Colhuehuapian	Oligocene
Guaranienne	Pyrotheréen		Deseadan	
	Astraponotéen		Mustersan	Eocene
	Notostylopéen		Casamayoran	
	[Notostylopéen basal]	Río Chico group	Riochican	Paleocene
	Salamanquéen[a]	Salamanca formation[a]	[Salamancan]	

[a] Marine.

SYSTEMATICS

ARRANGEMENT AND CONVENTIONS

"SYSTEMATICS" IS HERE TO BE UNDERSTOOD in the broadest sense. It includes not only formal classification and nomenclature, but also a discussion of the affinities and of the morphology of each taxonomic unit. When materials permit, special attention has also been paid to the variability manifested by various species. Some general morphological problems, such as that of notoungulate ear structure, are considered in connection with species or genera, available specimens of which are particularly significant for these problems.

Unless omissions have accidentally been made, every technical name previously proposed for species and genera of these faunas is listed, whether it is here considered valid or not. Many of these names are reduced to synonomy, but in each case the reasons for doing this are explicitly given and the supposed distinctions are mentioned. In this way, the reader is not wholly at the mercy of my personal judgment and can find the characters of units that I consider invalid as well as of those I consider valid.

There are, as it happens, some names, especially in Ameghino's work, the validity of which can hardly be judged one way or the other at present. When working with fragmentary materials and without knowledge of associated parts or of range of variation, Ameghino sometimes gave diagnoses descriptively correct but not really diagnostic with respect to related species or genera. In many of these cases new materials elucidate the situation and establish the name either as valid or a synonym. In other cases the supposed unit still cannot really be defined either on the basis of the original diagnosis or from the available specimens. Such names are not now known to be valid, and they cannot be applied to any specimens other than the type or syntypes. It is improbable but is conceivable that some of them can be clearly validated by future work. It would be misleading to list these names and to use them on the same basis as names of reasonably established status, because they really have no meaning or value at present. On the other hand, they are not technically homonyms, synonyms, or *nomina nuda*, and they maintain a standing in nomenclature although they have none in zoology. They are now, and in most cases probably will remain, mere empty names without real meaning. Where I have little doubt that this is the real status of a name, I designate it as a "*nomen vanum*," i.e., "empty name."

Basic information on each species is given in a standard sequence which is self-explanatory: accepted name and synonyms, with citations, type or syntypes and lectotype (which is always chosen when syntypes were originally used), hypodigm (i.e., all the specimens on which my concept of the group is based), horizon and locality, and diagnosis. Such of these standard items as are pertinent are given for genera. For families and higher units, for which the bibliographic information is already easily available, only definitions and distribution are usually given. Additional information, such as morphological descriptions, views on affinities, and reasons for synonymy, are given as convenient in discussions without standard or separate headings.

Locations of specimens are abbreviated as follows:

A.M.N.H., in the American Museum of Natural History, New York, New York, U.S.A.
C.N.H.M., in the Chicago Natural History Museum, Chicago, Illinois, U.S.A.
M.A.C.N., in the Museo Argentino de Ciencias Naturales, "Bernardino Rivadavia," Buenos Aires, Argentina
M.L.P., in the Museo de La Plata, La Plata, Argentina

Throughout the memoir, measurements of specimens are in millimeters, and the following abbreviations are used in tables of measurements and statistics:

L = length
W = width
N = number of specimens measured (size of sample)
OR = observed range
SR = standard range
M = arithmetic mean

σ = standard deviation
V = coefficient of variation
± = plus or minus, standing before the standard (not probable) error

MARSUPIALIA

Marsupials play an important part in the early Tertiary Patagonian faunas. The variety is considerable, although the number of specimens is not great. In the Río Chico six species and a doubtfully marsupial seventh are indicated by one specimen each in the materials known to me, and in the Musters only five species, mostly of rather doubtful status, are known. The Casamayor species and specimens are much more numerous, but still form only a small proportion of the fauna and of collections. The true proportion of marsupials in the living fauna was probably greater than is shown by collections. They are for the most part very small and probably had habits opposed to their abundant representation as fossils. Many were probably arboreal, and another large group was composed of predaceous carnivores—both ecological groups normally rather poorly represented as fossils.

Although marsupials continued to be of importance throughout the Tertiary in South America, they were at their greatest in variety in the Casamayor beds, where they are more varied than in any other known fauna outside of Australia. Ecologically they replace several groups of placentals not yet present or at least exceedingly rare in Patagonia in Casamayoran time. Thus they are more or less parallel to, and occupy the life stations of, insectivores, primates, rodents, and carnivores. Expressed in other words the whole unguiculate division of the fauna was confined to the Marsupialia and Xenarthra, in sharp contrast to contemporaneous Holarctic faunas where these groups are rare or absent and the ecologically unguiculate element is distributed in half a dozen placental orders absent in the early Tertiary of South America.

The wide divergence of the group is seen in the number of families present, five, greater than in any other time or place outside of Australia which has (in a broad classification) six recent families and which had seven known in the Pleistocene. These Casamayoran families are as follows:

Didelphidae
Caroloameghiniidae
Borhyaenidae
Caenolestidae
Polydolopidae

In the Río Chico only Borhyaenidae and Polydolopidae have been reported, but all five families were almost certainly present, and the absence of the other three in collections may be imputed to the general scarcity of fossils from this formation. In the Musters, borhyaenids and, somewhat doubtfully, caenolestids are known. Didelphids were unquestionably present although not yet discovered. Negative evidence is of little value when so few specimens are known in all, but it is possible that caroloameghiniids and polydolopids were already extinct by Musters time, as they almost certainly were before the Deseado.

Of the Didelphidae and Caenolestidae we know simply that they were present in the Casamayor, at least, but little else is known about them at this time. None of the other families is represented by as much as a complete skull or by any skeletal material of certain reference, but the dentitions are fairly well known in two or more species of each. The most divergent and specialized family, the Polydolopidae, includes far the largest number of named and identifiable species.

This diversity of marsupials in the early Tertiary clearly indicates great antiquity for the group and must almost surely date from the Cretaceous, perhaps well back in the Cretaceous. The Cretaceous didelphoids of North America indicate the same thing. They are quite diversified, although with much less fundamental variance of pattern than in the Casamayor. There is no direct and positive evidence that these South American specialized marsupials were derived from the North American Cretaceous fauna. This lack of evidence does not warrant the belief that they were not so derived, since no other evidence points to a theory more probable, but it leaves the whole question unsettled. None of the known North American Cretaceous marsupials shows any evidence of special affinity with any of the four more specialized South American families.

Paleontology and comparative anatomy

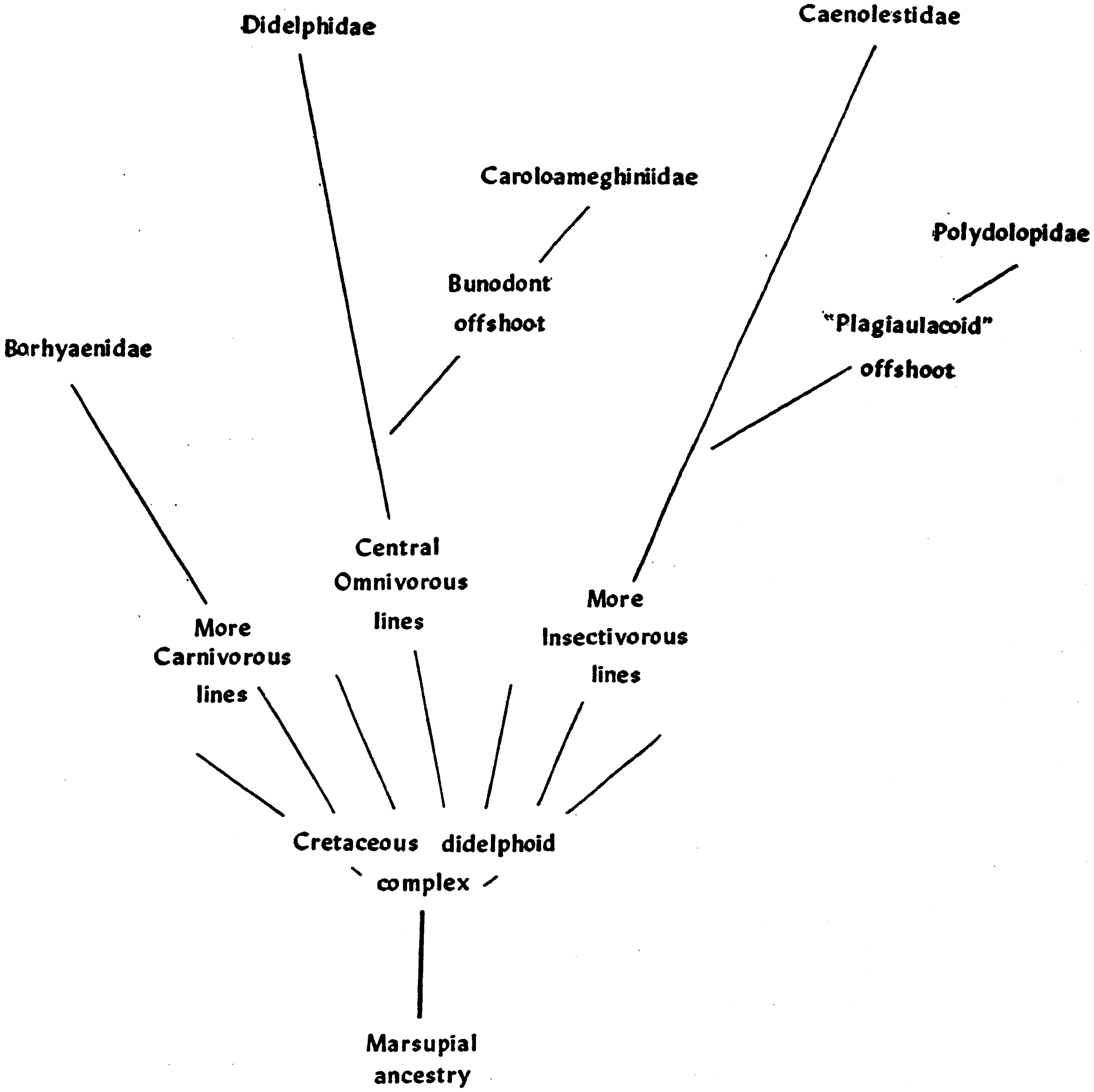

FIG. 2. Suggested ancestry and relationships of the South American families of marsupials.

point without any serious contradiction to a single primitive marsupial stock closest to the Didelphidae on one hand and to the Dasyuridae on the other. This stock must have combined the more primitive characters of both groups, but was probably closer, structurally, to the later Didelphidae because that family retains, on the whole, more primitive characters than do the dasyurids. By Casamayoran time, evolution from this central group had proceeded for different distances along several distinct lines. Least divergent were the Caroloameghiniidae, which seem, as far as the dentition is concerned, to be still definitely didelphoid, but to be progressing towards a frugivorous-omnivorous type of multicuspid bunodont dentition paralleling some of the primates. The Borhyaenidae accentuated the carnivorous tendencies fundamental in the didelphoid ancestry and had already progressed far and become rather strongly divergent among themselves, some being small and still rather opossum-like forms, others great predators.

Widest divergence from the ancestral type is seen in the caenolestoid group, primarily distinguished in the dentition by the development of large procumbent incisors and reduction of the teeth between them and the last premolar or first molar. In addition to its primitive family or central line, the Caenolestidae, themselves quite diverse at a somewhat later epoch and probably also at this time although poorly known, this stock had already given rise to the extraordinarily specialized Polydolopidae.

The affinities of the several families are discussed separately below. The evidence now available seems to me to indicate some such phylogeny as is shown in figure 2.

DIDELPHIDAE

This family may be used in a broad sense for all the most primitive polyprotodonts of the Western Hemisphere, a group rather circumscribed in structure although several diverse tendencies are manifest, especially in the Cretaceous. Ameghino lists one wholly dubious specimen from the Casamayor as mentioned below. This hardly suffices even to establish the presence of the family in this fauna, but that it was present is shown by specimens in our collection (below). Didelphids have not yet been found in the Río Chico or Musters.

IDEODELPHYS Ameghino, 1902, nomen vanum

Ideodelphys Ameghino, 1920a, p. 43; 1906, p. 468.

Ideodidelphys, Schlosser, 1923, p. 442.

Type: *Ideodelphys microscopicus* Ameghino.
Distribution: Casamayor, Patagonia.
Diagnosis: Generic characters unknown.

Teeth are as yet unknown in this genus, and the jaw fragments reveal no characters fairly considered generic. Yet if jaws were found with teeth they probably could be referred to Ameghino's species and probably would be generically distinctive from later forms. Reference to this family (or to the included Microbiotheriidae of Ameghino) depends on the small size, large number of evenly graded alveoli, and apparent absence of an enlarged incisor. This is far from conclusive, but is probable.

Ideodelphys microscopicus Ameghino, 1902

Ideodelphys microscopicus Ameghino, 1902a, p. 43.

Type: M.A.C.N. No. 10344, lower jaw, no teeth, alveoli probably for P_{1-3} M_{1-2}.

Horizon and Locality: Type from south of Lago Colhué-Huapí, referred specimen from Cañadón Vaca. Casamayor.

Diagnosis: Eleven alveoli occupying a space of 7 mm., mandible 2 mm. in height (Ameghino).

We found another specimen (A.M.N.H. No. 28423) apparently of this same species but also without teeth. Its practical significance is at present nil.

COÖNA Simpson, 1938

Coöna Simpson, 1938b, p. 1.

Type: *Coöna pattersoni* Simpson.

Distribution: Casamayor formation, Eocene, Patagonia.

Diagnosis: Small didelphids with lower jaw and dentition of generally didelphine aspect. P_3 (alveoli) about as large as M_1. M_3 (probably also $_{1-2}$) 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, near entoconid. Talonid of M_4 as wide as trigonid or slightly wider and of about the same area, fully basined and closely similar to that of M_3, with three quite distinct cusps, the hypoconulid not enlarged or produced but about as on M_3. M_4 as a whole smaller than M_3.

Coöna pattersoni Simpson, 1938

Text figure 3

Coöna pattersoni Simpson, 1938b, p. 2, fig. 1.

Type: A.M.N.H. No. 28907, left lower jaw with alveoli of P_4–M_2, whole crown of M_3, and M_4 with trigonid broken. Collected by C. S. Williams and G. G. Simpson, March, 1931.

Horizon and Locality: Casamayor, green bentonite series at type locality of *Sebecus icaeorhinus*, *Crossochelys corniger*, etc., in Cañadón Hondo, Chubut, Agentina.

Diagnosis: Sole known species of *Coöna*.

The alveoli show that P_3 was about as long as M_1 and nearly as wide. M_1–M_3 were progressively larger, and M_4 abruptly smaller, perhaps about the size of M_1. The posterior alveoli of M_1–M_2 are noticeably larger than the anterior, and the preserved crown of M_3 shows the reflection of this in the wide talonid. As in most didelphids, this tooth has oblique anterior and posterior cingula, the latter running into the hypoconulid. The other dental characters are adequately represented in the diagnosis and the figure.

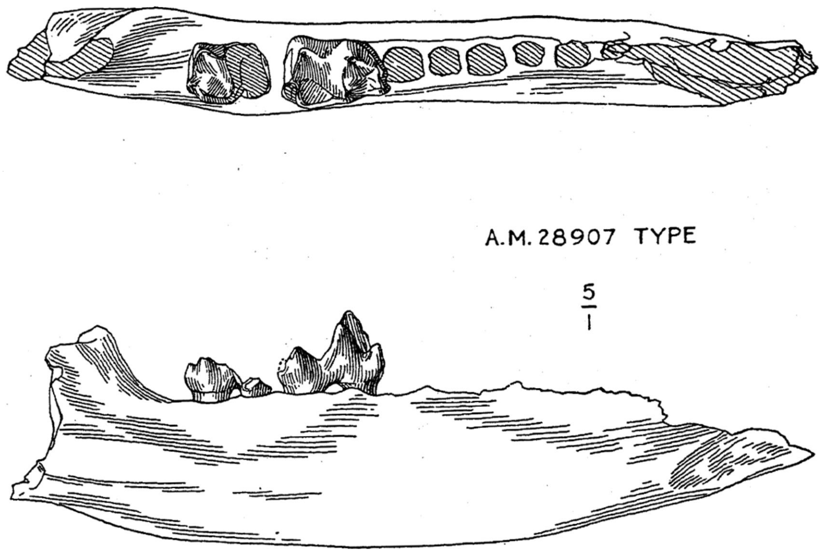

FIG. 3. *Coöna pattersoni* Simpson. Type A.M.N.H. No. 28907, left lower jaw with M_3, talonid of M_4, and alveoli of other teeth. ×5.

The jaw is slender, simple, and much as in other small didelphids. The long, open symphysis reaches nearly to the anterior end of P_3. There is a mental foramen beneath the posterior root of M_1. On the outer side of the ramus beneath M_3 there is a prominent oblique groove, evidently pathological or a postmortem injury.

Didelphids, although forming a very small fraction of the collections, are well represented in various South American faunas from the Colhué-Huapí formation (probably latest Oligocene) to the recent. Before the Colhué-Huapí the only records have been the practically unidentifiable *Ideodelphys microscopicus* Ameghino (see above) and *Proteodidelphys praecursor* Ameghino, each represented only by a single specimen. The latter was supposed to be from the Cretaceous "areniscas abigarradas," but I have elsewhere shown (Simpson, 1932a) that there is no credible evidence of this, that the specimen is morphologically indistinguishable from mid-Tertiary forms, and that everything suggests that it is, in fact, from the mid-Tertiary.[1] In any case it cannot be accepted as of greater age and should, lacking any confirmation, be omitted from considerations of marsupial history.

The minute jaw of *Ideodelphys* is much smaller than that of *Coöna pattersoni*, and the alveoli have quite different proportions, so that it is certain that the species are distinct and all but certain that the genera are.[2]

Coöna is thus really the only definable South American didelphid known to be from beds older than the Colhué-Huapí. Its most

[1] It was not found by Carlos Ameghino, who would not have made such an error, but by a worker whose field data are not reliable. Scott (1937) has recently compromised the argument by assigning the specimen to the Río Chico, which is practically impossible, or at least is contrary to all the evidence and claims on either side.

[2] In any case there would be no excuse for referring the present species to *Ideodelphys* simply because it cannot be absolutely proved not to belong to it; in that case all opossums described since 1902 would have to be referred to *Ideodelphys* since none of them can be rigidly proved not to belong to it.

surprising and important characteristic is that it is definitely not a member of the Microbiotheriinae, the subfamily to which all the other defined South American didelphids older than the Pliocene belong. As I have elsewhere pointed out (Simpson, 1935d), M_4 of the microbiotheres is very distinctive because it is markedly reduced in size and has a very narrow, nearly unbasined heel, with only one really distinct, posteromedian cusp. M_4 of *Coöna* not only does not have these talonid characters, but also suggests an even greater difference from them than is seen in the Didelphinae, for instance, because the latter do commonly have the talonid of M_4 narrower than the trigonid and with a relatively large and posteromedian hypoconulid. The microbiotheres also appear usually or always to have the hypoconulid of M_3 (and the more anterior molars) more median than in *Coöna* and more coordinate with the hypoconid and entoconid as an element of the talonid rim.

In a general way *Coöna* compares rather with the Cretaceous Pediomyinae and the earlier Tertiary Didelphinae of North America than with the Microbiotheriinae. I am not, however, acquainted with any pediomyine that has exactly the structure and proportions of M_3 seen in *Coöna*, or with any pediomyine or didelphine that is known to have a closely similar M_4. *Peradectes elegans*, a didelphine from the Tiffany, Upper Paleocene, of North America, seems to compare as closely with *Coöna pattersoni* as does any other previously known form. Its M_3 is very similar, differing only in minute details of doubtful value, such as the facts that the entoconid does not so nearly reach the height of the paraconid and that the disparity in width between trigonid and talonid is less marked. The talonid of M_4 is, however, definitely unlike that of *Coöna* and more like that of the later true didelphines, being somewhat elongate, narrower, and with a projecting hypoconulid which is the highest talonid cusp.

As hitherto known, the most probable interpretation of the history of the modern opossums has been as follows. In the Cretaceous of North America (and very likely also on other continents, although not yet discovered elsewhere) opossums were very abundant and extraordinarily varied. Probably from one group of these, the relatively unspecialized Pediomyinae, arose the didelphine stock, also varied as regards very minor characters but extraordinarily unprogressive and stereotyped in basic morphology. These occurred in the older Tertiary in Europe, but died out there in the Miocene. In North America they are known from the Paleocene to the Miocene and again in the Pleistocene and Recent. It is probable that their apparent absence towards the end of the Tertiary is merely caused by non-discovery, that they lived in North America continuously, and that the living genus *Didelphis* was autochthonous here. In South America the known Middle Tertiary forms are microbiotheres and could not be ancestral to the living South or North American opossums. Opossums of recent type appear with apparent suddenness in the later Tertiary of South America, and it seemed probable that they were invaders from the North American didelphine stock, making entry in advance of the major wave of continental intermigration.

As regards *Coöna*, three possibilities are worthy of special consideration:

1. That it is an ancestral microbiothere, these animals becoming typically developed only towards the middle Tertiary;
2. That it is an ancestral didelphine and that these modern opossums did develop in South America instead of, or as well as, in North America despite their non-discovery in the Middle Tertiary, which, after all, is represented only by faunas very limited facially and geographically; or
3. That it is simply another offshoot of the generalized, opossum-like, perhaps pediomyine, stock that must have entered South America sometime before the Eocene, and represents an extinct minor phylum ancestral neither to microbiotheres nor to recent didelphines.

This one specimen, so incomplete and so vastly isolated in space and in time, certainly can make possible no definite choice between these alternatives, and any one of them remains possible. Such as it is, however, the evidence favors the third view. As noted above, the known peculiarities of *Coöna* hint at a trend rather away from than towards the microbiotheres. Although it is, in the known parts, rather more didelphine- than microbiothere-like, it seems in these parts to be slightly less fit morphologically as an ancestor of living oppossums than are contemporary and older North American forms.

DIDELPHID INCERTAE SEDIS

A.M.N.H. No. 28410 is an isolated lower molar from the Casamayor 1½ leagues northeast of Cabeza Blanca. Its structure is characteristically didelphid, but this single tooth is not considered adequate for definition. It represents a species and probably also a genus otherwise unknown. It is much larger than *Ideodelphys microscopicus* and at least as large as *Coöna pattersoni.* It cannot belong to *Coöna,* if only because the elevation of the trigonid is much less, hardly greater than that of the talonid. The tooth is of rather generalized structure, paraconid distinct and internal, metaconid slightly wider than protoconid, entoconid large, hypoconulid very small and close to entoconid, hypoconid simple and crescentic, other cusps absent.

CAROLOAMEGHINIIDAE

DEFINITION: Small marsupials with bunodont cheek teeth without shearing modification. Upper molars nearly symmetrical, small but distinct parastyle, metastyle, protoconule, and metaconule, two larger stylar cusps immediately external to the subequal paracone and metacone, and no significant cingula. Lower dental formula 4. 1. 3. 4. Lower molars bunodont, with metastylid in addition to the six primitive cusps.

DISTRIBUTION: Casamayor, Patagonia.

In Ameghino's system these aberrant little animals occupy an extremely curious position. He placed them in the group Protungulata and considered them as crucial proof of his theory that ungulates arose in Patagonia from marsupial ancestors.

"La présence de *Caroloameghinia* dans le crétacé supérieur de Patagonie," he says (1906, p. 289), "et la ressemblance de ce genre avec le *Proteodidelphys* du crétacé inférieur de la même contrée, prouvent non seulement que les Ongulés descendent directement des marsupiaux polyprotodontes, mais aussi que cette transformation a eu lieu sur l'ancien continent patagonien."

So *Caroloameghinia* came to figure in Ameghino's phylogenies as the common ancestor of all the ungulates. No one has accepted this view. The resemblances signalized by Ameghino do exist: on the one hand to primitive marsupials (Didelphidae, Microbiotheriinae), and on the other to bunodont condylarths, and, it may be added, to other bunodont forms among rodents, primates, etc. The interpretation of these resemblances can now only be in one way, and that opposed to Ameghino. Real affinity is with the marsupials, adaptive or habitus resemblance with some bunodont placentals.

Dental formula, jaw form, and basic molar pattern are clearly marsupial or even didelphid. The peculiarities are adaptive and have led to a bunodont, multicuspid type. In the upper molars the presence of distinct conules and subequal paracone and metacone is merely the retention of primitive characters, and the chief specialization is in the styles, which contrast with any other family or genus. Of the five primitive styles of Cretaceous didelphids, the first and fifth remain about the same, the third is reduced or lost, and the second and fourth are enlarged and have become almost as important as the paracone and metacone. In the lower molars, the six primitive cusps are all retained and in their ancestral positions, but they are more bunodont than is usual among polyprotodonts and a new cusp, the metastylid, is developed.

In short, all the evidence shows *Caroloameghinia* as a slightly aberrant omnivorous or frugivorous side branch of primitive marsupials, probably didelphids.

CAROLOAMEGHINIA AMEGHINO, 1901

Caroloameghinia AMEGHINO, 1901, p. 354; 1902b, p. 22; 1906, p. 466; SCHLOSSER, 1923, p. 442.

TYPE: *Caroloameghinia mater* Ameghino.

DISTRIBUTION: As for the family.

DIAGNOSIS: Sole known genus of the family.

Caroloameghinia mater Ameghino, 1901

Plate 2, figures 1–6

Caroloameghinia mater AMEGHINO, 1901, p. 355; 1902b, p. 22, figs. 4–6; 1904b, p. 131, fig. 153; 1906, p. 287, figs. 67–68; SCHLOSSER, 1923, p. 442, fig. 561.

TYPE: The original of Ameghino, 1902b,

figures 4–5, a right lower jaw with the canine and all cheek teeth. Not found in the Ameghino Collection.

NEOTYPE: M.A.C.N. No. 10348, right lower jaw with P_{2-3} M_{1-4}.

HYPODIGM: Type (publication only), neotype, and the following:

A.M.N.H. No. 28441a. Isolated upper molar.
A.M.N.H. No. 28441b. Isolated upper molar.
A.M.N.H. No. 28445. Broken lower molar.

HORIZON AND LOCALITY: Exact origin of type unknown. Neotype and A.M.N.H. No. 28441 from south of Lake Colhué-Huapí. A.M.N.H. No. 28445 from Cañadón Lobo (Punta Casamayor). All from Casamayor formation.

DIAGNOSIS: Relatively large. Length M_{1-4} (neotype) 14.5 mm. Representative upper molars as much as 4 mm. in length and 5 mm. in width.

Caroloameghinia tenuis Ameghino, 1901

Caroloameghinia tenue (*sic*) AMEGHINO, 1901, p. 355.

Caroloameghinia tenuae (*sic*), AMEGHINO, 1904b, p. 98, figs. 108, 152.

TYPE: M.A.C.N. No. 10345, left maxilla with M_{1-4}.

HYPODIGM: Type and A.M.N.H. No. 28928, isolated upper molar.

HORIZON AND LOCALITY: Type without locality data but from the Casamayor beds of Patagonia. A.M.N.H. No. 28928 is from the Rinconada de los Lopez, also in the Casamayor.

DIAGNOSIS: About 35 per cent or more smaller than *C. mater*. Length M^{1-4} 8.2 mm. Upper molars more than 2 mm. in length.

This species is so much smaller than *C. mater* that its validity is very probable, although the types offer no points of comparison and no definite morphological differences have been detected in referred specimens. The species is extremely rare.

BORHYAENIDAE

DEFINITION: Carnivorous marsupials with formula $\frac{4\text{–}3.1.3.4}{3\text{–}2.1.3.4}$ (except *Thylacosmilus*). Tooth replacement sometimes greater than in recent marsupials. Incisors small, canines enlarged, more or less laniary. Paracone and metacone approximated on M^{1-3}, paracone often reduced, protocone moderate or reduced. Metastylar shear. M^4 reduced, transverse, metacone small or absent. M_4 enlarged, main lower shearing tooth. Lower talonids more or less reduced and often imperfectly or not basined. Metaconids always smaller than paraconids and usually absent, at least in later forms. No palatal vacuities. Naso-lacrimal contact present (except *Thylacosmilus*). Lacrimal foramen marginal or intraorbital. Single basisphenoid perforation.

DISTRIBUTION: Riochican to Chapadmalalan, South America.

This exclusively South American family includes the only predaceous mammals of that continent previous to the Pliocene. In collections from pre-Deseadan beds borhyaenids are a very minor element numerically. The Ameghino Collection contains fragments of about 12 individuals from the Casamayor, and our collection has about 15. They probably formed a considerably more abundant element in the fauna than is indicated by these figures. That they were highly varied is attested by the fact that these 25 or 30 specimens seem to represent about 15 species, varying in size from that of a small opossum to that of a large wolf and also widely variant in structure, although only a few of these can now be clearly defined.

The broader affinities of the group have been the subject of long dispute. Ameghino (1906, etc.), who did not recognize the marsupials as a natural group, placed the so-called polyprotodont marsupials, Insectivora, and Carnivora in a group Sarcobora. The Borhyaenidae, divided into various families as noted below, were grouped together as Sparassodonta, considered as indirectly related to the Australian carnivorous marsupials and as directly ancestral to the Creodonta and through them to the Fissipeda and Pinnipedia. Sinclair (1906) emphatically referred the "sparassodonts" to the Marsupialia and did not think them separable as to family from the Thylacinidae. Tomes (1906) considered them as placental rather than marsupial carnivores, but his view never received wide credence and his evidence was later completely controverted (Carter, 1920).

All authorities are now agreed that the

"sparassodonts" are marsupials. The discussion at present turns on the degree of affinity with the various Australian forms. There are two principal opinions: that they are definitely thylacinid (as opposed even to dasyuroid) and therefore postdate not only the origin of the Dasyuroidea but also its own subdivision into the recent families whenever and wherever this occurred (Sinclair, 1906; Wood, 1924; and others); that they are of dasyuroid origin as opposed to didelphoid, but that the separation is very ancient and antedates the Australian differentiation of the group (Cabrera, 1927; not very clearly stated by anyone else, but adumbrated by Gregory, 1910; Loomis, 1914, 1921; and others more or less casually); or that they are of didelphoid origin and parallel the Australian carnivores without any more special affinity (chiefly Matthew, 1915, and as regards the origin of the group this was also Ameghino's opinion). I have discussed the problem in a previous paper (Simpson, 1941a) of which the following remarks are a summary.

In considering the view of Sinclair and Wood, which has been most carefully supported and fully expressed and is the most commonly quoted opinion at present, one must constantly keep two facts in mind. First, they were dealing in South America with a small number of relatively specialized genera, all of the same age (Santa Cruz). Second, they were not suggesting affinities with the Australian carnivorous marsupials as a whole, but were explicitly excluding the Dasyuridae (following Bensley and others in considering these as markedly distinct from the Thylacinidae) and considered the relationship to be specifically with *Thylacinus*, a very highly specialized marsupial of recent age.

The main features of the morphological evidence have been rather thoroughly set forth by Ameghino, Sinclair, Wood, Cabrera, and others, except for a few important new observations given in the systematic review below. This evidence, however, requires brief revaluation on a somewhat broader basis.

In the first place, the "sparassodonts," or borhyaenids as I prefer to call them, anticipating the conclusion here reached, must be considered as a unit and not solely as represented by the few best known Santa Cruz genera. Cabrera (1927, p. 273) has also made a strong claim for this point of view. Although they are so varied and although this divergence is even older than the Casamayoran beds, the borhyaenids from *Patene* (below) to the most specialized Pliocene forms do bear the stamp of common ancestry. They all have common characters which distinguish them from all other groups of marsupials, a point not in dispute but not much emphasized in this connection except by Cabrera. If, then, they are especially related to *Thylacinus*, rather than to Australian carnivorous marsupials in general, they must all either be derived from a definite thylacinid (not dasyurid) or *Thylacinus* must be derived from them. All the evidence opposes either view. *Patene* and other primitive genera have none of the truly distinguishing characters of the Thylacinidae so that to suppose the borhyaenids derived from that family is really gratuitous. The resemblances between *Borhyaena*, say, and *Thylacinus* were developed within the Borhyaenidae either as parallelisms or as ancestral progressive traits. But they were not ancestral either: even the earliest borhyaenids are more specialized than *Thylacinus* in some particulars (e.g., closed palate, lacrimal) and the specialized forms are to a considerable degree divergent, the evolutionary tendencies not being wholly in the direction of *Thylacinus* (e.g., reduction of protocone and talonid, nearly complete fusion of paracone and metacone). These and the almost insuperable geographic difficulties have prevented anyone from claiming the groups to be ancestral and descendent in this way.

Wood lists 19 important characters as indicating thylacinid relationships of the borhyaenids, 11 being shared with the dasyurids. Of them eight are invalid as evidence because not present in primitive borhyaenids or highly variable in the group. One, in fact, is distinctly didelphoid in primitive borhyaenids (as *Patene*): the development of the stylar cusps. Of the remaining 11 characters listed by Wood, 10 are not known in borhyaenids aside from a few very specialized forms, and of these 10 seven are as dasyurid as they are thylacinid. The other three are thickened posterior edge of palate, vertebral formula (D13, L6, S2, as against D12, L7, S2 which is probably primitive for both didelphids and dasyurids, or at least occurs in both), and absence of marsupial bones. The latter hardly can be counted a very important resemblance as it is a negative character and as marsupial bones are present in *Thylacinus* although small. It is, furthermore, very likely that these few characters not now known outside of a few specialized borhyaenids will prove to be variable or absent in other typical genera, as did eight of the supposedly thylacinid characters. The remaining one character known in numerous genera and resembling the thylacinids is the absence (or reduction) of the mesostyle, which is, however, very small on some didelphids. In the most primitive Borhyaenidae the styles in general are distinctly more didelphoid than dasyuroid (or thylacinid) so that what real weight the styles in general have opposes dasyuroid relationships. In fact this character of the mesostyle might have been classed with the eight characters above, as primitive borhyaenids do have a vestigial mesostyle almost as large as in some didelphids.

The apparently imposing array of evidence for definitely thylacinid relationship thus boils down to two items: the thickened, ridgeless posterior edge of the palate and the vertebral formula. The palate otherwise is different in the two groups, and the vertebral formula is known in borhyaenids only in *Cladosictis* and there doubtfully. Loss of one rib in the supposed formula (a variation common within single families and sometimes merely individual) would give a didelphid vertebral formula. In short, there is no valid structural evidence for specifically thylacinid affinities, thus agreeing with the phylogenetic considerations already mentioned.

There is better evidence for dasyuroid affinities, that is, affinities with the Australian carnivorous marsupials as a whole, but it is still not very convincing. In the dentition the only definitely dasyuroid characters are specializations such as very commonly occur by convergence in animals of similar habits, for instance reduction of the incisors and progressively greater (but not identical) shearing adaption in the molars, and these surely or probably are not present in the most primitive borhyaenids—the number of incisors is not known in the most generalized forms, but in other characters they approach the didelphids as much as, or more than, the dasyuroids. With the possible exception of the retracted nasals, the skeletal resemblances also are generally adaptive in nature.

Traced as far as possible to its fundamentals, the structure of borhyaenids in general seems clearly derivable from a primitive stock certainly pre-thylacinid and comparable only to the didelphids and the most primitive dasyurids. It resembles both these stocks (which are very similar in essentials), and there is no conclusive evidence of relations to one or the other. Adaptively the group parallels the dasyuroids, but its inferred structural ancestry appears rather more didelphoid. The most probable conclusion is that in the Upper Cretaceous the didelphoids and dasyuroids had a common ancestry sharing the primitive characters of both groups, somewhat more like the Didelphidae than the Dasyuridae as we know them because the former are more conservative. From this stock the borhyaenids arose. They may very well have arisen from a carnivorous line progressing in the direction of the Dasyuridae, but not very far along this line, and surely before it had acquired its most characteristic specializations.

This view rather nearly accords with that of Cabrera, but is somewhat nearer to Matthew than he was. The truth appears to me probably to lie between the views of those two workers, certainly in agreement with Sinclair in the essential point he had to prove, that these are polyprotodont marsupials, but not in agreement with the particular part of his opinion that Wood selected for special emphasis. These South American carnivorous marsupials seem best placed in a distinctive family. Their superfamily reference is less secure, but in view of their generally, although perhaps not greatly, distinctice character, very ancient separation, and geographic isolation as well as because of the doubt as to whether they are closer to Didelphoidea or Dasyuroidea or rather intermediate between the two, I prefer to place them in a superfamily Borhyaenoidea. An acceptable alternative would be to place all the so-called polyprotodonts in a single superfamily, perhaps justifiable on the basis of range of variation, but not on the basis of antiquity as separate entities.

Ameghino listed six genera now considered borhyaenids as occurring in the Casamayor and one of these as occurring also in the Musters. *Arminiheringia* is the best founded of these. It is known from both upper and lower dentitions. *Pseudocladosictis* was based on a single premolar, said to be a lower but perhaps an upper, and the genus is unrecognizable. *Dilestes* is a synonym of *Arminiheringia*. *Procladosictis* was based on a good upper dentition from the Musters, where it is clearly definable. Its supposed presence in the Casamayor is based on a lower premolar. There is no real reason for referring this to *Procladosictis* and it is indeterminate. *Nemolestes*, based on two broken lower molars, and *Argyrolestes*, on one broken upper molar, were supposed to be insectivores but are borhyaenids, although otherwise hardly determinable on the type material. Thus in spite of an imposing list, only one genus (with two species) has really been adequately defined from the Casamayor. To this I now add one more, as well as supplementary observations on isolated specimens which are of interest in showing the variety and general characters of the sparassodonts of that time but are not of much taxonomic value. The Río Chico and Musters specimens show that the family is present, but all except *Procladosictis* are dubious for one reason or another.

The classification of the borhyaenids within the family and the distinction of definite phyla are as yet impracticable. Aside from those which he erroneously referred to other orders, Ameghino recognized six families: Arminiheringiidae, Hathlyacynidae, Proborhyaenidae, Borhyaenidae, Prothylacinidae, and Amphiproviverridae. These were for the most part based on real structural differences but not such differences as are now believed to characterize natural units of more than generic value. The only recent competent effort to group the numerous genera into subfamilies is that of Cabrera (1927) who divides them as follows:

Proborhyaeninae: Metaconid small but well defined

Cladosictinae: Metaconid absent, talonid forming a cusp more or less excavated above

Borhyaeninae: Metaconid absent, talonid widened and compressed anteroposteriorly, forming a shelf behind the trigonid

As a key for the convenient recognition of the various genera, such an arrangement is admirable, but it is not a natural classification of the group as a whole. It is based on but two related characters, and excludes other characters (such as the development of the canines, for instance) of equal importance in distinguishing natural groups. It is, furthermore, a classification based only on stages in progressively evolving characters. The ancestral Borhyaeninae had surely been successively Proborhyaeninae and Cladosictinae of Cabrera. Horizontal classification is frequently not only convenient but also necessary in practice. In this form, however, it will inevitably bring together genera which happen to have preserved one primitive character or to have achieved one specialized character but otherwise are very different in structure and origin, and separate other genera which happen to have diverged in one character but otherwise are closely similar and intimately related.

The evidence at hand shows that there were a number of distinct phyla, although none of these can be traced clearly or for long. There was in the group as a whole tendency to pass through the progressive steps of Cabrera's key, but the rate at which this occurred was apparently different in different lines of descent. Some lost the metaconid before the Casamayoran beds, and others retained it into the Pliocene. Similarly for the reduction of the heel; in some the heel remained small, in others it became large. Some had compressed laniaries, some dog-like canines, some great canine tusks, and some *Smilodon*-like sabers. These and many other characters suggest a very complex phylogeny not yet decipherable. The evidence does support a common origin for the group, and its scope is apparently not greater than that of most mammalian families in conservative classification. The extraordinary genus *Thylacosmilus* Riggs (see Riggs, 1934) is clearly a derivative of this ancestry, but is so highly specialized, far beyond any other known genus, that it may best be placed in a separate subfamily, Thylacosmilinae, leaving all the genera discussed in this work in the more typical Borhyaeninae, which is taken to embrace all the subfamilies of Cabrera and all the families of Ameghino.

ARMINIHERINGIA Ameghino, 1902

Arminiheringia Ameghino, 1902a, p. 44; 1906, p. 468; Simpson, 1932e, p. 1; Scott, 1937, pp. 704, 716, fig. 417.

Dilestes Ameghino, 1902a, 46; 1906, 468.

Type: *Arminiheringia auceta* Ameghino.

Distribution: Casamayor, Patagonia.

Diagnosis: Large borhyaenids with formula $\frac{3\cdot\ \cdot3\cdot4}{2\cdot1\cdot3\cdot4}$. Lower incisors much crowded. Canines very large, oval in section, with very long roots, those of both upper and lower jaws extending back into the molar region. Lower canines procumbent and closely appressed in the symphysis. Premolars all two-rooted. Molars in general agreement with those of *Borhyaena*. Symphysis thick and very long, ending beneath posterior part of M_1. Skull very massive, with widely expanded zygomata, suggesting that of *Borhyaena* but choanae significantly narrower and considerably posterior to M^4. Premaxillae with long ascending processes ending at a point about P^{1-2}.

This is an unusually well characterized and very distinctive genus. Occurring, as it does, among the oldest South American faunas it is extraordinary in being one of the most specialized members of its family. Its large size, massive skull, very peculiar anterior teeth, and very advanced molars all show it to be one of the most advanced of all borhyaenids. In spite of this fact and of its absence in our own collections, it undoubtedly does belong in the Casamayor fauna. The principal specimen was found by Carlos Ameghino after he had distinguished this fauna and was thoroughly familiar with it, comes from a true Casamayor locality, was apparently found in place,[1] and differs from any known later genus. Moreover, another species of the genus was later found in the same beds. Ameghino described three species, two of which are probably synonymous.

Dilestes was founded on isolated teeth, and the only clearly defined distinction was the supposed absence of a talonid. This was simply broken off, and the teeth are identical in structure with those of *Arminiheringia*. The genera are surely synonymous. They were described simultaneously, but *Arminiheringia* was given precedence by the author, was much more correctly and adequately defined, and was based on incomparably better material.

There were only two pairs of lower incisors, the smallest number known among Borhyaeninae. They are much crowded, the first pair anterior to the second rather than between them. The great canines, much worn in the known specimens, show no enamel, which must have been very thin or confined to the tips. The roots of opposite lower canines are immediately contiguous in the symphysis, their alveoli separated only by a film of bone. These long roots are still open in the known specimens, which are adult or even aged to judge from the cheek teeth, so that the canines appear to have been of long-continued or even continuous growth.

Arminiheringia considerably resembles *Borhyaena* of the Santa Cruz. It must, however, be considered more specialized in spite of its greater age, and it is not likely that the two are in exactly the same line of descent. Scott (1937) has suggested that *Arminiheringia* might be ancestral to *Thylacosmilus*, the Pliocene saber-tooth borhyaenid. The vast gap between the two might allow for such a transformation, but there is little positive evidence to favor it beyond the too general resemblance that *Arminiheringia* is large and specialized for its age. The enlargement of both upper and lower canines and the shallow rather than flanged symphysis hardly suggest the beginning of saber-tooth specialization.

Arminiheringia auceta Ameghino, 1902

Plate 3, figures 1–5; text figure 4

Arminiheringia auceta Ameghino, 1902a, p. 44; Simpson, 1932e, p. 1, fig. 1.

Dilestes dilobus Ameghino, 1902a, p. 46.

Syntypes: M.A.C.N. No. 10972, facial part of skull, alveoli of incisors, left C, root of all cheek teeth and crowns of left P^3 and M^{2-3}, and right P^1–M^4, all deeply worn and left M^3 broken.

M.A.C.N. No. 10970, lower jaw lacking the posterior part, roots of all teeth and crowns of left C, P_{1-3}, and M_{2-4}, right C, P_1, and P_{3-4}, all deeply worn.

Although separated as found in the collec-

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[1] A relatively complete and fragile specimen still partly embedded in undisturbed matrix.

tion, these almost surely are parts of the same individual, so that it is unnecessary to select one of the nominal syntypes as lectotype.

TYPES OF *Dilestes dilobus:* M.A.C.N. No. 10324, one nearly complete lower molar, one slightly broken, and a fragment of another.

HYPODIGM: M.A.C.N. Nos. 10324, 10970, and 10972, as above.

HORIZON AND LOCALITY: Casamayor, Patagonia. The types of *A. auceta* are labeled "Colhuapi Norte," i.e., the region north or northeast of Lago Colhué-Huapí. The type of *Dilestes dilobus* is from "Colhuapi," i.e., south of Lago Colhué-Huapí.

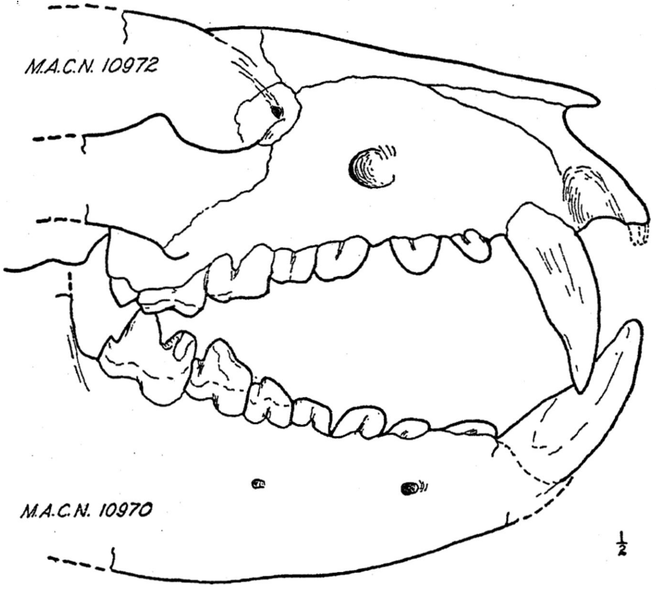

FIG. 4. *Arminiheringia auceta* Ameghino. Types, M.A.C.N. Nos. 10972 (skull) and 10970 (lower jaw), probably parts of one individual, anterior parts of skull and lower jaw. Right lateral view. ×½.

DIAGNOSIS: Size large, C–M$_4$ about 135 mm. Premolars spaced. Symphysis unfused in adult.

The best tooth of *Dilestes dilobus*, essentially the type, is slightly smaller than M$_4$ of the type of *A. auceta* and also a little narrower, but these seem inadequate for specific distinction. *A. auceta* is an unusually well-defined and distinctive species which cannot be confused with anything else.

Arminiheringia cultrata Ameghino, 1902

Arminiheringia cultrata AMEGHINO, 1902a, p. 46.

Arminiheringia contigua AMEGHINO, 1904a, vol. 58, p. 265.

TYPE: M.A.C.N. No. 10329, isolated upper molar, apparently M^3.

TYPE OF *A. contigua:* M.A.C.N. No. 10317, symphysis with incisive alveoli, and right C–M$_1$.

HYPODIGM: M.A.C.N. Nos. 10317 and 10329, as above.

HORIZON AND LOCALITY: Casamayor, Patagonia. Both types are from south of Lago Colhué-Huapí.

DIAGNOSIS: Over 25 per cent smaller than *A. auceta*. Lower premolars crowded. Symphysis fused in adult.

The present disposal of these two species of Ameghino may not be the correct one, but seems best at this time. *A. cultrata* is essentially based on a single upper molar of rather dubious character, apparently an M^3 and if so closely similar to that of *A. auceta* but much smaller. Ameghino speaks of M^{1-3}, but he often inferred the characters of missing teeth and his whole description could be, and I believe was, based on this one tooth. He stated that in *A. cultrata* M^{1-3} are narrower than in *A. auceta* and have an internal heel [protocone] missing in the latter. The difference in this respect is due to wear, and *A. auceta* also had a small protocone. The type of *A. contigua*, a partial lower jaw, is not comparable with that of *A. cultrata*. The two were of about the same size, *A. contigua* perhaps slightly smaller, and they came from the same locality. These facts, as well as the fact that *A. cultrata* would otherwise be practically indeterminate, lead me to consider the two as probable synonyms and to treat them as such. The fusion of the symphysis is not entirely an age character, because the type of *A. contigua* with symphysis fused is, if anything, younger than that of *A. auceta* with symphysis open.

PATENE SIMPSON, 1935

Patene SIMPSON, 1935a, p. 3; SCOTT, 1937, pp. 704, 716.

TYPE: *Patene coluapiensis* Simpson.

DISTRIBUTION: Río Chico and Casamayor, Patagonia.

DIAGNOSIS: Borhyaenids of medium to small size in the known species, with upper molars of primitive stamp. Paracone present and well separated from metacone on M^{1-3}, slightly smaller than metacone, these cusps more external on M^{1-2}, median on M^{3}. Increasingly great metastylar spur on M^{1-3}, that of M^{3} projecting strongly posteriorly as well as externally. Distinct conical stylar cusps immediately external to, and separate from, the paracone on M^{1-2}. Protocone large on all molars. M^{1-3} with distinct vestigial protoconules and metaconules. M^{4} as wide as M^{3}, with strong parastylar spur, paracone median, metacone represented by a basal cuspule, this tooth still retaining distinct molar-like character.

This genus is, in general, distinguished by its primitive, almost generalized, borhyaenid character. Indeed, were not much more specialized forms contemporaneous with it, it would be an almost ideal prototype for the whole group. Among its contemporaries, only *Arminiheringia* can be adequately compared, and it is obviously very different. *Procladosictis*, from the Musters, is rather closely comparable but in it the paracone and metacone are less external and M^{3} is less oblique and more compressed anteroposteriorly. *Pseudocladosictis* and *Nemolestes* are practically indeterminate and based on types not comparable with this. *Argyrolestes* is also poorly established and was apparently larger than this species, with paracone and protocone more reduced. Among later borhyaenids, *Lycopsis* Cabrera from the Santa Cruz, an extraordinarily conservative relict, is most closely comparable. The resemblance is close, but the *Lycopsis* M^{1-3} are considerably more oblique and more compressed laterally. The great difference in age also militates against accepting this resemblance in the upper molars as necessarily proving very close relationship.

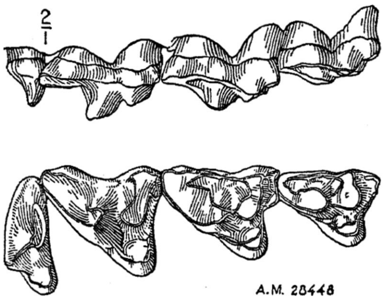

FIG. 5. *Patene coluapiensis* Simpson. Type, A.M.N.H. No. 28448, right M^{1-4}. External and crown views. ×2.

Patene coluapiensis Simpson, 1935

Text figure 5

Patene coluapiensis SIMPSON, 1935a, p. 4.

TYPE: A.M.N.H. No. 28448, part of right maxilla with M^{1-4}. Found by C. S. Williams.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayor, south of Lago Colhué-Huapí, Chubut, Argentina.

DIAGNOSIS: Sole defined species of the genus. M^{1-4} 24.5 mm.

The outstanding characters have been given in the generic diagnosis, and details are well shown in the figure.

An isolated upper molar from the Casamayor in Cañadón Vaca suggests the presence of a second, somewhat larger species, but it is inadequate for certain determination.

Patene sp.

A.M.N.H. No. 28532, from the *Kibenikhoria* faunule in the Río Chico of Cañadón Hondo, is an isolated, broken upper molar differing so little from *P. coluapiensis* as to be tentatively referable to the same genus. It is not more exactly identifiable, but the occurrence of so primitive a borhyaenid at this ancient horizon is worthy of note.

PROCLADOSICTIS Ameghino, 1902

Procladosictis Ameghino, 1902a, p. 46; 1906, pp. 468, 470; Schlosser, 1923, p. 440; Scott, 1913, p. 627; 1937, p. 704.

Type: *Procladosictis anomala* Ameghino, 1902.

Distribution: Musters formation,[1] Patagonia.

Diagnosis: Small borhyaenids. Simple P^3 obliquely implanted. Protocone distinct but low on M^{1-2}, reduced on M^3. Paracone and metacone confluent basally, metacone slightly larger than paracone on M^1, paracone progressively smaller on M^{2-3}, vestigial on M^3, and metacone progressively larger. Paracone and metacone median on M^1, progressively more internal on M^{2-3}. Broad outer shelf produced into a strong, triangular metastylar spur, projecting nearly posteriorly on M^{1-2} and nearly externally on M^3. Outer margin nearly straight on M^{1-2}, deeply bilobed on M^3. Twin styles, the anterior larger, external to paracone and metacone on M^2, small or absent on M^1 and M^3.

Ameghino's description and figure of the type of this genus are accurate and clear and call for no comment. *Procladosictis* is a distinctive and well-defined genus as regards details of molar structure, but it is basically similar to the smaller, typical borhyaenids throughout the Tertiary. Among well-defined Casamayor forms, it is decidedly more progressive than *Patene* and more primitive than *Arminiheringia*. The Deseado, also, has no known genus of closely comparable character. Among Santa Cruz forms, there is, as the name implies, much resemblance to *Cladosictis* and perhaps even more to *Amphiproviverra*. *Procladosictis* is not clearly more primitive than that genus.

We found an isolated lower molar, A.M.N.H. No. 29433, at the Cerro del Humo that may possibly belong to this genus. Its size is comparable with that of the type and its structure apparently harmonious. It, too, considerably resembles *Amphiproviverra* (for instance, M_3), but it has a minute metaconid. The talonid is narrow, with a long external slope, but is basined and has a hypoconulid, poorly distinguished from the entoconid.

Procladosictis anomala Ameghino, 1902

Plate 2, figure 7

Procladosictis anomala Ameghino, 1902a, p. 46; 1906, p. 354, fig. 191.

Type: M.A.C.N. No. 10327. Right upper jaw with P^3–M^3. Ameghino Collection.

Hypodigm: Type only.

Horizon and Locality: Musters formation, Patagonia. No other data.

Diagnosis: Sole species surely referable to the genus, as defined above. Measurements in table 2.

TABLE 2

Procladosictis anomala

P^3		M^1		M^2		M^3	
L	W	L	W	L	W	L	W
9	4.5	9	6.5	9.5	8	7.5	10

"Procladosictis" erecta Ameghino, 1902, nomen vanum

Procladosictis erecta Ameghino, 1902a, p. 47.

Type: M.A.C.N. No. 10328. A lower premolar.

Hypodigm: Type only.

Horizon and Locality: Casamayor, Patagonia. Type from north of Lago Colhué-Huapí.

Diagnosis: Indeterminate.

There is no real reason for referring this to *Procladosictis*, a genus based on upper teeth from a different horizon. Nor does there seem to be any way in which this supposed species

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[1] The Casamayor species *Procladosictis erecta* was referred to this genus on inadequate evidence.

can now be defined or distinguished. The type is a lower premolar, 9.3 mm. long and 4.0 mm. wide, with central cusps and sloping, non-cuspidate heel. It may be kept on record, since a neotype might show the species to be distinctive, but its present value and significance are nil.

PSEUDOCLADOSICTIS AMEGHINO, 1902, NOMEN VANUM

Pseudocladosictis AMEGHINO, 1902a, p. 47; 1906, p. 468; SCHLOSSER, 1923, p. 440; SCOTT, 1913, p. 627; 1937, p. 704.

TYPE: *Pseudocladosictis determinabile* Ameghino.

DISTRIBUTION: Casamayor, Patagonia.

DIAGNOSIS: Indeterminate.

This genus was based on a single premolar, by Ameghino considered a lower but in my opinion more probably an upper. There is nothing particularly distinctive about it, and I see no way in which the genus can be distinguished.

Pseudocladosictis determinabile Ameghino, 1902, nomen vanum

Pseudocladosictis determinabile AMEGHINO, 1902a, p. 47.

TYPE: M.A.C.N. No. 10325, isolated premolar.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayor, upper part, *fide* Ameghino. South of Lago Colhué-Huapí.

DIAGNOSIS: Indeterminate.

The type measures 8.8 by 6.1 mm. and has a central cusp and small, partly transverse, cuspidate heel. Like *Procladosictis erecta*, the species is essentially no more than preëmptive, based on no good evidence but securing the species to its author in case later work shows it to be valid. It is reluctantly included here in the interests of completeness.

NEMOLESTES AMEGHINO, 1902

Nemolestes AMEGHINO, 1902a, p. 48; 1906, p. 468.

TYPE: *Nemolestes spalacotherinus* Ameghino.

DISTRIBUTION: Casamayor and possibly Río Chico, Patagonia.

DIAGNOSIS: A borhyaenid with triangular trigonid and small metaconid. Otherwise indeterminate.

Ameghino described this as a triconodont of the Jurassic family Spalacotheriidae. He later (1906) considered it as an insectivore, probable ancestor of the whole order Insectivora. The chief error lay in not recognizing that the tooth once had a talonid, now broken off. In fact, it is a typical borhyaenid of the group called Proborhyaeninae by Cabrera. Otherwise it is indeterminate.

Nemolestes spalacotherinus Ameghino, 1902

Nemolestes spalacotherinus AMEGHINO, 1902a, p. 48; 1906, p. 391, fig. 252.

TYPE: M.A.C.N. No. 10330, tip of canine and two broken lower molars, not associated and of somewhat different character. The one figured by Ameghino may be taken as the lectotype.

HORIZON AND LOCALITY: Casamayor, north of Lago Colhué-Huapí.

DIAGNOSIS: About the size of *Cladosictis lustrata*, but with small metaconid.

This would probably prove to be a valid species if adequately known, but on this material it is practically indeterminate. The unfigured specimen is larger and has a large metaconid.

?Nemolestes sp.

Nemolestes spalacotherinus CABRERA, 1935, p. 12, perhaps not *N. spalacotherinus* Ameghino.

Cabrera referred a specimen from the uppermost Río Chico horizon in the Bajo de la Palangana to *N. spalacotherinus* and discussed it as follows (translated from Spanish): "Of this species, which evidently is nothing but a primitive marsupial, there is a lower molar like the type specimen of Ameghino but a little smaller, doubtless because it occupied a more anterior position in the series. Its dimensions are: anteroposterior diameter 6 mm., transverse diameter 3.5 mm., height of crown 8 mm. It is from 10 meters below the red clays . . . "

It is with hesitation that I query an identification by so eminent an authority, but I cannot feel that a positive specific identification is tenable under these circumstances. All the relatively well-preserved, truly identifiable specimens from this horizon have proved to be specifically distinct from definitely Casamayor specimens. Through a probable stratigraphic confusion, Cabrera had the apparently mistaken idea that the level is synchronous with part of Ameghino's Casamayor ("*Notostylops*") fauna, and a bias in favor of conspecific identifications exists. *Nemolestes* is essentially indeterminate, and a single tooth, not exactly like the type, can hardly have been so precisely determinable. Finally, some others of Cabrera's identifications in this faunule are internally inconsistent (for instance, separate references of fragments to genera and species that are synonymous).

ARGYROLESTES Ameghino, 1902

Argyrolestes Ameghino, 1902a, p. 48; 1906, p. 468.

Type: *Argyrolestes peralestinus* Ameghino.

Distribution: Casamayor, Patagonia.

Diagnosis: A borhyaenid with strong external cingulum, well-developed parastyle, and small paracone. Otherwise indeterminate.

Ameghino placed this with *Nemolestes* and believed it to have the same affinities, comparing it especially with *Peralestes*. This was, I believe, owing to mistaken interpretation of its morphology. The main cusp is not the internal cusp, protocone, but the metacone. The paracone was small but distinct and had been almost removed by wear. A true protocone was present, but is broken on the specimen. So interpreted, the tooth is that of a typical, rather primitive borhyaenid. It is fairly distinctive and may well be valid, although comparisons are rather futile on this worn, broken, isolated tooth.

Argyrolestes peralestinus Ameghino, 1902

Argyrolestes peralestinus Ameghino, 1902a, p. 48.

Type: M.A.C.N. No. 10331. Broken upper molar.

Hypodigm: Type only.

Horizon and Locality: Casamayor, Patagonia. No other data.

Diagnosis: Sole species referred to genus. Width of upper molar without protocone, 5.5 mm.

PHARSOPHORUS Ameghino, 1897

Pharsophorus Ameghino, 1897a, p. 502.

Plesiofelis Roth, 1903a, p. 154; Cabrera, 1927, p. 274 [as synonym of *Pharsophorus*]; Simpson, 1936d, pp. 66, 71 [citing Cabrera].

Type of *Plesiofelis*: *Plesiofelis schlosseri* Roth, 1903.

The genus *Pharsophorus* is typically of Deseado age and as such is not redescribed or revised here, but the possibility of its occurrence in the Musters must be discussed. In 1903, Roth described the (then) new genus and species *Plesiofelis schlosseri* and the new referred species *P. cretaceus*. The former is based on a good lower jaw with six teeth, the latter on one tooth. The provenience was given in each case as "Formación cretácea superior, Lago Musters (Territorio del Chubut)." Cabrera (1927) concluded that most of the specimens with these data, including these two, were from the Deseado of Colhué-Huapí, and hence that *Plesiofelis schlosseri* was contemporary with *Pharsophorus lacerans*, with which he considered it to be synonymous. Later study (Simpson, 1936d and the present work) shows, however, that almost all Roth's specimens with these data are really from the Musters of Cerro del Humo, a very distinct horizon and locality from the type of *Pharsophorus lacerans*. The type of *Plesiofelis schlosseri* is an excellent specimen, and Cabrera's statement is adequate authority for its being inseparable from *Pharsophorus lacerans*. This anomalous situation involves one of the following alternatives:

1. *Pharsophorus lacerans*, unquestionably a Deseado species, also occurs in the Musters. This is extremely improbable, not to say impossible, in view of the decidedly different ages and characters of these two faunas.
2. Roth's specimen is in fact of a distinct species, or even genus, from *Pharsophorus lacerans* although indistinguishable on the basis of the unique type specimen. This is improbable, since the horizontal ramus and P_2–M_4 are known and these are generally adequately determinable among borhyaenids; still, it is a possibility.

3. Roth's specimen is really from the Deseado. This is improbable, since all Roth's other specimens with these data are clearly older than the Deseado. The only possible exception is two fragments of *Parastrapotherium*, typically a Deseado genus, said by Roth to be from "Lago Musters," but explicitly stated to have been found in drift above the "upper Cretaceous" (i.e., Musters) and not, as was "*Plesiofelis*," in the "upper Cretaceous." On the other hand, a few Deseado fossils do occur in place near this locality.

Of these three alternatives, one is thus nearly impossible and the other two both improbable, yet one of them must be true. It is not certainly known whether Roth's species and genus are valid or whether they are from the Musters.

Pharsophorus lacerans Ameghino, 1897

Plate 3, figure 6

Pharsophorus lacerans AMEGHINO, 1897a, p. 503.

Plesiofelis schlosseri ROTH, 1903a, p. 154; CABRERA, 1927, p. 274, fig. 1 [as synonym of *Pharsophorus lacerans*]; SIMPSON, 1936d, p. 66 [citing Cabrera].

TYPE OF *Plesiofelis schlosseri*: M.L.P. No. 11–114. Left lower jaw with P_2–M_4. Roth Collection.

[The species is not redefined or further discussed, being typically Deseado and so outside the scope of this revision.]

Pharsophorus cretaceus (Roth, 1903)

Plate 3, figure 7

Plesiofelis cretaceus ROTH, 1903a, p. 155.

Pharsophorus cretaceus CABRERA, 1927, p. 278, fig. 2; SIMPSON, 1936d, p. 66.

TYPE: Museo de La Plata. Part of left lower jaw with M_4. Roth Collection.

HYPODIGM: Type only.

HORIZON AND LOCALITY: "Cretáceo superior de Lago Musters" *fide* Roth. See discussion above.

DIAGNOSIS: M_4 as in "*Plesiofelis schlosseri*" or *Pharsophorus lacerans*, but with a minute cuspule on the anterior base of the trigonid. Mandible less deep.

Cabrera remarks that the accessory cuspule on M_4 is probably without taxonomic value and relies on the depth of the mandible to define the species. Even this seems to me to be of little or no taxonomic value in this case, and I suspect that this is only another individual of "*Plesiofelis schlosseri*," or *Pharsophorus lacerans*, but the whole question is so insoluble at present that I follow Cabrera's nomenclature without change.

BORHYAENIDAE INDET.

To illustrate the variety of the borhyaenid element in the Casamayor fauna and its general character, a number of isolated specimens too imperfect for exact taxonomic placing may be mentioned here.

The Ameghino Collection contains two lower jaws referred by Ameghino to *Procladosictis* and apparently intended as type of an unpublished species. The animal is small, with canine nearly vertical, P_1 small and single-rooted, P_2 two-rooted, P_3 largest of the premolars and with a small posterior heel. The species doubtless is new, so far as comparable with named forms, but cannot well be placed in the system and the specimens are inadequate as types. Another distinctive but poorly known form in the Ameghino Collection has a procumbent canine, premolars spaced and all single-rooted.

Four isolated lower molars in our collection represent at least three species, no one of which can be surely identified with any yet named. Only one of these wholly lacks the metaconid. It is also above the average in size and may belong to *Arminiheringia*, although not to one of the named species. Three have very small metaconids. The only one of these that preserves the heel has a talonid of moderate size, with a median main cusp and vestigial internal basin with crenulated rim. This tooth and one of the others have an adventitious anteroexternal basal cuspule. These teeth, as well as *Nemolestes*, are fairly typical of the Proborhyaeninae of Cabrera, a group primitive in the retention of the metaconid but probably an ancestral stage through which all borhyaenids passed. The metaconid was retained, but accompanied by various specializations in other characters, in one or two post-Casamayor phyla. The presence of a metaconid appears to have been relatively more common in Casamayor than in any later time, as would be expected.

BORHYAENIDAE OR DIDELPHIDAE INDET.

Text figure 6

There remain for mention five isolated molars, three upper and two lower, that are particularly interesting and important. They are all relatively small and represent more than one species and probably more than one genus, although similar or harmonious in structure.

The lower molars have trigonids of normal triangular form, with metaconids large but somewhat smaller than the paraconids. In one case (text fig. 6A) the trigonid is far elevated above the talonid, in the other (text fig. 6D) little elevated. The talonids are of completely didelphid type, large, basined, with large crescentric hypoconid and smaller, more conical, approximated entoconid and hypoconulid.

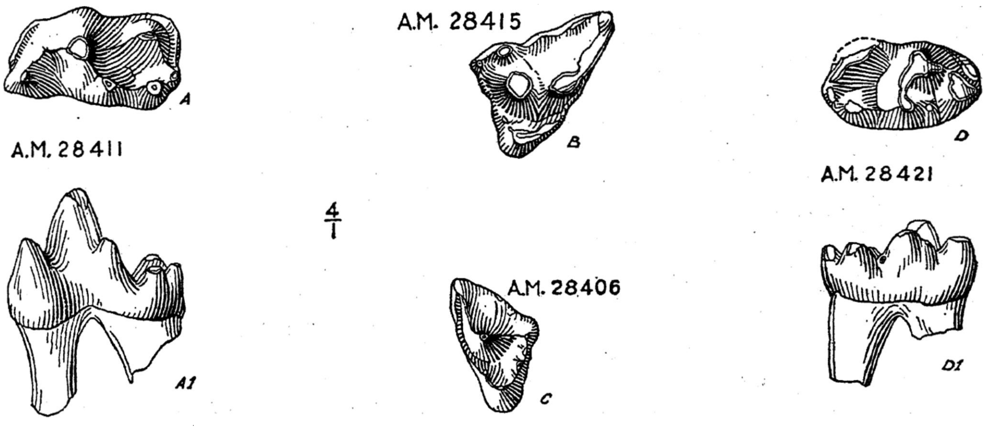

FIG. 6. Borhyaenidae or Didelphidae *incertae sedis*. A, A1. A.M.N.H. No. 28411, right lower molar. Crown and internal views. B. A.M.N.H. No. 28415, right upper molar. Crown view. C. A.M.N.H. No. 28406, left upper molar. Crown view. D, D1. A.M.N.H. No. 28421, left lower molar. Crown and internal views. All ×4.

Two of the upper molars, closely similar except for size, resemble those of *Patene* but are still more didelphid in general character. (Text fig. 6B.) Paracone and metacone are large, median to external and nearly equal. The protocone is large. The outer border is wide, oblique, with moderate metastylar shear. The five primitive didelphid styles are all present, the second enlarged and the others small and subequal. The other upper molar appears to be M^4. (Text fig. 6C.) It is definitely but not greatly more primitive than the homologous tooth in *Patene* or any other known borhyaenid, but slightly more specialized than in didelphids. The strongly oblique outer border has a strong parastylar projection and bears only one style, the first. Paracone and protocone are about equal, and a considerably smaller but distinct metacone is present.

These various teeth appear to represent a morphological group of fairly unified nature and intermediate in its (admittedly too few) known characters between borhyaenids and didelphids. The isolated teeth could be referred to either family. Among the Borhyaenidae they would be the most primitive known forms, among the Didelphidae the most advanced in the borhyaenid (or predaceous) direction. On the whole, I think them somewhat closer to borhyaenids, but they are almost perfectly intermediate as far as they go. In conjunction with the almost equally primitive *Patene*, they give a clue, slender but real, to the ancestry of the Borhyaenidae.[1]

CAENOLESTIDAE

Knowledge of this family in these faunas is even more scanty than that of the Didelphidae: practically it amounts to no more than bare assurance that the family was pres-

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[1] *Perazoyphium* Cabrera from Monte Hermoso might be a conservative survivor of this group, but it is equally possible that it is a more recent and somewhat convergent didelphid offshoot.

ent. This, placed on a firmer basis now, is of some importance. It seemed highly anomalous that the very specialized polydolopids should precede their simpler and more primitive relatives, the caenolestids. Now it is clear, as was to be expected, that the caenolestids were present, although very rare. This great rarity of the group, which was the only one of the two to survive this fauna, is probably due to differences of facies. However that may be, the polydolopids were the successful members of the caenolestoid series at this time. They vanished before or with (and in the latter case probably because of) the introduction of rodents, of similar adaptation, while the caenolestids proper continued to flourish and even increased, probably because they occupied ecological stations, in large part analogous to those of the Insectivora, not filled by any other South American group.

In addition to Ameghino's lost specimens, as mentioned below, we found one isolated tooth in the Casamayor (A.M.N.H. No. 28442) belonging to the most primitive subfamily, Caenolestinae, in which there is no strong shear on M_1 and the paraconid is internal. This tooth, a lower molar too small for probable assignment to Ameghino's species of this age, has the characters of the earlier Caenolestinae, especially the high, nearly bicuspid heel with entoconid about equal to metaconid. The paraconid is reduced and the hypoconulid small and spurlike.

PROGARZONIA AMEGHINO, 1904

Progarzonia AMEGHINO, 1904a, vol. 58, p. 260; 1906, p. 468; SCOTT, 1937, p. 717.

TYPE: *Progarzonia notostylopense* Ameghino.

DISTRIBUTION: Casamayor, Patagonia.

DIAGNOSIS: According to Ameghino, P_3 lower crowned than in *Garzonia*, *Stilotherium*, etc., compressed laterally and elongate anteroposteriorly, with a compressed anterior cusp followed by a very elongate talonid terminating in a rather thick but low cusp.

The true affinities of this genus are unknown, but it may be tentatively accepted as a caenolestine in the absence of contrary evidence.

Progarzonia notostylopense Ameghino, 1904

Progarzonia notostylopense AMEGHINO, 1904a, vol. 58, p. 260.

TYPE: A left lower jaw with P_3; not figured and not found in the Ameghino Collection.

HORIZON AND LOCALITY: Casamayor beds south of Lake Colhué-Huapí.

DIAGNOSIS: (Ameghino) P_3 3 mm. long, a little over 1 mm. wide; jaw 3.5 mm. deep on external side beneath P_3.

The original specimen is lost, and no others are known.

?CAENOLESTIDAE INCERTAE SEDIS

"?Promysops" primarius Ameghino, 1902,
nomen vanum

?Promysops primarius AMEGHINO, 1902a, p. 36.

Promysops primarius, AMEGHINO, 1903a, p. 89, fig. 6; 1906, p. 363, fig. 209.

TYPE: Lost. An isolated incisor.

HORIZON AND LOCALITY: Musters formation, Patagonia. No other data.

DIAGNOSIS: Indeterminate.

Although the type of this species is lost, it was fully described and figured from four different aspects by Ameghino so that its character is well known. It is, however, quite indeterminate at present, and probably permanently. It is an incisor, somewhat gliriform, with the crown enameled and the enamel not extending into the alveolus. It is perhaps from a caenolestid or a polydolopid, but even this is not certain. It is almost surely not "*Promysops*" (="*Propolymastodon*" = *Eudolops*, see below). Near the alveolar mouth its diameters are given by Ameghino as 4.5 and 2.5 mm.

POLYDOLOPIDAE

DEFINITION: Early Tertiary South American marsupials with one pair of lower incisors much enlarged, other lower antemolar teeth in part absent and in part vestigial (upper teeth anterior to P^3 unknown). P^3–M^1 and M_1 trenchant, with serrate edges, no distinct trace of normal cuspidate structure. M^{2-4}_{2-4} multicuspidate, basined, enamel of crown finely wrinkled when unworn. Trigonid of M_2 elevated to a shearing apex. M_{3-4} with one internal and two external cusps in trigonid, poorly differentiated from talonid. M^{2-3} generally with three imperfectly differentiated inner and three or (especially on M^2) more outer cuspules.

DISTRIBUTION: Riochican and Casamayoran, Patagonia.

This strongly specialized group is very difficult to handle taxonomically. Ameghino's arrangement (especially 1903a) derives it from the "Garzonidae" and derives from them the Rodentia on one hand and the "Abderitidae" on the other, yet he also derives some Multituberculata from them and the group itself is placed in the Allotheria. This close juxtaposition of three groups which more orthodox recent classifications refer to three different sub-classes is typical of Ameghino's startling originality in phylogenetic theory. As in most of his work, he does recognize as real the relationships that are supported by later study, but likewise claims relationships where now only convergence can fairly be admitted. As has also happened in other cases, some students without opportunity for thorough restudy have rejected the relationships pointed out by Ameghino that are real (as I believe) and accepted those merely apparent. In the present instance almost every earlier student but Gregory rejected caenolestoid and rodent affinities and accepted collocation with the Allotheria or Multituberculata. I have elsewhere (Simpson, 1928) argued at some length that the polydolopids are really aberrant caenolestoids. Renewed study, with Ameghino's original material and a number of new specimens, strengthens this opinion, without greatly adding to the evidence for it. The argument may here be restated in briefer form.

In the first place, it may be accepted that the Multituberculata, Caenolestoidea, and Rodentia are three distinct groups which have almost nothing in common beyond being, by definition, mammals. The multituberculates appear to belong in a distinctive subclass, Allotheria, and however that may be, the present rather good knowledge of their anatomy shows beyond reasonable doubt that they cannot be ancestral or closely related either to caenolestoids (or other Tertiary or Recent marsupials) or to rodents. The caenolestoids are true marsupials and certainly are far removed from the placental rodents. It is impossible to believe that the polydolopids really bridge the gaps between these groups which are about as diverse as three divisions of mammals could be. The polydolopids must be related to one only, or to none, of these three.

Little is known of their osteology, but it is known that they had inflected angular processes and palatal vacuities, both characters highly indicative of marsupial affinities although not absolutely diagnostic.

In the dentition, the dental formula and molar structure are fundamentally unlike those of the Multituberculata. The resemblance is so vague and so counteracted by more fundamental distinctions that the polydolopids may really be categorically denied any real relationship to the multituberculates. Shearing teeth are present, but shearing teeth quite as similar, if not more so, are also present independently in two groups of marsupials, in insectivores, and in primates. The molars have more than the average number of cusps, but this is also true of members of many other groups of mammals, insectivores, rodents, primates, sirenians, artiodactyls, etc., and the arrangement and shape of the cusps are not in agreement with the multituberculates but are fundamentally different.

On the other hand, there is a clear resemblance in the polydolopid dentition to that of the caenolestoids. The enlarged procumbent incisors and reduced antemolar teeth are very closely similar. Undoubted caenolestoids (Abderitinae) show a similar, but less advanced, shearing specialization. The lower molar pattern, as seen in the simpler forms of M_3 in the Polydolopidae, also has a basic resemblance to the Abderitinae: trigonid and talonid poorly differentiated, trigonid with one internal and two external cusps, talonid much enlarged, basined with cuspidate rim. The upper molar specializations conceal the ancestral type to a somewhat greater degree, yet here, too, the proliferation of cusps seems to overlie a distinctly caenolestoid heritage, subquadrate, broad molars with median basin, outer and inner cuspidate crests, inner side originally bilobed.

The marsupial caenolestoid affinities of the Polydolopidae seem to be beyond much doubt. They are much the most specialized of known caenolestoids, at least as far as the dentition is concerned, and this is extraordinary in view of their early occurrence. It is known that more primitive caenolestoids were present in the same fauna, although beyond their mere existence virtually nothing has yet been learned of them. An unexpectedly ancient divergence of this group is indicated.

The classification of the polydolopids themselves is also confused and confusing. Ameghino placed them in three families: Promysopidae (*Promysops* and *Propolymastodon*), Neoplagiaulacidae (*Anissodolops*), and Polydolopidae (other genera). It will be shown below that *Promysops* and *Propolymastodon* are synonymous with each other and also with *Eudolops* and that this genus, while clearly valid, is not very unlike *Polydolops* and should be placed in the same family. *Anissodolops* is synonymous with *Polydolops*. All the known genera are to be placed in a single family, Polydolopidae.

There are several other Patagonian genera that Ameghino considered as related more or less closely to this group. *Eomannodon* from the *Colpodon* beds (i.e., Colhué-Huapí formation), referred to the "Neoplagiaulacidae," was based on a single lower molar. I do not know what its affinities may be, but it is very unlike any polydolopid. *Mannodon*, from the Santa Cruz, is probably a caenolestid, and in any event is not a polydolopid. *Paradoxomys*, from the Entrerrian, was based on an imperfect incisor, inadequate for any opinion except that it is hardly possible that it represents a polydolopid, or a marsupial of any sort. Ameghino also referred to "*Promysops*" a species from the Deseado, *P. primarius*, based on an isolated incisor. I have not seen the original. Judging from Ameghino's figures and description, the tooth is indeterminate as to affinities. It might belong to this group, to the Caenolestidae, or to some rodent. Its definite reference to the Polydolopidae, and still more its placing in "*Promysops*," are unjustified.

Since Ameghino, undoubted polydolopids have been found in the Río Chico.

So far as is surely known, the Polydolopidae are thus confined to the Río Chico and Casamayor, where they form an element not very abundant but so characteristic and so widespread as to be one of the best indicators of pre-Deseadan age for the field worker.

The genera of Ameghino accepted as pertaining to this group are as follows, with the disposition here made of them:

Polydolops Ameghino, 1897	=*Polydolops*
Eudolops Ameghino, 1897	=*Eudolops*
Promysops Ameghino, 1902	=*Eudolops*
Pseudolops Ameghino, 1902	Probably =*Polydolops*
Pliodolops Ameghino, 1902	Probably =*Polydolops*
Amphidolops Ameghino, 1902	=*Amphidolops*
Propolymastodon Ameghino, 1903	=*Eudolops*
Anadolops Ameghino, 1903	=*Amphidolops*
Orthodolops Ameghino, 1903	=*Polydolops*
Anissodolops Ameghino, 1903	=*Polydolops*
Archaeodolops Ameghino, 1903	Probably =*Polydolops*

A distinction is made between those synonymies that seem to be demonstrated beyond reasonable doubt by the specimens now in hand and those that are probable but not demonstrated. In the latter case, involving *Pseudolops*, *Pliodolops*, and *Archaeodolops*, the known specimens do not make any valid, real, generic distinction and they show it to be improbable, but at the same time it may be that further discoveries would resuscitate these now undefinable genera. In any case all three are certainly closely allied to *Polydolops*, more closely than to any other form, and if they ever prove to be separable, this will be on relatively minor and unimportant characters.

As with most of the families of this fauna, generic classification is here extraordinarily difficult, principally for the following reasons:

1. The material is scanty in number and fragmentary in preservation.

2. Associated upper and lower jaws are unknown, and association of any sort is uncommon.

3. The real variety is great.

4. Morphological differences between teeth of the same dentition are very marked.

5. The types are not all comparable.

6. Numerous names, certainly too many, have already been applied to fragmentary materials and cannot be rejected, yet often cannot be validated.

These same difficulties arise time after time in the present revision, and it is necessary to keep them in mind.

The Ameghino Collection, all from the Casamayor, includes about 25 specimens, which were supposed to represent 11 genera and 16 species. The American Museum of Natural History Scarritt Collection (plus one specimen from the Chicago Natural History Museum) includes 43 specimens from the Casamayor and thus much more than doubles the available material. As with the older collection, most of the new specimens are isolated teeth, but there are nine jaws with two to four teeth in each. While the nomenclatural problem and that of detailed taxonomy still are not completely soluble, the more important broader features of the group and its fundamental diversity are now clearly shown. The Roth, Feruglio, and American Museum collections add four specimens from the Río Chico, one of which represents a genus distinct from any of Ameghino: *Seumadia*.

There are only four really distinctive morphological groups within the family, and these are here defined as genera: *Polydolops*, *Amphidolops*, *Eudolops*, and *Seumadia*. *Seumadia*, although fully distinctive, is known only from M^4. The other three clear-cut genera are most readily distinguished as follows:

Polydolops	*Amphidolops*	*Eudolops*
Vestigial teeth in lower diastema	(Unknown)	Vestigial teeth absent or reduced in number
Shearing teeth large, strongly denticulated	Very large. (Denticulations unknown)	Small, denticulation slight
Molar crowns moderate in height, well basined, cuspules small but distinct, enamel somewhat wrinkled	Molar crowns high, basins shallow, cuspules very small and indistinct, enamel very wrinkled	Molar crowns low, cusps large and distinct, enamel wrinkled
M^{2-3}_{2-3} moderate, M^4_4 reduced	M^2_2 relatively enlarged, M^4_4 reduced	M^{2-3}_{2-3} subequal, M^4_4 enlarged
Molar accessory cuspules present, M^2 with disconnected, conical external cuspules	Molar accessory cuspules abundant, M^2 with linear row of external cuspules	Molar accessory cuspules few or lacking, no external cuspules on M^2

Of these three, *Polydolops* is much the most abundant and, whether for this reason or another, it is also the most varied. The variations, however, are all in size, proportions, or minor details of cuspule development. They involve no important morphological character.

POLYDOLOPS AMEGHINO, 1897

Polydolops AMEGHINO, 1897a, p. 497; 1902a, p. 38; 1906, p. 468; SCHLOSSER, 1923, p. 433; SIMPSON, 1928, p. 2, figs. 1D, 2C, 6B; 1933d, p. 100, figs. 1D, 2C; SCOTT, 1913, p. 627; 1937, p. 723.

Pseudolops AMEGHINO, 1902a, p. 40; 1906, p. 468; SCHLOSSER, 1923, p. 433; SIMPSON, 1928, p. 3, figs. 1G, 7C.

Pliodolops AMEGHINO, 1902a, p. 41; 1906, p. 468; SCHLOSSER, 1923, p. 433; SIMPSON, 1928, p. 3, fig. 7B; SCOTT, 1937, p. 723.

Orthodolops AMEGHINO, 1903a, p. 130; 1904a, vol. 58, p. 257[1]; 1906, p. 468; SCHLOSSER, 1923, p. 433; SIMPSON, 1928, p. 3, fig. 1E; SCOTT, 1937, p. 723.

Anissodolops AMEGHINO, 1903a, p. 148; 1904a, vol. 58, p. 257[1]; 1906, p. 468; SIMPSON, 1928, p. 3, fig. 5B.

Archaeodolops AMEGHINO, 1903a, p. 150; 1904a, vol. 58, p. 257[1]; 1906, p. 468; SIMPSON, 1928, p. 3, fig. 3A; SCOTT, 1937, p. 723.

TYPE: *Polydolops thomasi* Ameghino.

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[1] These three genera were said to be new in 1904, but their publication in 1903 was prior and valid.

TYPES OF SYNONYMS: *Pseudolops: P. princeps* Ameghino. *Pliodolops: P. primulus* Ameghino. *Orthodolops: O. sciurinus* Ameghino. *Anissodolops: Amphidolops serrifer* Ameghino. *Archaeodolops: Polydolops clavulus* Ameghino.

DISTRIBUTION: Río Chico and Casamayor formations, Patagonia.

DIAGNOSIS: P_3 present. Shearing teeth large, denticulated. Molar crowns moderate in height, well basined, cuspules small but distinct, enamel somewhat wrinkled. M^{2-3}_{2-3} moderate in size. M^4_4 reduced, ovate. M^2 with a few disconnected, conical, external cuspules.

GENERIC SYNONYMY

Pseudolops was based on a number of teeth, the association of which is extremely dubious. This doubt and an error in the identification of the teeth deprive the original description of most of its distinction. The tooth described and figured by Ameghino as P^3 (his "M^3") is certainly M_1. This tooth and also M_3 and M^{2-3} differ from *Polydolops thomasi* in details that now appear only of specific value or less. The only other teeth included in the original lot, P^3 and M^1, differ in being relatively larger and more compressed laterally, and M^1 has rather small denticulations and is rounded in lateral contour. In view of the generally unsatisfactory nature of the specimens, it seems unwarranted to accept these minor distinctions as generic, but they make the synonymy slightly dubious.

Pliodolops was based on a single upper jaw fragment with two teeth, identified by Ameghino as M^{3-4} but now found to be M^{2-3}. A similar and closely related form is represented in our collection by a jaw with M^{2-3} (and parts of alveoli for M^1 and M^4) and by three isolated teeth, all M^2. The original definition is descriptive and not comparative, but the distinction from *Polydolops* is apparently meant to rest mainly on the greater development of the outer cuspules on M^2. At first sight, and especially in the published figures, the difference is striking. On study, the difference almost vanishes. The cuspules agree very closely with those on teeth surely referable to *Polydolops*. They are probably a little larger, but much of the apparent difference in this respect is caused merely by the fact that the type of *Pliodolops* is unworn, while the compared material of *Polydolops* was well worn. All intermediate stages are now shown. There are some minor differences, as given below in the specific diagnosis, but these do not seem to have generic value.

Orthodolops seems to have been based principally on the thick mandible. Ameghino also described the molar structure, but did not definitely state whether or in what way it was supposed to differ from *Polydolops*. The thick mandible, in part accentuated by crushing and perhaps even in part pathological, is almost exactly as in *Polydolops crassus*. The molar structure differs from *Polydolops thomasi* only in the presence of five tubercles on the inner side of the talonid of M_4, whereas these are variable in *P. thomasi* but do not appear commonly to exceed four. At best this can hardly be more than a specific difference.

Anissodolops was based on an error. Ameghino's description reverses the inner and outer sides of the type teeth, and he states that on the inner (really outer) side the fourth or last cusp is largest, and they diminish regularly anteriorly, whereas the third from the end is really larger than the second. In fact the molar structure is exactly that of *Polydolops*.

Archaeodolops was distinguished as having M_1 smaller, crown less oval and more pointed, border trenchant, denticles and salients absent, and as lacking P_2. The difference in form of M_1 is very slight, and denticles and salients were present and as in *Polydolops*, perhaps a little less prominent or perhaps only reduced by wear. P_2 was probably present in *Polydolops*, and its presence in *Archaeodolops* is not certainly confirmed by the original specimen. The genotype is much smaller than any other species of *Polydolops*, which may suggest a generic distinction, but no morphological distinction can really be established, and it seems necessary to return the type species to *Polydolops* where Ameghino himself first placed it.

MORPHOLOGY

The following description is based principally on specimens close or belonging to

Polydolops thomasi, but the outstanding variations are also taken into consideration.

P^3 and M^1 are shearing teeth.[1] P^3 has one anterior and two opposite posterior roots. It is a high tooth rising to a sharp apex. The anterior border continues the line of the root, becomes sharper as it nears the point, and bears a few denticles (only two distinctly defined in the type of *Polydolops thomasi*). The posterior crest is less steep, ends at the height of the following tooth, and has, in the type, four well-defined denticles. Inner and outer faces have two carinae each, the anterior one sharper in each case and rising forward and upward from the apex, the posterior less well defined and running almost straight upward. The posterior margin on both sides is also raised into a sharp angulation.

M^1 is similar but smaller, with three roots arranged in the same way. The apex is more central, and the anterior and posterior shearing crests are almost equal. Both are at a low angle to the horizontal and at the height of the adjacent tooth. Each has four denticles. There is a slight posterointernal heel. The carinae are about as on P^3 but the surfaces anterior to them relatively larger. In "*Pseudolops*" *princeps* what appears to be the homologue of this tooth is larger and less pointed than in other known specimens.

M^2 is quadrangular, with four main roots and a very small supplementary median external root. An internal notch divides this side of the tooth into two lobes, the anterior smaller and with one cusp, the posterior with two cusps, the first somewhat larger, and perhaps with accessory cuspules when unworn. The outer border has four nearly equal cusps, the third (from the anterior end) a little external to a line joining the other three. The first has a nearly connate posteroexternal accessory cusp, and the otherwise simple median longitudinal valley has another accessory cusp between, and internal to, the third and fourth main outer cusps and nearly connate with the latter. The outer border of the crown is sloping and bears in some cases apparently two, in others as many as five, small conical cuspules. Those specimens with only two cuspules are worn, and may have had more. Probably the number varies from three to five. In size they also vary, both from wear and from genetic but probably mostly individual variation, some being barely visible and others nearly as large as the cusps of the main external row.

M^3 is smaller, ovoid, with the anterior half wider. There are three subequal inner cusps and two distinct outer cusps, the anterior longer. Each of the external cusps has a tiny cuspule on its inner slope, in the valley, that on the first main cusp being extremely faint. The main cusps tend to be duplicated, so that a wholly unworn tooth has four apices in this row. There are two, one, or, rarely, no external cuspules, and these are always minute. M^3 and M^4 apparently had the crown enamel wrinkled when unworn, and rim crenulations may have been present.

M^4 is known in only one specimen (A.M.N.H. No. 28440), on which it is rounded, triangular, basined, with a raised rim all around. The cusp structure is obscure, but there appear to have been distinct anteroexternal and anterointernal cusps, a less definite posteromedian cusp, and obscure cuspules or crenulations elsewhere along the rim.

The lower incisor is unknown. It was followed by a diastema in which a vestigial tooth may have occurred. P_3, closely crowded against M_1, is very small but either two-rooted or with a grooved root. The crown has no cusps but is flattened and irregularly oval in outline.

M_1 is a large shearing tooth. In general it resembles P_3 but is higher and usually more compressed. In the best Ameghino specimen there are five anterior, one apical, and probably five posterior denticles. In A.M.N.H. No. 28444 there are four anterior and six posterior. From the apex sharp carinae run forward and downward on each side to the anterior root or the notch behind it, and less marked angulations run straight down to the posterior root.

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[1] Throughout this section I designate the teeth on the assumption that these are caenolestoids and derived from forms with a dental formula either really $P^3_3M^4_4$ or most conveniently so expressed. M^1_1 are in fact very different in form from the following teeth. As the abbreviations are used here, these are the fourth molars of Ameghino (who numbered premolars and molars as one series and called them all molars).

M_2 has a basined crown sharply elevated at the anterior end. When quite unworn, the apex has three cuspules, the largest central, another nearly connate with it on the anterior side, and a very faint cuspule lower down on the internal side. The inner side of the basin rim, falling away from this point, has four small cusps, their relative sizes varying greatly and apparently not of systematic value although the first is usually longest. The outer rim has a posterior cusp and several smaller cuspules between this and the apex.

The inner sides of M_{2-4} are low and nearly vertical, the outer slopes longer and more inclined. All have the crown enamel wrinkled where unworn.

M_3 has distinct trigonid and talonid, the latter considerably longer, but the difference in height is slight, and they are divided only by a low transverse ridge. The trigonid is very exceptional and agrees with that in the Abderitinae in having a single high inner cusp and two lower outer cusps. The basined heel has two inner and two outer cusps, but one to three accessory cuspules may appear on the inner side. M_4 is narrower than M_3, oval, narrowing posteriorly, but the cusp arrangement is about the same as on M_3.

SPECIFIC TAXONOMY

Ten species of Ameghino, all from the Casamayor, are now referred to this more broadly defined genus. Three species (one of doubtful reference to this genus) have been found in the Río Chico. Confining attention, for the moment, to the Casamayor species and to the best series of comparable specimens, the lower jaws, there appear three groups:

1. *Polydolops thomasi* group:
    - a. *Polydolops thomasi*
      Polydolops fur
      Polydolops simplex
    - b. *Polydolops crassus*
      "Orthodolops" sciurinus
2. *Polydolops serra* group:
    - *Polydolops serra*
    - *"Anissodolops" serrifer*
3. *Polydolops clavulus* group:
    - *Polydolops clavulus*

The last two groups, poorly represented in collections, seem to include only one species each, *"Anissodolops" serrifer* being a synonym of *Polydolops serra*, as will be shown below. The first group, relatively abundant, perhaps includes two species, but if so these are much closer to each other than to either of the other two species recognized. The first three species listed above are clearly synonymous, all being *P. thomasi*, and the next two are synonymous, being *P. crassus*.

Twelve of the new specimens are lower jaws or teeth of *Polydolops*, and clearly fall into the *P. thomasi* group, although most of them differ as much from *P. thomasi*, *sensu stricto*, as does *P. crassus* and so must be distinguished specifically if the latter species is recognized. Considering all these manifestly related but considerably varied specimens as a single sample (both the Ameghino and later specimens), the constants (table 3) of the most important available dimensions were calculated.

TABLE 3

Polydolops thomasi

Variate	N	OR	M	σ	V
LM_1	10	4.9–5.8	5.4 ± .1	.32 ± .07	5.9 ± 1.3
LM_2	9	3.6–4.4	4.1 ± .1	.25 ± .06	6.2 ± 1.5
LM_3	12	3.4–3.9	3.7 ± .04	.16 ± .03	4.2 ± .9

There is nothing in the figures to prove, or even necessarily to suggest, the presence of more than one species. Morphologically, also, the specimens present the familiar general characteristics of one rather variable species. No two are alike, most of them are nevertheless closely similar, but the extremes are markedly different and would be taken as taxonomically distinct were not the more numerous intermediate specimens known.

The sample is, in fact, of heterogeneous origin. All are from the same formation, but not at a single level, and all from the same general area, but several different localities are represented:

South of Colhué-Huapí: 5 specimens (3 in Museo

Argentino, 1 in Chicago Museum, 1 in American Museum)
Locality unknown, probably south of Colhué-Huapí for some or all: 3 specimens (all in Museo Argentino)
Cañadón Vaca: 4 specimens (all in American Museum)
Rinconada de los Lopez: 6 specimens (all in American Museum)

There is also in fact some discontinuity in the distributions of the variable characters, although in no case is the discontinuity clearly significant. Certain morphological associations do appear to be consistent, even though the specimens are too few to prove their significance, as may be seen in tables 4 and 5 of the relations between the lengths of M_1 and M_2.

TABLE 4

SUBSPECIES OF *Polydolops thomasi*

Group	Length M_1	Length M_2 of Same Specimen
A	4.9	4.3
	5.0	—
B	5.1	4.0
	5.2	3.9
	5.2	—
C	5.4	—
	5.6	—
	5.7	—
	5.8	4.4
D	5.8	3.9

TABLE 5

SUBSPECIES OF *Polydolops thomasi*

Group	Length M_2	Length M_1 of Same Specimen
D	3.6	—
	3.9	6.0
B	3.9	—
	3.9	5.2
	4.0	5.1
	4.1	—
A	4.3	4.9
C	4.4	5.8
	4.4	—

A few other associations are fairly consistent in supporting this fourfold grouping; for instance, a massive, swollen jaw is associated with group A. Altogether there seems to be a reasonable probability that these are natural groups, and they are tentatively defined below as subspecies of *P. thomasi.* Group A corresponds to Ameghino's *P. crassus* (and synonym), becoming *P. thomasi crassus.* Group B is *P. thomasi* proper and its several synonyms, becoming *P. thomasi thomasi.* The other two groups do not seem to occur (at least among lower jaws) in the Ameghino Collection and are defined below, group C as *P. thomasi paahi* and group D as *P. thomasi mara.* These are defined as subspecies, rather than species, because they are more closely related to each other than to the more clear-cut species of the same genus, because the total variation is not greater than does occur in single species, because this permits the identification (as simply *P. thomasi*) of specimens of upper jaws and of other specimens that would be *incertae sedis* were the specific criteria made so detailed, and because it is entirely possible that future work will necessitate considerable further revision which is a simpler matter if the somewhat dubious forms have not been given specific rank.

In some cases there is a definite association between morphological groups and provenience, but this is not clear in the present instance as is seen in the table (table 6) of the number of specimens from each locality referred to each subspecies.

It is, however, noteworthy that the best specimens in our collection from each of the three localities belong to a different subspecies for each locality: *P. t. thomasi* from Cañadón Vaca, *P. t. paahi* from Colhué-Huapí, and *P. t. mara* from the Rinconada de los Lopez. This may indicate that there is a real geographic (and perhaps a corresponding temporal) separation and that the seeming discrepancy results from lack of knowledge of the variability of single teeth. If this is true, no confusion should result from the misidentification of single teeth here, for the subspecies are based on the

TABLE 6

SPECIMENS OF SUBSPECIES OF *Polydolops thomasi*

	South of Colhué-Huapí	Cañadón Vaca	Rinconada de los Lopez	Locality Doubtful
P. t. thomasi	2	1	1	2
P. t. crassus	1	0	0	1
P. t. paahi	2	1	1	0
P. t. mara	0	0	2	0
Subspecies doubtful	0	2	2	0

more surely distinct relatively complete jaws.

Among the upper jaws, those belonging to *P. thomasi* are not numerous enough or distinctive enough to permit their association with subspecific groups of lower jaws, or to warrant attempting a detailed classification of the upper jaws themselves. There are three other groups of upper jaws that seem to be very distinctive from one another and from *P. thomasi* and that merit specific rank: Ameghino's "*Pseudolops*" *princeps* and *Pliodolops primulus* and a new form named *Polydolops bocurhor* below. It is very unlikely that these correspond to any of the subspecies of *P. thomasi* based on lower jaws. It is conceivable that they might include upper jaws of *P. serra* or *P. clavulus*, but even this seems unlikely, for the size relationships do not permit approximate occlusion among the known specimens.

The three Río Chico species are quite sharply distinct from any known in the Casamayor and are defined below, after the more typical Casamayor forms.

Polydolops thomasi Ameghino, 1897

Plate 6, figures 3–4; see also figures of subspecies

For synonymy, see the subspecies.

TYPE: M.A.C.N. No. 10338. Right upper jaw with P^3–M^3.

HYPODIGM: The type, the hypodigms of the subspecies, and (among others) the following A.M.N.H. Nos.: 28440, 28428, 28429, 28920, 28926, 28927.

HORIZON AND LOCALITY: Casamayor beds, Patagonia. Type from south of Lago Colhué-Huapí. Other specimens from Cañadón Vaca and Rinconada de los Lopez.

DIAGNOSIS: Denticles and carinae of M_1 well developed. M_3 with two to four internal talonid cuspules and M_4 with four to five talonid cuspules (in all). M^1 of moderate size and pointed apex. External cuspules of M^{2-3} feebly developed. Length and width of M^2 nearly equal. M^3 somewhat smaller than M^2 and with width slightly exceeding length. For dimensions see statistical constants given above and tabular comparison of specimens below.

Polydolops thomasi thomasi (Ameghino, 1897)

Plate 2, figure 8; plate 4, figures 1–2

Polydolops thomasi AMEGHINO, 1897a, p. 497, fig. 73; 1898, p. 185; 1902a, p. 38; 1903a, p. 141, figs. 63, 68, 101, 102, 104; 1904d, p. 43, fig. 26; 1906, p. 358, fig. 198; SCHLOSSER, 1923, p. 433, fig. 544A, B, C.

Polydolops fur AMEGHINO, 1902a, p. 39.

Polydolops simplex AMEGHINO, 1903a, p. 185, fig. 119; 1904a, vol. 58, p. 256.[1]

TYPE: M.A.C.N. No. 10338. Right upper jaw with P^3–M^3.

TYPES OF SYNONYMS: *Polydolops fur:* M.A.C.N. No. 10342. Right lower jaw with M_{2-4}, somewhat broken.

Polydolops simplex: M.A.C.N. No. 10335. Lower jaw, relatively complete but with crowns of M_1 and M_3 only.

HORIZON AND LOCALITY: Casamayor beds, Patagonia. The three types are from south of Lago Colhué-Huapí. The Ameghino referred specimens have no data. Ours is from Cañadón Vaca.

HYPODIGM: The three types, as above, and the following:

M.A.C.N. No. 10337. Right lower jaw with P_3–M_4
M.A.C.N. No. 10343. Right lower jaw with M_{2-4}

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[1] Said to be new in 1904, but publication in 1903 prior and valid.

A.M.N.H. No. 28444. Right lower jaw with P_3–M_2

DIAGNOSIS: Length P^3–M^3 in type 17 mm. In referred lower jaws, length M_1 5.1–5.2, length M_2 3.9–4.1, ratio LM_1:LM_2 1.25–1.33. Width M_1 3.8–3.9. M_1 pointed. Mandible slender.

Polydolops fur was founded on supposedly larger size, lower molars narrower, and more complex, horizontal ramus higher. The difference in size is considerably less than 10 per cent at most, and the molars are not unusually narrow—the small width given by Ameghino is due to the breaking of one side of the teeth. The crown pattern is identical with that of specimens referred by Ameghino to *P. thomasi*. The difference in jaw depth is negligible.

Polydolops simplex was referred to the genus doubtfully at first, and many supposed distinctions from *P. thomasi* were given. The teeth were said to be more slender, M_1 large with two external and one internal anterior vertical angulation, upper edge curved, denticles little accentuated, P_3 extremely small, symphysis long, turned up, rodent-like, and horizontal ramus long, slender, with lower border strongly curved. I see no essential difference in tooth size or form. P_3 is not over 0.4 mm. smaller (root, the crown being absent), a difference of no importance in a vestigial tooth. M_1 has the same size and shape as in *P. thomasi* and the denticles are, if anything, coarser, but the difference is unimportant. The symphysis is better preserved than in any other specimen referred to *P. thomasi*, but there is no evidence that it is different. The characters of the ramus are exactly matched in specimens referred to *P. thomasi* by Ameghino. The different preservation of the specimen makes it appear very distinct at first sight, but I find no way of separating it from *P. thomasi*.

Polydolops thomasi crassus (Ameghino, 1902)

Plate 2, figure 9

Polydolops crassus AMEGHINO, 1902a, p. 39.
Orthodolops sciurinus AMEGHINO, 1903a, p. 131, figs. 54, 106; 1904a, vol. 58, p. 257[1]; 1906, p. 367, fig. 220.

TYPE: M.A.C.N. No. 10349. Left lower jaw with M_{1-4}.

TYPE OF *Orthodolops sciurinus:* M.A.C.N. No. 10336. Right lower jaw with broken P_3–M_2 and complete M_{3-4}.

HYPODIGM: The two types, as above.

HORIZON AND LOCALITY: Casamayor beds, Patagonia. M.A.C.N. No. 10349 from south of Lago Colhué-Huapí. No data with other type.

DIAGNOSIS: Length M_1 4.3 mm., slightly (probably not significantly) longer than *P. t. thomasi*. Ratio LM_1:LM_2 1.14, lower than in available specimens of *P. t. thomasi*. Width M_1 5.0, markedly greater than in *P. t. thomasi*. M_1 pointed. Mandible very stout.

It has already been noted that the characters supposedly distinguishing *Orthodolops sciurinus* do not in any way separate it from *Polydolops crassus*. This subspecies is very close to *P. t. thomasi* and rests on little more than the swollen horizontal ramus, a feature not surely of taxonomic value.

Polydolops thomasi paahi,[2] new subspecies

Plate 5, figures 1–2

TYPE: A.M.N.H. No. 28434. Right lower jaw with M_{1-3}. Collected by G. G. Simpson.

HYPODIGM: The type and the following:

C.N.H.M. No. P14717. Lower jaw with M_{2-3}
A.M.N.H. No. 28443. Isolated M_1
A.M.N.H. No. 28934. Isolated M_1

HORIZON AND LOCALITY: Casamayor beds (below main fossil level; see elsewhere), south of Lago Colhué-Huapí, Chubut, Argentina.

DIAGNOSIS: Length M_1 5.4–5.8, somewhat greater than in either *P. t. thomasi* or *P. t. crassus*. Length M_2 4.4, greater than in *P. t. thomasi*. Ratio LM_1:LM_2 1.32, about as in *P. t. thomasi*. Width M_1 4.4–4.6, intermediate between *P. t. thomasi* and *P. t. crassus*. Shape of M_1 about as in those subspecies. Mandible as in *P. t. thomasi*.

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[1] Said to be new in 1904, but publication in 1903 prior and valid.

[2] *Paahi*, Patagonian hare in Tehuelche or Tsoneca Indian, according to Musters. Signalizing the rodent-like habitus.

TABLE 7

MEASUREMENTS OF ALL SUBSPECIES OF *Polydolops thomasi*

Upper Teeth (Subspecies Uncertain)

	P^3		M^1		M^2		M^3		M^4		
	L	W	L	W	L	W	L	W	L	W	
M.A.C.N. No. 10338	5.5	4.6	3.3	4.0	4.4	4.3	3.7	3.8	—	—	(Type of species)
A.M.N.H. No. 28440	—	—	3.0	3.1	4.4	4.5	3.5	4.0	3.5	3.4	

Lower Teeth

	M_1		M_2		M_3		M_4		Locality	Subspecies
	L	W	L	W	L	W	L	W		
M.A.C.N. No. 10337	5.2	3.9	3.9	3.4	3.4	2.9	—	—	?	*thomasi*
M.A.C.N. No. 10343	—	—	3.9	3.7	3.5	3.1	3.8	2.9	?	*thomasi*
M.A.C.N. No. 10342	—	—	—	—	3.7	3.1	—	—	Colhué-Huapí	*thomasi* (type *P. fur*)
M.A.C.N. No. 10335	5.2	3.8	—	—	3.6	2.8	—	—	Colhué-Huapí	*thomasi* (type *P. simplex*)
A.M.N.H. No. 28444	5.1	3.9	4.0	3.1	—	—	—	—	Cañadón Vaca	*thomasi*
M.A.C.N. No. 10349	4.9	5.0	4.3	3.9	3.9	3.4	4.2	2.9	Colhué-Huapí	*crassus* (type)
M.A.C.N. No. 10336	5.0	—	—	—	3.8	3.4	4.1	3.0	?	*crassus* (type *Orthodolops sciurinus*)
A.M.N.H. No. 28434	5.8	4.6	4.4	3.7	3.7	3.3	—	—	Colhué-Huapí	*paahi* (type)
C.N.H.M. No. P14717	—	—	4.4	3.6	3.8	3.3	—	—	Colhué-Huapí	*paahi*
A.M.N.H. No. 28443	5.6	4.4	—	—	—	—	—	—	Cañadón Vaca	*paahi*
A.M.N.H. No. 28934	5.4	4.5	—	—	—	—	—	—	Lopez	*paahi*
A.M.N.H. No. 28921	5.8	4.5	3.9	3.3	3.4	3.2	—	—	Lopez	*mara* (type)
A.M.N.H. No. 28930	5.7	4.8	—	—	—	—	—	—	Lopez	*mara*
A.M.N.H. No. 28429	—	—	3.6	2.7	—	—	—	—	Cañadón Vaca	?
A.M.N.H. No. 28428	—	—	—	—	3.6	2.8	—	—	Cañadón Vaca	?
A.M.N.H. No. 28927	—	—	4.1	3.6	—	—	—	—	Lopez	?*thomasi*
A.M.N.H. No. 28926	—	—	—	—	3.8	3.1	—	—	Lopez	?
A.M.N.H. No. 28920	—	—	—	—	3.7	2.9	—	—	Lopez	?

Polydolops thomasi mara,[1] new subspecies

Plate 4, figures 3–4

Type: A.M.N.H. No. 28921, left lower jaw with M_{1-3}. Collected by Second Scarritt Expedition.

Hypodigm: Type and A.M.N.H. No. 28930, M_1 in mandibular fragment.

Horizon and Locality: Casamayor beds, near "puesto" of Don Mariano, Rinconada de los Lopez, Chubut, Argentina.

Diagnosis: Length M_1 5.7–5.8, comparable to *P. t. paahi.* Length M_2 3.9, comparable to *P. t. thomasi.* Ratio $LM_1:LM_2$ 1.49, larger than in other subspecies. Width 4.5–4.8, comparable to *P. t. paahi.* Apex of M_1 more rounded than in other subspecies, its highest part not a point of the upper end of the carinae but the rounded edge posterior to this. Mandible about as in *P. t. thomasi.*

Polydolops serra Ameghino, 1902

Polydolops serra Ameghino, 1902a, p. 39.

Amphidolops serrifer Ameghino, 1902a, p. 42.

Polydolops serrifer [error for *Amphidolops serrifer*], Ameghino, 1904a, vol. 58, p. 257.

Anissodolops serrifer, Ameghino, 1903a, p. 148, fig. 72; 1904a, vol. 58, p. 257; 1906, p. 360, fig. 203.

Type: Ameghino's description included P_3–M_4, not figured. No one specimen now in the collection has all these teeth. There are three specimens that are conspecific and bear Ameghino's label as being of *Polydolops serra*. They are probably syntypes, and may be so considered.

M.A.C.N. No. 10341. Part of lower jaw with P_3, M_1, and fragment of M_2. Lectotype

M.A.C.N. No. 10361. Part of lower jaw with M_{2-3}

M.A.C.N. No. 10363. Part of lower jaw with M_4 and fragment of M_3.

Type of *Anissodolops serrifer:* M.A.C.N. No. 10359. Isolated broken M_3.

Hypodigm: The four types, as above.

Horizon and Locality: M.A.C.N. No. 10341 has no data. The others are all from the Casamayor beds south of Lago Colhué-Huapí.

Diagnosis: Denticles and carinae of M_1 well developed. Significantly smaller than *P. thomasi.* Differences from means for *P. thomasi* divided by corresponding σ of the latter: $LM_1-3.4$, $LM_2-2.4$, $LM_3-3.1$. Various tooth proportions and ratios within range of *P. thomasi.* M_3 with five or more tiny cuspules on internal side of talonid. Talonid of M_4 with six or seven tubercles in all.

Ameghino did not compare his *Amphidolops serrifer*, afterwards made type of *Anissodolops*, with *Polydolops serra*. In size and all other observable characters they are the same.

TABLE 8

Polydolops serra

	M_1		M_2		M_3		M_4	
	L	W	L	W	L	W	L	W
M.A.C.N. No. 10341	4.3	3.5	—	—	—	—	—	—
M.A.C.N. No. 10361	—	—	3.5	3.1	3.2	3.0	—	—
M.A.C.N. No. 10363	—	—	—	—	—	—	3.0	2.0
M.A.C.N. No. 10359	—	—	—	—	3.1	—	—	—

Polydolops clavulus Ameghino, 1902

Polydolops clavulus Ameghino, 1902a, p. 40.

Archaeodolops clavulus, Ameghino, 1903a, p. 150, figs. 75, 103; 1904a, vol. 58, p. 257.

Type: M.A.C.N. No. 10356. Lower jaw with P_3–M_2. It is not clear whether this or the other Ameghino specimen (see hypodigm) was the type, or whether both were syntypes, but in any event I select this, as it undoubtedly does typify the species and was figured under this name.

Hypodigm: Type (or lectotype) and the following:

M.A.C.N. No. 10360. Lower jaw with M_{1-3}

Horizon and Locality: Casamayor beds, Patagonia. No other data.

Diagnosis: Denticles and carinae of M_1 poorly developed. Much the smallest known species of the genus. Deviations from means of *P. thomasi* divided by corresponding σ of the latter: $LM_1-7.8$, $LM_2-9.6$, $LM_3-11.9$. M_2 somewhat smaller relative to M_1 and M_3 than in *P. thomasi* or *P. serra.*

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[1] *Mara*, Araucanian Indian name for native rodents (probably species of *Dolichotis*), used to signalize the rodent-like habitus of this animal.

TABLE 9

Polydolops clavulus

	LM_1	LM_2	LM_3
M.A.C.N. No. 10360	2.9	1.8	1.8
M.A.C.N. No. 10356	2.9	1.6	

Polydolops princeps (Ameghino, 1902)

Pseudolops princeps Ameghino, 1902a, p. 40; 1903a, p. 149, figs. 73, 108.

Type: M.A.C.N. No. 10332. Isolated incisor, P^3, M^1, M_1, and M_3 and surely associated M^{2-3}. As the association is otherwise doubtful, M^1, the most distinctive tooth, is made lectotype.

Hypodigm: Type or types, as above.

Horizon and Locality: Casamayor beds, south of Lago Colhué-Huapí, Patagonia.

Diagnosis: M^1 much larger than in *P. thomasi*, strongly compressed laterally, rounded rather than pointed in apical outline and denticulation slight. M^2 with external cuspules better developed than in *P. thomasi*.

The tooth described and figured by Ameghino as P^3 is really M_1, but P^3 is present in the lot of type material and is peculiar in being large and strongly compressed as is M^1. The other teeth (which may not really belong with these) differ very little from *P. thomasi* and might even belong to that species, but these peculiar upper shearing teeth are distinctive. The development of cuspules on M^2 is intermediate between *P. thomasi* and the following two species.

TABLE 10

Types of *Polydolops princeps*

(P^3 is somewhat broken. P^3 and M^1 are isolated teeth)

P^3		M^1		M^2		M^3	
L	W	L	W	L	W	L	W
7.3	3.7	5.7	4.2	4.5	4.6	3.9	4.0

Polydolops primulus (Ameghino, 1902)

Pliodolops primulus Ameghino, 1902a, p. 41; 1903a, p. 109, figs. 27, 65, 116; 1906, p. 359, fig. 201; Schlosser, 1923, p. 433, fig. 544D.

Type: M.A.C.N. No. 10353. Right M^{2-3}.

Hypodigm: Type only.

Horizon and Locality: Casamayor beds, south of Lago Colhué-Huapí, Chubut, Argentina.

Diagnosis: External cuspules of M^2 large. M^2 markedly and M^3 very slightly wider than long.

TABLE 11

Type of *Polydolops primulus*

M^2		M^3	
L	W	L	W
3.2	3.7	2.8	2.9

Polydolops bocurhor,[1] new species

Plate 6, figures 1–2

Type: A.M.N.H. No. 28427. Right M^{2-3}. Found by C. S. Williams.

Hypodigm: Type and A.M.N.H. Nos. 28425, 28426. Both isolated M^2.

Horizon and Locality: Casamayor beds, Cañadón Vaca, Chubut, Argentina.

Diagnosis: External cusps of M^2 as in *P. primulus*. M^3 much wider than long, M^2 nearly equidimensional and relatively larger than in *P. primulus*.

TABLE 12

Type of *Polydolops bocurhor*

M^2		M^3	
L	W	L	W
3.8	4.0	2.9	3.7

Polydolops rothi Simpson, 1936

Text figure 7

Polydolops rothi Simpson, 1935b, p. 14 (*nomen nudum*); 1936d, p. 71, fig. 1.

Type: M.L.P. No. 11-122, Roth Collection. Left ramus with M_{1-3}.

Hypodigm: Type only.

Horizon and Locality: Río Chico beds, near Gaiman, Chubut.

Diagnosis: About the size of *P. serra*, but

---

[1] *Bocur*, wide or thick, *hor*, tooth, Tehuelche Indian. In reference to the wide M^3.

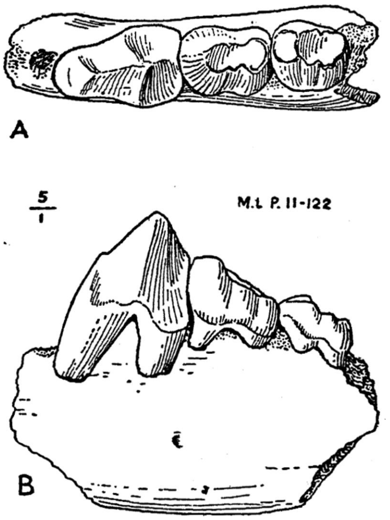

FIG. 7. *Polydolops rothi* Simpson. Type, M.L.P. No. 11-122, left lower jaw with M_{1-3}. A. Crown view. B. External view. ×5. Drawing by Cabrera, from Simpson, 1936d.

structure simpler, more like *P. clavulus.* M_1 with the denticles of the cutting edge weakly developed, apex acute and posterior border falling away sharply. Anterior end of M_2 less elevated than in *P. thomasi*, three external cusps on the talonid, of which the median cusp is small. M_3 with two external and probably three internal cusps on the talonid.

TABLE 13

TYPE OF *Polydolops rothi*

M_{1-3}	M_1		M_2		M_3	
L	L	W	L	W	L	W
9.7	4.0	2.9	3.2	3.0	3.0	2.6

Polydolops winecage Simpson, 1935

Text figure 8

Polydolops winecage SIMPSON, 1935a, p. 4, fig. 1.

TYPE: In Feruglio Collection, part of left lower jaw with M_1 and M_2. Cast, A.M.N.H. No. 27893.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Río Chico about 6 meters below the lowest true ash bed of the Casamayor, Bajo de la Palangana, Chubut, Argentina.

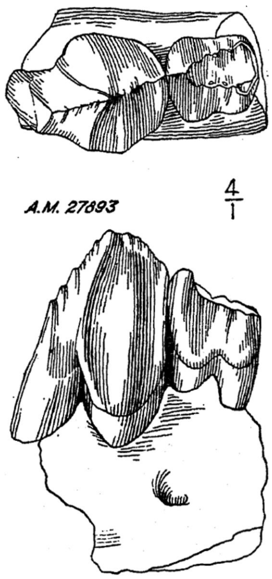

FIG. 8. *Polydolops winecage* Simpson. Type, Feruglio Collection (no catalogue number, cast A.M.N.H. No. 27893), left lower jaw with M_{1-2}. Crown and external views. ×4.

DIAGNOSIS: M_1 length 4.5 mm., width 4.0 mm. M_2 length 3.2 mm., width 2.8 mm. General structure close to *P. thomasi*, but M_1 considerably wider relative to its length, and M_2 much smaller both absolutely and relative to M_1.

Polydolops crassus has M_1 even wider relative to its length, and M_2 is much larger, *P. serra* has a smaller and more slender M_1 and a larger M_2, and *P. clavulus* is smaller than *P. winecage.*

?Polydolops kamektsen Simpson, 1935

Plate 5, figures 3–4

?Polydolops kamektsen SIMPSON, 1935a, p. 5, fig. 2.

TYPE: A.M.N.H. No. 28525. Part of right lower jaw with M_3.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Río Chico formation, Cañadón Hondo, Chubut, Argentina.

DIAGNOSIS: M_3 very small, length 2.4 mm. and width 2.0 mm. in type, rounded oval in contour, trigonid narrower than talonid.

This species is intermediate between *P. clavulus* and *P. serra* in size, and not close enough to either to be possibly synonymous. It is morphologically so distinctive that it probably belongs to a new genus, but the specimen is inadequate for definitive decision on this point. M_2 (as indicated by alveoli) was considerably smaller than in *P. winecage.*

AMPHIDOLOPS AMEGHINO, 1902

Amphidolops AMEGHINO, 1902a, p. 42; 1906, p. 468; SCHLOSSER, 1923, p. 433; SIMPSON, 1928, p. 3, fig. 1F; SCOTT, 1913, p. 627.

Anadolops AMEGHINO, 1903a, p. 186; 1904a, vol. 58, p. 258[1]; 1906, p. 468; SIMPSON, 1928, p. 3, fig. 3B.

TYPE: *Amphidolops serrula* Ameghino.

TYPE OF *Anadolops*: *Anadolops thylacoleoides* Ameghino.

DISTRIBUTION: Casamayor beds, Patagonia.

DIAGNOSIS: Shearing teeth very large. Molar crowns moderately high but basins and coronal relief as a whole shallow, cusps all small, tending to become very numerous and indistinct. Enamel strongly wrinkled. M^2_2 enlarged relative to other teeth, M^4_4 reduced. M^2 with a continuous external row of accessory cuspules, nearly or quite as prominent as the main row immediately internal to them.

The supposedly distinctive characters of *Anadolops* were all based on the identification of the three teeth of the type specimen as M_{1-3}. They are really M_{2-4} and cannot be distinguished specifically from the genotype of *Amphidolops*. Ameghino also proposed a species *Amphidolops serrifer* which he later made type of a new genus, *Anissodolops*. As shown above, it is a synonym of *Polydolops serra*, and so has no closer relationship to *Amphidolops*.

Of the known lower teeth, the isolated M_3 on which the genotype is based is the best preserved. Its outstanding characters are the high crown with shallow apical pattern and the wrinkled enamel. The enamel of *Polydolops* (and of *Eudolops*) is also wrinkled when unworn, but this feature is exaggerated in *Amphidolops*. The usual three trigonid cusps of M_3 are visible, but they are poorly differentiated and the whole anterior border is finely denticulated. The talonid has four main internal and two or three external cusps, but these are obscured and made hardly distinguishable by the presence of numerous tiny denticles.

M_2 is shown in very poor preservation in the type of "*Anadolops thylacoleoides*," and we have a well-preserved isolated M_2, A.M.N.H. No. 28922, surely of this genus. It shows analogous characters to those of M_3 and is also more elongate than is usual in *Polydolops*, has the anteroposterior trigonid blade more distinctly developed, the external talonid cusps indistinct and of nearly equal size, in contrast to the definite differentiation in *Polydolops*, and the internal talonid cusps likewise undifferentiated and also more numerous and much less distinct than in *Polydolops*. M_4 is present in "*Anadolops*" but is so poorly preserved that no important additional distinctions from *Polydolops* can be seen.

The diagnostic characters of the upper teeth depend on the reference to this genus of three specimens found by us, and particularly of A.M.N.H. No. 28929, a left maxilla with M^{2-3} and the roots of M^1 and M^4. The evidence for this reference is as follows:

1. The upper teeth in question have a very shallow apical pattern, much wrinkled enamel (except when deeply worn), poorly differentiated main cusps, and many accessory cuspules, all characters found only in *Amphidolops* among the known lower jaws.
2. Occlusion with *Amphidolops* lower teeth is apparently possible, although this cannot be well established with the available specimens. The elongation of M^{1-2} is harmonious with that of M_2 in *Amphidolops* lower jaws.
3. In a small pocket at a single horizon and locality in the Rinconada de los Lopez there were found six lower teeth and jaws and two upper teeth of *Polydolops*, one lower tooth surely of *Amphidolops*, and one upper tooth and one upper jaw that could not belong to *Polydolops* but could well belong to *Amphidolops*. No other polydolopids were found in this deposit, and no other genus is known to which these upper teeth could belong.

The characters of these teeth have been sufficiently stressed in the preceding pages and are well shown in the figures. All are

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[1] Said to be new in 1904, but publication in 1903 was valid and prior.

tentatively placed in the type species, since they are of approximately the same size and cannot reasonably be distinguished. The Lopez specimens may well prove to be distinct when comparison becomes possible.

Amphidolops serrula Ameghino, 1902

Plate 6, figure 5; plate 7, figures 1–2

Amphidolops serrula AMEGHINO, 1902a, p. 42; 1903a, p. 148, fig. 71.

Anadolops thylacoleoides AMEGHINO, 1903a, p. 186, fig. 120; 1904a, vol. 58, 258.[1]

TYPE: M.A.C.N. No. 10357. Isolated left M_3.

TYPE OF *Anadolops thylacoleoides:* M.A.C.N. No. 10339. Left lower jaw with M_{2-4}, somewhat broken.

HYPODIGM: Types and the following (but specific ascription not considered quite certain):

A.M.N.H. No. 28929. Palatal fragment with M^{2-3}
A.M.N.H. No. 28438. Isolated M^2
A.M.N.H. No. 28923. Isolated M^3
A.M.N.H. No. 28922. Isolated M_2
A.M.N.H. No. 28933. Isolated M_2

HORIZON AND LOCALITY: Casamayor beds. Type from south of Lago Colhué-Huapí. Type of *A. thylacoleoides* without data. A.M.N.H. No. 28438 from south of Lago Colhué-Huapí. Other A.M.N.H. specimens from Rinconada de los Lopez.

DIAGNOSIS: Only known species. Type M_3 measuring 3.8 mm. in length by 3.6 mm. in width.

SEUMADIA SIMPSON, 1935

Seumadia SIMPSON, 1935a, p. 5; SCOTT, 1937, p. 723.

TYPE: *Seumadia yapa* Simpson.

DIAGNOSIS: M^4 triangular, slightly wider than long, the corners somewhat elevated but without any distinct cusps. Crown very low, with a very shallow basin, with numerous irregular, anastomosing small grooves and ridges.

The proportions and the cusp structure, or its absence, sharply distinguish this from the homologous tooth of *Polydolops*. *Amphidolops* has similarly wrinkled enamel and small cusps, but the cusps (also in the upper teeth), while small, are numerous, sharp, and distinct, and the crowns are rather high although the apical pattern is shallow. No other genus suggests comparison.

The genus is surely distinct and has been named, even though the material is so limited, because of the great interest in this form which belongs to the oldest South American faunule.

Seumadia yapa Simpson, 1935

Plate 6, figure 6

Seumadia yapa SIMPSON, 1935a, p. 6, fig. 3.

TYPE: A.M.N.H. No. 28431, isolated M^4.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Río Chico formation, 37 meters above the "Banco Verde" of the Salamanca, Cerro Redondo, west of Puerto Visser, Chubut, Argentina.

DIAGNOSIS: Sole known species of the genus. M^4 measures 3.4 mm. in length and 3.6 mm. in width.

EUDOLOPS AMEGHINO, 1897

Eudolops AMEGHINO, 1897a, p. 498; 1906, p. 468; SIMPSON, 1928, p. 2, fig. 7A; 1933d, p. 105; SCOTT, 1937, p. 723.

Promysops AMEGHINO, 1902a, p. 36; 1906, pp. 468, 470; SCHLOSSER, 1923, p. 433; SIMPSON, 1928, p. 3, fig. 5A.

Propolymastodon AMEGHINO, 1903a, p. 100; 1906, p. 468; SCHLOSSER, 1923, p. 433; SCOTT, 1913, p. 627; 1937, p. 723; SIMPSON, 1928, p. 3, figs. 1H, 4; [=*Eudolops*] SIMPSON, 1933d, pp. 104–105.

TYPE: *Eudolops tetragonus* Ameghino.

TYPES OF SYNONYMS: *Promysops:P. acuminatus* Ameghino. *Propolymastodon:P. caroli-ameghinoi* Ameghino.

DISTRIBUTION: Casamayor beds, Patagonia.

DIAGNOSIS: P_3 (and probably C and P_{1-2}) absent. Shearing teeth relatively small, denticulation slight. Molar crowns low, with large distinct cusps, and relatively few accessory cuspules. M^{2-3}_{2-3} subequal, M^4_4 enlarged. No external accessaory cuspules on M^2.

Although it was placed in a different family from "*Promysops*" and "*Propolymastodon*" by Ameghino, there is now no doubt that *Eudolops* is the same as those better known

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[1] Said to be new in 1904, but publication in 1903 was prior and valid.

forms. This is proved by our discovery of an upper jaw which includes the homologue of the type of *Eudolops tetragonus.* This is certainly not distinct generically from the latter, perhaps not specifically, and is perfectly adapted to be the upper jaw of "*Propolymastodon*" and of no other known lower teeth.

Promysops rested entirely on a toothless fragment with the root of an incisor and the alveoli of M_1. The size, form, absence of P_3, and alveoli of M_1 agree exactly with the specimen later named "*Propolymastodon cardatus*," and the front part of the jaw is exactly as in "*P. caroli-ameghinoi*," except for its slightly smaller size.

Ameghino believed that there were two lower incisors, but this is improbable. In the available specimens (types of "*Promysops acuminatus*" and "*Propolymastodon caroli-ameghinoi*") the jaw is broken anterior to M_1 and shows a root of a procumbent incisor and anterior to it a larger cavity which may or may not be an alveolus. The canine and all the premolars were probably absent. At any rate, P_3, constantly present in other polydolopids, was absent. The form of M_1 is also unlike that of any other polydolopid, although it is a shearing tooth. M_{2-3} are basically similar to *Polydolops*, differing in detail. As Ameghino restored the lower jaw (e.g., 1903a, fig. 18) it is very unlike that of any other polydolopid or caenolestoid and much as in *Taeniolabis*. I have elsewhere (1928) pointed out that this restoration is conjectural. After studying the original and a new specimen, I have confirmed that the jaw was closely similar to *Polydolops* and other caenolestoids. The incisor was more procumbent than in Ameghino's restoration, and an inflected angle was surely present. The horizontal ramus is almost exactly as in *Polydolops* except in minor proportions. The condyle is not preserved, but surely was distinct from the angle and more elevated than in Ameghino's restoration. I would now change my restoration in details, but not in essentials, making the symphysis a little longer, more curved, the postdental part of the jaw shorter, angle more inflected, and coronoid more nearly vertical.

M_1 differs from that of *Polydolops* in being smaller relative to the other molars, symmetrical in contour, rising to a sharp median point, and with the serrations less pronounced, although they are present. M_2 in the (known) specimens has two distinct external talonid cusps with one cuspule between them, and in one specimen one, in the other two, anterior internal cusps followed in each case by a smaller but well-developed posterointernal cusp. On all the grinding molars the cusps are more distinct and larger than in *Polydolops.* On M_3 the trigonid has the usual two external and one internal cusp, while the poorly differentiated talonid has in one supposed species (*E. caroli-ameghinoi*) two cusps each on internal and external side and in the other (*E. cardatus*) two internal and three external, the extra external cusp being relatively small and intercalated between the other two. M_4 is relatively much larger than in *Polydolops* and is less oval. In the two known specimens (both *E. caroli-ameghinoi*) it is almost exactly like M_3 but has the heel more elongated. In one there is a very faint trace of an intercalated external cuspule (cf. M_3 of *E. cardatus*, but much less pronounced than in the latter).

P^3 and M^1 are unknown, and M^{2-4} are principally represented by a single specimen, A.M.N.H. No. 28932, tentatively referred to the type species but possibly distinct. Presumably the cusps varied considerably, but the following remarks are based on this specimen only. M^{2-4} are of approximately equal size and similar form, but M^3 is shorter than M^2 or M^4, and M^4 is narrower than the others and tapers posteriorly so as to be an elongate oval rather than quadrate. The internal face has a marked vertical groove, least pronounced on M^4, separating it into smaller anterior and larger posterior lobes. The internal cusps are deeply worn. The anterior lobe had probably two poorly differentiated cusps, and the posterior lobe had two or possibly three. The main external cusps are on the edge of the tooth, there being no long outer slope with stylar cuspules as in *Polydolops* and *Amphidolops.* On M^{2-3} there are four outer cusps of varying size (see figures). On M^4 there is one main anteroexternal cusp followed along the outer margin by four small cusps or cuspules. On M^{2-3} there is an accessory cusp posterointernal to the largest external cusp of the posterior lobe and nearly connate with it; this cusp apparently is constant in the Polydolopidae. On all these molars the crown is much higher on the internal than on the external side, so that the coronal surface is markedly inclined outward.

The number of species really represented in the collections is very doubtful. As far as size is concerned, all known specimens could be of one species, but there are differences in cusp number and size, the significance of which is dubious. In some groups they would be generic, but in this group, in which the individual cusps are obviously highly variable, they may not even be specific.[1] The upper and lower teeth cannot be associated specifically. The following specific diagnoses therefore merely meet taxonomic requirements and do not have much real meaning.

Eudolops tetragonus Ameghino, 1897

Plate 7, figure 3

Eudolops tetragonus AMEGHINO, 1897a, p. 498, fig. 74; 1898, p. 185.

TYPE: M.A.C.N. No. 10358, isolated right M^3.

HYPODIGM: The type and, tentatively, the following: A.M.N.H. No. 28932, palatal fragment with left M^{2-4}. Found by Justino Hernandez.

HORIZON AND LOCALITY: Casamayor beds. No data with type, but probably from south of Lago Colhué-Huapí. Referred specimen from the Rinconada de los Lopez.

DIAGNOSIS: M^3 measuring 6.2 by 5.4 mm. in type. Not directly comparable with other supposed species, but possibly slightly larger.

Ameghino considered the type as M^2, which may be correct, but it compares more closely with M^3 of the referred specimen. In the type the anterior and posterior external cusps are larger and the two between them smaller and subequal. In the referred specimen the second and fourth outer cusps are smaller than the first and third (and on M^2 the third is smaller than the other three). These proportions are of very dubious taxonomic value.

TABLE 14

Eudolops tetragonus

	M^2		M^3		M^4	
	L	W	L	W	L	W
M.A.C.N. No. 10358	—	—	6.2	5.4	—	—
A.M.N.H. No. 28932	7.0	5.6	6.5	5.3	7.0	4.9

Eudolops acuminatus (Ameghino, 1902)

Promysops acuminatus AMEGHINO, 1902a, p. 36; 1903a, p. 86, figs. 3, 7, 8, 44; 1906, p. 363, fig. 208.

Propolymastodon cardatus AMEGHINO, 1903a, p. 105, fig. 23.

TYPE: M.A.C.N. No. 10340. Anterior part of lower jaw without teeth.

TYPE OF *Propolymastodon cardatus:* M.A.C.N. No. 10333. Part of left lower jaw with M_{2-3} (M_1 also shown in Ameghino's figures, but not now present).

HYPODIGM: The two types, as above.

HORIZON AND LOCALITY: Casamayor beds. No other data. (Probably from south of Lago Colhué-Huapí.)

DIAGNOSIS: Length M_{2-3} 11.2 mm. M_2 with three external and three internal talonid cusps, M_3 with three external and two internal. M_2 longer than M_3.

The diagnosis, contrasting with that of the next species, is based on the type of *Propolymastodon cardatus*, but there is little doubt that it is synonymous with *Eudolops acuminatus* as the types agree exactly so far as comparable. For measurements see after following species.

Eudolops caroli-ameghinoi (Ameghino, 1903)

Plate 2, figure 10; plate 7, figures 4–5

Propolymastodon caroli-ameghinoi AMEGHINO, 1903a, p. 100, figs. 18, 19, 20, 21, 22; 1904d, p. 43, fig. 27; 1906, p. 362, fig. 206; SIMPSON, 1928, p. 8, fig. 4.

TYPE: M.A.C.N. No. 10334. Left lower jaw with M_{1-4} and isolated incisor.

HYPODIGM: Type and A.M.N.H. No. 28435. Right lower jaw with M_{3-4}.

HORIZON AND LOCALITY: Casamayor beds.

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[1] Ameghino's three genera were not based on such differences, but on three specimens that were not comparable at all. He placed two comparable specimens with marked differences in the cusps in the same genus, and in this I follow him.

No other data with type. Our specimen is from Cerro Blanco, a few miles west of the great barranca south of Colhué-Huapí which is probably the type locality.

DIAGNOSIS: About 5 per cent larger than *E. acuminatus*. M_2 with three external and two internal talonid cusps, M_3 with two external and two internal. M_2 and M_3 of nearly equal length.

A.M.N.H.No. 28435 is almost identical with Ameghino's type in size and structure. None of our other good polydolopid specimens enters so exactly into one of his species.

It is not clear that the broken incisor preserved with the type is truly associated, but this may be the case. It is somewhat rodent-like, but with enamel band ending on the crown.

TABLE 15

MEASUREMENTS OF LOWER TEETH OF *Eudolops*

	M_1		M_2		M_3		M_4	
	L	W	L	W	L	W	L	W
E. acuminatus								
M.A.C.N. No. 10333	—	—	5.8	3.7	5.4	3.9	—	—
E. caroli-ameghinoi								
M.A.C.N. No. 10334	4.7	3.3	5.9	4.0	5.8	4.2	6.3	4.1
A.M.N.H. No. 28435	—	—	—	—	5.8	4.2	6.5	4.1

Eudolops sp.

A.M.N.H. No. 28430 is a right M^2 clearly of *Eudolops* but of doubtful species, in view of the unsatisfactory status of the supposed species of this genus. It is smaller than the most probable range of *E. tetragonus*, measuring 6.0 by 5.0 mm., and so might belong to the probably small but otherwise questionable *E. acuminatus*. Its special interest is that it is completely unworn and so shows the cusp structure perfectly. The coronal enamel is extensively wrinkled, as in all unworn polydolopid grinding teeth. The anterointernal lobe has two subequal cusps and the posterointernal likewise two, somewhat higher than the anterior cusps, followed posteroexternally by a third, much smaller. The external cusps are five in number, the first two large and well separated, the third much smaller, the fourth and fifth as high as the first two but smaller in area and less separated. The median cuspule is immediately anterointernal to the last external cusp. This specimen is from the Casamayor of Bahia Solano, a locality where Casamayor fossils are not abundant.

?MARSUPIALIA INCERTAE SEDIS

ODONTOMYSOPS AMEGHINO, 1902

Odontomysops AMEGHINO, 1902a, p. 35; 1906, p. 468.

TYPE: *Odontomysops spiniferus* Ameghino.

DISTRIBUTION: Casamayor beds, Patagonia.

DIAGNOSIS: (*Fide* Ameghino) enlarged incisor followed by three one-rooted teeth, then by a large tooth with a trenchant anterior lobe with several denticles and a small, low, pointed posterior lobe.

Ameghino considered this as an allothere (or multituberculate) and placed it in a new family Odontomysopidae. If he interpreted its relationships correctly (according to his own individualistic taxonomy), it should resemble the polydolopids, but this it does not seem to do at all closely. I did not locate any specimens in the Ameghino Collection, and the descriptions and figure leave the affinities of this genus altogether doubtful.

Odontomysops spiniferus Ameghino, 1902

Odontomysops spiniferus AMEGHINO, 1902a, p. 35; 1903a, p. 97, fig. 13.

TYPE: Upper incisor and fragment of lower jaw with incisor root, three alveoli, and an unerupted tooth. Present whereabouts of type unknown.

HYPODIGM: Ameghino's published data only.

HORIZON AND LOCALITY: Casamayor beds, Patagonia.

DIAGNOSIS: Sole species of the genus.

GASHTERNIA SIMPSON, 1935

Gashternia SIMPSON, 1935a, p. 6.

TYPE: *Gashternia ctalehor* Simpson.

DISTRIBUTION: Río Chico beds, Patagonia.

DIAGNOSIS: Metaconid higher than, and directly internal to, procotonid. Paraconid conical, anteroexternal to metaconid, smaller than metaconid and basally confluent with it. Anterior wing of protoconid crescent, at least on $M_{2?}$ running to anterior border at its median point and not to the paraconid. Talonid about equal in size to trigonid and hypoconid about as high as protoconid. Entoconid posterointernal, somewhat elongate anteroposteriorly. Apparently no hypoconulid.

The type jaw has two teeth which appear to be M_{1-2} but could be P_4–M_1. The more anterior tooth is slightly broken, but on it the paraconid was apparently larger, nearer the protoconid and farther from the metaconid, and the peculiar anterior protoconid wing was less developed or absent.

Alveoli indicate that there was a large semiprocumbent canine, followed by a very small, one-rooted, crowded P_1, a larger two-rooted P_2, closely crowded and planted obliquely so that its anterior root is posteroexternal to that of P_1, and a still larger two-rooted P_3.

This peculiar little jaw is quite unlike anything else known to me. It clearly is not a notoungulate, and while it could conceivably be a condylarth- or litoptern-like animal, it is too unlike any other known to warrant such a theory of relationships. There is some suggestion that it may be marsupial, chiefly the fact that the probabilities somewhat favor the presence of only three premolars, but this is not certain. The molars are as much like those of some marsupials as of any other group, although not enough to prove relationships. *Caroloameghinia* is remotely similar, but very different in detail, with separate entoconid and hypoconulid, distinct metastylid, etc. Comparison with any caenolestoids is excluded not only by the somewhat different molar structure, but also by the character of the premolar roots and the large canine.

Gashternia ctalehor Simpson, 1935

Text figure 9

Gashternia ctalehor SIMPSON, 1935a, p. 7, fig. 4.

TYPE: A.M.N.H. No. 28533. Part of right lower jaw with two cheek teeth and several alveoli.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Río Chico formation, Cañadón Hondo, Chubut, Argentina.

DIAGNOSIS: Sole known species of genus. First tooth of type, length 4.9 mm., width 3.2 mm.; second tooth, length 5.0 mm., width 3.5 mm.

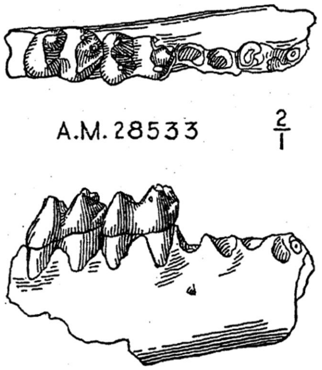

FIG. 9. *Gashternia ctalehor* Simpson. Type, A.M.N.H. No. 28533, right lower jaw with two teeth. Crown and external views. ×2.

INSECTIVORA

Ameghino reported two insectivores in the Casamayor, *Argyrolestes* and *Nemolestes*, and referred both to the Jurassic family Spalacotheriidae. These are based on borhyaenid teeth and have been discussed in their proper place. There is no trace of any insectivore from this or any other fauna of southern South America, recent or fossil, with the possible exception of the puzzling *Necrolestes* of the Santa Cruz beds.

PRIMATES

Ameghino referred many Casamayor and Musters genera not to the Primates, by his definition, but to the Prosimiae, which would fall under Primates in most classifications if the original conception of these were correct.

Here were placed the numerous genera ending in *-pithecus* as well as *Henricosbornia*, *Othnielmarshia*, *Guilielmoscottia*, and *Selenoconus*. It is now clear beyond possible question that these are all notoungulates, and they will be discussed with that group. No undoubted primates are known from pre-Colhué-Huapí beds in South America. They were either Tertiary invaders from some other land mass or else were confined to, or common only in, other parts of South America before the Colhué-Huapí. Early Tertiary Patagonia was perhaps unsuited to these predominantly arboreal and tropical animals.

RODENTIA

Ameghino did not believe that rodents were present as such in the Casamayor beds, but he traced their ancestry to the "Promysopidae" [= Polydolopidae]. As generally recognized by other workers, this is an untenable theory. The curious fact is that rodents do not appear in Patagonian collections until the Deseado, where they are abundant, even if not extremely varied. Their absence in Casamayor time is an outstanding negative characteristic of the fauna. We found no tooth or bone that could possibly belong to this order.

ORDER **EDENTATA**

SUBORDER **XENARTHRA**

One of the striking negative characteristics of the early Patagonian faunas is the scarcity of edentates among known materials. In the Río Chico the four fragmentary specimens known to me barely suffice to show that armadillos did exist. In the Casamayor armadillos are not uncommon, but they form a small percentage of the known specimens. This is the more noticeable because armadillos (and glyptodonts), when present, are usually disproportionately well represented as fossils. Each individual has hundreds of easily preserved and readily recognized bones not present in other mammals. There is so far no evidence of glyptodonts in the Casamayor, and the only evidence of ground sloths is *Protobradys*, based on one specimen, now lost and of highly dubious affinities (see below). In the Musters, armadillos form perhaps about the same proportion of the fauna as in the Casamayor, but are even rarer in absolute numbers, as this fauna is less well represented in collections. Glyptodonts are still less common than armadillos, but are surely present. Ground sloths are rarest of the three groups but are probably present, although this is not absolutely certain.

These three groups of edentates are all surely present and somewhat more common in the Deseado, while in the Colhué-Huapí and all later faunas, through the Pleistocene, they are exceedingly abundant.

It is most improbable that glyptodonts and ground sloths were really lacking until Mustersan time or that armadillos were not well differentiated even in Riochican time. These groups may, indeed, have been really rare in the early Tertiary, but in addition or alternatively it is possible that the facies is unfavorable to them in the earlier deposits.

?MEGALONYCHOIDEA INCERTAE SEDIS

PROPLATYARTHRUS AMEGHINO, 1905

Proplatyarthrus AMEGHINO, 1905a, p. 59; 1906, p. 470; SCHLOSSER, 1923, p. 500.

TYPE: *Proplatyarthrus longipes* Ameghino, 1905.

DISTRIBUTION: Musters formation, Patagonia.

DIAGNOSIS: A probable megalonychid with the astragalus strongly compressed dorsoventrally, trochlea very long and narrowing posteriorly, crests of equal height, head large.

The isolated astragalus on which alone this genus was based was not found in the collection, and Ameghino's description was very summary, but most of the characters can be made out in his figure (1905a, fig. 69). This is unquestionably a ground sloth of generally megalonychid aspect and quite distinct from any in the Santa Cruz. As far as I know, no astragali from the Deseado or Colhué-Huapí are available for comparison.

Ameghino emphasizes that his specimen came from the highest part of the Musters ("de la parte más superficial" and "parte la más superior"), and there is thus perhaps a possibility that it is a drift specimen from the Deseado, but there is no reason to assume this. At the Cerro del Humo, on and almost certainly from the Musters, we found a broken and worn ungual, A.M.N.H. No. 29460, that is indeterminate but is probably a gravigrade of some sort. To some degree, this tends to confirm the presence of gravigrades in the Musters.

Proplatyarthrus longipes Ameghino, 1905

Proplatyarthrus longipes AMEGHINO, 1905a, p. 59, fig. 69.

TYPE: Lost. A left astragalus.

HYPODIGM: Ameghino's published data only.

HORIZON AND LOCALITY: "Parte la más superior" of the Musters formation, Patagonia. No other data.

DIAGNOSIS: Sole known species.

PROTOBRADYS AMEGHINO, 1902

Protobradys AMEGHINO, 1902a, p. 49; 1906, p. 468.

TYPE: *Protobradys harmonicus* Ameghino.

DISTRIBUTION: Casamayor beds, Patagonia.

DIAGNOSIS: According to Ameghino, with palate widened in advance of first tooth, five upper teeth in continuous series, each with undivided roots or rootless, first and third to fifth small and cylindrical, second large and transversely elliptical, zygoma with no descending process.

This very interesting little specimen could not be found in the collection, and as Ameghino did not figure it and his interpretation of it leaves room for doubt, the record is tantalizingly inconclusive. In addition to the characters given above, Ameghino believed that milk teeth had been present and also rudimentary anterior teeth, and chiefly on these characters he made a new family for the genus. As evidence for this interpretation, Ameghino cited the presence in the tooth region of supposed vestiges of alveoli in addition to those of (presumably) the permanent teeth, and the presence anterior to the latter of a groove with transverse divisions. The specimen was very small, the five teeth occupying a space of only 15 mm. None of the teeth was in place, the description being based on the alveoli only.

There is no reason to question Ameghino's actual description of the specimen, which is doubtless accurate here as almost always, but it is clear that the real distinction and classification of the genus rest altogether on personal interpretation of a very small, very fragmentary, toothless specimen, and this cannot be granted unquestioning credence. That the main alveoli really each contained one Xenarthra-like tooth, that the supposed vestiges of alveoli really are such, that they did not hold other roots of the permanent teeth, that they were for milk teeth, that the anterior pits were for vestigial teeth—all these and other points are matters of personal interpretation for which there is now no conclusive evidence and most of which seem rather improbable.

The form is very interesting and suggestive. It might have been a gravigrade, but in the absence of the crucial evidence and the total lack of any other specimen of this age suggesting any xenarthrans but armadillos, there must be returned a verdict of not proved.

Protobradys harmonicus Ameghino, 1902

Protobradys harmonicus AMEGHINO, 1902a, p. 49.

TYPE: Fragment of maxilla with alveoli. Present location unknown.

HYPODIGM: Ameghino's published data only.

HORIZON AND LOCALITY: Casamayor beds. No other data.

DIAGNOSIS: Sole known species of genus. Five alveoli occupied a space of 15 mm.

DASYPODIDAE

The indeterminate Río Chico armadillos are described at the end of this section as dasypodids *incertae sedis*. The Casamayor and Musters specimens were placed by Ameghino in 16 genera and 32 species, 11 genera and 20 species from the Casamayor and eight genera and 12 species from the Musters. Several genera from the Musters and one from the Casamayor were also reported in the Deseado, undoubtedly a reflection of the fact that these are form genera and not genetic genera. On the evidence of other, more precisely identifiable, groups, it is most improbable that Musters and Deseado had so many or that Casamayor and Deseado had any genetic genera in common.

Although Ameghino named so many genera and species, he did not figure any of the types, and each was based on scanty material. So poorly known have they been that one authority, Matthew, was inclined to deny their presence in these faunas. As will be abundantly supported by the details given below, armadillos certainly were present in Casamayoran and even in Riochican time. In the Casamayoran they are now represented not only by scutes so typical that no mistake is possible but also by even less equivocal parts of the skeleton. Many of these have been found surely in place, so that no error of horizon makes their presence apparent rather than real.

Ameghino's dasypod species from the Casamayor and Musters are all based on scutes, isolated and generally few in number. The best type (*Prostegotherium notostylopianum*) includes 33 loose but supposedly associated scutes. Most species are based on fewer than 10 and several on a single scute. When it is noted that an average recent armadillo may have 1000 scutes or more and that no two of these are exactly alike, the inadequacy of these types and the difficulty of classifying armadillos on isolated scutes alone are apparent. These materials are insufficient to determine the true number, character, and relationships of the dasypods present.

Knowledge of these early xenarthrans is placed on a new and incomparably better basis by the discovery of a Casamayor specimen, described below, which includes not only about 250 separated scutes, but also several groups of articulated scutes, vertebrae, pelvis, some limb and foot bones, lower jaws with the teeth, and part of the skull. This specimen puts a definite end to any doubts about the occurrence of armadillos at this horizon and also for the first time gives real data as to their affinities and stage of development.

This specimen also shows that many of the names based on isolated scutes are synonymous, since on the basis of its various scutes this single individual belongs in several different genera and species as previously defined.

Beyond this specimen and the genera and species which it unites, classification must still be based on scute characters, and mainly on isolated scutes. Their extremely variable nature within a species, with position, with age, and with different individuals, makes their use very difficult and the results often uncertain. The situation is not quite a hopeless one. As can be seen by extensive examination of recent armadillos, they can be roughly divided into fairly natural units on the basis of scutes alone, even of isolated scutes. The groups so formed, although conveniently called genera in dealing with fossils, are found to be broader in scope than genera based on more complete materials, yet if drawn broadly and with care they are essentially natural, as checked by other anatomical data. There is no reason to believe that this would not also be true of fossils, using the same criteria in the same way.

Armadillo scutes may be divided into the following categories on form and position in any one individual:

1. CASQUE SCUTES: From the top of the head. Usually distinctive, but sometimes confused with buckler scutes
2. BUCKLER SCUTES: The immovable or only slightly movable scutes from the shields or bucklers over the pectoral and pelvic regions. Pectoral buckler scutes can seldom be distinguished from pelvic in isolated materials (when both bucklers occur), but the following subdivisions are usually recognizable:
   A. Central buckler scutes, i.e., away from any margin
   B. Lateral marginal buckler scutes
   C. Posterior pectoral buckler scutes
   D. Anterior pelvic buckler scutes
   These four divisions are usually clearly distinguishable even as isolated scutes. The following two may be confused with each other or with lateral marginal buckler scutes:
   E. Cervical notch buckler scutes
   F. Caudal notch buckler scutes
3. MOVABLE BAND SCUTES: From the overlapping bands. Easily recognized, and readily divided into:
   A. Central movable band scutes
   B. Marginal movable band scutes

3a. CERVICAL RING SCUTES: These are not infrequent and may be almost indistinguishable from the movable band scutes

4. CAUDAL SCUTES: Usually distinctive, and sometimes divisible as follows:
   A. Anterior row of biseriate or triseriate ring
   (B. Median row of triseriate ring; such are not common, but some essentially biseriate rings are partly triseriate)

   C. Posterior row of biseriate or triseriate ring
   D. Uniseriate ring
   E. Terminal tube
5. LIMB SCUTES: Often recognizable, but probably confused with buckler scutes at times

Any classification of isolated scutes obviously presupposes that the scutes compared belong to a single category of this list. In practice, central buckler scutes are usually most abundant and are the most practical basis for arrangement. Each of Ameghino's types, with one possible exception, includes at least one central buckler scute, and I have selected lectotypes from these only, to make all types as nearly comparable as possible and to avoid confusion from possible incorrect association.

In dealing with the edentate carapace, it is convenient to apply the name "scute" to the bony dermal plates, and "scales" to the horny overlapping superficial plates, not preserved in fossils although the scale arrangement is reflected in grooves on the scutes. Scute and scale patterns are frequently different, and their relationships give valuable taxonomic characters.[1] The most median scale over each scute may be called "central scale," and others "intercalary scales." Intercalary scales may be absent, may cross sutures between underlying scutes, or may be confined to the marginal areas of each scute. Central and intercalary scales frequently tend to fuse in adult recent armadillos, but as they arise separately and as fusion seldom obliterates evidence of their individuality and its reflection on the scute, this need not be especially considered.

It would appear to be the most reasonable *a priori* hypothesis and has in fact been advanced as a theory that the ancestral condition in armored edentates was identity of scale and scute patterns, that is, each scute overlain by a single scale of nearly the same size and shape. This I believe to be untrue, on embryological, comparative anatomical, and paleontological grounds. In recent forms even those with manifestly several scales per scute show a strong tendency for the scales to fuse in the adult, and those with apparently simple scales, one per scute, are found usually to have more numerous scales at an early stage of ontogenetic development. Forms such as *Priodontes*, which approach or attain essential identity of scale and scute patterns, are in general advanced and specialized animals, while the more primitive types have multiple scales, imperfectly or not fused in the adult. Finally, reviewing the paleontological evidence, there is no known case of a phylum with simple scales preceding the multiple condition, and on the contrary in these oldest scutes from the Casamayor in every known case the scale and scute patterns were clearly different, and intercalary scales were always present, even in *Machlydotherium* which appears to be ancestral or at least related to later forms without intercalary scales.

The principal central buckler scute characters available for description and definition are as follows, the condition in our single best specimen being given in brackets to show a normal range of variation due to position, even when dealing with scutes of one individual and from the same general region.

1. OUTLINE: Highly variable, but essential in determining position in the carapace and of some taxonomic value; e.g., some forms have mainly polygonal buckler scutes, others mainly quadrangular, others both. [Elongate quadrangular to equidimensional hexagonal]
2. SIZE: Highly variable, but of taxonomic value when very marked and more or less constant. [About 25 per cent variation in maximum central buckler scute diameters]
3. THICKNESS: Of very little taxonomic value on isolated scutes. [Nearly 100 per cent variation]
4. SUTURES: Smooth or spicular, plane or concave, vertical or imbricating. Variable but of some taxonomic value in approximately homologous scutes. [Smooth to slightly spicular; plane to concave; vertical to slightly imbricating]
5. SURFACE: Smooth to punctate to rough. Taxonomic when very marked and fairly constant. [Smooth to moderately punctate]
6. PERIPHERAL FOLLICLES: Variable, but fairly constant averages of size, number, and position have taxonomic value. [Nearly constant size, one to five in number, always on posterior border only]
7. CENTRAL PERFORATIONS: Rarely a good character in size, number, and arrangement and only where differences are extreme. [Ex-

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[1] For a previous use of these relationships and diagrams showing them, see Holmes, W. W., and G. G. Simpson, 1931, especially figures 7, 8, and 20, and text pages 397–400 and 408–415.

tremely variable in size, two to five in number, arrangement of a given number fairly constant]

8. Scale Areas: With large allowance for variation, the number and the arrangement of these areas are the most useful separate taxonomic characters. [Four to six intercalary scales, arrangement, relative size, etc., fairly constant]

Ameghino's genera and species utilize all these characters for definition, and allow for very little variation in any of them. As proved by our fine specimen and strongly suggested by studies of variability in later armadillos, the result was the designation of far too many taxonomic units. Ameghino's definitions constitute a key for the classification of scutes, but do not correspond to reality in the classification of animals.

Employing what seems to be the minimum permissible allowance for variation, individually and due to position or age, an allowance much broader than that of Ameghino, we may define the various groups present in the Casamayor and Musters as follows, gathering them together here for easier contrast. (See text fig. 10.) So far as valid, these form "genera" are probably not coextensive with genetic genera that might be based on skeletal parts if known, but they do appear to approximate natural units. In almost all cases, I believe it to be impossible to recognize a true species from isolated scutes, and those of Ameghino given in the succeeding revision are recognized not as natural but only for convenience.

The following genera as represented in the Casamayor and Musters beds are fairly well defined and probably are distinct natural units:

Machlydotherium: Irregularly polygonal. Very large, thick. Spicular sutures, punctate surface. Few peripheral follicles. Central perforations few and large or absent. Intercalary scales small, confined to one side or absent. Main scale area usually with rounded longitudinal ridge. A rare but almost surely valid genus. Casamayor and Musters

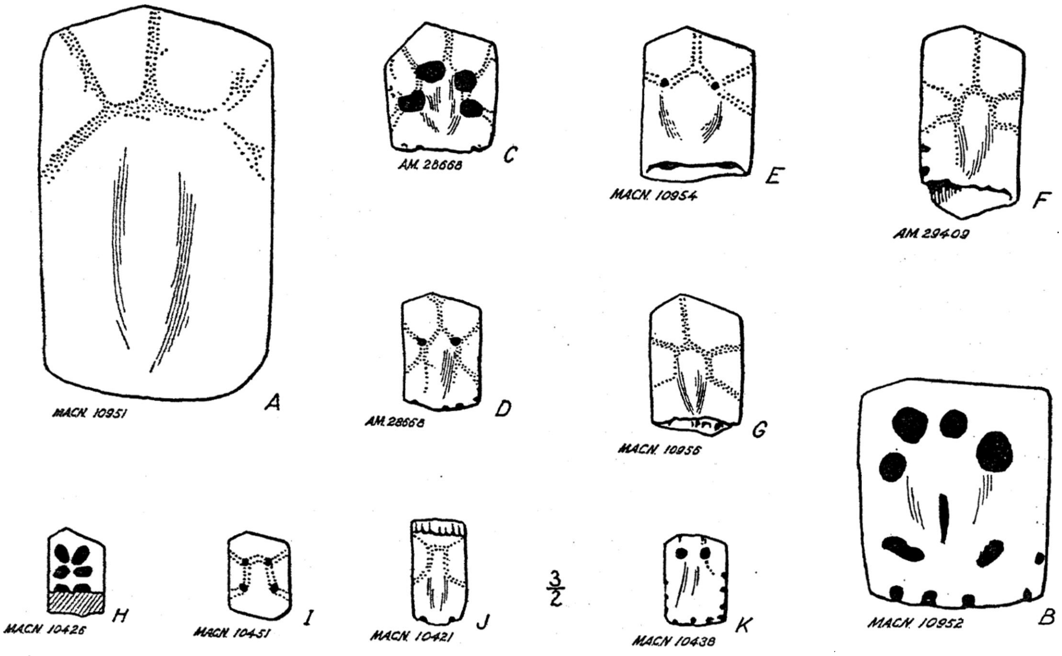

FIG. 10. Diagrams of representative buckler scutes of Casamayoran and Mustersan genera of armadillos. In each case the diagram is based on a particular species and specimen (as numbered in the figure), but the figures are diagrammatic rather than strictly pictorial. A. *Machlydotherium asperum.* B. *Machlydotherium ater.* C. *Utaetus buccatus.* D. *Utaetus buccatus*, same individual as C, showing the marked variation that may occur within one individual. E. *Meteutatus confluens.* F. *Meteutatus confluens.* G. *Pseudeutatus cuneiformis.* H. *Coelutaetus cribellatus.* I. *Prostegotherium notostylopianum.* J. *Astegotherium dichotomum.* K. *?Pseudostegotherium chubutanum.* ×3/2.

Meteutatus (synonym: *Sadypus*): Polygonal. Size intermediate. Spicular sutures, slightly punctate surface. Few peripheral follicles (two in type), very large, united in groove at posterior edge. Central perforations absent in known material. Intercalary scales large, anterior and anterolateral, main scale area sharply keeled (in type). A single scute from the Casamayor but so unlike other material that it is probably distinct. There is, however, a distinct possibility that it really came from a higher horizon. The (form) genus is more typical of the Musters, and the genotype is from the Deseado

Utaetus (synonyms: *Anteutatus*, *Posteutatus*, *Parutaetus*, *Orthutaetus*): Quadrangular to hexagonal, slightly elongate to equidimensional. Size generally small. Sutures slightly spicular to smooth. Peripheral follicles small, generally few, 1–6, confined to posterior border. Central perforations 0–7, around anterior and anterolateral borders of main scale area, very small to very large. Intercalary scales well developed, generally 4–6, posterolateral pair often poorly defined or apparently absent, others well defined and excluding central scale from anterior border. Main scale area usually convex but not keeled. Relatively extremely abundant, including almost all the material from these beds. Probably containing some extraneous elements, but not separable and scutes not essentially different from the various types present in our single specimen. Typically Casamayor, with a few generically inseparable scutes from the Musters

"*Pseudostegotherium*"[1]: Scutes generally slightly elongate and imbricating, size generally small. Peripheral follicles small but numerous, up to 14, and occurring on posterior and both lateral edges. Central perforations 0 to 8. Intercalary scales 2 to 4, areas rather poorly defined, anterior and anterolateral. Central scale area usually lightly keeled. This type grades into others to some extent, but from comparison with Santa Cruz forms and from the fact that nothing like it occurs in our good specimen, it is probably distinct. The genotype is of much later age, Colhué-Huapí, and the genus is not reported from the intervening Musters and Deseado.

Pseudeutatus (with the possibly partly distinct but not clearly separable *Isutaetus*, *Anutaetus*, and *Pachyzaedyus*): Generally quadrate, sometimes polygonal. Size small to moderate. Sutures with short spicules. Surface smooth to somewhat punctate. Peripheral follicles small, 5 or more, confined to posterior border where they tend to form a groove. Central perforations few and small or absent. Intercalary scales anterior and anterolateral, large, generally 4–6. Central scale area with a slightly convex lageniform figure, distinguished posteriorly from flatter posterolateral areas, possibly for further intercalary scales. Musters

The following three Casamayor genera cannot definitely be reduced to synonymy but are ill defined, and probably one or more are synonyms:

Coelutaetus: Similar to *Utaetus* but with central follicles (in known specimen) in three symmetrical pairs, very large, leaving very little room for scales, the areas of which are very vague. This is known by a single scute, which may well be a variant of *Utaetus*, but this cannot be demonstrated

Astegotherium: Differing from the *Utaetus* group in the small number of follicles, 0–2 posteriorly and 0–2 centrally, all of small size, and the intercalary scales only 2–3 in number, anterior, sometimes not excluding the central scale area from the anterior border. The type includes a number of similar scutes, none exactly like those of other genera, so that this is probably valid

Prostegotherium: Intermediate in character between *Astegotherium* and *Utaetus*, with 0–4 small posterior and 0–8, usually 4 or 5, small central perforations. Two to four intercalary scales, anterior and anterolateral. Some of the scutes placed here by Ameghino are completely indistinguishable from *Astegotherium*, while others approach *Utaetus*. The genus is probably a synonym of one of these two, but its proper position is not wholly clear

The genera have been defined as they occur in the Casamayor and Musters. Actually the genotypes of three are of later age:

Machlydotherium, type *M. asperum*, Musters
Meteutatus, type *M. lageniformis*, Deseado
Pseudostegotherium, type *P. glangeaudi*, Colhué-Huapí

Casamayor and Musters specimens of *Machlydotherium*, are so similar that the reference must stand, at least for the present. Inasmuch as all species referred to *Meteutatus* have the characteristic few large posterior follicles, united in a groove, the reference of the Casamayor and Musters species may be permitted to stand tentatively, although it is rather improbable that the genus is really common to these three very different faunas. The genotype of *Pseudostegotherium* is known to me only by Ameghino's unillustrated de-

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[1] Probably not really this genus; see comment below.

scription. It appears to have differed quite definitely from the Casamayor scutes placed in this genus, and the probabilities are enormously against actual generic identity, as the time lapse was certainly large, no other genus is common to the two faunas, and the genus is not reported in the two intervening formations.

There are some scutes and supposed species that do not enter very well into any of these supposed genera, but they may be tentatively retained in them nevertheless, as none is particularly striking or important and it seems very undesirable to establish any more names than absolutely necessary on such material.

In the Santa Cruz there are five well-established genera of armadillos (see Scott, 1903–1904):

Stegotherium
Prozaedius
Stenotatus
Proeutatus
Peltephilus

Although well distinguished from any of these later genera, the most common Casamayor forms, members of the *Utaetus* group, are more nearly similar to *Prozaedius* than to any other. In the description, below, this similarity will be further mentioned. In part it is simply due to the fact that *Prozaedius* is the most primitive of the Santa Cruz armadilos. The other early genera, known from a few scutes only, offer no certain basis for comparison. *Meteutatus* is somewhat suggestive of *Proeutatus*, but is particularly poorly known in these beds. *Pseudostegotherium* may really be allied to *Stegotherium* if the general and not wholly exact resemblance in the scutes is trustworthy. *Machlydotherium* of the Casamayor and Musters seems to resemble *Proeutatus* most closely among Santa Cruz forms, although the very inadequate evidence suggests a closer and to that extent somewhat anomalous resemblance to the still later chlamytheres. *Pachyzaedyus* and its allies and synonyms somewhat, but only incompletely, resemble *Stenotatus*. Thus the buckler scutes, at least, suggest that armadillo differentiation in the early Tertiary was about the same in character and variety as in the mid-Tertiary Santa Cruz, except for the Peltephilidae (see below).

Ameghino (1906, pp. 468–469) placed these armadillos in the families "Chlamydotheriidae" (Chlamytheriidae or Chlamytheriinae), "Dasypidae" (= Dasypodidae), and Astegotheriidae. How poor is the evidence for such separation is obvious upon learning that his Dasypidae and Astegotheriidae include genera which are now found to be synonymous without any doubt. The only practical usage is to place them all in the family Dasypodidae, *sensu lato*. Only *Utaetus*, with its synonyms, is well enough known to be definitively classified. A family could readily be based on it, but it would be defined entirely by primitive characters, and I see no necessity for such an arrangement in this case. It seems to me to be a primitive but none the less typical member of the Dasypodidae in the strict sense, or Dasypodinae.

Ameghino also stated (1902a, p. 70) that scutes belonging without any doubt to the Peltephilidae were found in the Casamayor, although he later (1906) omitted this family from the faunal list. The presence of this group in these beds is to be expected, but in fact I have seen no clear evidence of it. In the Ameghino Collection there are some broken movable band scutes from the Musters labeled by Ameghino with a manuscript name implying relationship to *Peltephilus*. The name has never been published, as far as I know, and Ameghino did not cite Peltephilidae in the Musters. The specimens are not really identifiable.

MACHLYDOTHERIUM AMEGHINO, 1902

Machlydotherium AMEGHINO, 1902a, p. 52; 1906, pp. 468, 470.

TYPE: *Machlydotherium asperum* Ameghino, 1902.

DISTRIBUTION: Casamayor and Musters formations, Patagonia.

DIAGNOSIS: See page 74.

The type species is relatively well known and is of great interest. The referred species are imperfectly known and of somewhat doubtful relationship.

Machlydotherium asperum Ameghino, 1902

Plate 8, figure 1; text figure 10A

Machlydotherium asperum AMEGHINO, 1902a, p. 52.

TYPE: M.A.C.N. No. 10951. Twenty-eight scutes, many broken, and one tooth. Ameghino Collection.

HYPODIGM: Type and A.M.N.H. No. 29407, two scutes.

HORIZON AND LOCALITY: Musters formation, Patagonia. No exact data with type. Referred specimen from Cerro Blanco.

DIAGNOSIS: Buckler scutes generally slightly elongate, with parallel lateral margins; intercalary areas present, small, anterior; central follicles generally absent on these scutes, sometimes present on band and tail scutes; keel of central area usually prominent. Size large.

The scutes seem generally to have two to four intercalary areas, but they are small and poorly defined. They are usually somewhat elevated above the main area and more rugose. The whole scute is highly punctate. Central follicles are absent on scutes surely of the buckler in the known material, but one or two very large follicles are present at the anterior margin of the main area on scutes probably of the tail and movable bands. The band scutes are larger and, especially, more elongate than those of the buckler and are remarkable for the poor development of their anterior articular areas, which are very short, poorly differentiated, and rugose. A typical buckler scute measures 35.5 by 22 mm. and a band scute 48 by 29.5 mm.

With these scutes there is a tooth, described by Ameghino and implied to have been found at the type locality, although this is not certain. It is amazingly similar to teeth of Pliocene-Pleistocene chlamytheres, the cross section similarly elongate, with two large terminal lobes and a narrower and less sharply distinguishable median lobe between them. The anteroposterior diameter, near the wear surface, is 17.9 mm. and the transverse diameter 9.0 mm. across one end lobe and 8.5 mm. across the other.

Machlydotherium ater Ameghino, 1902

Text figure 10B

Machlydotherium ater AMEGHINO, 1902a, p. 53.

TYPE: M.A.C.N. No. 10952. Ten scutes and partial scutes. Ameghino Collection.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Musters formation, Patagonia. No other data.

DIAGNOSIS: Buckler scutes generally quadrate and elongated; intercalary scale areas very poorly marked and probably extending farther posteriorly than in *M. asperum*, keel generally less prominent; three or four large central follicles usually present as well as a few smaller posterior and posterolateral marginal follicles. Size averaging smaller; one scute is 29.5 by 20.5 mm. and another 20 by 16.5 mm.

?Machlydotherium intortum Ameghino, 1902

?*Machlydotherium intortum* AMEGHINO, 1902a, p. 53.

TYPE: M.A.C.N. No. 10953. Three scutes, all obscure and two of them broken. Ameghino Collection.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Musters formation, Patagonia. No other data.

DIAGNOSIS: Most complete scute, of unknown and probably special position, arched anteroposteriorly, thin, smaller than average of *M. asperum*, with eight central follicles arranged in a semicircle; 22 by 17.5 mm.

Machlydotherium sparsum Ameghino, 1902

?*Machlydotherium sparsus* AMEGHINO, 1902a, p. 54.

TYPE: M.A.C.N. No. 10427. Two broken buckler scutes. Lectotype: single scute described below.

HYPODIGM: Types only.

HORIZON AND LOCALITTY: (According to Ameghino) upper part of *Notostylops* beds, south of Lago Colhué-Huapí, Chubut, Argentina.

DIAGNOSIS: Not now clearly distinguishable from *M. asperum.*

While not identical, the scraps of this genus said to be from the Casamayor are so similar to the genotype that at present I see no way to distinguish the supposed species. This fact and the further facts that only these two broken scutes have ever been reported from the Casamayor and that they are said to be from the upper part lead to the definite suspicion that the specimens were really derived from the overlying Musters beds and picked up in the surface below their actual horizon. This cannot be definitely established, and the supposed Casamayor species may be listed very tentatively.

The best preserved scute was apparently roughly hexagonal, 32.5 by 25.0 mm., with three small, purely anterior intercalary scales, low carina on main scale area, and a rugose surface but no follicles. At the thickest point, the posterior angle, the thickness is 10.8 mm. This scute may become the lectotype.

METEUTATUS Ameghino, 1902

Meteutatus Ameghino, 1902a, p. 54; 1906, pp. 468, 470, 472.

Sadypus Ameghino, 1902a, p. 64; 1906, pp. 470, 472.

Type: *Proeutatus lagenaformis*[1] Ameghino, 1897, Deseado beds. [One of the few genotypes definitely designated by Ameghino.]

Type of *Sadypus: Sadypus confluens* Ameghino, 1902, Musters beds.

Distribution: Supposedly Casamayor, Musters, and Deseado formations.

Diagnosis: See above.

Of the seven species referred to this genus by Ameghino, four are from the Deseado,[2] two from the Musters, and one from the Casamayor. It is improbable that all do belong to one genus, but they are similar and are best so placed, at least until better known.

It seems to me quite impossible to distinguish *Sadypus confluens* from the contemporaneous species referred to *Meteutatus*, and so *Sadypus* is tentatively considered synonymous with *Meteutatus*. It is, of course, possible that better specimens will show that the Musters species of *Meteutatus* were incorrectly referred to that genus, and in that case *Sadypus* would perhaps become valid for all four Musters species placed by Ameghino in the two genera concerned. These supposed species are separately defined below, but they differ less than is common in the scutes of a single individual, not to mention species, so that their synonymy is probable. Even the dubious Casamayor species may be synonymous and in any case is not well defined.

Meteutatus attonsus Ameghino, 1902

Meteutatus attonsus Ameghino, 1902a, p. 55.

Type: M.A.C.N. 10957. Six scutes, all heavily coated in manganese concretion. Lectotype: a quadrate buckler scute. Ameghino Collection.

Hypodigm: Type only.

Horizon and Locality: Musters formation, Patagonia. No other data.

Diagnosis: Lectotype buckler scute measuring 20 by 14.5 mm., central area depressed.

Meteutatus rigidus Ameghino, 1902

Meteutatus rigidus Ameghino, 1902a, p. 55; Simpson, 1936d, p. 72.

Type: M.A.C.N. No. 10958. Twelve scutes and broken scutes, in concretion. Lectotype: an elongate buckler scute with two posterior follicles. Ameghino Collection.

Hypodigm: Type and a specimen in the Roth Collection, Museo de La Plata.

Horizon and Locality: Musters formation, Patagonia. No other data with type. Roth specimen from his "Lago Musters," i.e., probably Cerro del Humo.

Diagnosis: Lectotype measuring 22.5 by 10 mm., more elongate than lectotype of *M. attonsus* and center less depressed.

The individual characters do not really distinguish this species from *M. attonsus*. Some of the scutes in the type lot are indistinguishable from *Pachyzaedyus*, and if they really belong to the same individual would unite *Pachyzaedyus*, and probably other similar genera, with *Meteutatus*.

Meteutatus confluens (Ameghino, 1902), new combination

Text figure 10E–F

Sadypus confluens Ameghino, 1902a, p. 64.

Type: M.A.C.N. No. 10954. Eight scutes. Lectotype: a pentagonal buckler scute. Ameghino Collection.

Hypodigm: Type and A.M.N.H. No. 29409, single scute.

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[1] Later spelled "*lageniformis*," but the original spelling, while less correct orthographically, was apparently intentional and is therefore retained.

[2] While Loomis (1914) briefly describes M. *lagenaformis*, he leaves it in *Proeutatus* and seems to have overlooked the generic name *Meteutatus* and the description of other species.

Horizon and Locality: Musters formation, Patagonia. No other data with type. Our specimen is from Cerro Blanco.

Diagnosis: Lectotype measuring 14 by 10 mm., smaller and shorter than lectotypes of preceding species.

The different preservation makes the intercalary areas seem more clearly bounded on this form than in *M. attonsus*, but this is probably illusory, and the two species are probably based on scutes of different proportions such as occur on single individuals.

Meteutatus ascendens (Ameghino, 1902), new combination

Sadypus confluens Ameghino, 1902a, p. 64.

Type: M.A.C.N. 10955. One scute. Ameghino Collection.

Hypodigm: Type only.

Horizon and Locality: Musters formation, Patagonia. No other data.

Diagnosis: Type measuring 17 by 11 mm. Intercalary areas sharply defined.

This does not appear to be really distinguishable from any of the preceding three species.

Meteutatus percarinatus Ameghino, 1902

Meteutatus percarinatus Ameghino, 1902a, p. 55.

Type: M.A.C.N. No. 10453. Single buckler scute.

Hypodigm: Type only.

Horizon and Locality: (According to Ameghino) upper part of Casamayor beds, south of Lago Colhué-Huapí, Chubut, Argentina.

Diagnosis: A central buckler scale pentagonal, with sharply incised pattern, and posterior follicular groove distinctly narrower than the scute.

In the known scutes of the genus from the Musters, there is none exactly like this, but this is very insufficient basis for comparison, and any or all of the supposedly diagnostic characters of this species may well be individual or due to position in the carapace. As with *Machlydotherium sparsum*, the facts that this is known only from one scute, similar to a Musters species, found in or very likely on the upper part of the Casamayor where the Musters is known to occur above it give rise to active suspicion that the fossil was really from the later fauna, but it may be very tentatively retained.

The scute measures 13.9 mm. in width at the anterior end, 10.9 at the posterior end, 18.1 in maximum length, and 6.5 in maximum thickness. It has four large anterior and anterolateral intercalary areas, and a very distinct keel on the main scale area. Central perforations are absent or inconspicuous.

UTAETUS Ameghino, 1902

Utaetus Ameghino, 1902a, p. 59; 1906, p. 469; Simpson, 1932d, p. 2; Scott, 1937, pp. 675, 681, fig. 405.

Anteutatus Ameghino, 1902a, p. 58; 1906, pp. 468, 470.

Posteutatus Ameghino, 1902a, p. 60; 1906, p. 468.

Parutaetus Ameghino, 1902a, p. 62; 1906, p. 468.

Orthutaetus Ameghino, 1902a, p. 63; 1906, p. 468.

Type: *Utaetus buccatus* Ameghino.

Types of Synonyms: *Anteutatus lenis* Ameghino. *Posteutatus indentatus* Ameghino. *Parutaetus chicoensis* Ameghino. *Orthutaetus crenulatus* Ameghino.[1]

Distribution: Casamayor and possibly also Musters beds, Patagonia.

Diagnosis: See above.

In publishing the five genera here considered synonyms, Ameghino did not compare them with one another, nor did he distinguish generic from specific characters. The only clear distinction between *Utaetus* and the other four supposed genera is the presence in the former of much larger central perforations. This has no taxonomic value, as both conditions, and a complete intergrading between them, are seen in A.M.N.H. No.

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[1] All these genera, and *Utaetus* as well, were published with two or more species. In each case that followed by "n. g., n. sp." is taken as being the type. *Anteutatus* has page priority over *Utaetus*, but as the latter was based on better and more characteristic material, as Ameghino referred more species and specimens to it than to any of the other synonyms, and as publication was absolutely simultaneous, I select *Utaetus* for preservation.

28668, a single individual. *Anteutatus* was based on a few relatively larger scutes with the follicles poorly developed, but still well within the range of our No. 28668 except in size, at best a specific character. There is nothing in Ameghino's diagnoses or in the specimens to separate *Posteutatus*, *Parutaetus*, and *Orthutaetus*, and only the invalid character of smaller central perforations to separate them from *Utaetus*. The follicles are a little better developed than in *Anteutatus*.

The structure of the genus is described in detail under *U. buccatus* below.

Utaetus buccatus Ameghino, 1902

Plate 9; text figures 10C–D, 11–22

Utaetus buccatus AMEGHINO, 1902a, p. 59; 1906, p. 384, fig. 244; SIMPSON, 1932d, p. 2, fig. 1.
Utaetus argos AMEGHINO, 1902a, p. 59.
Utaetus laxus AMEGHINO, 1902a, p. 59.
Posteutatus indentatus AMEGHINO, 1902a, p. 60.
Posteutatus scabridus AMEGHINO, 1902a, p. 61.
Posteutatus indemnis AMEGHINO, 1902a, p. 61.
Parutaetus chicoensis AMEGHINO, 1902a, p. 62.
Parutaetus clusus AMEGHINO, 1902a, p. 62.
Parutaetus signatus AMEGHINO, 1902a, p. 62.
Orthutaetus crenulatus AMEGHINO, 1902a, p. 63.
Orthutaetus clavatus AMEGHINO, 1902a, p. 63.

TYPE: M.A.C.N. No. 10457. Eighteen scutes, metacarpal, and calcaneum. Lectotype: an irregularly pentagonal fixed buckler scute measuring 14.3 by 10.0 mm.

NEOTYPE: A.M.N.H. No. 28668. Two hundred to three hundred separated scutes from all parts of the body. Part of cephalic shield, two areas of associated buckler scutes, two areas of movable bands (one with much of six bands); connected parietals with parts of squamosals and temporals, fragments of occipitals, crushed maxilla with four teeth, both sides of lower jaw with most of the teeth, nine isolated teeth; parts of nine vertebrae, one chevron bone, several rib fragments; parts of both scapulae, one humerus and ulna, and both radii; one ilium and fragment of the other, parts of one ischium and pubis, parts of one femur and fibula, and various tarsals, metatarsals, and phalanges. Found by C. S. Williams south of Lago Colhué-Huapí.

TYPES OF SYNONYMS: *Utaetus argos:* M.A.C.N. No. 10445, three scutes. Lectotype: quadrangular fixed buckler scute measuring 8.8 by 11.6 mm.

Utaetus laxus: M.A.C.N. No. 10424, two scutes. Lectotype: quadrangular fixed buckler scute, 11.8 by 16.1 mm.

Posteutatus indentatus: M.A.C.N. No. 10464, three scutes. Lectotype: quadrangular fixed buckler scute, 9.6 by 11.7 mm.

Posteutatus scabridus: M.A.C.N. No. 10463, three scutes. Lectotype: quadrate-pentagonal fixed buckler scute, 13.1 by 18.2 mm.

Posteutatus idemnis: M.A.C.N. No. 10442, eight scutes (mostly broken). Lectotype: anterior scute of pelvic buckler.

Parutaetus chicoensis: M.A.C.N. No. 10429, six scutes. Lectotype: hexagonal fixed buckler scute, 6.5 by 10.5 mm.

Parutaetus clusus: M.A.C.N. No. 10436, two scutes. Lectotype: fixed buckler scute.

Parutaetus signatus: M.A.C.N. No. 10422, six scutes. Lectotype: quadrangular fixed buckler scute, 5.4 by 10.0 mm.

Orthutaetus crenulatus: M.A.C.N. No. 10430, one scute.

Orthutaetus clavatus: M.A.C.N. No. 10440, one scute.

HYPODIGM: The various types listed above.[1]

HORIZON AND LOCALITY: Casamayor formation, Chubut, Argentina.

DIAGNOSIS: Size small to moderate. Follicles usually well developed and scale areas mostly well marked.

* * *

It is possible that more than one species is included in this group, but certainly the majority of the names listed above are synonymous and none can at present be separately defined. The range in size, while slightly too great for a single individual, is clearly not too great for different individuals, some of different ages, but all of one species. The other characters are no more variable than in different scutes of one individual, as evidenced by the neotype.

There seems no reason for discussing the supposedly distinctive characters of each species in detail, but the most aberrant and hence possibly, but improbably, distinct forms will be mentioned. *Utaetus laxus* is essentially based on one scute which is of more than average size for this group, with a shallow

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[1] Many other specimens are referred to *Utaetus* and mostly to *U. buccatus*, but they do not add notably to knowledge of this species and are not formally included in the hypodigm.

median transverse depression, and rather poorly defined scale areas. *Posteutatus scabridus* is also above the average size, but not otherwise unusual. *Parutaetus signatus* has fixed scutes slightly more elongate and evenly rectangular than is usual. These distinctions seem hardly of specific value, and the other types all differ even less from specimens identified beyond any reasonable question as *Utaetus buccatus.*

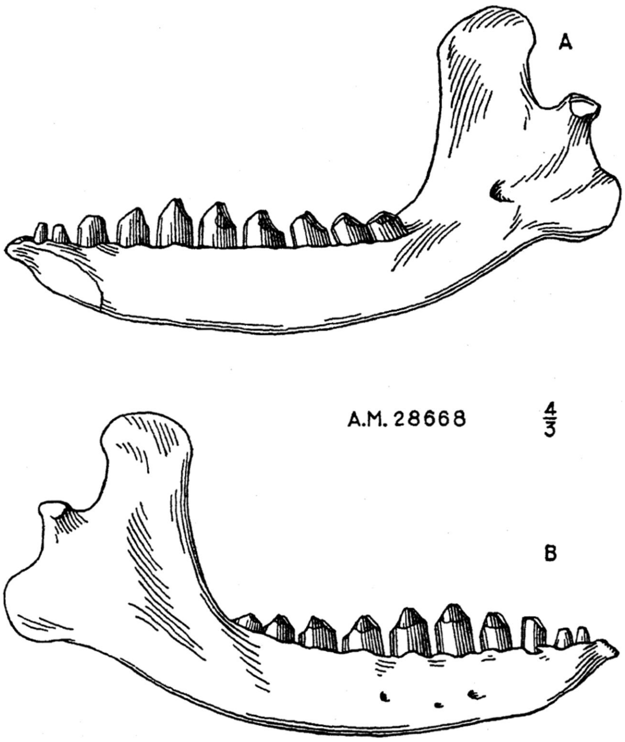

FIG. 11. *Utaetus buccatus* Ameghino. A.M.N.H. No. 28668. Right lower jaw. A. Internal view. B. External view. More heavily shaded areas on tips of teeth are enamel. ×4/3.

Description of this species, and of the genus, is based on A.M.N.H. No. 28668, here designated neotype, far the best edentate yet found in pre-Santa Cruz formations. The individual was not quite full grown, having the epiphyses unfused and most sutures open. It was probably slightly smaller than the type of this species, but this may be attributed to its lesser individual age. Aside from areas of the carapace and one or two other minor exceptions, the bones had become disarticulated and jumbled, but were all in a limited block of matrix without admixture of foreign elements and surely are of one individual.

DESCRIPTION

DENTITION

Upper teeth are represented by four in association with fragments of the crushed maxilla. These are not perfectly preserved and no enamel can be definitely seen. Otherwise they are similar to the lower teeth. The largest has a height of 10 mm. from the worn crown to the end of the open root. Other isolated upper teeth show enamel as on the lowers.

The lower teeth are all preserved in place in the right ramus, and the last six in the left ramus. A summary description has already been published (Simpson, 1932d). There are 10 teeth in each jaw, a common number in armadillos.[1] The first two are small and peg-

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[1] The evidence is too insecure for any definite theory,

like. The third is abruptly larger, and they then increase gradually in horizontal dimensions to the seventh and eighth, then decrease to the tenth. The form is very simple. In transverse section they are oval, elliptical, or circular. The first two nearly simple ovals, the third to eighth elliptical, the width becoming progressively greater relative to the length, the third to fifth tending to be somewhat flattened on the inner side, and the last two nearly circular. The height of the crowns above the alveoli has perhaps been slightly modified by postmortem movement, but the first two were about the same, then it increased to the fifth or sixth, then decreased to the tenth. The crown is typically armadilloid also, rounded on the first two, then on the third and fourth with a larger anterior oblique and smaller posterior horizontal surface, then on the rest with steeply oblique anterior and posterior surfaces, the latter somewhat steeper and larger except on the last tooth. There seems no doubt that these are all permanent teeth, although the individual is perhaps not quite adult and they may not have been in use for long. All grew from persistent pulps. They are nearly vertical in position, although the ninth is slightly, and the tenth distinctly, procumbent.

The most interesting peculiarity of the teeth is the presence of true enamel, unknown on the permanent functional teeth of any other xenarthran, although vestiges have been discovered on the germs of milk teeth of recent armadillos. To distinguish it from the dense shiny dentine common in xenarthrans and sometimes hard or impossible to distinguish from enamel macroscopically, several thin sections were cut. These show that unequivocal enamel is present, thin and simple in structure, with straight prisms all apparently extending through the whole thickness in the limited material available for microscopic study. It is present only on the internal and external sides of the teeth, wear presumably having obliterated it on the apex and anterior and posterior sides. It is absent on the first three teeth, present on the outer but not inner sides of the fourth and fifth, both sides of sixth and seventh, although only in small patches on the inner side, outer side only of the eighth, and both sides of the ninth and tenth, although very small on their inner sides. On the left ramus the distribution is the same on the teeth preserved in place as that just given for the complete right ramus, except that wear seems to have removed even the minute vestige of enamel on the inner side of the ninth.

SKULL

The occipital condyles, all of the parietals, and much of the frontals, squamosals, basisphenoid, and alisphenoids are preserved.

The condyles are simple, sessile, oval, transversely cylindrical, and not notched on the medial side. The condylar foramen occupies the usual position and is very small.

The lambdoid crest is of moderate development, sharp, and only slightly notched (for-

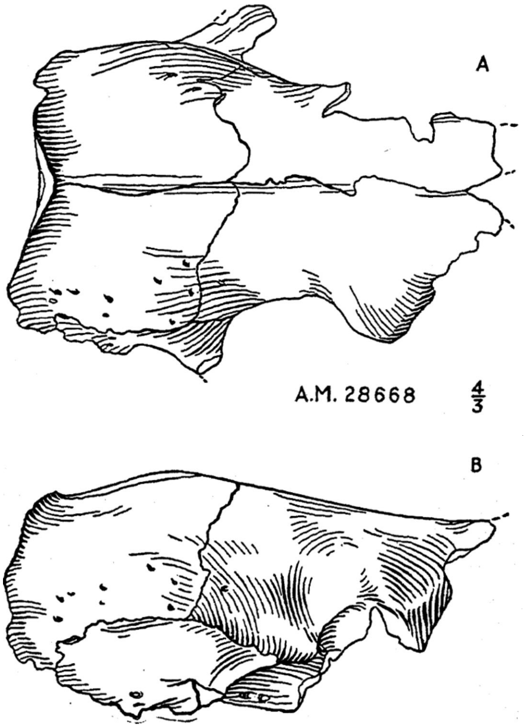

FIG. 12. *Utaetus buccatus* Ameghino. A.M.N.H. No. 28668. Incomplete cranium. A. Dorsal view. B. Right lateral view. ×4/3.

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but the possibility that the true dental formula is 2.1.4.3 is very tentatively suggested. The smallest, peg-like teeth may be incisors, the next abruptly larger but still without enamel in this worn stage, a canine, the next four, more protruded and all with enamel in progressively larger areas to the last of them, premolars, and the last three, progressively less protruded again and with enamel progressively less on all of them than on the last "premolars," molars.

ward) at the midline, less than in most armadillos. The sagittal crest is single and very feebly indicated, dying out on the frontals, without distinct connection with the supraorbital processes. The cranium is gently domed, without any sharp descent from parietals to frontals. The parietals together form a quadrate transverse arch, almost evenly rectangular. The width, along the curve, is almost exactly twice the length, i.e., each parietal is almost square. The two parietals are fused, although the suture between the frontals is still open. The postorbital constriction is moderate, much as in *Prozaedius*, etc., and as in other armadillos the anterior parts of the frontals contain extensive sinuses.

The squamosals are rather small, their zygomatic processes very slender. Both squamosals and parietals are pierced by various vascular foramina. The glenoid fossae are transverse and nearly flat. They are underhung by the external auditory meati posteriorly, where each has a prominent foramen. The most interesting features of this whole skull fragment are that the glenoid fossa is somewhat more anterior than in later armadillos, and that it is nearly on a level with the basisphenoid, instead of far above it as in later forms. Both are points of resemblance to the palaeanodonts, and the latter is probably a very primitive character.

The foramen ovale is relatively small. The still smaller canal which in *Dasypus* is parallel to, and has a common external opening with, the foramen ovale is here more separate, relatively more anterior.

The endocranium is remarkably like that of recent *Dasypus*. The olfactory lobes seem to have been smaller, but this region is not well preserved and this unexpected condition may be illusory. In any event, they were fully dorsal and were larger relative to the cerebrum than in the majority of specialized mammals. As in *Dasypus* the cerebellum was unusually wide but rather short, and the vermis was lodged against the occiput, only the lateral lobes being in part covered by the parietals. There apparently were a few simple cerebral convolutions, but the details are not clear. The small portion of internal basicranium preserved also resembles that of *Dasypus*, with a large groove and canal for III, IV, V^1, V^2, and VI, apparently without separate courses, and a smaller, more posterior, lateral, and slightly lower outlet for V^3, and a shallow sella turcica.

MANDIBLE

The anterior end of the lower jaw is somewhat protruded and incipiently spout-like, but it is less prolonged in front of the teeth than in later armadillos, despite the fact that the number of lower teeth is not unusual. The symphysis is long, even, and unknit without any genal spine or expansion. The horizontal ramus is rather slender, its lower border a sweeping, regular curve, and the alveolar border nearly straight. There are three mental foramina, between fourth and fifth, fifth and sixth, and sixth and seventh teeth, respectively, the latter being much more posterior than is usual.

The ascending ramus is very unlike that of any later armadillo and decidedly more primitive throughout. It has little relief, the only well-defined sculpture being a thickening of the lower border on the internal side. The angle is small, not at all recurved or hook-like, and separated by shallow emarginations from the condyle and the horizontal ramus. The condyle is relatively less elevated above the tooth level than in later forms and is not, as in them, developed as a flattened and somewhat concave plate, directed upward and forward, but, as in more primitive mammals, is a transverse cylinder directed upward and backward. The coronoid is expanded anteroposteriorly, rounded at the end, and not recurved or hooked.

VERTEBRAE

Vertebrae are poorly represented, but there are axis, atlas, parts of two very imperfect posterior dorsals or (more probably) lumbars, two anterior caudals, and unimportant frag-

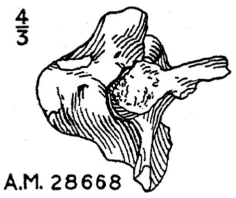

FIG. 13. *Utaetus buccatus* Ameghino. A.M.N.H. No. 28668. Occipital condyle and articulated atlas. Right lateral view. ×4/3.

FIG. 14. *Utaetus buccatus* Ameghino. A.M.N.H. No. 28668. Anterior caudal vertebra. Anterior view. ×4/3.

ments of three others. The atlas is very like that of *Dasypus*, save in details of proportion, etc., and the relatively smaller foramina. On the axis the odontoid and atlanteal facets are less separate than in *Dasypus*. The bone had not fused with the third cervical, and since a working facet seems to be present, probably did not do so at any time—another very primitive character for an armadillo, as these are already fully fused in the Santa Cruz forms. Little can be learned from the thoracic vertebrae except the very important fact that the xenarthrous articulation was already present. The anterior caudals are somewhat shorter relatively than in *Dasypus*, with flatter ventral surfaces, but otherwise are about the same. One chevron bone is preserved. It is simple, with none of the specializations of various later forms, of Y shape closed above, and with the united stem somewhat expanded anteroposteriorly.

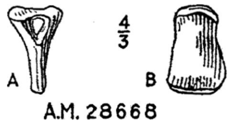

FIG. 15. *Utaetus buccatus* Ameghino. A.M.N.H. No. 28668. Chevron. A. Anterior view. B. lateral view. ×4/3.

FORE LIMB

The fragmentary scapulae show that the posterior process of the acromion was larger than in later forms, and that the second spine is a mere thickening of the posterior border, both characters strongly suggestive of palaeanodonts. Even at its narrowest point, the prespinous fossa is wider than the postspinous.

The ends of the humerus are not preserved, but the shaft is very distinctive. It is more slender and elongate, less twisted and with weaker processes than those of later armadillos. The deltoid crest is broken but seems to have been much less expanded. It is continued to the distal end by a definite angulation on the shaft. The supinator crest, while strong and continuing probably about halfway up the shaft, is not so wide as in most armadillos and is almost straight rather than strongly sigmoid.

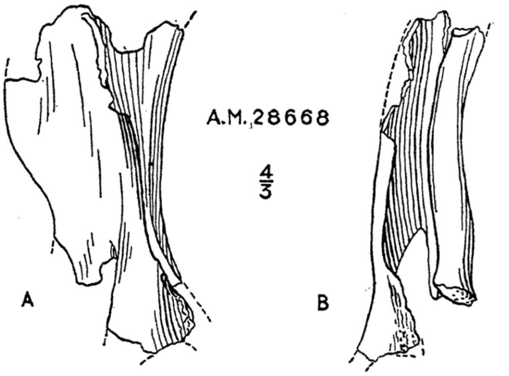

FIG. 16. *Utaetus buccatus* Ameghino. A.M.N.H. No. 28668. Left scapula. A. Lateral view. B. Anterior view. ×4/3.

The ulna suggests that of *Dasypus* but is less curved, perhaps in part due to crushing, and less specialized. The trochlear facet is narrower transversely. The articulation for the radius is a nearly flat single surface. Save for its flatter and single proximal ulnar facet, the radius is as in most later forms, and the distal ends of radius and ulna are not present.

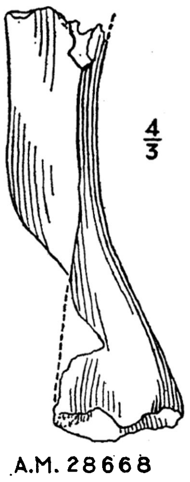

FIG. 17. *Utaetus buccatus* Ameghino. A.M.N.H. No. 28668. Left humerus. Posterior view. ×4/3.

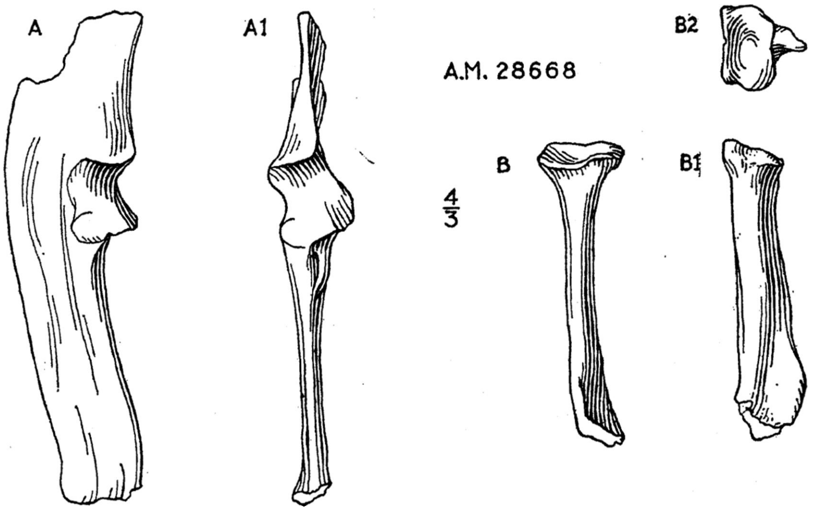

FIG. 18. *Utaetus buccatus* Ameghino. A.M.N.H. No. 28668. A. Right ulna, lateral view. A1. Same, anterior view. B. Right radius, anterior view. B1. Same, lateral view. B2. Same, proximal view. ×4/3.

Various fragments apparently belong to the manus, but they are too uncertain of interpretation to be of much use.

HIND LIMB

The pelvis has acquired the fundamental xenarthran characteristics, but with little or no further specialization. The ilium is a long and rather slender blade. The lateral crest is well developed throughout and parallel to the lower border. On the posterior third it forms the upper border, but anterior to this a larger triangular, nearly vertical articular flange is developed. The pubis is a still more slender bar and arises wholly beneath the anterior part of the acetabulum, a xenarthran (and palaeanodont) character. The anterosuperior part of the ischium is much as in *Dasypus*, with the ischiocaudal (or false sacral) contact already established.

Of the femur, only the crushed shaft is preserved. This is of generalized armadilloid structure, with a strong, *Dasypus*-like third trochanter somewhat above the middle of the shaft. The shaft of the fibula also suggests *Dasypus*, but with a much less definite interosseous crest.

In the tarsus, we have the calcaneum, astragalus, navicular, entocuneiform, and ectocuneiform of one side or both. The astragalus is characteristically xenarthran, but differs from that of *Dasypus* in being shallower dorsoventrally; with shallower and less coiled trochlea, not extending so far proximally, and not invaded by any distinct emarginations; malleolar facets somewhat

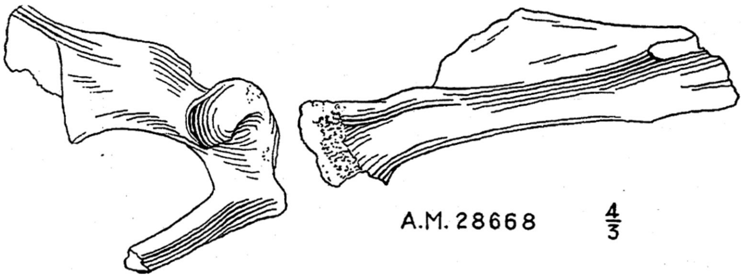

FIG. 19. *Utaetus buccatus* Ameghino. A.M.N.H. No. 28668. Right innominate. Lateral view. ×4/3.

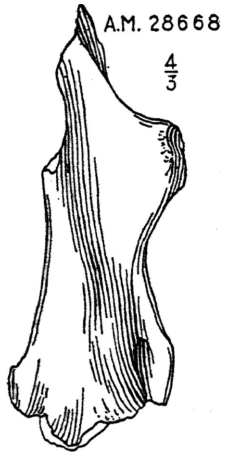

FIG. 20. *Utaetus buccatus* Ameghino. A.M.N.H. No. 28668. Left femur. Anterior view. ×4/3.

smaller but external projection definitely longer; sustentacular facet oval and distinctly separated from any other; ectal facet relatively longer and narrower and less concave. On the poorly preserved calcaneum, the most clearly visible peculiarity is the much flatter ectal facet. Save for being relatively shallower dorsoventrally and with a smaller entocuneiform facet, the navicular is like that of *Dasypus*. On the entocuneiform, the distoexternal angle is more acute than in *Dasypus*, making the dorsal face of this bone less square, and the navicular facet is less produced transversely. The entocuneiform had a distinct contact with the fourth metatarsal. The indifferently preserved three median metatarsals seem to differ from *Dasypus* only in quite minor details. Judging from various dissociated fragments, the phalanges were of the same general character as in the recent genus, but they display less aberrant specialization.

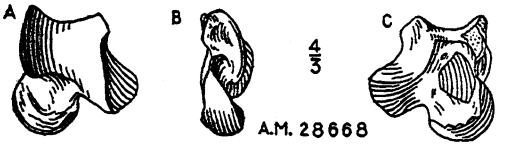

FIG. 21. *Utaetus buccatus* Ameghino. A.M.N.H. No. 28668. Left astragalus. A. Dorsal view. B. Medial view. C. Plantar view. ×4/3.

CARAPACE

A fragment of the head shield shows a mosaic of irregular, simple, thin scutes with finely punctate surface (in texture rather like an egg shell) without follicles or scale patterns.

In one case, a patch of buckler scutes is so placed with respect to movable bands as to appear to be from a pectoral buckler, but in view of the facts that this is not an actual contact and that no Santa Cruz (or older) armadillo is known to have a pectoral buckler, this collocation is probably fortuitous. There is an isolated scute fixed anteriorly and imbricating at the posterior edge, hence resembling a posterior pectoral buckler scute, but this might be a posterior cephalic, posterior pelvic buckler, or even, but less probably, a caudal scute, and a pectoral buckler was probably absent. Our largest group of associated movable band scutes has parts of six bands; the total number of bands is unknown and was probably at least 12. There are at least 14 in the Santa Cruz *Prozaedius*.

On the movable band scutes, the articular anterior part is generally a little less than a third of the total length of the scute and is slightly wider than long. The exposed part is generally less than twice as long as wide and is marked by a narrow median longitudinal ridge, divided by grooves from a similar lateral ridge on each side. These merge at the distal end of the scute. The lateral areas are often, but rather vaguely, divided into anterior and posterior scale areas. In some cases the two longitudinal grooves have one or two perforations each, so small as to be hardly or not at all distinguishable from the general surface punctations. From the associated groups, these appear to be the more lateral scutes. In other cases, apparently more central, there are in each groove two relatively very large follicles, and between these two very distinctive types (distinct generically in Ameghino's classification) there may be others with one large perforation in each groove. Many of the movable band scutes have one or two small posterior marginal follicles, but none has more than two and in many cases none is visible.

As already suggested, the central buckler scutes are highly varied. In general they have a convex main scale area and usually four anterior and anterolateral, sharply defined, intercalary scale areas, with occasion-

FIG. 22. *Utaetus buccatus* Ameghino. A.M.N.H. No. 28668. Right pes. Dorsal view. ×4/3.

ally another ill-defined posterolateral pair. There are no lateral marginal follicles, but small posterior follicles are usually present in moderate numbers, generally two or four. With respect to shape and central perforations, there are two fairly well-defined types: one slightly elongate, rectangular, with two or occasionally four small central perforations, the other nearly equidimensional, polygonal (usually irregularly hexagonal), with much larger central perforations, almost always four in number. Every intergradation between these extremes is present, as well as a number of more aberrant scutes. These two types are so unlike that placing them in different genera on the basis of isolated scutes would seem justifiable, but there is no doubt that both belong to this single individual. Their distribution in the buckler is not known. The buckler scutes were not so immovably fixed as in most modern forms. The sutural surfaces are plane or, frequently, concave, never convex, with spicules very poorly developed or even absent, and there is commonly a slight degree of imbrication, although this is not comparable with that of the true movable bands.

Five associated scutes represent a posterolateral corner. They are thicker than average, and more definitely imbricating, with only two or three small intercalary scales and very small and few central perforations. Other isolated marginal scales have no central perforations and no differentiated sculpture.

Scott states that no certain caudal scutes were found in the Santa Cruz. With the present specimen are a few small, unsculptured, lozenge-shaped or polygonal, strongly arched scutes with non-articular edges which seem almost surely to belong to a flexible caudal tube, rather like the distal part of tail of *Dasypus*, for instance. Whether definite caudal rings were also developed is unknown. It may be that the tail investiture in the earlier armadillos was generally of this looser, more flexible type and that to this is due the non-recognition of its remains.

RELATIONSHIPS

Utaetus has acquired all the fundamental xenarthran and armadillo characters. Almost all the positive features shared by all recent armadillos, and hence presumably present in their immediate common ancestry, are displayed in characteristic form in this Eocene relative: e.g., strong dermal armor of armadilloid structure and pattern, degenerate rootless teeth, xenarthrous vertebrae, scapula with two spines and very large acromion, ischiocaudal suture, large third trochanter of femur, and highly characteristic astragalus. With only isolated scutes, it was perhaps possible, as Matthew implied, that we were dealing with primitive forms only superficially armadillo-like, but now it is obvious that *Utaetus*, at least, is a real armadillo in every respect.

On the other hand, closer study quickly demonstrates that, with very few exceptions, it is only the basic armadillo characters that have been acquired, that definite phyletic advances are almost absent, and that in almost every character *Utaetus* either is in the most primitive condition known in later allies or is definitely more primitive. The cranium is armadilloid, but its very low glenoid fossa and long basicranium are more primitive; the jaw is elongate and rather armadillo-like, but the protruded edentulous symphysis is only incipient, and the ascending ramus is quite different from any later form and more primitive; the teeth are cylindrical and rootless, but they have functional enamel—and so on, more clearly in some characters than others, but visible throughout the whole skeleton of the animal.

The only known character which is, with reasonable probability, aberrant is the development of very large central perforations on some, but not all, of the scutes. This is probably not of fundamental importance, as considerable variation is shown in this respect by later forms which are, on other and more impelling grounds, seen to be nearly allied.

Among Santa Cruz armadillos, *Prozaedius* most nearly resembles *Utaetus*. The resemblance, however, is almost entirely negative, that is, due to the absence in *Prozaedius* of various specializations present in other Santa Cruz genera. The two differ in many respects, mostly owing to the more primitive character of *Utaetus*, and are divergent in details of scute sculpture. Among recent armadillos, *Utaetus* most nearly resembles the *Zaedyus-Dasypus* [or *Euphractus*]- *Chaetophractus* group. But here again, the resemblance is largely or wholly due to the fact that these are the most primitive recent armadillos, and definite points of resemblance in specializations such as would indicate phyletic relationship seem to be absent. It is probable that *Utaetus* is not directly ancestral to any of these later forms, but that it stands near the structural ancestry of all.

I have elsewhere discussed the ancestry of the edentates in some detail (Simpson, 1931b), concluding that they were probably derived from pre-Eocene, possibly lower Paleocene, Palaeanodonta. The present material tends, morphologically, to support that view. In the following principal points, *Utaetus* shows some special resemblance to the palaeanodonts:

1. Presence of enamel on the teeth
2. Shape of occiput (so far as known) and of cranial roof
3. Post-glenoid elongation[1]
4. Low position and general structure of glenoid fossa
5. Shape of lower jaw
6. Unfused axis and third cervical, atlas and axis generally very palaeanodont-like
7. Scapula with second spine only incipient, large posterior branch of acromion[2]
8. Pelvis definitely xenarthran rather than pre-xenarthran, but distinctly more palaeanodont-like than in later armadillos
9. Astragalus slightly more *Metacheiromys*-like than in later armadillos

Thus in a high percentage of the known characters *Utaetus* makes a more definite approach to the palaeanodonts than do any or most of the later edentates. In view of the fact that *Utaetus* is the oldest xenarthran in which these parts are known, this is very impelling evidence for this theory of xenarthran origin.

From a temporal point of view, however, *Utaetus* raises an apparent difficulty, or at least demands some further consideration. If the rate of evolution was constant and if the Xenarthra arose from the Palaeanodonta in not earlier than late Cretaceous or later than Paleocene time, an Eocene xenarthran should be closer to the Palaeanodonta than to its Recent descendants. Now *Utaetus* is literally intermediate between the two, but distinctly closer to modern armadillos than to any known palaeanodont. This difficulty, however, is more apparent than real. The possibility of change from the palaeanodont to this most primitive known xenarthran condition, even in the minimum time available, can hardly be doubted, as it is not greater than is known to have occurred in an equal time in some other lines. In estimating the rate of evolution it is not valid to compare *Utaetus* with its most primitive Recent allies, for these are static forms whose rate of change has demonstrably been remarkably slow, far below the average not only for mammals in general but also for this group in particular. If we compare *Utaetus* with the more specialized recent armadillos, such as *Priodontes* or *Chlamyphorus*, it is about as close to the palaeanodonts as to those, and if we consider Pleistocene glyptodonts or, still more, other Pleistocene or Recent Xenarthra, *Utaetus* is decidedly closer to the palaeanodonts than to these. Furthermore it is

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[1] This was considered aberrant in *Metacheiromys* (Simpson, 1931b, p. 368), but the intermediate condition in *Utaetus* suggests that it was really an ancestral edentate character and is peculiarly suggestive of real relationship.

[2] This was suggested as possibly independently acquired in the two groups (Simpson, 1931b, p. 369) in an effort not to overstate the evidence, but it now appears probably to be an ancestral character and a valid item of evidence.

unjustifiable to assume a constant rate of evolution for any one line or a constant average for the Xenarthra as a whole, as it is clear that the origin of the basic characters of such a group may, perhaps generally does, involve more rapid fundamental evolution than the later differentiation of the group.

Utaetus lenis (Ameghino, 1902)

Anteutatus lenis AMEGHINO, 1902a, p. 58.

TYPE: M.A.C.N. No. 10425. Seven scutes. Lectotype: central buckler scute, roughly quadrangular, measuring 10.6 by 15.7 mm.

HYPODIGM: Types and M.A.C.N. No. 10459, five scutes.

HORIZON AND LOCALITY: Locality not given. Upper part of Casamayor beds. Referred specimens from south of Lago Colhué-Huapí.

DIAGNOSIS: Intermediate in size. Scutes heavy. Sculpture low. Follicles and perforations few in number and small.

This may be a valid species, but certainly present evidence does not warrant generic separation from *Utaetus*, and even the specific distinction is not well established.

Utaetus deustus Ameghino, 1902

? *Utaetus deustus* AMEGHINO, 1902a, p. 60.

TYPE: M.A.C.N. No. 10431. Four scutes. Lectotype: fixed buckler scute, measuring 14.0 by 17.1 mm.

HYPODIGM: Types only.

HORIZON AND LOCALITY: (According to Ameghino) upper part of Casamayor beds, south of Lago Colhué-Huapí, Chubut, Argentina.

DIAGNOSIS: Larger than average *U. buccatus*, with unusually heavy scutes and tending to form a keel on central scute areas. Probably associated movable scutes likewise large and heavy, with raised lateral edges and a central depression with median keel.

Ameghino thought that this might be a distinctive genus, and indeed it does differ more from *U. buccatus* than do a number of his supposedly distinct genera. The material is very scanty and is so heavily encrusted with manganese that fine details are lacking, but it may well represent a valid species. Only the type specimens are known.

?Utaetus laevus (Ameghino, 1902), new combination

Anteutatus laevus AMEGHINO, 1902a, p. 58.

TYPE: M.A.C.N. No. 10960. Six scutes, some broken. Lectotype: a quadrate buckler scute. Ameghino Collection.

HYPODIGM: Types only.

HORIZON AND LOCALITY: Musters formation, Patagonia. No other data.

DIAGNOSIS: Closely similar to *U. lenis*, but averaging smaller. Lectotype measuring 10 by 7 mm.

As Ameghino recognized, this cannot be distinguished generically from "*Anteutatus*" *lenis*, which in turn cannot be adequately distinguished from *Utaetus*. It is somewhat improbable that this Musters material belongs to *Utaetus*, but the actual specimens show no good distinction.

PSEUDOSTEGOTHERIUM AMEGHINO, 1902

Pseudostegotherium AMEGHINO, 1902d,[1] p. 137; 1902a,[1] p. 68; 1906, p. 469.

TYPE: *Pseudostegotherium glangeaudi*[1] Ameghino. Colhué-Huapí formation.

DISTRIBUTION: Supposedly in the Casamayor and Colhué-Huapí of Patagonia.

DIAGNOSIS: For distinctive generic characters of the Casamayor species see page 75; this is probably not really *Pseudostegotherium*, which will not be redefined here.

?Pseudostegotherium chubutanum Ameghino, 1902

Text figure 10K

Pseudostegotherium chubutanum AMEGHINO, 1902a, p. 68.

TYPE: M.A.C.N. No. 10438. Fifteen iso-

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[1] There are two separate papers, both in the Bol. Acad. Nac. Cien. Cordoba, vol. 17. 1902a begins on page 5 and is dated only 1902; 1902d begins on page 71 and is dated May, 1902. *P. glangeaudi* is labeled "n. g., n. sp." but appears in the second of the two papers. *P. chubutanum* is in the first paper, and hence must have some degree of priority, but is labeled only "n. sp." I therefore conclude that the genus *Pseudostegotherium* is a *nomen nudum* in the first paper, being quoted from the manuscript of the second, the publication of which established or validated it, and that its type was intended to be and is in fact by original indication *P. glangeaudi*. As the older species probably does not belong in the same genus as *P. glangeaudi*, this is of nomenclatural importance.

lated scutes. Lectotype: central buckler scute measuring 6.5 by 8.9 mm.

HYPODIGM: Types only.

HORIZON AND LOCALITY: (According to Ameghino) upper part of Casamayor beds, south of Lago Colhué-Huapí, Chubut, Argentina.

DIAGNOSIS: With distinct lageniform sculpture and small central perforations.

Ameghino's description of the genotype suggests that this species is very different morphologically and it is also very improbable that the genus really occurs in both the Casamayor and Colhué-Huapí as no other is known to do so. Without further material, however, it seems unwise to erect a new genus. The species is quite surely valid and does not appear to belong in any other named Casamayor genus.

COELUTAETUS Ameghino, 1902

Coelutaetus AMEGHINO, 1902a, p. 64; 1906, p. 468.

TYPE: *Coelutaetus cribellatus* Ameghino, 1902.

DISTRIBUTION: Casamayor beds, Patagonia.

DIAGNOSIS: See page 75.

Coelutaetus cribellatus Ameghino, 1902

Text figure 10H

Coelutaetus cribellatus AMEGHINO, 1902a, p. 64.

TYPE: M.A.C.N. No. 10426. One broken plate.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayor beds, "Río Chico," Chubut, Argentina.

DIAGNOSIS: Sole known species.

The genus and species rest on a very insecure basis, being known only from a single broken scute. This measures 5.1 by 7.8 mm. and has a maximum thickness of 3.8 mm.

ASTEGOTHERIUM Ameghino, 1902

Astegotherium AMEGHINO, 1902a, p. 67; 1906, p. 469.

TYPE: *Astegotherium dichotomum* Ameghino, 1902.

DISTRIBUTION: Casamayor beds, Patagonia.

DIAGNOSIS: See page 75.

Astegotherium dichotomum Ameghino, 1902

Text figure 10J

Astegotherium dichotomus AMEGHINO, 1902a, p. 67.

TYPE: M.A.C.N. No. 10421. Twenty-two scutes. Lectotype: a central buckler scute measuring 5.3 by 8.4 mm.

HYPODIGM: Types only.

HORIZON AND LOCALITY: No data with specimen. Casamayor beds, Patagonia.

DIAGNOSIS: Sole known species.

These scutes are fairly distinctive, generally quadrangular, somewhat imbricating, thickness generally one-third to one-half the width, follicles and intercalary scales few. Ameghino held that this species proved that scales antedated hair, and that it was a direct ancestor of the very hairy *Stegotherium* of the Santa Cruz. This theory can hardly be taken seriously. Aside from the tremendous probability on other evidence that hair preceded the scales in the armadillos, this less hairy genus appears to be contemporaneous with others quite as hairy as any later forms, and there is no clear or credible evidence that it is really ancestral or closely related to the very different *Stegotherium*.

PROSTEGOTHERIUM Ameghino, 1902

Prostegotherium AMEGHINO, 1902a, p. 69; 1906, p. 469.

TYPE: *Prostegotherium notostylopianum* Ameghino, 1902.

DISTRIBUTION: Casamayor beds, Patagonia.

DIAGNOSIS: See page 75.

It is very doubtful whether this genus or either of its species is valid, but their true position is not now determinable.

Prostegotherium notostylopianum Ameghino, 1902

Text figure 10I

Prostegotherium notostylopianum AMEGHINO, 1902a, p. 69.

TYPE: M.A.C.N. No. 10451. Thirty-three scutes. Lectotype: central buckler scute measuring 5.1 by 7.8 mm.

HYPODIGM: Types only.

HORIZON AND LOCALITY: (According to Ameghino) upper part of Casamayor beds, south of Lago Colhué-Huapí, Chubut, Argentina.

DIAGNOSIS: Fixed scutes generally 7.5 to 9.5 mm. in length. Posterior follicles generally one or two, central perforations generally two to four.

Prostegotherium astrifer Ameghino, 1902

Prostegotherium astrifer AMEGHINO, 1902a, p. 69.

TYPE: M.A.C.N. No. 10444. Eighteen scutes. Lectotype: central buckler scute measuring 6.5 by 11.5 mm.

HYPODIGM: Types only.

HORIZON AND LOCALITY: (According to Ameghino) upper part of Casamayor beds, south of Lago Colhué-Huapí, Chubut, Argentina.

DIAGNOSIS: Fixed scutes generally 9.5 to 11.5 mm. in length. Posterior follicles generally three or four, central perforations generally eight to 10.

Some scutes form a complete intergradation between this and the preceding species, and it is highly probable that the two are synonymous, and both may also be synonymous with *Astegotherium dichotomum*, but they are tentatively retained. *Prostegotherium notostylopianum* and *astrifer* is a (or are) rather common species relatively, some 10 or more different lots of scutes being referable to this group. These additional specimens are not added to the specific hypodigms because they do not add to knowledge of the species and in general cannot be allocated with any confidence to one species rather than to the other.

PSEUDEUTATUS AMEGHINO, 1902

Pseudeutatus AMEGHINO, 1902a, p. 57; 1906, p. 470.

Isutaetus AMEGHINO, 1902a, p. 65; 1906, pp. 470, 472.

Anutaetus AMEGHINO, 1902a, p. 66; 1906, pp. 470, 472.

Pachyzaedyus AMEGHINO, 1902a, p. 67.

Pachyzaedius, AMEGHINO, 1906, p. 470.

TYPE: *Pseudeutatus clypeus* Ameghino, 1902.

TYPES OF SYNONYMS: *Isutaetus depictus* Ameghino, 1902. *Anutaetus circundatus* Ameghino, 1902. *Pachyzaedyus cuneiformis* Ameghino, 1902.

DISTRIBUTION: Musters and perhaps Deseado formations, Patagonia.

DIAGNOSIS: See page 75.

The four genera here united were based on very unsatisfactory materials, *Isutaetus* on three scutes, and the other three supposed genera on once scute each. As has been noted above, these scutes have all their most probably diagnostic features in common, cannot reasonably be separated generically, and could even be all of a single species. Their species are nevertheless separately listed and diagnosed below, because positive association is not demonstrated and in order not to prejudice the possiblity that they are distinguishable.

The distinction of this group as a whole from *Machlydotherium* is clear enough. The difference from the Musters species referred to *Meteutatus* (including *Sadypus*) is less satisfactory, amounting to little more than the smaller number of peripheral follicles in *Meteutatus* and their situation in a more definite and continuous groove. It is possible that the Musters species of "*Anteutatus*" belong in *Pseudeutatus* rather than in *Utaetus*, of which (typical) *Anteutatus* is a synonym.

Ameghino also referred Deseado specimens to *Isutaetus* and *Anutaetus*, but in both the genotypes are from the Musters. The pertinence of the Deseado species to this group is dubious.

Pseudeutatus clypeus Ameghino, 1902

Plate 8, figure 2

Pseudeutatus clypeus AMEGHINO, 1902a, p. 57.

TYPE: M.A.C.N. No. 10959. One scute. Ameghino Collection.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Musters formation Patagonia. No other data.

DIAGNOSIS: Buckler scute subquadrate, with dense surface with many punctations. Numerous irregular follicles on posterior margin only. Intercalary scales anterior, very poorly defined. Lageniform central figure vague. Type measuring 14 by 12 mm.

Pseudeutatus depictus (Ameghino, 1902), new combination

Plate 8, figures 3–4

Isutaetus depictus AMEGHINO, 1902a, p. 65; SIMPSON, 1936d, p. 72.

TYPE: M.A.C.N.No. 10961. One band and two buckler scutes. Lectotype: approximately hexagonal buckler scute. Ameghino Collection.

HYPODIGM: Types and specimen in Roth Collection, Museo de La Plata.

HORIZON AND LOCALITY: Musters formation, Patagonia. No other data with type. Referred specimen from Roth's "Lago Musters," probably Cerro del Humo.

DIAGNOSIS: Punctations less pronounced than in *P. clypeus* and intercalary scale boundaries sharper and deeper. Peripheral follicles numerous and small. Lectotype measuring 12½ by 11 mm.

Pseudeutatus circundatus (Ameghino, 1902), new combination

Anutaetus circundatus AMEGHINO, 1902a, p. 66.

TYPE: M.A.C.N. No. 10962. One scute. Ameghino Collection.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Musters formation, Patagonia. No other data.

DIAGNOSIS: Scale areas well marked. Apparently only one intercalary scale, which is along anterior margin. Central ridge well defined. Posterior follicles few and united in groove. Type quadrangular, measuring 10 by 6½ mm.

Ameghino said that the type has a "rebord périphérique . . . non divisé en figures séparées," i.e., in my terminology, intercalary scale areas not distinguishable, but this is erroneous as the grooves separating these are clear but were filled with matrix when Ameghino studied the specimen. The Deseado "*Anutaetus*" *tortuosus* is said to have the lateral parts rugose. They are smooth in this species and in its allies or synonyms in the Musters fauna.

Pseudeutatus cuneiformis (Ameghino, 1902), new combination

Plate 8, figure 5; text figure 10G

Pachyzaedyus cuneiformis AMEGHINO, 1902a, p. 67.

TYPE: M.A.C.N. No. 10956. One scute. Ameghino Collection.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Musters formation, Patagonia. No other data.

DIAGNOSIS: Almost indistinguishable from *P. depictus*, but surface still smoother and flatter, scale boundaries unusually sharp, type relatively elongate and thick, measuring 12 by 8 mm.

DASYPODIDAE INCERTAE SEDIS

There are many Casamayor and some Musters specimens that cannot surely be referred to a named species, but this is largely or wholly because the species are so ill defined and their intra-individual and intra-specific variation not established. These additional specimens do not suggest any greater diversity than is established by the named specimens.

We have only four scutes from the Río Chico, and I know of no others. These cannot be placed with any likelihood in named genera or species and are sufficiently distinctive to be probably new, but no new names are proposed on such a slender basis. A.M.N.H. No. 28490 is a thick, short, imbricating scute, perhaps from a uniserial caudal ring, from 3 kilometers southwest of Pico Salamanca. A.M.N.H. No. 29100, from the top of Cerro Redondo, includes a fragment of an imbricating scute and a buckler scute, complete but somewhat weathered. The latter scute is elongate hexagonal, 8.7 by 6.2 mm. Anterior intercalary areas are vague. Four small central perforations are on and around the anterior end of the main scale area, which has a low and vague central carina. Marginal follicles are only two in number and are on the posterior half of one lateral edge, not on the posterior edge. A.M.N.H. No. 28488, from near the south end of the barranca of Las Violetas, is rather like the scute just described but is thinner, smaller, and more elongate, 7.8 by 4.8 mm. It has two marginal follicles on each lateral border and none on the posterior edge.

GLYPTODONTIDAE

Undoubted glyptodonts occur in the Musters for the first time, but they are here extremely rare, only four (or possibly five) specimens being known to me. Ameghino described three species, placed in as many genera, but each is based on a single specimen, in no case including even one whole scute, so that their real relationships are very doubtful aside from the interesting fact that they are glyptodonts. He also had one isolated tooth, and we found a jaw fragment with all of one tooth and part of another, indeterminable but figured here as conclusive assurance that glyptodonts are present (fig. 23).

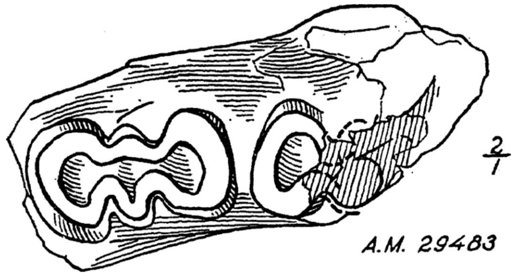

FIG. 23. Glyptodont, *incertae sedis*, perhaps *Glyptatelus*. A.M.N.H. No. 29483, fragment of lower jaw with one tooth and part of another. Crown view. ×2.

GLYPTATELUS AMEGHINO, 1897

Glyptatelus AMEGHINO, 1897a, p. 507; 1902a, p. 50; 1906, pp. 470, 472; LOOMIS, 1914, p. 206.

TYPE: *Glyptatelus tatusinus* Ameghino, 1897, from the Deseado.

DISTRIBUTION: Musters and Deseado formations, Patagonia.

This is a poorly known Deseado genus and is not revised here. The following nearly indeterminate species is not separable from this genus, but there is little assurance that it belongs to it.

Glyptatelus fractus Ameghino, 1902

Glyptatelus fractus AMEGHINO, 1902a, p. 51.

TYPE: M.A.C.N. No. 10949. A small fragment of a scute (lectotype) and an isolated tooth. Ameghino Collection.

HYPODIGM: Lectotype only.

HORIZON AND LOCALITY: Musters formation, Patagonia. No other data.

DIAGNOSIS: Smaller than *G. tatusinus*. Surface of scute dense with few and small punctations, large central figure, and various well-defined intercalary areas, one of which is 13.5 mm. in greatest diameter; thickness of lectotype about 8 to 9 mm.

Since there is inevitably some doubt as to the association of the tooth and scute fragment syntypes of this species, I have selected the scute, poor as it is, because it alone is comparable with the other types in this fauna and in the Deseado. Ameghino has pointed out the principal characters of the tooth, which are also seen in A.M.N.H. No. 29483, from Cerro Blanco. It has the usual trilobed pattern but is peculiar in having the lobes rounded, cylindrical rather than prismatic, and in being composed of hard outer and soft central dentine, without the secondary hard median pattern of Santa Cruz and later glypotodonts. The length is 10.2 mm., and the widths across the three lobes 5.1, 4.3, and 3.4 mm., respectively.

LOMAPHORELUS AMEGHINO, 1902

Lomaphorelus AMEGHINO, 1902a, p. 51; 1906, p. 470.

TYPE: *Lomaphorelus depstus* Ameghino, 1902.

DISTRIBUTION: Musters formation, Patagonia.

DIAGNOSIS: Small scute with dense, glistening surface, obscurely marked into a large central area with a vague longitudinal elevation and small intercalary areas; numerous radiating punctations, especially on the very vague scale boundaries.

The single broken scute on which this genus is based is unlike any other known, in details, and probably represents a valid genus, but its affinities can hardly be guessed.

Lomaphorelus depstus Ameghino, 1902

Plate 8, figure 6

Lomaphorelus depstus AMEGHINO, 1902a, p. 51.

TYPE: M.A.C.N. No. 10950. Single broken scute. Ameghino Collection.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Musters formation, Patagonia. No other data.

DIAGNOSIS: Sole species referred to genus. Type measuring about 13 by 20 mm., and 5 to 7 mm. in thickness.

PALAEOPELTIS AMEGHINO, 1895

Palaeopeltis AMEGHINO, 1895, p. 659; 1897a, p. 506; 1902a, p. 52; 1906, p. 470; LOOMIS, 1914, p. 205.

TYPE: *Palaeopeltis inornatus* Ameghino, 1895, from the Deseado.

DISTRIBUTION: Musters and Deseado formations, Patagonia.

This Deseado genus is, in a sense, characterized by its lack of character, being based on scutes practically devoid of any decoration. The referred Musters fragment is similar to that extent, but will probably prove to represent a different genus when adequately known. It seems to be a glyptodont, but this is not absolutely certain.

Palaeopeltis tesseratus Ameghino, 1902

Palaeopeltis tesseratus AMEGHINO, 1902a, p. 52.

TYPE: M.A.C.N. No. 10948. Broken fragment of shield with most of one scute and small parts of three others. Ameghino Collection.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Musters formation, Patagonia. No other data.

DIAGNOSIS: Scutes with dense, porcelain-like outer surface, few follicles; small punctations; outer face slightly convex and devoid of any pattern; very strongly sutured. Greatest diameter of best scute of type 33 mm., thickness 8 to 10 mm.[1] The sutures are somewhat dendritic and so strong that this broken fragment does not follow them anywhere.

TUBULIDENTATA

This order is not present in any Patagonian fauna, but Ameghino's report of *Archaeorycteropus* in the Casamayor requires comment.

The type of *Archaeorycteropus* is *A. gallicus*, based on an isolated tibia from the Phosphorites de Quercy (Mouillac), France. This seems to me so different from *Orycteropus* that I am little impressed by the evidence for relationship. *A. patagonicus* was based on the distal part of a tibia from the Casamayor, in a very poor state of preservation. The specimen was not found by me in the Ameghino Collection. Ameghino's figures suffice to show that it can hardly be related to *A. gallicus*. Whatever the affinities of the latter may be, *A. patagonicus* surely does not belong in the same genus. The species is so surely indeterminate that one need have no compunction in striking it from the record. As for its relationship to *Orycteropus*, which Ameghino held to be a scaleless armadillo, this hardly merits discussion. Whatever the ancestry of *Orycteropus* may be, the Casamayor fragment bears so little real resemblance to that genus and is so devoid of diagnostic features anyway, that its reference to the Orycteropodidae can most charitably be forgotten.

ARCHAEORYCTEROPUS AMEGHINO, 1905

Archaeorycteropus AMEGHINO, 1905b, p. 223; 1906, p. 469.

TYPE: *Archaeorycteropus gallicus*, from the Phosphorites de Quercy, France.

DISTRIBUTION: France. Erroneously reported in the Casamayor of Patagonia.

DIAGNOSIS: Omitted as not pertinent to these faunas.

"Archaeorycteropus" patagonicus Ameghino, 1905, nomen vanum

Archaeorycteropus patagonicus AMEGHINO, 1905b, p. 226, fig. 61; 1906, p. 374, fig. 228.

TYPE: Broken distal part of tibia, not found in Ameghino Collection.

HYPODIGM: Ameghino's published data only.

HORIZON AND LOCALITY: Casamayor, Patagonia. No other data.

DIAGNOSIS: Not *Archaeorycteropus*. Otherwise indeterminate.

CONDYLARTHRA

DEFINITION: Primitive and generalized ungulates. Dental formula $\frac{3\cdot1\cdot4\cdot3}{3\cdot1\cdot4\cdot3}$ so far as known. Brachyodont. Bunodont or, more rarely, bunoselenodont. Incisors subequal, primitive, canines simple, usually slightly larger than incisors. Posterior premolars becoming molariform in more advanced members. Upper molars generally subquadrate, with nearly equal paracone, metacone, protocone, and usually hypocone; prominent conules. Trigonids little elevated, shortened, paraconid generally fusing with metaconid or otherwise reduced. Large basined cuspidate

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[1] Ameghino gives 18 which is surely a misprint.

heels. M_3 with prominent projecting hypoconulid. Skull, where known, very generalized, bullae not inflated, skull carnivore-like in general outline. Feet, where known, pentadactyl and plantigrade to semidigitigrade; tarsus serial. Astragalus with shallow trochlea, somewhat elevated on fibular side, often with foramen, neck oblique, constricted, head moderately compressed anteroposteriorly or planto-dorsally), articular surface convex in all directions.

The foregoing definition is presented in order to permit and at the same time to justify the reference to this order of a number of Río Chico and Casamayor forms here united in the family Didolodontidae. Several different lines are present, and the distinction between some of these and the Litopterna is sometimes difficult to draw. Although the Condylarthra are defined chiefly on primitive characters and although the Didolodontidae do thus tend towards a more specialized order, the arrangement now adopted seems justified by the morphological facts given below. According to this view, the Litopterna are, in effect, no more than advanced condylarths surviving in South America long after this general structural grade had been replaced elsewhere by still more progressive condylarth derivatives, the perissodactyls and artiodactyls. In the Musters, there are several persistently primitive forms that still are near the line between condylarths and litopterns, but these are tentatively classified as Litopterna because of a few relatively advanced features that are litoptern-like. The ordinal reference of these early genera is more or less formal, and the disappearance of condylarths after the Casamayor is in part a necessary artifact of classification. There were, nevertheless, already some animals in the late Río Chico that were clearly differentiated as litopterns.

DIDOLODONTIDAE SCOTT[1]

This family comprises a possibly somewhat artificial assemblage of early Patagonian ungulates with tooth characters the same as those defining the Condylarthra. It is at present impossible to frame a purely morphological definition which would include all these genera and exclude the North American condylarth families.

The poorly known forms which will be considered under this heading have had a very checkered career. Ameghino (e.g., 1906, p. 467) referred 21 genera from the Casamayor to this order, distributing them in the Patagonian family Pantostylopidae and the Holarctic families Phenacodontidae, Catathleidae [= Periptychidae], Pantolambdidae, and Arctocyonidae.[2] His "Pantostylopidae" seem to me to be notoungulates, and his Patagonian genera of "Catathleidae" (except *Argyrolambda*) and Pantolambdidae appear to be litopterns. The specimen that served for the listing of "*Claenodon*?" in the fauna was incorrectly determined and otherwise practically indeterminate, so that his supposed Patagonian Arctocyonidae may be ignored. There remain, then, the nine[3] supposed genera placed by Ameghino in the Phenacodontidae, to which must be added some other forms by Ameghino placed in widely different groups, as detailed below. Ameghino not only considered these Patagonian forms as ancestral to the Holarctic condylarths, but also placed them in various phylogenetic trees as ancestral to most later ungulates.

Roth placed what was essentially this group (with somewhat different limits) in a group apart, Didolodia, and opposed the view that they were related to the Litopterna (e.g., 1927, pp. 201, 227, etc.). Scott (1913) also recognized essentially the same group, and applied to it the name Didolodidae. He called them "Condylarthra like" but placed them in the Litopterna. Loomis (1914, especially p. 41) placed all the litoptern-like genera of the Deseado in Santa Cruz families and clearly implied that these bunodont Casamayor forms were true litopterns, with no further suggestion as to their origin. Winge (1923–1924, vol. 3, p. 21, etc.) also considered them as litopterns (without using that name) as *Didolodus* is placed in a subfamily of the Macraucheniidae. Schlosser (1923, p. 525)

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[1] Emended from Didolodidae in Scott, 1913. Didolodontidae in Simpson, 1934d.

[2] Contrary to more common usage, he placed all these families in the Condylarthra.

[3] Through some oversight the most typical and best known genus, *Didolodus*, is omitted in Ameghino's final faunal list, 1906, page 467.

replaced Scott's name "Didolodidae" [Didolodontidae] by the invalid name "Bunolitopternidae,"[1] but otherwise he followed Scott, placing the group in the Litopterna and comparing them with condylarths. On this last score he is more definite than Scott, explicitly stating that the Litopterna as a whole were derived from North American Condylarthra. Osborn (1910) placed this group in the Condylarthra as of uncertain family, and Gregory (1910) also considered them doubtful condylarths, suggesting that they form a link between condylarths and notoungulates. Abel (1928) has exactly followed Schlosser's views. The majority of these opinions, and others not cited, derive from Ameghino's published descriptions and figures and from previous workers, since, as with almost this whole fauna, no one but Ameghino has hitherto added any significant new data for the solution of this problem. The more or less orthodox attitude at present seems to be essentially that first and most clearly expressed by Scott: that the Didolodontidae are primitive litopterns with certain resemblances to condylarths, resemblances suggestive of possible relationship but to be viewed with some suspicion.

All the material of Ameghino and more having been reviewed, the present conclusion is that Didolodontidae cannot be separated from the Condylarthra on the available evidence, that more nearly than any other known group they represent the common structural ancestry of all native South American ungulates, and that they are closest to the Litopterna among these but cannot be placed in that order and resemble it particularly because it includes forms rather less progressive dentally than most members of other orders. The known genera are not directly ancestral to any other family or order, for even the Litopterna were already present in Río Chico time and distinct from the Didolodontidae, although, as would be expected, less so than in any later formation.

Didolodus and its allies are thus among the most interesting and important of South American Eocene ungulates, on one hand because they most nearly compare with the primitive ungulates of the rest of the world and on the other because they most nearly represent the structural ancestory of all other South American forms. Unfortunately they are relatively rare, and the available material is scanty and very incomplete.

Didolodus, the best known genus, differs no more from various North American condylarths than they do among themselves. The resemblance in the dentition is remarkably close, so close that were the genus found in North America it would probably be referred to the Phenacodontidae with little question. The outstanding difference from North American genera is in P^{3-4}_{3-4}, these teeth, of upper and lower jaws, respectively, being of almost the same size and structure in *Didolodus*, instead of having P^4_4 definitely more complex than P^3_3, and at least P^4 is somewhat less molariform than in the true phenacodonts. The true molars, upper and lower, can with difficulty be distinguished from those of *Phenacodus* or *Ectocion*, except that in the latter M^3_3 tend to be reduced whereas in *Didolodus* they tend to be enlarged, or at least lengthened. The maxilla and what is known of the lower jaw of *Didolodus* do not differ from those of the Condylarthra in any significant way.

No astragali have been found in certain association with didolodont teeth, but there are astragali in the collection that I refer to this family with little doubt. Their abundance relative to other astragali is about that of didolodont teeth relative to other teeth. Their size range is within that of the known Didolodontidae. In form they are markedly unlike any contemporaneous or later astragali referable to other families or orders and definitely resemble the Condylarthra more closely than they do other contemporaneous mammals. They most closely resemble the astragali of Litopterna among other orders, but lack litoptern specializations. There are other astragali in the Casamayor beds that are almost exactly like those of later litopterns and doubtless do belong to the true Litopterna of that epoch.[2]

These are not the astragali referred by Ameghino to members of this group. These seem to me to belong in various divisions, and

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[1] There is no genus "*Bunolitopterna*."

[2] A general discussion of the astragali of primitive South American ungulates will be given in a later section.

several of them have unmistakable notoungulate characters and hence could hardly belong to didolodonts. In the astragali that I consider probably didolodont, the trochlea is broad but well excavated, the fibular crest more elevated and the bottom of the trochlea more on the tibial side, both crests fairly sharp. The internal tibial facet is small. The neck is oblique, rather short, somewhat constricted, the head somewhat flattened dorsoventrally and with convex navicular facet. The body has no internal projection, but a *Phenacodus*-like external projection. There is no foramen, and no extension of the trochlear groove (very characteristic of most notoungulates). The sustentacular facet is short, the ectal facet fully separate, relatively wide, oblique, and deeply concave. No other astragali like these are known from South America, and their differences from phenacodonts and other condylarths are not more than would be expected in related genera or, at most, families. The only really definite distinction is the rather shorter neck. Although the evidence is somewhat indirect and open to question, these astragali seem to me to add to the probability that the didolodonts are correctly placed in the Condylarthra.

If the Didolodontidae are Condylarthra, it is important to attempt to determine their relationships within the group and degree of evolution as closely as possible for purposes of phylogeny and correlation, but the results are mostly inconclusive.

The North American Mioclaeninae, especially characterized by small or absent hypocone and triangular upper molars, are rather similar to the Casamayoran *Asmithwoodwardia*, but the latter is too poorly known for one to rely on a resemblance in isolated teeth which is far from amounting to identity. Most of the Patagonian forms compare much more readily with the Phenacodontidae than with any other known North American family. In *Asmithwoodwardia* and *Ernestokokenia* the mesostyle is absent, as in *Tetraclaenodon*. *Asmithwoodwardia* is a minute form, hardly comparable in detail with *Tetraclaenodon*, with rather simple upper molars with wider anterointernal cingulum and smaller hypocone. *Ernestokokenia* (with *Notoprotogonia*) is closely similar to *Tetraclaenodon* so far as can be judged from isolated upper and lower molars, but with somewhat simpler, less rugose crowns and the paraconid less distinct.

The best known genera, *Didolodus*, *Paulogervaisia*, and *Proectocion*, have distinct mesostyles and in that and some other features are closer to *Phenacodus* and *Ectocion* among Holarctic forms. The differences already noted between *Didolodus* and *Phenacodus* show the former to be as highly specialized as *Phenacodus* and on a different line of descent. *Paulogervaisia* is rather similar to *Didolodus* in general but is a larger, heavier form and probably more specialized. *Proectocion*, known from P^4–M^3, is of special interest as it is definitely more *Ectocion*-like than is *Didolodus*. Its P^4 is tricuspid and submolariform, and M^3 is reduced, more trigonal, with smaller hypocone, points of difference from *Didolodus* and of resemblance to the lower Eocene phenacodonts. Its structure in general differs from *Ectocion* only in minor details so far as known, and Ameghino was certainly justified in considering the two genera to be closely similar and hence probably closely allied.

The family considered as a whole is an assemblage too advanced to be compared with Paleocene Holarctic condylarths. If it did have a common ancestry with the latter and if the evolution of the known structures proceeded at approximately equal rates in North and in South America, the most reasonable assumption although not yet open to proof, then the family Didolodontidae in the Casamayor is in approximately a Lower Eocene stage of evolution, certainly not significantly earlier, possibly as late as Middle Eocene but probably not so late and surely no later.

In a comparison of the Didolodontidae with other South American ungulates, the closest resemblance is with certain rather atypical or primitive litopterns. Indeed, on the basis of the imperfect specimens usually available, it is very difficult to draw a clear-cut line between didolodontids, which are probably condylarthrans, and certain other forms which are very primitive litopterns. The groups perhaps do intergrade to some extent, as is natural if one is really derived from the other, but the few better specimens suggest that they could be more clearly separated if really well known. Such litopterns as the Mustersan *Megacrodon*, described and discussed below, are of particular interest in this connection.

The generic contents of the group here united tentatively are drawn from several families widely separated by Ameghino. In his definitive classification of 1906 (pp. 466–469), he placed them as follows:

- Condylarthra
  - Phenacodontidae
    - Whole family as listed by Ameghino, plus *Didolodus* inadvertantly omitted by him, and minus the genotype of *Lambdaconus*, see below
  - Catathleidae
    - *Argyrolambda*
- Perissodactyla
  - Hyracotheriidae
    - *Archaeohyracotherium*
    - *Proectocion*
- Proboscidea
  - Carolozitteliidae
    - *Paulogervaisia*

The group that was thus spread through three dissimilar orders by Ameghino is not a very homogeneous one, but it does appear to consist of genera related at least ordinally and probably much more closely, and the heterogeneity does not follow the lines drawn by Ameghino. Formal subdivision does not seem profitable now, the majority of the genera being based on material too imperfect to give a stable basis for such action. They are therefore retained in one family. An artifical key to the upper molars of the valid genera follows:

DIDOLODUS AMEGHINO, 1897

Didolodus AMEGHINO, 1897a, p. 437; 1902b, p. 24; SCOTT, 1913, p. 489; 1937, p. 490, fig. 309; SCHLOSSER, 1923, p. 525.

Didalodus, ROTH, 1927, pp. 200, 249. [Error.]

Lonchoconus AMEGHINO, 1901, p. 379; 1904b, p. 79; 1906, p. 467; ROTH, 1927, p. 249; SCHLOSSER, 1923, p. 525.

Nephacodus AMEGHINO, 1902a, p. 19; 1902b, p. 24; 1906, p. 467.

Cephanodus AMEGHINO, 1902b, p. 25; 1906, p. 467.

TYPE: *Didolodus multicuspis* Ameghino.

TYPES OF SYNONYMS: *Lonchoconus lanceolatus* Ameghino. *Nephacodus latigonus* Ameghino. *Cephanodus colligatus* Ameghino.

DISTRIBUTION: Casamayor of Patagonia.

DIAGNOSIS: Upper molars with strong mesostyle and wide, continuous, external cingulum. Hypocone about equal to protocone. Anterior, posterior, and, sometimes, weaker internal accessory cuspules. Posterior cingulum relatively weak and feebly cusped on M^{1-2}. P^{3-4} nearly equal, strongly transverse, and with paracone and metacone completely confluent or barely separated at tips.

Ameghino did not compare *Lonchoconus* directly with *Didolodus*. The characters given by him which seem to contrast with *Didolodus* are chiefly: paracone and metacone high, lanceolate; protocone and hypocone conical; cusps all sharp and well separated; median tubercle on posterior border; cingulum completely surrounding the tooth. Reëxami-

KEY TO THE UPPER MOLARS OF THE VALID GENERA OF DIDOLODONTIDAE

- Distinct mesostyle present.
  - External cingulum strong. Posterior cingulum relatively weaker.
    - Protostyle weak . . . . *Didolodus*
    - Protostyle strong . . . . *Argyrolambda*
  - External cingulum weak or absent. Strong posterior cingulum.
    - Species much larger.
      - Mesostyle weaker . . . . *Paulogervaisia*
    - Species much smaller.
      - Mesostyle stronger . . . . *Proectocion*
- Mesostyle weak or absent.
  - Rudimentary mesostyle. Other distinct marginal accessory cuspules on anterior, posterior, and internal borders . . . . *Enneoconus*
  - No mesostyle. Marginal accessory cuspules very poorly developed or absent.
    - External cingulum incomplete. Hypocone smaller . . . . *Asmithwoodwardia*
    - External cingulum continuous. Hypocone larger.
      - Molars considerably wider than long . . . . *Ernestokokenia*
      - Molars with length and width more nearly equal . . . . *Archaeohyracotherium*

nation shows, however, that the protocone and hypocone are not conical but subcrescentic, that the median tubercle is anterior, not posterior,[1] and that the cingulum is interrupted on the internal face; in all these characters it is exactly as in *Didolodus*. The lanceolate outer cusps and the generally tall, sharp, well-separated cusps are merely unworn. The sole specimen is simply a *Didolodus multicuspis* molar which is unworn but not otherwise unusual in any way.

Nephacodus was separated from *Didolodus* by Ameghino on the sole character of having the hypoconulid relatively more posterior. The other characters given were not explicitly said to be distinctive and are not so in fact. Even the hypoconulid differs little from *Didolodus*, and the genus cannot be maintained as separate.

Cephanodus was founded on a species formerly placed in *Didolodus*, and the only stated reason for generic separation was the supposedly higher trigonid, with the cusps still independent but forming a transverse crest. This apparent difference is simply an effect of advanced wear, and the genera are certainly synonymous.

With these additions, *Didolodus* is a well-characterized genus. The only form that can be confused with it is *Paulogervaisia*, but it seems almost certain that they are distinct and that better material of the latter will increase the apparent difference between them. *Didolodus* is far the best known genus of this group. It is described below, under its type species, to which the better specimens so far discovered all belong.

Didolodus multicuspis Ameghino, 1897

Plate 10, figures 1–8; text figures 24–28

Didolodus multicuspis Ameghino, 1897a, p. 437; fig. 22; 1902b, p. 24, figs. 9–10; 1904b, p. 80, figs. 80, 150, 181, 272, 397, 398, 545, 546, 572; 1904d, p. 67, fig. 56; 1906, p. 295, fig. 83; Roth, 1927, p. 247.

Didolodus crassicuspis Ameghino, 1901, p. 376; 1902b, p. 25, fig. 11; 1904a, vol. 57, p. 333; 1904b, p. 121, figs. 137, 182, 450, 547; 1904d, p. 67, fig. 57; 1906, p. 297, fig. 93; Schlosser, 1923, p. 525, fig. 648 [unites *D. crassicuspis* and *D. multicuspis* under this name without reference to the latter species, which has clear priority].

Didolodus dispar Ameghino, 1904a, vol. 57, p. 333.

Lonchoconus lanceolatus Ameghino, 1901, p. 379; 1904b, p. 79, figs. 79, 170, 260, 307, 544, 571; 1906, p. 295, fig. 85.

Didolodus colligatus Ameghino, 1902a, p. 18.

Cephanodus colligatus, Ameghino, 1902b, p. 25, fig. 12; 1906, p. 329, fig. 153.

Type: M.A.C.N. No. 10690. Most of left maxilla with P^2–M^3 and alveoli of P^1 and the canine.

Types of Synonyms: *Didolodus crassicuspis:* M.A.C.N. No. 10689. Right P$_2$–M$_3$.

Didolodus dispar: M.A.C.N. No. 10733. Isolated, broken right M^2.

Lonchoconus lanceolatus: M.A.C.N. No. 10730. Isolated left M^1.

Didolodus colligatus: M.A.C.N. No. 10736. Right and left M$_3$, and left P$_{3-4}$.

Hypodigm: The types and the following:

M.A.C.N. No. 10720. Right lower jaw with M$_3$ and possibly associated isolated M^1 and C
M.A.C.N. No. 10738. Right P^1 and left P^2
M.A.C.N. No. 10729. Left M^2
A.M.N.H. No. 28475. Right lower jaw with P$_4$ and M$_{2-3}$
A.M.N.H. No. 28738. Left M^3
A.M.N.H. No. 28774. Left P$_4$

Doubtfully referred:

M.A.C.N. No. 10728. Right M$_3$. (From west of the Río Chico)
A.M.N.H. No. 28899. Right M$^{1-2}$. (From Bahía Solano)
C.N.H.M. No. P13499. Left M$_{2-3}$. (From Punta Casamayor)

Horizon and Localities: Casamayor, Patagonia. No other data are available for the types of *D. multicuspis*, *D. crassicuspis*, or *D. dispar*. The other surely identified specimens of known origin are all from south of Lake Colhué-Huapí. The specimens listed as doubtfully referred are from other localities and are sufficiently unlike the Colhué-Huapí specimens to suggest distinct temporal or geographic races, but the material does not suffice for definition.

Diagnosis: Length M$^{1-3}$ about 26.5 mm.; M$_{1-3}$ about 28.5 mm. Molars broad relative to length. Hypoconulid on M$_{1-2}$ almost in line with entoconid and hypoconid.

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[1] Ameghino called the sole specimen a right molar, whereas it is really from the left side. In 1904b he calls it a right tooth in the legends to figures 79 and 544, but correctly labels it as left in figures 170, 260, 307, and 571, and in all figures the cusps are correctly labeled as for a left molar.

Didolodus multicuspis and *D. crassicuspis* are clearly based on upper and lower dentition, respectively, of the same species. Ameghino said that *D. crassicuspis* is somewhat larger and also has the molars relatively narrower than the genotype, but these differences, too slight to be significant in any event, were based not on direct comparison of types but on very dubiously referred fragments. The type specimens are perfectly adapted for occlusion with each other, beyond the fact that they are different individuals and opposite sides.

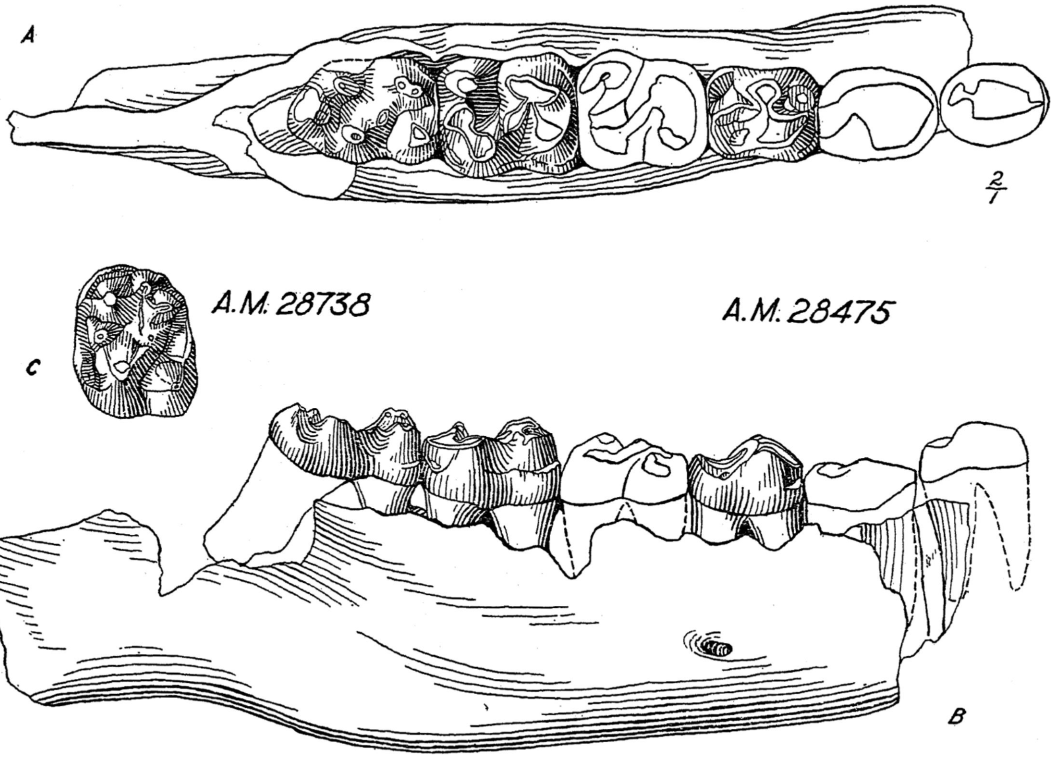

FIG. 24. *Didolodus multicuspis* Ameghino. A. A.M.N.H. No. 28475, right lower jaw with P_4, M_1, and M_3 (P_{2-3} and M_2 restored in outline from M.A.C.N. No. 10689), crown view. B. Same, external view. C. A.M.N.H. No. 28738, left M^3, crown view. ×2.

Didolodus dispar, based on one broken tooth, was described in some detail, but on direct comparison I am at a loss to find any difference from *D. multicuspis* except that this type is rather less worn. Aside from also being less worn, the single tooth of "*Lonchoconus lanceolatus*" differs from *D. multicuspis* in the slightly weaker cingulum across the paracone, somewhat less protuberant hypocone base, and in being about 10 per cent narrower transversely. These do not appear to be of probable specific value, and the species must be considered synonymous. It is possible, however, that this is an upper tooth of the doubtfully distinct form *D. latigonus*.

Didolodus colligatus was supposed to be differentiated by strong external cingulum on lower molars, crested rather than tuberculate lower premolar heels, union of hypoconulid and entoconid of M_3 by a crest, and similar union of the trigonid cusps of the lower molars. Except for the cingula, which hardly seem to differ enough to be of specific value, all these differences appear to me to be due largely or wholly to wear and not to original structure. They have probably been accentuated by malocclusion, for in the type it seems probable that P_3 and P_4 are not normal in position but that P_3 never rose fully to the level of the following tooth.

The dentition of this species is fairly well known and will be described in detail as characteristic of this whole very important group.

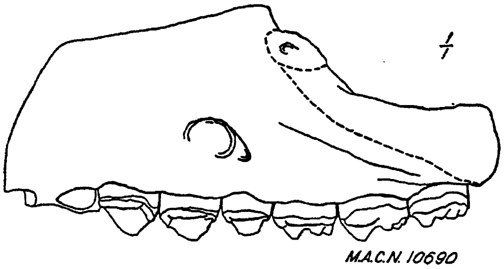

FIG. 25. *Didolodus multicuspis* Ameghino. Type, MA.C.N. No. 10690, left maxilla with P^2–M^3. External view. ×1. (Drawn from a cast and photograph in the A.M.N.H.)

The formula is $I^?_3$ C^1_1 P^4_4 M^3_3. All the known teeth are very brachyodont and all, when unworn, are covered with enamel, the surface of which is finely wrinkled. The canines, upper and lower, are separated by small spaces from the neighboring teeth, but no definite diastemata are developed and the other teeth are all in contact. No part of the dentition shows any clear tendency towards reduction or loss.

The upper canine is known from its alveolus only, which is only slightly larger than that of P^1 and is somewhat procumbent. P^1 (known only in M.A.C.N. No. 10738) has the roots nearly confluent but divided at the tip into an anteroexternal and a posterior and internal part. The crown has a high anteroexternal main cusp, slightly compressed transversely, a small posteroexternal accessory cusp, and a low posterointernal heel. A cingulum surrounds the crown, forming a sharply elevated rim around the basined heel. The contour is triangular and longer than wide. P^2 is similar to P^1 but larger, higher, and with width nearly equal to length.

P^3 and P^4 closely resemble each other and differ markedly from the teeth on either side of them. They are transversely elongate, the outer part nearly quadrate in outline and the inner more rounded. On the outer side is a high cusp, laterally compressed and crested anteroposteriorly, which when quite unworn is seen to have two nearly connate apices, a large anterior and a smaller posterior. The protocone, sole internal cusp, is a little lower and is subcrescentic. There is a small but distinct protoconule, but the metaconule appears to be absent on P^3 and represented on P^4 only by a minute rudiment almost immediately removed by wear. Each tooth is surrounded by a cingulum, which may, however, be weak or absent on the inner face, and which rises to form small parastyles and metastyles immediately anterior and posterior to the outer double cusp.

M^1 is quadrate and wider than long, but the length is considerably greater relative to the width than on P^{3-4}. It consists essentially of a normal trigon, with conules, a large hypocone, and several stylar and accessory cuspules. Paracone, metacone, and protocone are of nearly equal size and height when unworn, the hypocone of nearly equal size but slightly lower. The conules are very sharp and distinct, about half the size of the primary cusps, the protoconule slightly the larger of the two. Paracone and metacone are somewhat compressed transversely and crested anteroposteriorly, the "lanceolate" structure noted by Ameghino for *Lonchoconus*, which is merely *Didolodus* without wear. The conules are slightly, and the protocone and hypocone distinctly, crescentic. The protoconules and metaconules are slightly anterior and posterior to lines from the tip of the protocone to the tips of the paracones and metacones, respectively. The apex of the hypocone is more internal than that of the protocone. There are four other cuspules of varying prominence, besides small and inconspicuous but nearly constant parastyles and

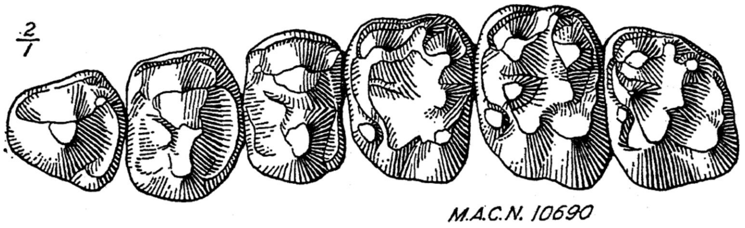

FIG. 26. *Didolodus multicuspis* Ameghino. Type, M.A.C.N. No. 10690, left P^2–M^3. Crown view. ×2. (Drawn from a cast and photograph in the A.M.N.H.)

metastyles. Most important is the mesostyle, a sharp spur extending outward and backward from the junction of the paracone and metacone crests and rising to a distinct apex when unworn. On each side of it is a strong, nodulated cingulum, passing through the parastyles and metastyles onto anterior and posterior sides of the tooth. The anterior cingulum bears a small but distinct cuspule anterior to the notch between protocone and protoconule. The posterior cingulum rises into the hypocone and may also bear a small accessory cuspule, which is, however, inconspicuous or perhaps sometimes quite absent on M^{1-2}. There is also usually but not invariably a tiny cuspule between the protocone and hypocone.

FIG. 27. *Didolodus* cf. *multicuspis* Ameghino. C.N.H.M. No. P 13499, left M_{2-3}. Crown view. ×2. (Drawing made under the direction of Riggs and Patterson, supplied by the Chicago Natural History Museum.)

M^2 is somewhat larger but otherwise differs very little from M^1. M^3 is narrower than M^2 although of approximately equal length, the external border is more oblique, the metacone is reduced, the hypocone projects farther posteriorly, and the posterior cingulum cuspule is larger and more distinct.

The anterior lower dentition is known from alveoli only in M.A.C.N. No. 10720, referred to this species. The symphysis is narrow, but the incisors are placed nearly transversely. They are markedly procumbent. The alveoli of I_1 and I_2 are about equal, that of I_3 slightly larger. The canine alveolus is only slightly procumbent and is about twice the size of the alveolus for I_3. The alveolus of P_1 is not procumbent and is for one root only, about as large as that of the canine at the mouth, but tapering more rapidly.

P_2–M_3 are known in M.A.C.N. No. 10689 and also from various less complete specimens, of which A.M.N.H. No. 28475, with P_4 and M_{2-3}, is the most important. P_2, deeply worn in the known material, seems to have had a single plump main cusp, followed by a small heel, much broader than long, with a single cuspule, from which a crest ran to the main cusp and also crests laterally on each side around the posterior edge of the heel. P_3 apparently was similar, but the trigonid cusps are wholly obliterated and the degree of molarization is unknown. P_4 has a well-developed trigonid with three cusps, the metaconid almost directly internal to, and smaller than, the protoconid, the paraconid still smaller and not fully internal. The talonid is larger than on the preceding premolars. From between the protoconid and metaconid, a crest extends posteriorly and slightly externally, forming a small cusp near the middle of the heel. From the posterior end of the crest, nodulated lesser crests extend internally and externally, falling as they go, around the edges of the heel which is thus developed into two small shallow basins, one external and one internal.

M_1 and M_2 have nearly the same structure. The talonid and trigonid are of nearly equal size, the former slightly wider, and the trigonid is somewhat more elevated. The large internal trigonid cusp appears to be bifid at the extreme tip when unworn, and probably represents fused paraconid and metaconid. The small, shallow, trigonid basin is closed by anterior and posterior crests from the protoconid to the internal cusp, the anterior crest with a tiny cuspule near the midline when unworn. The talonid has a large crescentic hypoconid, opposite, smaller, and more conical entoconid, and still smaller, subconical hypoconulid at the midline and very slightly posterior to the other two cusps. A crest runs from the metaconid to the hypoconid, and it bears an accessory cusp near the midline, distinct but early obscured by wear.

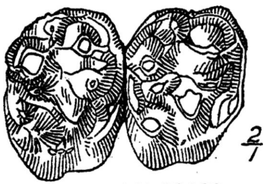

FIG. 28. *Didolodus* cf. *multicuspis* Ameghino. A.M.N.H. No. 28899, right M^{1-2}. ×2.

In closely related forms there is also a minute cuspule on the anterior slope of the entoconid, and while not seen in specimens surely referred to this species it may well have been present on quite unworn teeth. There are always a narrow anterior cingulum and also cingulum crests falling away laterally from the hypoconulid, while an external cingulum may be variously developed.

M_3 has the talonid narrower than the trigonid and elongate, with the hypoconulid relatively larger and most posterior, although not forming a distinct third lobe.

All that is known of the skull is the maxilla of the type. The maxillo-premaxillary suture can have slanted backward only slightly and the premaxillary (judging from relations to the lower jaw) was apparently short. The infraorbital foramen is above P^4 and the posterior end of P^3, less than halfway to the maxillo-nasal suture, and it is double, with a larger anterior and smaller posterior opening. The zygomatic root is little expanded and slopes rapidly backward, continuing the curve of the maxilla save for a shallow muscular excavation below and anterior to the root. The latter is chiefly above M^{2-3} and is based on the maxilla, but the maxilla forms little or none of the actual zygoma. The jugal overlies its external surface and reaches the lacrimal. The lacrimal has a small facial expansion, and the foramen is near but on the facial side of the orbital rim.

This part of the skull is not very distinctive. About the most that can be said is that it is primitive. It distinctly resembles that of Holarctic condylarths on one hand and of litopterns on the other, except that in both these groups the lacrimal foramen is usually marginal or intraorbital. The double infraorbital foramen recalls the triple foramen in some litopterns and multiple foramen of *Trigonostylops*.

The lower jaw is very poorly known. In M.A.C.N. No. 10720 it appears to have a moderately long and slender horizontal ramus, proportioned much as in *Phenacodus* and other primitive ungulates. The symphysis is narrow and ends opposite P_2. In this specimen there is a double mental foramen beneath P_1 and the posterior end of the canine, and another, small and single, between P_4 and M_1. The coronoid arises immediately posterior to M_3. In A.M.N.H. No. 28475 the jaw is shallow and rather plump, the posterior mental foramen beneath the posterior end of P_4.

Dental measurements of this species are given in table 16.

Didolodus latigonus (Ameghino, 1902), new combination

Nephacodus latigonus AMEGHINO, 1902a, p. 19; 1902b, p. 24, fig. 8; 1906, p. 295, fig. 84.

TYPE: M.A.C.N. No. 10725. Isolated M_2.[1]

HYPODIGM: Type only (but M.A.C.N. No. 10739 may belong here, see below).

HORIZON AND LOCALITY: Casamayor beds. West of the Río Chico, Chubut, Argentina.

DIAGNOSIS: Talonids relatively slightly longer than in *D. multicuspis* and hypoconulid slightly more posterior. Lower molars narrower relative to length, length about as in *D. multicuspis*.

It seems entirely impractical to maintain this as a separate genus, and even as a species it rests on no very secure basis, but may be retained tentatively. There is a specimen in the Museo Argentino, No. 10739, with P_4 and M_1, which possibly belongs to this species. It was referred by Ameghino to *D. multicuspis*, although its differences from that form are greater than between many of his genera. M_1 is relatively much narrower, has the trigonid wider than the talonid, and the protoconid-metaconid and hypoconid-entoconid lines rather more oblique. If it should prove referable to *D. latigonus*, it would support the validity of that species.

Didolodus minor, new species

Text figure 29

TYPE: A.M.N.H. No. 28473. Isolated left M^1.

HYPODIGM: Type and the following:

A.M.N.H. No. 28471. Right P^3
A.M.N.H. No. 28472. Right M_2
A.M.N.H. No. 28470. Right M_3
A.M.N.H. No. 28736. Inner portion of upper molar

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[1] In his description, Ameghino refers to M_1 and M_2. Only one tooth was labeled as of this species in his collection, however, and it is probably a second molar.

FIG. 29. *Didolodus minor*, new species. Type, A.M.N.H. No. 28473, isolated left M^1. Crown view. ×2.

Horizon and Locality: Casamayor beds, Cañadón Vaca, Chubut, Argentina.

Diagnosis: Between 10 and 15 per cent smaller than *D. multicuspis* in every dimension, and molars relatively narrower than in typical specimens of that species.

We have five specimens of *Didolodus*, representing as many individuals, from a single locality and horizon in Cañadón Vaca. Since all these are quite different in size and proportions from any teeth found elsewhere, and all differ in the same way and to about the same degree from typical specimens of *D. multicuspis* from south of Lago Colhué-Huapí,[1] it seems hardly open to question that they represent a distinct form, perhaps a geographic race or a temporal mutation but most conveniently described in the guise of a species. This is one of the cases where the data do show a difference between geographically separated faunules of the Casamayor beds, and it is valuable to signalize the fact.

Didolodus sp. innom.

It may be noted that an isolated M_3 (A.M.N.H. No. 28478) from Bahía Solano seems to represent an unnamed species of *Didolodus* or a closely related genus. Another specimen (A.M.N.H. No. 28899), also from Bahía Solano but not found with that just mentioned, includes M^{1-2} which differ slightly from typical specimens of *D. multicuspis* in dimensions (see table 16) but are almost identical in morphology (text fig. 28). It is possible that a distinctive species will prove to characterize this locality and its most fossiliferous horizon, but the material is inadequate for any useful conclusion.

ARGYROLAMBDA Ameghino, 1904

Argyrolambda Ameghino, 1904a, vol. 57, p. 338; 1904b, p. 122; 1906, p. 467; Schlosser, 1923, p. 525.

Type: *Argyrolambda conidens* Ameghino.

Distribution: Casamayor beds, Patagonia.

Diagnosis: Upper molar like that in *Didolodus*, but protostyle larger.

This genus is known only from one upper molar, now lost or mislaid, with the hypocone region broken away. Its position is therefore dubious in the extreme. Ameghino placed it with other genera now held to be litopterns. The illustrations given by him suggest that it does resemble the Casamayor litopterns in the large protostyle, but as it seems otherwise to be closer to *Didolodus* and as *Didolodus* does have a protostyle, although only about half this size, it seems preferable to grant *Argyrolambda* a very tentative position in the Didolodontidae.

Argyrolambda conidens Ameghino, 1904

Plate 10, figure 9

Argyrolambda conidens Ameghino, 1904a, vol. 57, p. 338; 1904b, p. 395, fig. 516; 1906, p. 298, fig. 94.

Argyrolambda conulifera Ameghino, 1904b, p. 123, fig. 140. [Error.]

Type: A broken upper molar. Not found.

Hypodigm: Published data on type, only.

Horizon and Locality: Casamayor beds of Patagonia. No other data.

Diagnosis: Sole species of the genus. Molar (according to Ameghino), length 8.5 mm., width 9.5 mm.

PAULOGERVAISIA Ameghino, 1901

Paulogervaisia Ameghino, 1901, p. 389; 1902b, p. 25; 1906, pp. 467, 470; Schlosser, 1923, p. 601; Scott, 1913, pp. 462, 488; 1937, p. 544.

Lambdaconus, in part [not including the genotype], Ameghino, 1897a, p. 439; 1906, pp. 467, 470, 471.

Type: *Paulogervaisia inusta* Ameghino.

Type of *Lambdaconus*: *Lambdaconus suinus* Ameghino (does not belong to *Paulogervaisia*).

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[1] Which is almost certainly the type locality of that species in spite of the poorness of the data. All the surely referable specimens are from there, and it seems probable that all the material of this age described by Ameghino in 1897 was from that locality.

TABLE 16

MEASUREMENTS OF *Didolodus*

Upper Teeth

	P^1		P^2		P^3		P^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
D. multicuspis														
M.A.C.N. No. 10690			7.6	7.4	7.5	9.5	7.0	10.0	8.1	11.1	8.4	12.0	8.3	10.7
M.A.C.N. No. 10738	6.8	6.0	7.6	7.2										
M.A.C.N. No. 10729											8.6	11.5		
M.A.C.N. No. 10730									8.1	9.9				
A.M.N.H. No. 28738													8.5	10.3
A.M.N.H. No. 28899[a]									7.8	10.4	7.9	11.3		
D. minor														
A.M.N.H. No. 28473									7.2	9.4				
A.M.N.H. No. 28471					5.7	7.8								

Lower Teeth

	P_2		P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W	L	W
D. multicuspis												
M.A.C.N. No. 10689	7.4	5.4	7.6	6.3	7.6	6.6	9.0	8.3	9.2	8.7	10.8	7.4
M.A.C.N. No. 10736			7.6	6.3	7.4	6.6	—	—	—	—	10.7	7.2
M.A.C.N. No. 10728[a]											10.0	7.6
A.M.N.H. No. 28475					7.5	6.4	—	—	9.2	8.1	10.7	7.3
C.N.H.M. No. P13499[a]									9.9	8.6	10.9	7.3
D. latigonus												
M.A.C.N. No. 10725									8.9	7.2		
D. ?latigonus												
M.A.C.N. No. 10739							8.7	6.5				
D. minor												
A.M.N.H. No. 28472									7.7	6.6		
A.M.N.H. No. 28470											9.0	6.7

[a] Slightly aberrant individuals, possibly of different subspecies or races; see data under "Hypodigm" and "Horizon and locality."

DISTRIBUTION: Casamayor beds, Patagonia.[1]

DIAGNOSIS: Mesostyle present, but weaker than in *Didolodus*. External cingulum of upper molars weak or absent. Posterior cingulum strong and cuspidate. Hypocone large.

This genus has been the subject of great confusion. *Paulogervaisia* was hailed by Ameghino as a link between the condylarths and Proboscidea. He made it directly ancestral to *Moeritherium* and also, through the pyrotheres, to all other true Proboscidea, and he considered it a direct descendant of *Didolodus*. He classified it in the family Carolozitteliidae. As in almost all his phylogenetic work, this conclusion involves recognition of the true affinities of the genus, but it

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[1] Ameghino (1906) lists *Lambdaconus* also in the Musters and Deseado faunas, *Paulogervaisia* also in the Musters fauna, but none of the specimens on which this was based belongs to the genus *Paulogervaisia* as here revised.

adds conjectural relationships which now appear to be nonexistent. He gave for the genus three lines of relationship: to the condylarths (or didolodonts), to the pyrotheres, and to proboscideans. As has happened in so many cases, to the greater confusion of science and with injustice to Ameghino, later commentators have ignored what was correct in his work and have rejected one false alternative only to adopt another equally improbable. Without any exception known to me, they have considered *Paulogervaisia* a pyrothere and overlooked Ameghino's more cogent evidence that it is really a close relative of *Didolodus*.

In describing the genotype, Ameghino referred to two teeth, M_1 and M_3, but he subsequently (1902b, 1906) figured only M_3 and did not again refer to M_1. In his collection only M_3 was found. It is to be presumed either that the M_1 was lost between 1901 and 1902 or that Ameghino concluded that it was incorrectly associated and did not belong in this genus. The M_3 is deeply worn, but it differs in no essential feature from that of other genera of didolodonts, and is very unlike that of any pyrothere. On the basis of this tooth alone, the only visible distinctions from *Didolodus* are: much greater size, more squarely truncated anterior end, more rugose enamel.

These are at best suggestive of not more than generic difference. It also seems beyond doubt that all materials referred to *Lambdaconus* from these beds except the genotype are congeneric with *Paulogervaisia inusta*, and these species of *Lambdaconus* have been accepted by everyone as didolodonts.

Lambdaconus suinus, genotype by monotypy, was based on a fragment of a lower jaw with one tooth (M.A.C.N. No. 10718). The tooth is labeled as if P_4 in the figure (Ameghino, 1897a, fig. 23), called M_1 in the text, and is probably M_2. It is very badly preserved, most of the enamel being broken off. Superficially it resembles the better teeth later referred to the genus, and the error is quite understandable, but detailed study shows that it does not belong to this group at all, chiefly for the following reasons:

The crown is relatively much higher than in any didolodont.

The hypoconulid is absent or very small, whereas it is large and prominent in all didolodonts.

The anterior trigonid crest falls away to the base of the tooth internally, as in notoungulates and astrapotheres, instead of rising again to the internal cusp as in didolodonts and most litopterns.

The entoconid is shorter, anteroposteriorly, and more limited to the posterior border than in any didolodont.

The real affinities of this fragment are uncertain, but it is certain that it is not a member of this family and that the other species later referred to *Lambdaconus* are not congeneric with the genotype.

These species are *Lambdaconus mamma* and *Lambdaconus porcus*,[1] the latter based on an upper jaw with M^3 and fragments of M^2, the former on a lower jaw with P_3–M_2 and probably not associated fragments of upper teeth. As these do not include M_3, direct comparison with *Paulogervaisia inusta* is not possible, but that they are congeneric, if not, in part at least, conspecific with the latter, is almost certain. Except for size, a difference specific at best, M_3 of *Paulogervaisia inusta* is exactly suited for occlusion with M^3 of "*Lambdaconus*" *porcus* and still better with an M^3 placed in "*L.*" *mamma*, and is structurally entirely concordant with M_2 of "*L.*" *mamma*.

Thus emended, the genus *Paulogervaisia* appears to be a close relative of *Didolodus*, including two or three species larger than those referred to the latter genus and the largest at present referred to the family. The upper molars (*P. mamma* and *P. porca*), aside from their greater size, differ from *Didolodus* in the smaller, but still well-developed mesostyle, weak or obsolete external cingulum, absence of cuspule between protocone and hypocone (sometimes absent in *Didolodus*), position of metaconule in a straight line from protocone to metacone, and stronger posterior cingulum cuspule on M^2.

The lower teeth are badly worn on all the available specimens and, while the general pattern was *Didolodus*-like, the details of

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[1] Ignoring, for the present, species or specimens supposedly of *Lambdaconus* which are not congeneric with either of the two genera already confused under this name.

cusp structure are not visible and probably presented some peculiarities. In *P. mamma* P_{3-4} are relatively more elongate and have relatively larger heels than in *Didolodus multicuspis*. On M_{1-2} the trigonids are wider than the talonids, whereas they are slightly narrower than the talonids in the other known genera of the family.

We did not find any specimens of this genus, and there are only three to five individuals represented in the Ameghino Collection. It is a very rare form.

Paulogervaisia inusta Ameghino, 1901

Plate 10, figure 10

Paulogervaisia inusta Ameghino, 1901, p. 389; 1902b, p. 25, fig. 13; 1906, p. 329, fig. 154.

Type: M.A.C.N. No. 10664. Isolated right M_3, deeply worn.

Hypodigm: Type only.

Horizon and Locality: (*Fide* Ameghino) upper part of Casamayor beds, Colhué-Huapí, Chubut, Argentina.

Diagnosis: The largest species of the genus (or of the family). M_3, length 17.3 mm., width 13.3 mm.

Paulogervaisia mamma (Ameghino, 1901), new combination

Plate 10, figures 11–14

Lambdaconus mamma Ameghino, 1901, p. 376; 1904b, p. 122, figs. 138, 203, 449, 548, 568, 570; 1906, p. 296, figs. 86, 174.

Type: M.A.C.N. No. 10719. Fragmentary right lower jaw with P_3–M_2, deeply worn. Fragmentary left maxilla with broken M^{2-3}. Isolated broken right M^2 (?), and other fragments.[1] Probably not all of one individual. Lectotype: the maxillary fragment with broken M^{2-3}.

Hypodigm: Lectotype. Other syntypes doubtfully referred.

Horizon and Locality: (*Fide* Ameghino) upper part of Casamayor beds, Colhué-Huapí, Chubut, Argentina.

Diagnosis: Distinctly larger than *P. porca* and with somewhat weaker mesostyle. Not directly comparable with *P. inusta* but probably smaller.

This may well be synonymous with *P. inusta*, but the type is apparently a smaller individual, and the species may be retained tentatively.[2]

The length of M^3 is roughly 13 mm., and of the isolated tooth, perhaps M^2, about 13.5 mm. The syntype lower teeth have the dimensions shown in table 17, in their much worn condition.

TABLE 17

Paulogervaisia mamma

P_3		P_4		M_1		M_2	
L	W	L	W	L	W	L	W
10.0	7.1	9.3	7.7	11.2	9.6	11.7	9.7

Paulogervaisia porca (Ameghino, 1901), new combination

Plate 10, figure 15

Lambdaconus porcus Ameghino, 1901, p. 377; 1904b, p. 437, fig. 569; 1906, p. 243, fig. 170.

Type: M.A.C.N. No. 10721. Fragment of right maxilla with broken M^2 and complete M^3.

Hypodigm: Type only.

Horizon and Locality: (*Fide* Ameghino) upper part of Casamayor beds, Colhué-Huapí, Chubut, Argentina.

Diagnosis: The smallest species of the genus. Mesostyle apparently somewhat stronger than in *P. mamma*. M^3 length 10.7 mm., and 12.1 mm.

The species is probably valid, although it is very poorly characterized by the known material. Ameghino states that the paracone is stronger, higher, and more isolated than in *P. mamma*, but this is due to the fact that it is better preserved and that on M^3 it is in any case larger relative to the metacone.

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[1] Ameghino, 1904b, figure 570 is of the fragmentary left M^{2-3}, but all the other illustrations listed above (all reproductions of a single drawing) are of the right tooth which they show as if it were complete. Ameghino called it M^1, but I think it probably M^2. It might even be M^3, in which case it does not belong to this species and probably is an upper molar of *Paulogervaisia inusta*.

[2] If they prove synonymous, it would appear preferable to give precedence to *P. inusta*. *P. inusta* was published on a later page than "*L.*" *mamma*, but simultaneously and it has long stood as typifying the valid generic name.

PROECTOCION AMEGHINO, 1904

Proectocion AMEGHINO, 1904b, p. 83; 1904a, vol. 58, p. 183; 1906, p. 307; SCHLOSSER, 1923, p. 525; SCOTT, 1937, p. 490.

Proectocyon, AMEGHINO, 1906, p. 467. [Changed spelling.]

TYPE: *Proectocion argentinus* Ameghino.[1]

DISTRIBUTION: Casamayor beds of Patagonia.

DIAGNOSIS: Upper molars with strong mesostyle, but weak external cingulum. Posterior cingulum strong. Hypocone large on M^{1-2}, relatively much reduced on M^3. P_4 triangular, not markedly transverse, with large, equal, well-separated paracone and metacone.

This genus was always placed in the Hyracotheriidae by Ameghino, but it certainly is not closely related to the true hyracotheres or even to Ameghino's Patagonian *Prohyracotherium*. As already noted, it is remarkably like *Ectocion* (which Ameghino also considered a hyracothere) in the known teeth. Among Patagonian forms, it most resembles *Didolodus*, and it may be placed in this family. P^4–M^3 of one individual are known, making it the best known genus of this group except for *Didolodus* itself.

If only the molars were known, very close relationship to *Didolodus* would seem indicated. The external cingulum is much less developed and the posterior cingulum relatively slightly stronger on M^{1-2}, but otherwise these teeth seem to be as in *Didolodus*. M^3 is more distinctive, with the anterior cingulum much weaker than in *Didolodus*, the hypocone much smaller relatively and projecting less posteriorly, and hence the contour more triangular and the whole tooth appearing more reduced relative to the others.

P^4 of *P. precisus*, however, is so unlike that of *Didolodus*, that the genera are obviously quite distinct and their relationship is not fully certain. The tooth here described is not dm^4, as its characters might suggest, for it is less worn than M^1 and the individual is old, with M^3 in place and well worn. It has a well-formed trigon, similar to the molar trigon but more symmetrical. The paracone and metacone are equal and well separated. The external border is so straight and flat that it appears broken, but this is not the case. There is a small parastyle, about as on the molars, but no mesostyle. There is no true hypocone, only a posterior cingulum which is little wider than the anterior cingulum. The tooth is more molariform than is P^4 of *Didolodus*, but differs from the molar in its symmetrical, triangular contour, much less developed hypocone, and absence of mesostyle.

Proectocion argentinus Ameghino, 1904

Plate 10, figure 16

Proectocion argentinus AMEGHINO, 1904a, p. 83, figs. 84, 85, 271 [original of fig. 85 later removed from this species to *P. precisus*]; 1904a, vol. 58, p. 184; 1906, p. 307, fig. 116.

TYPE: M.A.C.N. No. 10673. Right M^3.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayor beds, Colhué-Huapí, Chubut, Argentina.

DIAGNOSIS: 10–15 per cent larger than *P. precisus*, M^3 with more distinct anterior and external cingula. M^3 length 4.17 mm., width 6.1 mm.

Ameghino states or implies that the metacone is better developed than in *P. precisus* and the contour of M^3 more quadrate. These supposed distinctions do not seem to me to be appreciable.

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[1] This is one of the few cases where the different publication dates of 1904a and 1904b have more than purely bibliographic interest. 1904b was actually published first, but it contains no formal diagnosis, and the new names in it are quoted from the manuscript of 1904a. In 1904a they are formally proposed and given as new. In most cases this makes no difference, but in the present instance it unfortunately fixes *P. argentinus* as the genotype. Ameghino had two specimens of the genus, both of which he figured as *P. argentinus* in 1904b. He then decided that they belonged to different species, and in 1904a he left the less complete specimen in the species already published and created another species, *P. precisus*, for the much better specimen. The publication of 1904b is clearly valid, even though he calls the genus and both species new (but with reference to 1904b) in 1904a, and the genus was therefore monotypic when published. The actual specimen on which the genus was chiefly erected therefore does not belong to the genotypic species, but there is apparently no legal way in which this peculiar result can be counteracted. There seems to be some doubt even in the minds of members of the Commission, but the International Rules are sufficiently explicit that the type of a genus is a species, not a specimen.

Proectocion precisus Ameghino, 1904

Plate 10, figures 17–18

Proectocion argentinus [*pars*], Ameghino, 1904b, fig. 85 [labeled *P. argentinus*, later type of *P. precisus*].

Proectocion precisus Ameghino, 1904a, vol. 58, p. 185; 1906, p. 307, fig. 115.

Type: M.A.C.N. No. 10679. Fragment of right maxilla with P^4–M^3.

Hypodigm: Type only.

Horizon and Locality: Casamayor beds, Colhué-Huapí, Chubut, Argentina.

Diagnosis: Smaller M^3 with small non-cusped anterior cingulum and no external cingulum. M^3 length 4.2 mm., width 5.1 mm.

TABLE 18

Proectocion precisus

P^4		M^1		M^2		M^3	
L	W	L	W	L	W	L	W
4.2	5.2	4.6	6.4	5.2	6.4	4.2	5.1

ENNEOCONUS Ameghino, 1901

Enneoconus Ameghino, 1901, p. 378; 1904b, p. 78; 1906, p. 467.

Euneoconus, Roth, 1927, p. 249. [Error.]

Type: *Enneoconus parvidens* Ameghino.

Distribution: Casamayor beds, Patagonia.

Diagnosis: M^3 closely similar to *Didolodus*, but the mesostyle much weaker, almost lacking, the anterior cingulum cuspule large, almost equal to the protoconule, and an accessory cuspule present on the anterointernal slope of the hypocone.

Ameghino did not compare this genus directly with *Didolodus*, and the apparently most distinctive feature of his definition, paracone much larger than the metacone, is due to the fact that his specimen is M^3 and not, as he thought, M^1. It is a rather dubious form, but the very small mesostyle warrants acceptance as a separate genus. It is known from a single tooth.

Enneoconus parvidens Ameghino, 1901

Plate 11, figure 1

Enneoconus parvidens Ameghino, 1901, p. 378; 1904b, p. 78, figs. 78, 136, 169, 513; 1906, p. 296, fig. 87.

Type: M.A.C.N. No. 10726. Isolated right M^3.

Hypodigm: Type only.

Horizon and Locality: Casamayor beds, west of Río Chico, Chubut, Argentina.

Diagnosis: Sole known species of the genus. M^3 length (parallel to a line joining paracone and metacone) 8.0 mm., width (directly transverse to this) 8.5 mm., maximum diameter 9.5 mm., minimum diameter 6.7 mm.

ASMITHWOODWARDIA Ameghino, 1901

Asmithwoodwardia Ameghino, 1901, p. 379; 1902b, p. 23; 1906, p. 467.

Type: *Asmithwoodwardia subtrigona* Ameghino.

Distribution: Casamayor beds, Patagonia.

Diagnosis: No mesostyle. Accessory cuspules poorly developed. External cingulum incomplete or weak on the paracone. Hypocone relatively small. Species minute.

This genus and the next, *Ernestokokenia*, are poorly distinguished. The genotypes, however, are obviously distinct and differ greatly in size, so much so that it is reasonable to suppose that, as with *Didolodus* and *Proectocion*, for example, more complete dentitions would show that the small differences in isolated molars really are of generic value.

Ameghino also placed in this genus, and probably correctly, a lower molar. It resembles a *Didolodus* lower molar in miniature, except that there is no external cingulum and the cuspule on the hypoconid-metaconid crest is absent.[1]

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[1] Ameghino's description says that this cusp is present, but it is not shown in his figures (1906, fig. 80b, and elsewhere) and is not visible on the specimen. The figure does err in showing the internal trigonid cusp as simple rather than bifid, and in showing the trigonid equal in width to the talonid rather than slightly narrower.

Asmithwoodwardia subtrigona Ameghino, 1901

Plate 11, figure 2; text figure 30

Asmithwoodwardia subtrigona AMEGHINO, 1901, p. 379; 1902b, p. 23, fig. 7; 1904b, p. 66, figs. 62, 109, 262, 330; 1904d, p. 68, fig. 58; 1906, p. 293, figs. 80, 102.

TYPE: M.A.C.N. No. 10723. One left upper molar, probably M^2, possibly M^3, and one left lower molar, M_1 or M_2. Lectotype: the upper molar.

FIG. 30. *Asmithwoodwardia ?subtrigona* Ameghino. A.M.N.H. No. 28469, left M^2 (?). Crown view. ×4.

HYPODIGM: Types only, but A.M.N.H. No. 28469, a left upper molar, is doubtfully referred.

HORIZON AND LOCALITY: No exact data available for types. Referred specimen, not surely conspecific, from Cañadón Vaca.

DIAGNOSIS: Sole established species of genus. Upper molar length 3.7 mm., width 4.9 mm. Lower molar length 4.2 mm., width 3.4 mm. Smallest known species of the family.

A.M.N.H. No. 28469, probably M^2, has the characters of this genus but measures 4.1 by 5.4 mm. It is tentatively referred to this species.

ERNESTOKOKENIA AMEGHINO, 1901

Ernestokokenia AMEGHINO, 1901, p. 380; 1906, p. 467.

Notoprotogonia AMEGHINO, 1904a, vol. 57, p. 336.

Protogonia, AMEGHINO, 1906, p. 467. [Misprint?]

Protogonia (*Euprotogonia*) Cope, GAUDRY, 1904, p. 9. [Error.]

Notoprogonia, SCOTT, 1913, p. 489; 1937, p. 490. [*Lapsus.*]

TYPE: *Ernestokokenia nitida* Ameghino.

TYPE OF *Notoprotogonia*: *Notoprotogonia patagonica* Ameghino.

DISTRIBUTION: Río Chico and Casamayor beds, Patagonia.

DIAGNOSIS: Upper molars wider than long, no mesostyle, accessory cuspules poorly developed, continuous external cingulum, large hypocone. Lower molars without cuspule on hypoconid-metaconid crest. Teeth in general of simple construction, with smooth enamel, and bunoid cusps.

Ernestokokenia was based on lower teeth, *Notoprotogonia* on uppers. *Ernestokokenia* differs from other lower molars of this group in having smoother enamel, simpler construction, and relatively more bunoid cusps. *Notoprotogonia* differs in exactly the same respects. Teeth of the two genera occlude perfectly, and neither occludes well with any other known teeth. It seems justifiable to consider them synonymous. Both upper and lower teeth are very similar to those placed in the genus *Asmithwoodwardia* except for their much greater size and differences in minor structural details.

Ameghino at first referred the upper teeth to the North American Torrejon genus "*Euprotogonia*" [=*Tetraclaenodon*], to which they do show a striking resemblance, but he afterwards recognized them as distinct generically.

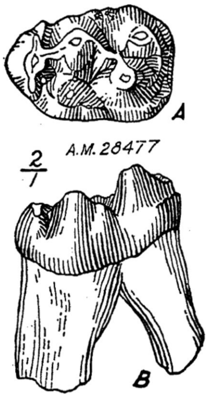

FIG. 31. *Ernestokokenia nitida* Ameghino. A.M.N.H. No. 28477, left M_3. A. Crown view. B. Internal view. ×2.

Ernestokokenia nitida Ameghino, 1901

Plate 11, figures 3–4; text figure 31

Ernestokokenia nitida AMEGHINO, 1901, p. 380.

Ernestokokenia marginata AMEGHINO, 1901, p. 380.

Type: M.A.C.N. No. 10735. Left M_2 and broken left M_3.

Type of *E. marginata:* M.A.C.N. No. 10722. Left M_1.

Hypodigm: Types and A.M.N.H. No. 28477, left M_3.

Horizon and Locality: (*Fide* Ameghino) basal Casamayor beds. No locality data available for types. Referred specimen from south of Lago Colhué-Huapí, Chubut, Argentina.

Diagnosis: Typical lower teeth of this genus. M_1 (type *E. marginata*) length 6.8, width 5.3 mm. M_2 (type *E. nitida*) length 7.6, width 6.2. M_3 (A.M.N.H. No. 28477) length 8.1, width 5.6.

The three individuals placed in this species may not be of quite the same size, but they are near enough to belong to a single species. Ameghino separated *E. marginata* as being smaller, with more pointed cusps and deeper hollows, smaller hypoconulid, and anterior and posterior basal cingula. I believe the difference in cusps and hollows to be illusory or due to wear and the size and smaller hypoconulid to be due in larger part or wholly to position, as the type is M_1 whereas the complete tooth of *E. nitida* seems to be M_2. The cingula are the same in both. They may be individuals of slightly different size, but they are in such perfect harmony that the types could even be of a single individual and cannot fairly be placed in distinct species.

Ernestokokenia patagonica (Ameghino, 1901), new combination

Plate 11, figure 5

Euprotogonia patagonica Ameghino, 1901, p. 375; 1904b, p. 76, figs. 74, 135.

Notoprotogonia patagonica, Ameghino, 1904a, vol. 57, p. 336.

Protogonia (*Euprotogonia*) *patagonica*, Gaudry, 1904, pp. 8, 12, figs. 2, 8.

Type: M.A.C.N. No. 10687. Isolated right upper molar, perhaps M^2.

Hypodigm: Type only.

Horizon and Locality: (*Fide* Ameghino) upper part of Casamayor beds, north of Lago Colhué-Huapí, Chubut, Argentina.

Diagnosis: Cingulum across protocone vague. Upper molar length about 7 mm., width 9.5 mm.

This cannot be directly compared with *E. nitida* and may be synonymous, but may be retained as separate provisionally. The horizon is given by Ameghino as somewhat higher, and the localities probably were not the same.

Ernestokokenia trigonalis (Ameghino, 1901), new combination

Plate 11, figure 6

Euprotogonia trigonalis Ameghino, 1901, p. 375; 1904b, p. 76, figs. 75, 76, 134, 180; 1906, p. 296, figs. 89, 91.

Notoprotogonia trigonalis, Ameghino, 1904a, vol. 57, p. 336.

Type: M.A.C.N. No. 10688. Isolated upper molar, M^1 or M^2.

Hypodigm: Type only.

Horizon and Locality: (*Fide* Ameghino) upper Casamayor beds, north of Lago Colhué-Huapí, Chubut, Argentina.

Diagnosis: Distinct cingulum across protocone. Upper molar length 6.2 mm., width 8.5.

This is probably the same as the preceding species, but this is too uncertain to reduce them to synonymy. Ameghino referred a lower molar (1906, fig. 91) to this species, but I was unable to find the specimen.

Ernestokokenia yirunhor Simpson, 1935

Text figures 32–33

Ernestokokenia yirunhor Simpson, 1935a, p. 7, figs. 5, 6.

Type: A.M.N.H. No. 28539. Part of right lower raw with M_{2-3}.

Hypodigm: Types and two specimens, M_3 and M^3, in Feruglio Collection.

Horizon and Locality: Río Chico formation, Cañadón Hondo, Chubut, Argentina.

Diagnosis: A didolodontid with very simple teeth, smaller than any other species of *Ernestokokenia* and larger than any known species of *Asmithwoodwardia*. M_2 length 6.2 mm., width 4.8 mm.; M_3 length 6.9 mm., width 4.7 mm.

Ameghino's genera *Asmithwoodwardia*, *Ernestokokenia* (including the upper teeth named *Notoprotogonia*), and *Archaeohyracotherium* are separated by only the most trivial

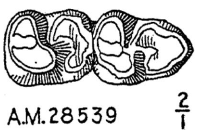

FIG. 32. *Ernestokokenia yirunhor* Simpson. Type, A.M.N.H. No. 28539, right M$_{2-3}$. Crown view. ×2. After Simpson, 1935a.

structural details and can be retained as separable at all only because the type species are distinct and the genera may prove to be so when more than isolated teeth are known. Incomplete as it is, this specimen is the best of this group yet found. Its generic assignment is, of course, unclear since it is also a very distinct species and the supposed generic differences are so minor and variable, but on the whole it seems most satisfactory to place it in *Ernestokokenia.*

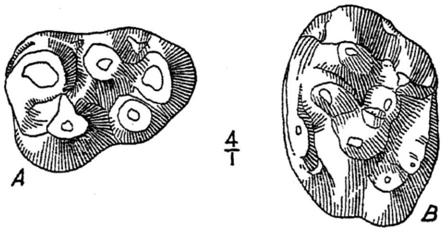

FIG. 33. *Ernestokokenia ?yirunhor* Simpson. Specimens in Feruglio Collection (casts, A.M.N.H. No. 27896). A. Right M$_3$. B. Left M^3. Crown views. ×4. After Simpson, 1935a.

In the Feruglio Collection from the upper sandstone of the Bajo de la Palagana there is an M$_3$, measuring 6.6 by 4.7 mm., which is probably of this species. In the same lot is an M^3 also possibly of this species. Except for characters clearly due to its being a last molar, this tooth is closely similar to those of other species of *Ernestokokenia* ("*Notoprotogonia*"), but indicates a smaller animal, length 5.4 mm., width 6.7 mm. (Casts, A.M.N.H. No. 27896.)

Ernestokokenia chaishoer Simpson, 1935

Text figure 34

Ernestokokenia chaishoer SIMPSON, 1935a, p. 8, fig. 7.

TYPE: In Feruglio Collection, isolated upper molar, probably M^2. Cast, A.M.N.H. No. 27892a.

HYPODIGM: The type and the following: Feruglio Collection, isolated lower molar, probably M$_2$. Cast, A.M.N.H. No. 27892b.

HORIZON AND LOCALITY: About 6 meters below lowest true tuff of the Casamayor, Bajo de la Palangana, Chubut, Argentina.

DIAGNOSIS: M$^{?2}$ longer relative to width than known teeth of *E. patagonica* or *E. trigonalis* and somewhat larger. No cingulum across protocone or hypocone, but continuous, sharp external cingulum. Much larger than *Archaeohyracotherium mediale.* M$_2$ larger than *E. nitida* and with small cusp on hypoconid-metaconid crest, as in *Didolodus*, trigonid and talonid of equal width. M$^{?2}$ length 7.9, width 9.4 mm. M$_{?2}$ length 8.2, width 6.4 mm.

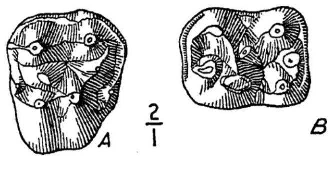

FIG. 34. *Ernestokokenia chaishoer* Simpson. Specimens in Feruglio Collection. A. Type (cast, A.M.N.H. No. 27892a), right M^2. B. (Cast, A.M.N.H. No. 27892b), right M$_2$. Crown views. ×2. After Simpson, 1935a.

The lower molar is with difficulty distinguishable from *Didolodus minor*, but the upper molar, having no mesostyle, obviously is not of *Didolodus*. As the two teeth are from the same horizon and locality, are harmonious in structure, and occlude well, it is proper to assume that they are of the same species. As already suggested, the generic division of this group is as yet very unsatisfactory. It is also unlikely that this robust species is really of the same genus as the dimunitive teeth from the same locality referred to *E. yirunhor* (above), but the material is still inadequate for full generic revision and it seems most conservative to place these similar forms in *Ernestokokenia* for the present.

ARCHAEOHYRACOTHERIUM AMEGHINO, 1906

Archaeohyracotherium AMEGHINO, 1906, pp. 307, 467.

TYPE: *Archaeohyracotherium mediale* (Ameghino).

Distribution: Casamayor beds, Argentina.

Diagnosis: Closely similar to *Ernestokokenia*, but upper molar more quadrate, length and width more nearly equal, external cingulum less sharp.

This genus was founded by Ameghino on a species formerly referred to *Prohyracotherium*. He was obviously correct in separating the two, and they are so different that it seems incorrect to retain them even in the same family or order as he did. Neither one is a hyracothere. *Prohyracotherium* seems to be a notoungulate, while *Archaeohyracotherium* is a didolodont. The single known tooth of this genus differs from *Ernestokokenia* in very little more than size and proportions. It might belong to a distinct species of that genus, or might be a milk tooth of it. The localities are different, and the data do not warrant any definite conclusion, so that both genera of Ameghino are retained, with much doubt.

Archaeohyracotherium mediale (Ameghino, 1902)

Plate 11, figure 7

Prohyracotherium medialis Ameghino, 1902a, p. 16.

Archaeohyracotherium mediale, Ameghino, 1906, p. 306, fig. 113a.

Type: M.A.C.N. No. 10677. Isolated left upper molar.

Hypodigm: Type only.

Horizon and Locality: (Ameghino) Casamayor beds, west of the Río Chico, Chubut, Argentina.

Diagnosis: Sole known species of the genus. Upper molar, length 6.6 mm., width 7.1 mm.

DIDOLODONTIDAE indet.

Text figure 35

A.M.N.H. No. 28945, an isolated M^3 from the Rinconada de los Lopez, clearly represents an otherwise unknown genus. It does not seem important enough to name on this single tooth, but is recorded for future comparison. It measures 9.1 by 12.7 mm., somewhat larger than *Didolodus multicuspis*, has no mesostyle, and is peculiar in this family in having a relatively very small hypocone which is posteroexternal to the protocone. Otherwise it somewhat resembles *Paulogervaisia*. Pertinence to this family is clear.

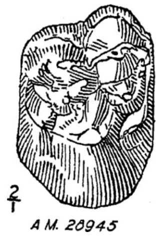

Fig. 35. Didolodontid, unnamed genus and species. A.M.N.H. No. 28945, isolated M^3. Crown view. ×2.

LITOPTERNA Ameghino

Definition: Extinct South American ungulates. Dental formula $\frac{3 \cdot 1 \cdot 4 \cdot 3}{3 \cdot 1 \cdot 4 \cdot 3}$ to $\frac{1 \cdot 0 \cdot 4 \cdot 3}{2 \cdot 1 \cdot 4 \cdot 3}$. Molars persistently brachyodont. Bunoselenodont to modified lophiodont. Incisors subequal, or one pair above and below enlarged and becoming rootless. Canines small, not differentiated. Cheek teeth unreduced, posterior premolars becoming molariform. Upper molars quadrate; paracone and metacone crescentic; protoloph imperfect, without full union of elements, and no true metaloph. Lower molars more or less bicrescentic, perfectly so in later forms, and trigonid and talonid usually subequal; talonid usually without transverse pillar; M_3 usually without third lobe. Skull condylarth-like in primitive forms, becoming modified in one line (Macraucheniidae) by retreat of the external nares. Tympanic not inflated, no epitympanic sinus posterior to the ear region, no ossified tubular meatus. Feet mesaxonic, functionally tridactyl to monodactyl, generally digitigrade. Carpus serial or nearly so; digital reduction inadaptive. Astragalus with deep trochlea, crests elevated, rounded, subequal, neck of moderate length, slightly oblique, slightly constricted, head depressed, extended transversely, straight transversely and convex dorsoventrally; no cuboid facet.

Ameghino (1889) proposed the name Litopterna for an order[1] of the group Perissodactyla, with substantially the contents

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[1] Or suborder; his intention is not quite clear.

now accepted, except that the Homalodotheriidae were at first placed here. He later (e.g., 1904b, 1906) abandoned the use of the name Litopterna. He modified the Order Perissodactyla of other authors by taking from it the later true horses and some South American forms (Notohippidae), placed in the Order Hippoidea. Aside from the Homalodotheriidae, whose lack of relationship to this group he had now recognized, and the Notohippidae,which he placed here for a time but removed to the Hippoidea, the contents of his former Order Litopterna were classified as the families Proterotheriidae and Macraucheniidae of the Order Perissodactyla. Scott (1910) showed that the litopterns are not perissodactyls, and revived the Order Litopterna, in which he placed three families: Macraucheniidae, Proterotheriidae, and Didolodontidae. This is the usual arrangement since that time, except that some authors place the Didolodontidae in the Condylarthra, as I have done here, and others (e.g., Loomis, 1914; Schlosser, 1923) keep Ameghino's family Adianthidae separate from the Macraucheniidae with which Scott tentatively united it. (Patterson, 1940, makes this group a subfamily, Adianthinae, of Macraucheniidae.)

Ameghino's view of perissodactyl relationship for the Litopterna was accepted, without critical restudy, by some of his contemporaries, but Scott returned to and much strengthened the opinion of Lydekker that the litopterns are of common origin with the Notoungulata, and have nothing directly to do with perissodactyls. That they are an isolated and non-perissodactyl order has since been almost universally accepted, but there are still many shades of opinion as to how close is the possible relationship to the Notoungulata. Gregory (1910) and Loomis (1914) classified the Litopterna as a suborder of Notoungulata. Scott (e.g., 1913) makes them a separate order, but one of common origin with the Notoungulata.[1] Others (e.g., Schlosser, 1923), tend to ignore the resemblance to the notoungulates and to emphasize derivation from the condylarths.[2]

Ameghino's definitive classification of the Casamayor fauna (Ameghino, 1906, pp. 466–469) places only two genera in families ordinarily referred to the Litopterna, *Eolicaphrium* in the Proterotheriidae and *Pseudadiantus* in the Adianthidae. These genera are practically indeterminate and of uncertain position at present. The types were very inadequate, not even including one molar in any case; they were rather briefly described, were not figured, and were not seen by me in the Ameghino Collection. These genera must be treated as *incertae sedis* and virtually ignored unless or until the types or unmistakable neotypes are found.

Aside from these ill-fated genera, however, eight of Ameghino's Casamayor genera seem to be litopterns, although referred by their author to the following Holarctic orders and families:

Condylarthra
  Catathleidae (=Periptychidae)
    [3 genera]
  Pantolambdidae
    [3 genera]
Perissodactyla
  Palaeotheriidae
    [2 genera]

There are also the very dubious genus, *Ernestohaeckelia*, by Ameghino referred to the Notohippidae, and its probable synonyms or allies *Rutimeyeria* and *Amilnedwardsia* (referred by Ameghino to the Albertogaudryidae) which may possibly be litopterns. These genera fall into two fairly well-defined groups, corresponding to Ameghino's "Condylarthra" and "Perissodactyla." I fail to see any natural division between his "Catathleidae" and "Pantolambdidae" within the former group. All the genera have the following characters in common:

1. Brachyodont
2. Primitive and more or less symmetrical trigons, with three main cusps and two strong conules
3. Hypocone present, but no true metaloph
4. Protoloph sometimes suggested, but never fully crested and continuous

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[1] That is, with his Toxodontia, not Toxodonta in a more limited sense. For better clarity I use the term Notoungulata here in the same sense as that given it throughout the memoir, and not in the sense given it by Scott himself.

[2] Also strongly emphasized by Gregory (1910) who places the litopterns in the Notoungulata in his formal classification, yet shows them in his phylogenetic chart as independently derived from the condylarths.

5. Crista, crochet, and similar secondary modifications absent or slight and atypical
6. Paracone and metacone crescentic
7. Mesostyle present
8. Parastyle a projecting external pillar
9. Hypocone much smaller than protocone
10. Two internal trigonid cusps
11. Anterior end of hypoconid crescent internal, at or near metaconid
12. Entoconid of M_{1-2} near or confluent with hypoconulid, not forming a transverse crest
13. Lower molars bunolophodont to lophiodont, more or less bicrescentic
14. Paraconid a distinct cusp, as large as the metaconid and sharply separated from the latter

Most of these characters are striking points of difference from the Notoungulata as a whole; 1–5 and 10–12, inclusive, are points of resemblance to the Didolodontidae, while 6–9 and 13–14 are differences from that family. While all these teeth differ more or less from those of any later litopterns, all these distinctive characters are to some degree characteristic of primitive undoubted litopterns of later formations. There seems little doubt that the genera here under discussion are litopterns.

The two major groups into which these genera fall are *Victorlemoinea* on one hand, *Josepholeidya* and all the other genera on the other.

Victorlemoinea	*Josepholeidya*
Upper molars subquadrate, asymmetrical	Upper molars generally subtriangular, more nearly symmetrical
Hypocone relatively large	Hypocone smaller or very small
Strong supplementary crests between hypocone and protocone and hypocone and metaconule	Uniting crest to metaconule weak or absent, to protocone variable but never prominent and in many cases completely absent
Posterior cingulum forming a closed fossette	No definite closed fossettes
Lower molars completely lophiodont, crescents subequal. Paraconid and entoconid visible as separate entities only on completely unworn teeth if at all	Lower molars much more bunodont, anterior crescent smaller and less open. Paraconid and entoconid separate entities

These molars, upper and lower, differ almost as much as do, for example, those of the Macraucheniidae and Proterotheriidae in the Santa Cruz fauna.

Victorlemoinea seems to be related to the later Macraucheniidae. The details of the upper molars are different, but the basic pattern and modifying tendencies are similar to those of *Theosodon*, for instance. The more lophiodont molars and tendency to form secondary crests and fossettes are much the same in the two and distinguish them rather sharply from the Proterotheriidae. The differences between *Victorlemoinea* and *Theosodon* are not greater than would be expected between genera of a single family separated by a considerable span of time. One tentative distinction, however, is the probable or possible absence in *Victorlemoinea* of a transverse talonid pillar, at least on M_1, but this is dubious.

The presence and development of this pillar are very puzzling in the litopterns. Scott believed its presence primitive for the group as a whole, and this probably influenced his opinion that litopterns and notoungulates are related. It is, however, absent in all the most primitive litopterns, notably the early proterotheriids. In its early form in that group the pillar appears as a normal entoconid, and such resemblance to the notoungulate condition as it later acquires is not very close and is rather clearly secondary.

The lower teeth called by Ameghino *Anisolambda longidens* do not have this macraucheniid type of pillar on M_1. These teeth probably belong to *Victorlemoinea* for they are in the size range of that genus and from the same locality or region. There is, however, one tooth, an M_1 or M_2, in our collection, A.M.N.H. No. 28682, which shows an entoconid crest well developed, much as in *Theosodon*. This is, to the best of my knowledge, the only evidence for such a structure in any Casamayor litoptern. It is too large for any known genus but *Victorlemoinea*, and the facts that no upper teeth surely of that genus have ever been found at this locality, while where they do occur there are lower teeth of different type at least as well adapted for occlusion, oppose reference to that genus.

In fact the tooth cannot be surely accepted as of Casamayor age. It suspiciously resembles *Cramauchenia* of the Colhué-Haupí, and it was found on the surface on the Casamayor but below a rich Colhué-Huapí exposure. The distance to which it would have had to be transported if derived from the later formation is considerable, but there is a distinct possibility that this is its history and it is very dubious. Although this single item of opposing evidence must be recorded, it appears highly probable that the transverse entoconid is a neomorph in all lines of litopterns, not yet present in Casamayor time and hence developing much later and wholly independent of the somewhat similar notoungulate character.

The other group, that of *Josepholeidya,* has also been known only from isolated teeth, but these are fairly numerous and our work adds not only many more single teeth, but also part of a lower jaw with all the molars of one side preserved. Furthermore, what appears to be either a progressive genus of the same group or a nearly allied collateral branch is represented in the Musters by good lower jaws. The general characters of this group link it with the Proterotheriidae as opposed to the Macraucheniidae. The principal differences of the Casamayor genera from the Santa Cruz proterotheres are as follows:

Average size smaller
Molar crowns lower
Upper molars more trigonal and symmetrical
Protocone-protoconule line more transverse
Hypocone smaller
Definite protostyle always present and often nearly or quite as large as hypocone
Protoconule and metaconule about equal
Lower molars distinctly more bunodont
Paraconid a distinct conical cusp nearly closing the internal opening of the trigonid crescent
Entoconid imperfectly fused with hypoconulid on M_{1-2} and almost separate on M_3
M_3 with hypoconulid projection forming an imperfect third lobe

These distinctions are great, but they do not wholly mask a fundamental similarity of plan. They are in general what would be expected in the proterothere ancestry, and some of them are approached by some Santa Cruz forms. Two features, the characters of the protostyle and paraconid, may possibly be aberrant, but except for these two points, and perhaps including them, the differences all seem to be due to the much more primitive character of the Casamayor species, consonant with their age.

The more recently discovered Río Chico litopterns are few and fragmentary, but they indicate the presence of the same groups, and probably of some of the same genera, as in the Casamayor without adding much to this broader review of structure and affinities.

Most of the Musters litopterns were described by Roth (1899, 1903), with critical remarks and emendations by Ameghino. Roth did not present a formal classification of these forms, but in describing them he made or suggested the following allocations:

Polyacrodon: Toxodontia
Glyphodon: Litopterna or Toxodontia
Megacrodon: No definite suggestion; detail compared with "*Eupithecops*"
Proacrodon: No definite suggestion; detail compared with "*Hyrachius*"
Polymorphis: No definite suggestion; details compared with "*Dydelphys*" and *Megacrodon*
Heteroglyphis: Derived from *Polyacrodon*
"*Lambdaconus*" *elegans:* "Didalodia"

The nomenclature is Roth's and requires some modification (see below). Roth also referred to the Casamayor genus *Anisolambda* Ameghino a species probably from the Deseado and quite surely not of this genus.

Of Roth's generic names, Ameghino recognized only *Heteroglyphis* as valid, but in terms of his own nomenclature he referred all Roth's genera now considered litopterns, as well as his own genera *Decaconus* and *Lambdaconus,* to the Condylarthra. *Heteroglyphis* was placed in the Pantolambdidae and the other genera in the Phenacodontidae (Ameghino, 1906).

In a preliminary paper (Simpson, 1936d), I have already suggested that these genera of Roth's are primitive litopterns, but in keeping with the general neglect of the Musters fauna other students since Ameghino have ignored them.

The macraucheniid-like *Victorlemoinea* group is as yet unknown in the Musters. This is certainly an accident of collecting, because members of this group occur in both Río Chico and Casamayor and typical macraucheniids in the Deseado. The absence of the group in the relatively small Musters collections is not surprising, as proterotheriids or proterotheriid-like genera are considerably the more numerous of the two sorts of litopterns throughout the early and middle Tertiary.

Many of the remarks made regarding the Casamayor *Josepholeidya* and its allies apply also to these rather similar Musters genera. The necessity of placing them in some family motivates reference of these Mustersan genera to the Proterotheriidae, but there is no evidence that any of them had characters such as enlarged incisors and diastemata typical of later proterotheres. Their molar structure is somewhat more proterothere- than macraucheniid-like.

Aside from a few indeterminate forms, four Musters genera are here recognized. *Polymorphis* is based on lower jaws and is the best known, there being three good lower jaws, one each in the Roth, Ameghino, and American Museum Collections. *Polyacrodon* is based on upper teeth, probably of the same genus as *Polymorphis*. *Xesmodon* is based on a skull, unfortunately very poorly preserved, and *Heteroglyphis* on a single broken upper tooth.

Polymorphis differs from known lower jaws of didolodonts in the more lophiodont lower molars, separation of metacone and paracone with reduction of the latter, and other details, all suggesting that it belongs rather on the litoptern side of the vague, perhaps artificial line separating early litopterns from condylarths. It is, however, much more condylarth-like than are the later undoubted litopterns. Among known Casamayor lower jaws, *Polymorphis* most resembles *Anisolambda*, but it differs markedly in the reduction of the paraconid, less crescentic trigonid, more spur-like and lophoid hypoconulid, and other characters that make the genera sharply distinct even though they are probably, in some measure, allied.

In the Deseado, the lower dentition referred by Loomis (1914) to *Protheosodon* has similar molars, but is likewise sharply distinct, most obviously in the much more molariform premolars.

If the attention is confined, for the moment, to lower jaws, the general group of *Anisolambda-Polymorphis-Protheosodon*, Casamayor, Musters, and Deseado, respectively, seems to be an assemblage of very primitive litopterns, probably including several minor phyla. Because of the complete dental formula and lack of enlarged incisors and diastemata the Deseado form was referred by Loomis to the Macraucheniidae, and the same logic could be extended to the earlier genera. But as already suggested in dealing with the Casamayor forms, the dental structure, although generically distinct and suggesting some aberrant lines, is really closer to the Proterotheriidae, and this seems more important than the retention of the primitive dental formula. More macraucheniid-like molars also do go back even into the Río Chico.

The situation is made somewhat exasperating by the Deseado skeletal remains described by Loomis (1914). If the hind limb referred by him to *Protheosodon* belongs to the same animal as the lower jaw referred to that genus, and if the lower jaw is really closely related to *Anisolambda* and to *Polymorphis*, then these animals can hardly be considered as belonging to either of the Santa Cruz families and must form a third, equally distinctive group. That they belong in a separate family is indeed quite possible, but the line of evidence just suggested is too hedged about with conditions to have much weight. Loomis does not give the evidence for associating his lower jaw and hind limb. Doubtless they were found together, but in a deposit as mixed and as rich as the Deseado at Cabeza Blanca the discovery of two remote and disconnected parts of a skeleton near each other is not sufficient evidence that they belong to one animal. They are not evidently harmonious, for the lower jaw is surely a litoptern while the hind limb may not be. It is certainly not proterothere, and I cannot agree with Loomis that it is much like *Theosodon*. That possibility is not excluded, but as far as I can judge from Loomis' figures this limb could belong to a notoungulate. Further confusion is provided by the hind limb that Loomis named *Notodiaphorus*. His figures and description suggest that he must be mistaken in referring this to the Proterotheriidae or considering *Diadiaphorus* as its closest ally, for it seems to be very close to *Theosodon* and must be a macraucheniid, thus showing that the typical macraucheniid limb was already developed and that the limb referred to *Protheosodon* is not simply a primitive forerunner of *Theosodon*.[1]

Polyacrodon, probably the upper dentition of *Polymorphis*, shows closely analogous resemblances and differences. It is more primitive, more condylarth-like than the later and typical litopterns, yet it is more litoptern-like than are the didolodonts, as seen in its more bicrescentic ectoloph, strong parastyle, etc. It differs from *Josepholeidya* and its allies in the less symmetrical molars, large hypocones, and several lesser details, and from *Victorlemoinea* in being less lophiodont, with few cusp connections. Of these early forms it seems clearly closest to the *Josepholeidya* group. In comparison with Deseado genera, it closely resembles *Protheosodon*, more closely than *Polymorphis* does the lower jaw referred to *Protheosodon* by Loomis. The differences are relatively minor, as in the greater development of styles and cingulum cusps, and the pattern is essentially the same. Resemblance to typical proterotheres is less close, but still noteworthy, while resemblance of *Polyacrodon* or of *Protheosodon* to *Theosodon* or other undoubted macraucheniids seems to me to be decidedly more distant than to the proterotheres.

If *Polymorphis* and *Polyacrodon* are considered as the lower and upper teeth, respectively, of the same group, and perhaps of the same genus, reference may be made to the list of characters given on a previous page as separating the Casamayor *Josepholeidya* group from the Santa Cruz proterotheres. *Polymorphis* and *Polyacrodon* show the following chief modifications with respect to the Casamayor genera in these characters:

Upper molars more quadrate and asymmetrical
Hypocone large
Protostyle still present, but much smaller than hypocone
Lower molars less bunodont than in the Casamayor, more than in the Santa Cruz
Paraconid not distinct or conical
Entoconid still a distinct entity, but more fully entering into the talonid crescent

These all suggest advancing specialization, and all are points of greater resemblance to the Santa Cruz proterotheres. The other primitive characters of the Casamayor genera are retained with little change in the Musters. In broad features, then, these Casamayor and Musters genera and the Santa Cruz proterotheres do show grades of structural advance in agreement with their relative ages, and to this extent the relationship is confirmed. This is not, however, true of the more minute and exact details of structure such as might designate exact phyletic lines of descent, and it seems impossible to trace any precise phylogeny from a known Casamayor genus through the Musters to a known Santa Cruz genus, and it is, indeed, likely that *Polymorphis-Polyacrodon* is off the main line leading to the later forms. This is further emphasized if Loomis' *Protheosodon* jaw belongs in this group, for it is contemporaneous with typical and more advance proterotheres. These considerations would not negative the existence of a generally progressive family Proterotheriidae through all these formations, with one or more of the various early offshoots surviving into the Deseado. On the other hand the evidence is obviously very imperfect and in part anomalous, especially as regards limb structure, and the early forms may have been more markedly aberrant and not really close to the true proterothere line.

Xesmodon apparently falls into this same vague and perhaps artificial group. As will be discussed more fully below, it resembles the didolodonts and the litopterns and among the latter is somewhat nearer the proterotheres than the macraucheniids in spite of probably having a closed tooth series and an open orbit. As in most of these genera, its presumably most diagnostic characters are very imperfectly known.

Heteroglyphis is known only from a single broken tooth and aside from probably being a litoptern is of a very uncertain status.

When these early litopterns are viewed as a whole it is clear that their teeth are in agreement with the theory of condylarth derivation for this order, and that they even add significantly to the evidence for that theory. Their differences from the teeth of later litopterns are for the most part points of resemblance to the condylarths as a whole, and in many cases specifically to the didolodonts. If, con-

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[1] In addition to this, it is not certain that Loomis' lower jaw belongs to *Protheosodon*, which was based on upper teeth, but it probably does, and in any case this is merely a matter of nomenclature and does not alter conclusions based on this lower jaw.

trary to my opinion, the latter be themselves considered litopterns, their very condylarth-like structure merely adds to the probability that litopterns were directly derived from condylarths, and with modifications not very profound. So far as present evidence goes, it might even be said that the litopterns appear to represent the direct further evolution of the Condylarthra, continuing in South America after they became extinct in the rest of the world.

The resemblance of the meniscotheres to the litopterns seems to me to extend only to the acquisition by both of a selenodont habitus. It is probably to be considered as evidence of a tendency for the condylarths to develop selenodont molars, independently of the other selenodont ungulates, rather than as an indication of special affinity between these two groups.

On the other hand, without attempting a complete review of the mid-Tertiary evidence already so ably presented by Scott, these early litopterns seem to me to be opposed to any very intimate relationships with the Notoungulata. In general their teeth are not more notoungulate-like than are those of later litopterns, as would be expected were this relationship real and close. On the contrary, in some respects they are less notoungulate-like. When what is known of notoungulate evolution is borne in mind, their relationship seems to be one of common derivation from the same basic stock, protoungulate in a broad sense and perhaps condylarth in a narrower sense. But the notoungulates seem to be the older group as such, that is, they diverged from the condylarths more widely and at an earlier date than did the litopterns. There is no strong evidence that either group was derived from the other, nor do I see how they can properly be placed together in a monophyletic taxonomic division which would exclude all typically Holarctic orders.

MACRAUCHENIIDAE

This family is based on later, Santa Cruz to Pampean, genera, and the Río Chico and Casamayor forms are placed in it with some doubt. There appears to be but a single well-characterized genus, *Victorlemoinea*, with the extremely dubious addition of *Ernestohaeckelia*, *Rutimeyeria*, and *Amilnedwardsia*.

VICTORLEMOINEA Ameghino, 1901

Victorlemoinea Ameghino, 1901, p. 383; 1906, p. 467.

Type: *Victorlemoinea labyrinthica* Ameghino.

Distribution: Casamayor beds, Patagonia.

Diagnosis: Upper molars strongly lophoselenodont. Protoconule and metaconule subequal, united to ectoloph only by low sharp crests at their posterior bases. Protoconule and protocone joined by a crest. Anterior cingulum terminating in an isolated protostyle. Hypocone much larger than protostyle but smaller than protocone, united by crests to protocone and metaconule. Sharp posterior cingulum enclosing a fossette.

The lower teeth which I very tentatively place in this genus have not been found in actual association with the uppers on which the name is based, but they are of about the same relative abundance, occur at the same horizons and localities, are of appropriate size, and occlude well with the upper teeth. Ameghino's species *Anisolambda longidens* is probably based on lower teeth of this genus. His genus *Anisolambda* included three species which appear to me to belong to three different genera and families. The species placed first in order by Ameghino, *A. fissidens*, is selected as genotype, and it seems to belong in the next group, referred to the Proterotheriidae. The alternative or supplementary possibility that a single lower molar from Colhué-Huapí, with a transverse talonid pillar, may belong here has been mentioned above.

In the upper molars, the paracone and metacone are subequal, crescentic, the inner side convex and the outer with crescentic crests, between which on each cusp there may be a slight rounded median ridge. Parastyle and metastyle are both sharp vertical crests, projecting strongly externally. Protoconule and metaconule are also about equal and are definite, sharply crescentic cusps, the posterior wing of each united basally with the corresponding external cusp, paracone and metacone, respectively. The large protocone is also crescentic, one wing running to the protoconule and the other to the hypocone, with a weaker branch uniting the metaconule also to these cusps. The apex of the hypocone is slightly lower than that of the protocone. It is continued externally in a sharp posterior cingulum which runs, with decreasing prominence, to the posterior side of the metacone and encloses a deep, narrow, transverse basin along the posterior margin of the tooth. There is also a well-developed, but narrower, anterior cingulum which ends freely in an elevation, protostyle, anterior to the notch between protocone and protoconule.

A.M.N.H. No. 28466 (text fig. 36) is probably M^3 of this genus. It is more triangular than the other molars, with outer border more oblique. Instead of distinct metaconule and hypocone, it has a single cusp which is intermediate in position and in size between those two cusps as developed on the other molars. Aside from its basal union with the protocone, it has three sharp crests, one posterior leading into the posterior cingulum, one posteroexternal abutting against the metacone, and one anteroexternal running into the trigon basin.

The lower molars which are referred to this genus are simply bicrescentic. A.M.N.H. No. 28467 is apparently M_3. It resembles the other molars except that the talonid is distinctly narrower than the trigonid. There is no trace of a third lobe.

The lower premolars are not certainly identified. Those with the type of "*Anisolambda*" *longidens*, perhaps of this genus, have a triangular trigonid with a high transverse crest and a curving, falling crest extending anterointernally from the external point of this. The heel is large and has a rather high and sharp median longitudinal crest. A.M.N.H. No. 28508, on the other hand, has a different structure, but one that might also belong to this genus. It resembles the molars and is bicrescentic, but is smaller and more pointed anteriorly.

It is interesting that all the known Casamayor specimens of this genus, including all the known lower molars of the kind described above, are from the same region, west of the Río Chico, and none from the classic locality south of Colhué-Huapí. Ameghino's specimens are labeled "Oeste de Río Chico" and ours are from Cañadón Vaca, which is also west of the Río Chico. The types are not comparable with each other and most of the known specimens are essentially isolated teeth. The species are purely nominal and specimens aside from the types are of uncertain specific identification.

Victorlemoinea labyrinthica Ameghino, 1901

Plate 11, figure 8

Victorlemoinea labyrinthica Ameghino, 1901, p. 383.

Type: M.A.C.N. No. 10671. Left P^4, badly preserved, and about a third of M^1.

Hypodigm: Type only.

Horizon and Locality: (*Fide* Ameghino) Casamayor beds, west of Río Chico, Chubut, Argentina.

Diagnosis: The larger species based on upper teeth. P^4 length about 17 mm., width about 20 mm.

Victorlemoinea emarginata Ameghino, 1901

Plate 11, figure 9

Victorlemoinea emarginata Ameghino, 1901, p. 383; 1904b, p. 125, fig. 144.

Type: M.A.C.N. No. 10672. Right M^1 nearly complete and M^2 with outer part much broken.

Hypodigm: Type only.

Horizon and Locality: (*Fide* Ameghino) Casamayor beds, west of the Río Chico, Chubut, Argentina.

Diagnosis: Smaller. M^1 length about 10 mm., width about 13.5 mm.

?Victorlemoinea longidens (Ameghino, 1901), new combination

Plate 11, figure 10

Anisolambda longidens Ameghino, 1901, p. 384.

Type: M.A.C.N. No. 10670. Fragment of right lower jaw with P_{2-3}. Fragment of right lower jaw with M_1 and trigonid of M_2. Association doubtful. Lectotype: the fragment with molars.

Hypodigm: Type only.

Horizon and Locality: (*Fide* Ameghino) Casamayor beds, west of the Río Chico, Chubut, Argentina.

Diagnosis: Not comparable with other species of *Victorlemoinea*. M_1 length 14.7 mm., width 9.8 mm.

If this species is correctly placed in the genus, it is very possibly synonymous with one of those based on upper teeth, but it appears to be somewhat too small for *V. labyrinthica* and too large for *V. emarginata.*

Victorlemoinea sp. indet., Casamayor

Text figure 36

We have four specimens probably and a fifth possibly of this genus, all from the same locality in Cañadón Vaca. These seem to represent a single species and appear to be intermediate in size between *V. labyrinthica* and *V. emarginata*, but the data are inadequate to determine to which of those species it should be referred or whether it represents a distinct species; the latter is more probable, but definition is impossible on these data.

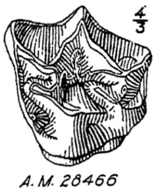

FIG. 36. *Victorlemoinea* sp. A.M.N.H. No. 28466, left M^3. Crown view. ×4/3.

Measurements of these teeth are as follows:

A.M.N.H. No. 28468. M^1 (?). Length about 14 mm.

A.M.N.H. No. 28466. M^3. Length 14.6 mm., width 15.8 mm.

A.M.N.H. No. 28465. M_1 or M_2. Width 7.6 mm.

A.M.N.H. No. 28467. M_3. Length 12.7 mm., width 7.1 mm.

Victorlemoinea sp. indet., Río Chico

Text figure 37

The presence of this genus, or an ally, in the late Río Chico is attested by a single specimen, right M^3, from the highest Río Chico fossiliferous level in the Bajo de la Palangana, in the Feruglio Collection (cast, A.M.N.H. No. 27895). This is quite distinct specifically from A.M.N.H. No. 28466, the only Casamayor M^3 known to me, and may be a different genus although in that case probably a close ally. The Río Chico tooth is smaller and more transverse, metacone shorter and more strongly ribbed, metaconule present and distinct from hypocone, protostyle smaller, and cingulum complete across inner face of protocone. It measures 11.7 by 14.2 mm.

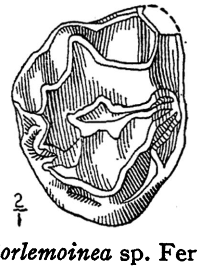

FIG. 37. *? Victorlemoinea* sp. Feruglio Collection (cast, A.M.N.H. No. 27895), right M^3. Crown view. ×2. After Simpson, 1935a.

ERNESTOHAECKELIA AMEGHINO, 1901

Ernestohaeckelia AMEGHINO, 1901, p. 382; 1906, p. 467.

TYPE: *Ernestohaeckelia aculeata* Ameghino.

DISTRIBUTION: Casamayor, Patagonia.

DIAGNOSIS: Protocone and hypocone subequal and well separated. Protoloph incompletely developed, protoconule large. One wing from the metaconule running to the ectoloph. A very inadequately known genus.

The genotype was not figured and its type specimen has not been located, but the genus may provisionally be taken as characterized by *E. acutidens*, also poorly known. The three genera *Ernestohaeckelia*, *Rutimeyeria*, and *Amilnedwardsia* are probably related. They have these characters in common:

1. Simple, basically six-cusped upper molars
2. No mesostyle (no data for *Ernestohaeckelia*)
3. A protoloph, involving the protoconule, but no metaloph
4. Hypocone near and slightly united to protocone
5. Metaconule independent or basically united to the ectoloph, generally elongate anteriorly
6. Tendency to develop a crista

These strange little teeth invite comparison with the henricosborniids, didolodontids, *Albertogaudrya*, and *Victorlemoinea*, representatives of four different orders. They are more bunodont than the henricosborniids and lack the metaloph. They are more lophiodont than the didolodontids, and have the protocone more separate from the metaconule and less from the hypocone. Possible relationship to *Albertogaudrya* (stressed by

Ameghino except in the case of *Ernestohaeckelia*) rests on the theoretical possibility of derivation of molar pattern, not on any definite resemblance, and cannot be accepted without further evidence. Despite the much smaller size, resemblance to *Victorlemoinea* is rather close, especially in *Amilnedwardsia*, but the mesostyle is absent and the anterior cingulum less developed. The real affinities of these genera cannot now be determined, and they are only very tentatively placed in the proximity of *Victorlemoinea.*

Ernestohaeckelia aculeata Ameghino, 1901

Ernestohaeckelia aculeata AMEGHINO, 1901, p. 382.

TYPE: Presumably an isolated upper molar. Not found.

HYPODIGM: Ameghino's published data only.

HORIZON AND LOCALITY: (*Fide* Ameghino) Casamayor beds. No other data.

DIAGNOSIS: M¹ length 8 mm., width 9 mm. (Ameghino).

Ameghino's description of the species contains a statement which would make the type extremely peculiar: "denticule médian antérieur [protoconule] oblique et s'unissant à la base du tubercule postérieur interne [hypocone]. Tubercule antérieur interne [protocone] isolé." This must be a *lapsus calami* and doubtless should read "denticule médian antérieur oblique et s'unissant à la base du tubercule antérieur interne. Tubercule postérieur interne isolé." This is true of the referred species and is a normal sort of structure.

Ernestohaeckelia acutidens Ameghino, 1901

Ernestohaeckelia acutidens AMEGHINO, 1901, p. 382; 1906, p. 313, fig. 129.

TYPE: M.A.C.N. No. 10731. A right upper molar lacking the posterior and posteroexternal portion. Two isolated inner halves of somewhat similar molars. The anteroexternal corner of an upper molar. The external wall of an upper molar. In all, five specimens, all incomplete, not correctly associated, and representing at least two very unlike genera. Lectotype: the most complete tooth.

HYPODIGM: Lectotype only. (Other types are doubtfully or not of this species.)

HORIZON AND LOCALITY (*Fide* Ameghino) Casamayor beds, west of the Río Chico, Chubut, Argentina.

DIAGNOSIS: Smaller than the genotype. The length of the lectotype upper molar was probably about 5.5 mm., and the width across the anterior half is 6 mm.

Ameghino's figures of his specimens are on the whole quite satisfactory from a scientific point of view, but the figure (1906, fig. 129) of this species is misleading. The crown view is of the specimen here made lectotype and represents the tooth as complete, whereas about one-third of it is missing.[1] The external view is not of the same tooth, as the legend implies, but of another specimen, about 25 per cent smaller, with higher crown, in general very unlike the lectotype, and probably belonging to *Notopithecus*. The most important point for any decision regarding the affinities of the species is the mesostyle. It is shown as completely lacking in the figure, but the actual specimen gives no authority for this.

RUTIMEYERIA AMEGHINO, 1901

Rutimeyeria AMEGHINO, 1901, p. 385; 1906, p. 467; SCHLOSSER, 1923, p. 618.

TYPE: *Rutimeyeria conulifera* Ameghino.

DISTRIBUTION: Casamayor, Patagonia.

DIAGNOSIS: Type upper molar more triangular than that of *Ernestohaeckelia acutidens*, hypocone smaller and nearer protocone, parastyle smaller. No mesostyle.

This genus may be based on M³ of *Ernestohaeckelia.*

Rutimeyeria conulifera Ameghino, 1901

Plate 11, figure 11

Rutimeyeria conulifera AMEGHINO, 1901, p. 385; 1904b, p. 127, figs. 149, 490.

TYPE: M.A.C.N. No. 12013. Isolated upper molar.[2]

HYPODIGM: Type only.

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[1] The wax used to mount the tooth for drawing was still on it when examined, and it shows that the tooth was not more complete when the drawing was made.

[2] This is labeled by Ameghino with an unpublished name, but is apparently the original of the specific description. He probably changed the name in his manuscript.

HORIZON AND LOCALITY: (*Fide* Ameghino) Casamayor, Colhué-Huapí.

DIAGNOSIS: Sole known species of the genus. Type measures 6.1 by 4.7 mm.

AMILNEDWARDSIA AMEGHINO, 1901

Amilnedwardsia AMEGHINO, 1901, p. 386; 1906, p. 467.

TYPE: *Amilnedwardsia brevicula* Ameghino.

DISTRIBUTION: Casamayor, Patagonia.

DIAGNOSIS: Upper molar very similar to *Ernestohaeckelia*, but crests less distinct and inner contour more quadrate.

This could well be synonymous with *Ernestohaeckelia*, *Rutimeyeria*, or both, but synonymy cannot now be proved.

Amilnedwardsia brevicula Ameghino, 1901

Plate 11, figure 12

Amilnedwardsia brevicula AMEGHINO, 1901, p. 386; 1904b, p. 151, figs. 185, 220, 313, 491.

TYPE: M.A.C.N. No. 12011. Isolated upper molar.

HYPODIGM: Type only.

HORIZON AND LOCALITY: (*Fide* Ameghino) Casamayor, west of the Río Chico, Chubut, Argentina.

DIAGNOSIS: Sole known species of genus. Type measures 6.7 by 4.7 mm.

PROTEROTHERIIDAE AMEGHINO

This family is based principally on Santa Cruz specimens, with others referred to it on good grounds from horizons as early as the Deseado and as late as the Monte Hermoso, but not the Pampean. The forms discussed below are placed here rather tentatively, as already pointed out.

The Casamayor and Musters genera in Ameghino (1906) that probably belong here and in any event certainly form a well-marked unit in the faunas are those placed by Ameghino in the Catathleidae, except *Argyrolambda* (tentatively removed to the Didolodontidae), those placed in the Pantolambdidae, the Musters (but not Casamayor) genera placed in the Phenacodontidae, and *Anisolambda*, placed in the Palaeotheriidae, 12 genera in all as classified by Ameghino. Except *Anisolambda*, all the Casamayor forms and several from the Musters are based on isolated upper teeth, in some cases imperfectly preserved. The criteria used for separating these genera, not to mention species, make virtually no allowance for differences due to position in the series or to individual variation. In one or two cases where Ameghino did allow some latitude in this respect, he later returned to the group and made a new genus of the variant specimen. On the criteria so established, every complete tooth in the known collections would become type of a species, and most of them would belong to separate genera. Even now, no two upper teeth are known in association in the Casamayor, but with the considerable additions to the series of isolated teeth afforded by our collection, it is possible to find intergradations between certain of the supposed genera. They seem to be reduced, so far as these upper teeth are concerned, to three fairly distinctive types which are here retained as genera, and the others are reduced to synonymy. It remains possible that even three are too many, and that only two genera, or even, but with much less probability, only one, is actually present. In the Musters, four genera, also rather unsatisfactory in definition, may be recognized. A specific revision is impossible. All of Roth's and all but one of Ameghino's species are separately listed, but the specific unit really has no value in this group as now classified. The majority of new specimens cannot be placed in any particular species without the proposal of numerous new names for which there seems to be no real need or justification. The Casamayor genera recognized are *Josepholeidya*, *Ricardolydekkeria*, and *Guilielmofloweria*. As defined below, these are well distinguished and readily recognizable morphologically, although the real taxonomic significance of these morphological distinctions is not at all clear. *Anisolambda* is also retained, although almost certainly synonymous with one or more of the genera based on upper teeth. It includes the lower teeth of this group in general. In the Musters, *Polyacrodon*, *Xesmodon*, and *Heteroglyphis* are recognized on the basis of upper teeth. *Polymorphis* is probably the lower dentition of *Polyacrodon* but is separately defined.

Twenty-four specimens in our collection from the true Casamayor represent this group, and all but one are from Cañadón Vaca, the exception being from near Cabeza Blanca. This geographic distribution is accidental, however, for the majority of Ameghino's types are from south of Colhué-Huapí, where we found only one possibly Casamayor litoptern.[1] Ameghino had about 13 Casamayor specimens now believed referable to this group, basing on them seven genera and eight species.

Musters specimens of this group are rare. Only two were first described by Ameghino or found in his collection. Roth described seven and mentioned another, which, however, was not found in his collection. Our collection includes only three specimens, two of which are, however, unusually good. Most of the known specimens are from the Cerro del Humo, although a few are from south of Colhué-Huapí.

Río Chico specimens of this group (all found since Ameghino and Roth) are still less common, with three specimens in the Feruglio Collection, three in our collection, and two in the Museo de La Plata. These include the distinctive, very early *Wainka* and late Río Chico forms generically similar to those from the Casamayor.

WAINKA SIMPSON, 1935

Wainka SIMPSON, 1935a, p. 9.

TYPE: *Wainka tshotshe* Simpson.

DISTRIBUTION: Río Chico, Patagonia.

DIAGNOSIS: Upper molar resembling *Ricardolydekkeria* in general structure, but paracone and metacone heavy, very close together, bases connate, and no trace of a mesostyle.

The tooth is heavier and more transverse than the type of *Ricardolydekkeria praerupta*, with the conules more distinct, somewhat more as in *Josepholeidya*, the metaconule somewhat larger and better separated from the protocone. The protostyle, or anterointernal cingulum cusp, is well developed and about as in *Ricardolydekkeria*, and the hypocone, or posterointernal cingulum cusp, is considerably smaller. The parastyle is strongly developed, also much as in *Ricardolydekkeria*, but there is a sharp, well-marked, continuous external cingulum and no trace of mesostyle or median external fold.

Although known only from one tooth, the genus is very distinctive and merits a name as one of the two oldest known South American mammals. Many isolated teeth of this general type are known from later beds, but all have strong mesostyles and other, less-marked distinctions. The affinities of *Wainka* are apparently with this group, *Josepholeidya*, *Ricardolydekkeria*, etc., very tentatively placed in the Proterotheriidae pending discovery of associated material which may determine the affinities more closely.

Wainka tshotshe Simpson, 1935

Text figure 38

Wainka tshotshe SIMPSON, 1935a, p. 9, fig. 8.

TYPE: A.M.N.H. No. 28505. Isolated left upper molar (M^1 or M^2).

HYPODIGM: Type and, doubtfully, A.M.N.H. No. 29101, left M_3.

HORIZON AND LOCALITY: Río Chico formation, 37 meters above the "Banco Verde" of the Salamanca, on Cerro Redondo west of Puerto Visser, Chubut, Argentine.

DIAGNOSIS: Sole known species of genus. Length of type 8.9 mm., width 12.8 mm.

The left M_3, from the same horizon and locality, A.M.N.H. No. 29101, is compatible with *Wainka tshotshe* in size and structure, and it resembles *Anisolambda* (which I believe to be the lower dentition of *Josepholeidya*, *Ricardolydekkeria*, or both) to about the same degree as *Wainka* resembles *Ricardolydekkeria*. The tooth measures 14.6

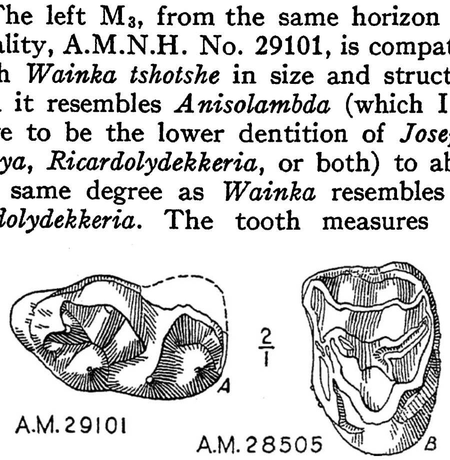

FIG. 38. *Wainka tshotshe* Simpson. A. A.M.N.H. No. 29101, left M_3. B. Type, A.M.N.H. No. 28505, left upper molar. Crown views. ×2. After Simpson, 1935a.

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[1] The doubtful *Theosodon*-like No. 28682, mentioned under *Victorlemoinea*, which may not really be from the Casamayor.

mm. by approximately 8 mm. (slightly broken). The general structure is as in *Anisolambda*, but the paraconid is slightly more external and is almost completely conical, being connected neither to the metaconid nor to the anterior crest from the protoconid. The latter crest does not curve so directly inward as in *Anisolambda*, but runs more forward and then turns internally at nearly a right angle. The hypoconulid projects very strongly, much more than in any species of *Anisolambda*, and there is a shelf, with sharp, denticulate rim, between and internal to it and the isolated, conical entoconid. The talonid, at least (broken off on the trigonid), has a sharp, continuous, but narrow external cingulum.

JOSEPHOLEIDYA AMEGHINO, 1901

Josepholeidya AMEGHINO, 1901, p. 384; 1904a, vol. 57, p. 340; 1904b, p. 124; 1906, p. 467; SCHLOSSER, 1923, p. 525; SIMPSON, 1935a, p. 10, fig. 10.

Josepho-Leidya = Plesiadapis Lemoine, GAUDRY, 1904, p. 9; 1906, p. 33, fig. 1.

Eulambda AMEGHINO, 1904a, vol. 57, p. 340; 1906, p. 467.

TYPE: *Josepholeidya adunca* Ameghino.

TYPE OF *Eulambda*: *Eulambda deculca* (Ameghino).

DISTRIBUTION: Río Chico and Casamayor, Patagonia.

DIAGNOSIS: Molars subquadrate to subtriangular. Parastyle and mesostyle[1] about equally prominent. Protoconule and metaconule well separated from the protocone, their bases nearly or quite in contact in the central valley. Hypocone tending to fuse basally with the protocone, constantly higher and often distinctly larger than the protostyle, except on M^3. An accessory cuspule constant in occurrence but variable in size and position on the posterior cingulum near or almost connate with the hypocone. Variable accessory cuspules tending to develop on base of inner sides of protocone.

The genus *Eulambda* was proposed in 1904, with a species formerly referred to *Josepholeidya* as type. The genera were treated henceforth as related. *Josepholeidya* was referred by Ameghino successively to the Meniscotheriidae (1901), Periptychidae (1904a), and Catathleidae (1906). Gaudry's equation of *Josepholeidya* with the primate *Plesiadapis* is an aberration unworthy of further attention.

Eulambda was supposed to be distinguished by many characters, of which the following seem to be real differences from the type specimen of the genotype of *Josepholeidya:*

Crown somewhat lower
Hypocone more closely applied to the protocone
Cingulum cusp so close to hypocone that latter appears bifid
A small accessory cuspule on the inner side of the base of the protocone

These characters seem very distinctive at first sight, but when a series of nine or 10 teeth of this general character is studied, as can now be done, it seems clear that these are highly variable characters and not of generic value. The basic plan of the tooth, and most of its details, are identical throughout, or as nearly so as would ever be true of a random sampling of upper molars of one genus or even one species. The variation in these details is an intergrading series that does not pass limits quite customary for such cuspule variation in one species of mammal teeth generally. It seems that Ameghino's original opinion was the more sound, and that only one genus is represented. A.M.N.H. No. 28512 is almost certainly, and A.M.N.H. No. 28513 is probably, M^3 of this genus. The characters are those usual in M^3 of most similar ungulates: size relatively smaller, contour more rounded or triangular, outer border more oblique, metacone smaller relative to paracone, and hypocone reduced (here not larger than the protostyle).

A.M.N.H. No. 28509 includes an upper premolar either of this genus or of *Ricardolydekkeria*, if indeed these are separate genera. It is probably P^2, or possibly P^3. The tooth is triangular with the shortest side posterior, and length and width equal. There are sharp, fairly well-separated, subequal paracone and metacone, small parastyle anterior to the paracone, no mesostyle, strong cingulum external to the metacone and there forming a cuspule, no conules or hypocone, cingulum-

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[1] Ameghino's figures of *J. adunca* give the impression that the styles are poorly developed, but this is because they are broken on the original specimen.

like internal heel forming a protocone much lower than the outer cusps.

None of our specimens will enter definitely into either of Ameghino's species, but any definite division into species is now futile in any event. Their variation is well shown in the accompanying figure (text fig. 39), in which I have placed the three principal types as if they were M^{1-3} of one form, which is quite possible, although of course hypothetical at present.

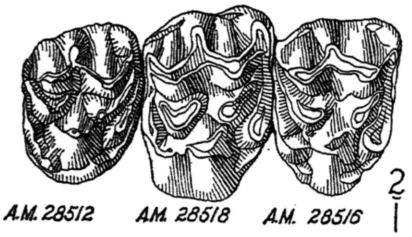

FIG. 39. *Josepholeidya* sp. Three isolated right upper molars, of different individuals, exemplifying the three main morphological types referred to this genus, assembled to illustrate the hypothesis that these teeth are M^{1-3} of the same species. A.M.N.H. Nos. 28512, 28518, and 28516, as labeled. Crown views. ×2.

Josepholeidya adunca Ameghino, 1901

Plate 11, figure 13

Josepholeidya adunca AMEGHINO, 1901, p. 384; 1904b, p. 124, figs. 142, 519.

Plesiadapis (*Josepho-Leidya*) *aduncus*, GAUDRY, 1904, p. 8, fig. 1.

TYPE: M.A.C.N. No. 10702. Left upper molar.

HYPODIGM: Type only, but eight upper molars in the American Museum may belong to this species.

HORIZON AND LOCALITY: (*Fide* Ameghino) Casamayor, west of the Río Chico, Chubut, Argentina. The American Museum of Natural History specimens possibly of this species are from Cañadón Vaca (seven specimens) and northeast of Cabeza Blanca (one specimen).

DIAGNOSIS: Crown of moderate height. Hypocone fairly well separated from protocone, posterior cingulum cusp distinct from hypocone. No internal accessory cuspules. Upper molar, length 7.9 mm., width 11.3 mm.

Josepholeidya deculca Ameghino, 1901

Plate 11, figure 14

Josepholeidya deculca AMEGHINO, 1901, p. 385.

Eulambda deculca, AMEGHINO, 1904a, vol. 57, p. 340; 1904b, p. 131, figs. 154, 518; CABRERA, 1935, p. 12.

TYPE: M.A.C.N. No. 10682. Left upper molar.

HYPODIGM: Type only.

HORIZON AND LOCALITY: (*Fide* Ameghino) Casamayor, south of Lago Colhué-Huapí, Chubut, Argentina. (Cabrera's reference of an uppermost Río Chico specimen to this species may be queried; see "*Josepholeidya* sp.," below.)

DIAGNOSIS: Hypocone partly confluent with protocone and nearly so with posterior cingulum cusp. Internal accessory cuspule present. Upper molar, length 8.2 mm., width 10.6 mm.

Josepholeidya sp.

Text figure 40

An upper molar in the Feruglio Collection (cast, A.M.N.H. No. 27890), from the late Río Chico of the Bajo de la Palangana, is referable to *Josepholeidya* and closely similar to *J. adunca* but is not considered specifically identifiable in the present unsatisfactory condition of specific definitions. Cabrera (1935) referred a specimen from the same horizon and locality to *Eulambda deculca*, and this I take also to be *Josepholeidya* sp. indet., as *Eulambda* seems to me quite surely synonymous with *Josepholeidya*, and I question the positive value of specific ascription of single teeth on the basis of the available data.

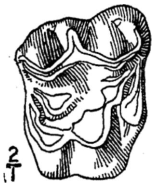

FIG. 40. *Josepholeidya* sp. Feruglio Collection (cast, A.M.N.H. No. 27890), right upper molar. Crown view. ×2.

RICARDOLYDEKKERIA AMEGHINO, 1901

Ricardolydekkeria AMEGHINO, 1901, p. 397; 1904b, p. 123; 1906, p. 467; SCHLOSSER, 1923, p. 525; SIMPSON, 1935a, p. 11, fig. 11.

Heterolambda AMEGHINO, 1904a, vol. 57, p. 338; 1904b, p. 67; 1906, p. 467.

Lopholambda AMEGHINO, 1904a, vol. 58, p. 36; 1904b, p. 97; 1906, p. 467.

TYPE: *Ricardolydekkeria praerupta* Ameghino.

TYPES OF SYNONYMS: *Heterolambda lunulata* Ameghino. *Lopholambda profunda* (Ameghino).

DISTRIBUTION: Río Chico and Casamayor of Patagonia.

DIAGNOSIS: Molars subtriangular. Parastyle and mesotyle about equally prominent. Protoconule and metaconule nearly confluent with protocone and not meeting in central valley. Hypocone cingulum-like, no tendency to fuse with protocone, little if any higher or larger than protostyle. Posterior cingulum cuspule usually absent, and no apparent tendency to form other cuspules.

Heterolambda has no essential differences from the type of *Ricardolydekkeria praerupta* except the facts that the crown is lower and that the width is less relative to the length. It seems unreasonable to maintain that these are in themselves of generic value. The specimens could well be, and I think probably are, non-homologous teeth not only of the same genus but also of the same species. *Heterolambda* may be a milk molar. *Lopholambda* was founded on a species at first referred to *Ricardolydekkeria*. It differs from the type of *R. praerupta* as follows:

Paracone and metacone with slightly more definite external convexities
Mesostyle relatively stronger
Protostyle slightly larger and with a feeble cingulum below it
Protoconule and metaconule slightly closer together

These differences in detail are not greater than often occur between different teeth of a single individual, and the agreement with *Ricardolydekkeria* is so close that the genera cannot be retained as really distinct.

With these genera added to it, *Ricardolydekkeria* is an unmistakable and easily distinguished morphological unit. It must be listed as a genus at present, and better specimens will probably confirm this. Yet it is distinctly possible that it is based on posterior upper premolars of *Josepholeidya*. In favor of this view are these facts:

The teeth differ most essentially from *Josepholeidya* in being simpler, more triangular, and with smaller hypocone.

They occur at the same horizons and localities.

In a series of teeth from the same locality, the specimens of *Ricardolydekkeria*, upon graphic analysis, prove to be of appropriate size and proportions to be P^3 and P^4 and those of *Josepholeidya* to be M^{1-3} of the same species.

The lower teeth of this group do not suggest the presence of more than one genus with species of about this size.

Opposed to it are these considerations:

Although in general the differences between the two genera suggest those between premolars and molars, in particular, they do not very closely follow these differences in the later proterotheres.

This relationship is probable only if some of the *Ricardolydekkeria* teeth are P^3, but *a priori* it seems improbable that P^3 would be so molariform at this time.

Teeth of *Ricardolydekkeria* are somewhat more numerous in collections than those of *Josepholeidya*, whereas an adequate sampling should show P^{3-4} only two-thirds as numerous as M^{1-3} and P^4 only one-third as numerous (the samples are, however, so small that the deviation from expectation is not significant).

Six well-preserved upper molars of *Ri-*

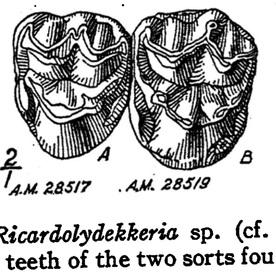

FIG. 41. *Ricardolydekkeria* sp. (cf. *praerupta*). Upper cheek teeth of the two sorts found together at Cañadón Vaca, dissociated specimens drawn together to illustrate the hypothesis that they are successive teeth of a single species. A.M.N.H. Nos. 28517 and 28519, as labeled. Crown views. ×2.

cardolydekkeria from the same place (in Cañadón Vaca) fall into two distinct groups. One group, with two representatives, is very little smaller than *R. praerupta* and probably includes close or exact equivalents of the type of that species. The other group, four teeth, is distinctly smaller, its largest specimen 10 per cent smaller than the smallest of the other group. The proportions and other characters are about the same. I take these groups to represent two different upper cheek teeth in the dentition of the same species, and figure them together to illustrate this hypothesis (text fig. 41).

As with *Josepholeidya* the supposed species of this genus seem at present to have little or no real value, but are listed as a matter of record.

Ricardolydekkeria praerupta Ameghino, 1901

Plate 11, figure 15

Ricardolydekkeria praerupta AMEGHINO, 1901, p. 397; 1904b, p. 123, figs. 141, 274, 524; 1906, p. 300, fig. 100.

TYPE: M.A.C.N. No. 10701. Right upper cheek tooth.

HYPODIGM: Type, but six American Museum of Natural History specimens from Cañadón Vaca may also belong to this species.

HORIZON AND LOCALITY: (*Fide* Ameghino) Casamayor, south of Lago Colhué-Huapí, Chubut, Argentina.

DIAGNOSIS: Metastyle inconspicuous. Mesostyle moderately prominent. Paracone and metacone ridges small. External cingulum discontinuous. Protoconule and metaconule far apart. Cingulum on protostyle. Upper tooth, length 9.2 mm., width 11.3 mm.

Ricardolydekkeria profunda Ameghino, 1901

Plate 11, figure 16

Ricardolydekkeria profunda AMEGHINO, 1901, p. 397.

Lopholambda profunda, AMEGHINO, 1904a, vol. 58, p. 36; 1904b, p. 97, figs. 105, 139, 523; CABRERA, 1935, p. 12.

TYPE: M.A.C.N. No. 10706. Right upper cheek tooth, lacking the posterointernal portion. Two other fragments of upper teeth. Two fragments of lower molars. Lectotype: the most complete upper tooth.

HYPODIGM: Lectotype only.

HORIZON AND LOCALITY: (*Fide* Ameghino) Casamayor, south of Lago Colhué-Huapí, Chubut, Argentina. (Cabrera's citation of *Lopholambda profunda* from the late Río Chico is queried as to species; see below.)

DIAGNOSIS: Mesostyle slightly more prominent. Paracone and metacone ridges more prominent. External cingulum more continuous. Protoconule and metaconule closer together. Faint cingulum on protostyle. Upper tooth, length about 10 mm.

The lower teeth with the type are of the sort grouped under *Anisolambda* below. They doubtless do belong to this genus or to *Josepholeidya*, but their exact association is doubtful.[1] This supposed species may well be synonymous with that preceding.

Ricardolydekkeria lunulata (Ameghino, 1904), new combination

Heterolambda lunulata AMEGHINO, 1904a, vol. 57, p. 338; 1904b, p. 67, figs. 63, 517.

TYPE: Isolated upper cheek tooth. Not found. An excellent cast of the type in sulphur, A.M.N.H. No. 11876, is, however, available and is as good for study as an original.

HYPODIGM: The sulphur cast of the type.

HORIZON AND LOCALITY: Casamayor of Patagonia. No other data.

DIAGNOSIS: Closely similar to *R. praerupta* but with lower crown and width less relative to length. Upper tooth (cast), length 8.9 mm., width 10.0 mm.

Ricardolydekkeria cinctula Ameghino, 1904

Plate 11, figure 17

Ricardolydekkeria cinctula AMEGHINO, 1904a, vol. 58, p. 35: 1904b, p. 158, figs. 196, 522; 1906, p. 300, fig. 99.

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[1] In this and most other similar cases, they doubtless were placed together because found at the same spot. Lest my refusal throughout to accept this as sufficient evidence of real association appear captious, it may be noted that in a number of cases the teeth so grouped together did not even belong to the same family, and that in general the chances are against isolated upper and lower teeth's being of the same individual under the field conditions here obtaining, even if found at exactly the same place. Association on the basis of field data only becomes probable when considerable parts of the dentition occur, without duplication or significant admixture of other forms, and only becomes certain when the jaws are preserved in contact or nearly so and, of course, are morphologically compatible.

TYPE: M.A.C.N. No. 10705. Right upper cheek tooth.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayor, Patagonia. No other data.

DIAGNOSIS: Metastyle slightly more prominent than in *R. praerupta*. Type considerably wider and slightly shorter than in the latter species.

Ricardolydekkeria sp.

Text figure 42

A right upper cheek tooth in the Feruglio Collection (cast, A.M.N.H. No. 27891), from the upper level of the Río Chico in the Bajo de la Palangana, resembles *R. cinctula* sufficiently for reference to this genus. It measures 7.2 by 9.8 mm., smaller than are the Casamayor specimens, and it also has the mesostyle weaker, the hypocone more internal, and a tendency to form an internal cingulum. This is probably a new species, but good definition is not now possible. The undescribed specimen from the same horizon and locality identified by Cabrera (1935, p. 12) as *Lopholambda profunda* may belong to this unnamed or indeterminate form.

FIG. 42. *Ricardolydekkeria* sp. Feruglio Collection (cast, A.M.N.H. No. 27891), right upper cheek tooth. Crown view. ×2. After Simpson, 1935a.

GUILIELMOFLOWERIA AMEGHINO, 1901

Guilielmofloweria AMEGHINO, 1901, p. 397; 1906, p. 467.

TYPE: *Guilielmofloweria plicata* Ameghino.

DISTRIBUTION: Casamayor, Patagonia. A probable ally, perhaps but probably not this genus, occurs in the Río Chico.

DIAGNOSIS: Based on large, robust, subtriangular upper teeth, with very prominent mesostyle, large conules closely appressed to each other and to the protocone but remaining separate to an advanced wear stage, cingulum-like hypocone simple and quite independent of protocone, and strong external cingulum on each side of the mesostyle.

This genus is based on a single tooth which resembles *Josepholeidya* and, even more closely, *Ricardolydekkeria*, to some extent combining characters of the two, but it is distinctive and probably is a valid genus. This tooth is definitely larger than the size range reasonably allowable for any known species of the other two genera, which considerably adds to the probability that its distinctions are really of taxonomic value and not due merely to position in the series or individual variation.

A.M.N.H. No. 28514 (text fig. 43) is an upper tooth measuring 11.1 by 15.0 mm., about the size of *G. plicata*. It differs in being less transverse, the mesostyle even larger, in fact relatively enormous and usurping the posteroexternal root, and the conules farther from each other and more confluent with the protocone. This differs at least as much from *Guilielmofloweria* as does *Ricardolydekkeria* from *Josepholeidya*, and on the established scale should become type of a new genus, but I suspect that it may be a position variant of *Guilielmofloweria* and classify it as such for the present.

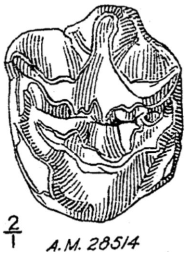

FIG. 43. *Guilielmofloweria* sp. A.M.N.H. No. 28514, left upper cheek tooth. Crown view. ×2.

A.M.N.H. No. 28572, the inner half of a worn upper molar from the Río Chico in Cañadón Hondo, is inadequate for identification but suggests this genus.

Guilielmofloweria plicata Ameghino, 1901

Plate 11, figure 18

Guilielmofloweria plicata AMEGHINO, 1901, p. 397; 1904b, p. 206, figs. 275, 520; 1906, p. 299, fig. 96.

TYPE: M.A.C.N. No. 10703. Left upper cheek tooth.

HYPODIGM: Type.

HORIZON AND LOCALITY: Casamayor, south of Lago Colhué-Huapí, Chubut, Argentina.

DIAGNOSIS: Sole established species of the genus. Length 11.1, width 15.7 mm.

ANISOLAMBDA AMEGHINO, 1901

Anisolambda AMEGHINO, 1901, p. 383.
Anissolambda, AMEGHINO, 1906, p. 467.

TYPE: *Anisolambda fissidens* Ameghino.

DISTRIBUTION: Casamayor, Patagonia.

DIAGNOSIS: Lower teeth probably belonging to the group of *Josepholeidya*, *Ricardolydekkeria*, and *Guilielmofloweria* and synonymous with one or more of these genera. Molars with small, high trigonid basins, closed on the inner side by the large conical paraconid, which is nearly or quite equal to the metaconid, from which it is separated by a narrow notch. Hypoconid large and crescentic, hypoconulid and metaconid approximated but separate until advanced wear stages. Hypoconulid of M_3 projecting and forming an imperfect third lobe. The metaconid somewhat compressed transversely and sending backward along the inner side of the tooth a rapidly falling sharp ridge.

The lower molars placed here closely resemble those of didolodonts from which they are, however, easily distinguished, especially by the character of the paraconid. I was at first inclined to agree with Ameghino in considering these lower teeth close to *Victorlemoinea*, but renewed study and discovery make it seem much more probable, if not certain, that they belong to this group of genera and that dissimilar, purely lophiodont, bicrescentic lower molars also known in the Casamayor are probably those of *Victorlemoinea*. The reasons for this are:

Morphology and Occlusion: These lowers are intermediate between bunodont (cf. didolodonts) and lophiodont molars (cf. *Victorlemoinea*), which is also true of *Josepholeidya*, etc. The high, closed trigonids suggest low, small hypocones, also strikingly true of *Josepholeidya* and its allies as opposed to any other Casamayor ungulates. Occlusion is easily possible between the two.

Size Range: *Anisolambda fissidens* is slightly large for average members of this group, yet within its size range. Our specimens from Cañadón Vaca seem to be of entirely appropriate sizes for correlation with the upper teeth of *Josepholeidya* and *Ricardolydekkeria* from the same locality. No species of *Victorlemoinea* small enough to occlude with these teeth is known.

Abundance: Relative abundance also favors this allocation. For instance, in the Cañadón Vaca material, most valid for this purpose as being a large series from the same horizon and locality, *Victorlemoinea* and the lophiodont lowers referred to it are both very rare, while members of the *Josepholeidya* group and *Anisolambda* are both several times as abundant.

Ameghino placed three species in *Anisolambda: A fissidens*, *A. longidens*, and *A. latidens*. Only the genotype belongs to the group here discussed. *A. longidens* is probably closer to *Victorlemoinea*, although not certainly so, and has been discussed there. *A. latidens* has a totally different structure: the trigonid is not crescentic, having the paraconid reduced and probably external; the anterior hypoconid crest runs to the protoconid and not to the metaconid; and the entoconid is widely separate from the hypoconid and forms a transverse crest. This cannot be a litoptern at all, but is certainly a notoungulate; see *Eochalicotherium* (in part 2 of this study).

Anisolambda will very probably be found synonymous with one or more of the genera based on upper teeth, but it may conveniently and properly be retained for the present as a formal genus for lower teeth only.

Anisolambda fissidens Ameghino, 1901

Plate 11, figures 19–21

Anisolambda fissidens AMEGHINO, 1901, p. 383.

TYPE: M.A.C.N. No. 10668. Right M_{1-3} and left M_{1-2} of two different individuals. Lectotype: the right M_{1-2}.

TABLE 19

LECTOTYPE OF *Anisolambda fissidens*

M_1		M_2		M_3	
L	W	L	W	L	W
9.6	7.4	10.8	8.0	11.2	8.0

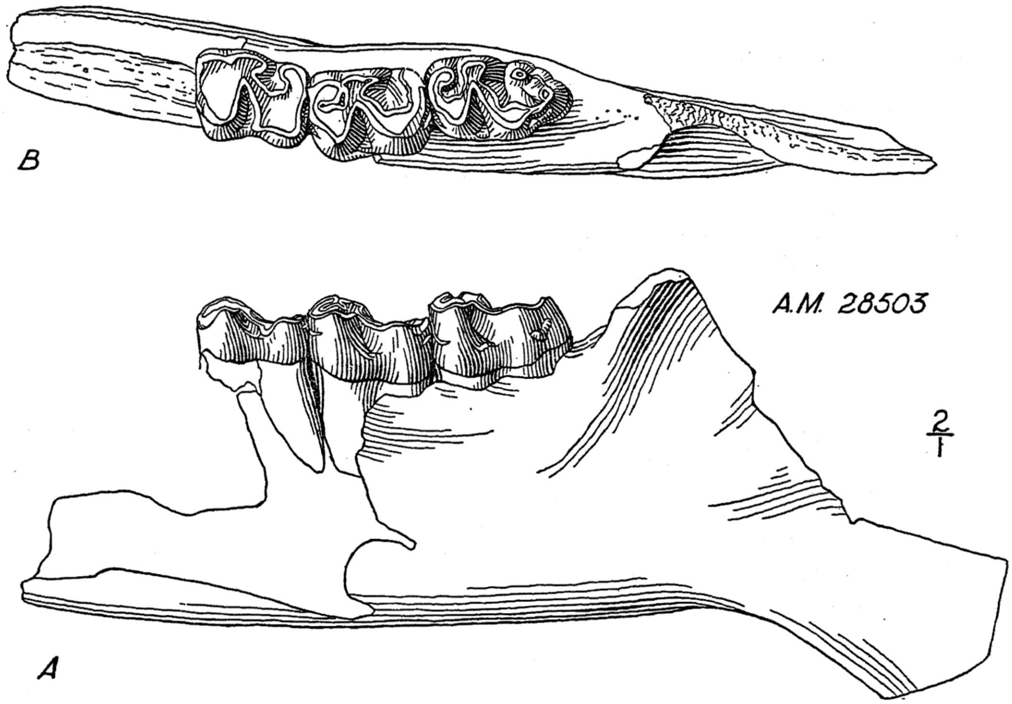

FIG. 44. *Anisolambda amel*, new species. Type, A.M.N.H. No. 28503, left lower jaw with M_{1-3}. A. External view. B. Crown view. ×2.

HYPODIGM: Both syntypes.

HORIZON AND LOCALITY: Casamayor, Patagonia. No other data.

DIAGNOSIS: Size relatively large. Strong external cingulum. Hypoconulid of M_3 relatively smaller.

Anisolambda amel,[1] new species

Text figure 44

TYPE: A.M.N.H. No. 28503. Left lower jaw with M_{1-3}. Collected by C. S. Williams.

HYPODIGM: Essentially the type. Three similar but slightly larger isolated lower molars are known from the same locality.

HORIZON AND LOCALITY: Casamayor, Cañadón Vaca, Chubut, Argentina.

DIAGNOSIS: Over 20 per cent smaller than *A. fissidens*. No external cingula. Hypoconulid of M_3 large.

As this is the best known specimen of this group and is certainly specifically distinct from *A. fissidens*, it must receive a name. Upper teeth from the same locality also suggest distinction from Ameghino's species and have not been named, so that even the

TABLE 20

Anisolambda amel AND *Anisolambda* SP.

	M_1		M_2		M_3	
	L	W	L	W	L	W
Type, A.M.N.H. No. 28503	7.3	6.0	7.8	6.0	9.5	5.8
Anisolambda sp., A.M.N.H. No. 28506	—	—	—	—	10.6	6.3
Anisolambda sp., A.M.N.H. No. 28510	—	—	—	—	10.6	6.4

---

[1] Amel, Tehuelche, child, in allusion to its smaller size.

union of upper and lower teeth, when that becomes possible, should not invalidate *A. amel.*

The only interesting peculiarity of the jaw is that the lower border turns down abruptly at the beginning of the angular region.

Measurements of the type and two other specimens from the same locality are given in table 20.

POLYMORPHIS Roth, 1899

Polymorphis Roth, 1899, p. 385; Simpson, 1936d, pp. 66, 73.

= *Trigonostylops*, Ameghino, 1899, p. 12.

Megacrodon Roth, 1899, p. 384; Simpson, 1936d, pp. 66, 72.

Parts = *Polyacrodon*, *Lambdaconus*, and *Didolodus*, Ameghino, 1899, p. 12.

Type: *Polymorphis lechei* Roth, 1899.

Type of *Megacrodon*: *Megacrodon planus* Roth, 1899.

Distribution: Musters formation, Patagonia.

Diagnosis: Dentition complete, incisors not enlarged, no marked diastemata. P_{3-4} with crescentic trigonids, paraconid low but present, internal, talonids with median longitudinal crest and vague posteromedian cuspule. Molar trigonids compressed anteroposteriorly, with strong transverse protoconid-metaconid crest, anterior crest from protoconid descending rapidly and ending without distinct paraconid. Talonids of M_{1-2} sublophiodont, crescentic, with large hypoconids and entoconid, hypoconulid smaller and projecting as a posteromedian spur. Vague third lobe on M_3, with large hypoconulid well connected with entoconid.

Roth defined *Megacrodon* solely on the low and round horizontal ramus of the mandible, a character of almost no diagnostic value in this group. He referred two species to the genus, *M. prolixus* and *M. planus*, in that order but both on the same page. Of these, *M. planus* was based on the better type and also shows Roth's supposed generic character most clearly; indeed one of the differences between the two species is that the ramus is less low and round in *M. prolixus*. I therefore selected *M. planus* as genotype in 1936 (p. 72), pointing out that Roth's two species of *Megacrodon* might not be congeneric and that *M. planus* might be congeneric with "*Lambdaconus*" *alius* Ameghino. In the light of renewed research and thorough comparison of all the material, including some excellent new specimens, it seems that *Megacrodon planus* and "*Lambdaconus*" *alius* cannot be separated generically from each other or from *Polymorphis lechei*. They certainly have nothing to do with *Lambdaconus*, and I select *Polymorphis* as the name of the genus. It was published one page after *Megacrodon*, but simultaneously. It was based on incomparably better and more diagnostic material and was more fully, adequately, and accurately defined by Roth. *Megacrodon prolixus* is here very tentatively referred to *Xesmodon*.

Roth compared *Polymorphis* and *Megacrodon* only by saying that in *P. lechei* P_{3-4} are somewhat like those of *Megacrodon* (i.e., *M. prolixus*) and by giving different, but not very distinctive, descriptions of these teeth in the two. This comparison, in any case, does not apply to the genotype of *Megacrodon*, in which P_{3-4} are unknown. *M. planus* was further likened to *Eupithecops* and *P. lechei* to *Didelphis* in some details, but neither comparison is useful. Ameghino in 1899 equated *Megacrodon prolixus* with *Lambdaconus suinus*, *M. planus* with *Didolodus multicuspis*, and *Polymorphis lechei* with *Trigonostylops wortmani*, but these proposed synonymies cannot be correct either as to genera or as to species. Unfortunately Ameghino's desire to invalidate Roth's genera and species, the types of which he had not seen, led him to reidentify Roth's materials in what were, as he later learned, completely unjustified ways.

The only noteworthy possible generic differences known between *Megacrodon planus* and *Polymorphis lechei* are the possible absence of I_1 and the possibly more bunodont M_3 of the former. The incisive region is broken in such a way that I_1 may have been present, and comparison with allied forms makes it probable that it was present. M_3 is deeply worn, and from other less worn specimens it seems probable that it may really have had the same degree of limited lophiodonty as in *Polymorphis*. All other known characters are so closely similar in the two forms that their generic separation seems unwarranted. They are from the same locality and, presumably, horizon.

Lambdaconus alius Ameghino, 1901, was, of course, referred to that genus because of comparison with forms like "*Lambdaconus*" *mamma*, which (as shown above) belongs to *Paulogervaisia*, and not with the genotype, *Lambdaconus suinus*, which is very different and is probably neither a condylarth nor a litoptern. The implied comparison with *Paulogervaisia* is apt, but does not involve generic identity. Ameghino was unable to make any close comparison with *Polymorphis*, adequate data on which were not then available to him, and there is little doubt that his species belongs in this genus. The relatively minor differences from the genotype are mentioned below, under the species.

Polymorphis lechei Roth, 1899

Plate 12, figure 1; text figure 45

Polymorphis lechei ROTH, 1899, p. 385; SIMPSON, 1936d, pp. 66, 73.

=*Trigonostylops wortmani*, AMEGHINO, 1899, p. 12.

TYPE: M.L.P. No. 12-2168. Left lower jaw and symphysis with left I_1–M_3 and right I_{1-3}. Roth Collection.

HYPODIGM: Type and A.M.N.H. No. 29480, lower jaw with left P_2–M_3.

HORIZON AND LOCALITY: Type from "Cretáceo superior de Lago Musters." Probably Musters formation of the Cerro del Humo, Chubut. Our specimen is from the Cerro del Humo.

DIAGNOSIS: I_1 well developed. Canine larger than P_1 (at least in type). Molars all sublophiodont. Length P_1–M_3 66.5 mm.

Roth (1899) stated that this was based on two lower jaws, one with the dentition complete on one side and the other with five cheek teeth. The first specimen is that here listed as type, which may be taken as a designated lectotype if the other be considered a syntype. The less perfect specimen was not found in the collection, and there is no evidence that Roth's original description derived any characters from it. A.M.N.H. No. 29480,

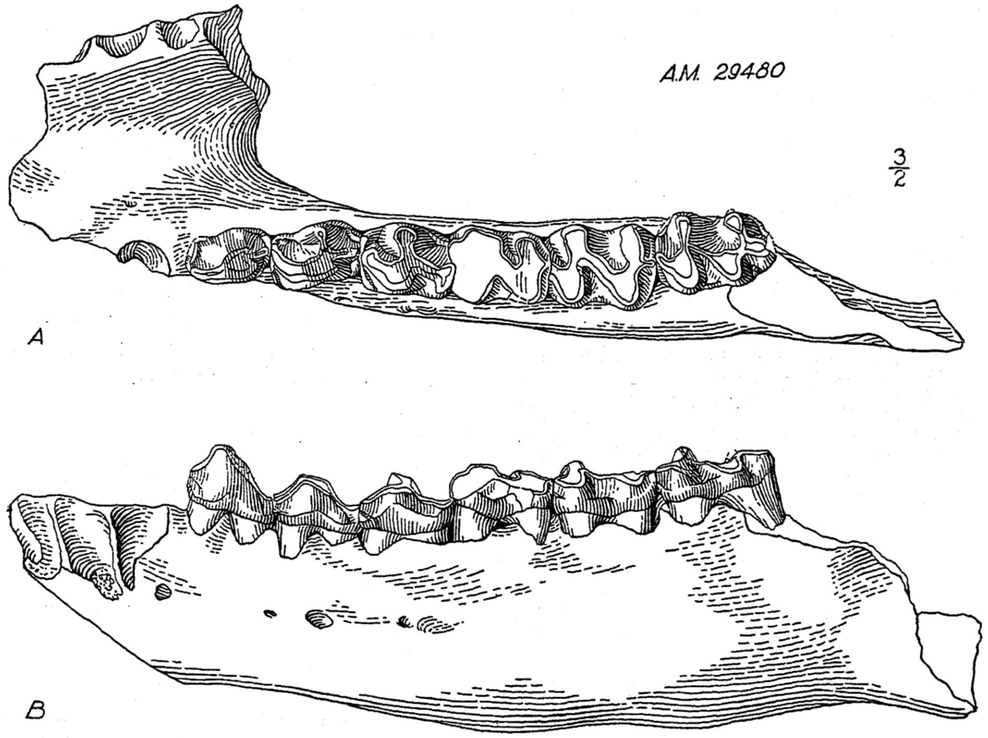

FIG. 45. *Polymorphis lechei* Roth. A.M.N.H. No. 29480, symphysis and left lower jaw with P_2–M_3. A. Crown view. B. External view. ×3/2.

symphysis with alveoli and left ramus with P_2–M_3, comes from what is probably the type locality. It differs about as much from the type as do some of the supposedly distinct species, yet these differences do not establish positive specific difference on the basis of single specimens.

The dental formula is $_{3.1.4.3}$. The incisors, canine, and especially P_1 are well spaced, but there are no decided diastemata. The incisors and canines of the two sides are arranged in a semicircle.[1] The cheek teeth are in an almost straight line.

The incisors are all simple, almost styliform teeth, increasing slightly in size from I_1 to I_3. All are procumbent. The canine is larger than I_3 or P_1 in the type, although in our referred specimen the roots of canine and P_1 seem to have been of the same size, and this seems also to be true in *P. alius* and *P. planus*. The canine is less procumbent than the incisors, little expanded, anteroposteriorly, and slightly recurved.

P_1 has a single, almost circular root and is a small, simple tooth. Each of the other cheek teeth has two subequal roots. As preserved in all specimens referred to the genus, P_2 is higher than the other cheek teeth and is long and compressed laterally. Its trigonid is an incipient crescent with very rudimentary paraconid and metaconid, while the heel is small, sharply sloping, with a pronounced median longitudinal crest, on either side of which is a small basin, and a vague posteromedian cuspule.

P_{3-4} have the trigonid well developed and strongly crescentic or triangular, relatively shorter and wider on P_4. The metaconid is large, about equal to the protoconid on P_4. The paraconid is small and not very distinct. In the type it seems to be larger on P_3 than on P_4, but this may be an effect of wear. In any case it is the end of a sharp, descending, anterior crest of the trigonid crescent. The talonid is larger than on P_2, but on both P_3 and P_4 it is shorter than the trigonid and in the type it is slightly narrower than the trigonid, while in A.M.N.H. No. 29480 the two are of about equal width.

The molar trigonids are short, barely equal to the talonid on M_1 and relatively shorter on M_{2-3}. At least in slightly worn specimens the metaconid is taller than the protoconid, and these two cusps are united by a strong, sharp, slightly oblique transverse crest. The likewise sharp but less prominent anterior wing of the protoconid crescent descends rapidly and ends without forming a distinct cusp, the paraconid as such being absent. This absence, with the weakness of the anterior crest and compression of the trigonid, gives an aspect markedly unlike the strong and relatively open trigonid crescent of most later litopterns. The talonid crescent on M_{1-2} is strongly crescentic with large hypoconid and entoconid and a well-marked basal metaconid-hypoconid-entoconid crest, while the hypoconulid is developed as a short, median, anteroposterior spur from the hypoconid-entoconid crest. The talonid of M_3 is more elongate, with a larger and more cuspidate hypoconulid united by a strong crest to the entoconid and by a slightly weaker crest to the hypoconid. There is a small basin internal to the hypoconulid and posterior to the entoconid.

As in most litopterns, the horizontal ramus is relatively long and slender, somewhat rounded on the external face. The symphysis

TABLE 21

Polymorphis planus

	P_2		P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W	L	W
M.L.P. No. 12-2168	9.2	5.5	9.6	5.9	8.8	6.8	9.5	7.4	11.0	8.0	11.5	7.3
A.M.N.H. No. 29480	8.6	4.8	8.5	5.8	8.7	6.5	9.3	6.7	9.7	7.4	11.1	7.3

---

[1] But if the incisor crowns were lacking and particularly if their alveoli were also broken, as in the other jaws referred to this genus, the rather broad and rounded effect of the present type would disappear and the front end of the jaw would seem to be narrower and somewhat pointed, an apparently distinct difference which does not seem to be real.

is completely fused and extends approximately to the posterior end of P_2.

M.L.P. No. 12-2168: Maximum diameters of crowns: I_1 3.7, I_2 4.1, I_3 4.6, C 5.6, P_1 5.0 mm. Depth of mandible on inner face below M_2 21.5. Other measurements are given in table 21.

Polymorphis planus (Roth, 1899), new combination

Plate 12, figure 2

Megacrodon planus ROTH, 1899, p. 384; SIMPSON, 1936d, pp. 66, 72–73.

=*Didolodus multicuspis*, AMEGHINO, 1899, p. 12.

TYPE: M.L.P. No. 12-1732. Symphysis and nearly complete right ramus with crown of M_3. Roth Collection.

HYPODIGM: Type only.

HORIZON AND LOCALITY: "Cretáceo superior de Lago Musters." Probably Musters formation of the Cerro del Humo, Chubut.

DIAGNOSIS: I_1 possibly reduced or (improbably) absent. Canine and P_1 subequal. M_3 slightly larger than in *P. lechei*, possibly more bunodont. Horizontal ramus relatively shallow and thick.

This species is very inadequately characterized. The surely established data do not sufficiently distinguish it from *Polymorphis lechei*, with which it might be synonymous, and on the other hand the most diagnostic features are doubtful or unknown, so that such synonymy cannot be established. M_3 measures 13.4 mm. in length by 9.0 in width, and the depth of the ramus internally beneath M_2 is 18.5 mm., its width here 13.5 mm.

Polymorphis alius (Ameghino, 1901), new combination

Plate 12, figures 3–4

Lambdaconus alius AMEGHINO, 1901, p. 377.

TYPE: M.A.C.N. No. 10893. Lower jaw with left P_2–M_1, right P_2–M_3, and alveoli. Ameghino Collection.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Musters formation, Patagonia. No exact data.[1]

DIAGNOSIS: Molars possibly more bunodont than in *P. lechei* and heel structure apparently somewhat different, more *Didolodus*-like, but these distinctions all very dubious. M_3 possibly more rounded and heel reduced, also doubtful. Size larger than *P. lechei* or *P. planus*.

The type of this species has the teeth so deeply worn that their real structure cannot be determined and its vestiges may be quite misleading. The general form of jaw and dentition, arrangement of incisors and canine, one-rooted P_1, relative sizes, shapes, molarization and other gross features of P_{2-4}, and many other characters so closely resemble *Polymorphis lechei* that I now see no reason to separate the genera. In their different stages of wear the molars are so unlike, superficially, that I was at first disinclined to compare them closely, but an individual variant of the *Polymorphis* type could, if deeply worn, produce the molar structure seen in "*Lambdaconus*" *alius*.

The real specific characters of the present form are not properly established, but the species will probably prove to be valid. The locality also, although unknown, is different from that of Roth's species which came from

TABLE 22

TYPE OF *Polymorphis alius*

P_2		P_3		P_4		M_1		M_2		M_3	
L	W	L	W	L	W	L	W	L	W	L	W
10.5	5.8	10.4	6.5	9.5	7.9	11.7	9.6	12.5	10.7	14.5	10.5

---

[1] A slip with the specimen says "*Notostylops Colhuapi*," i.e., Casamayor beds south of Lake Colhué-Huapí. The locality may be correct, but this slip was evidently never meant to apply to this specimen, since Ameghino placed the species in the *Astraponotus* fauna. Aside from his almost invariable accuracy in such respects, the independent discovery of several closely allied specimens in the Musters and none so closely allied in the Casamayor confirms Ameghino's statement as to the age of the specimen.

a locality never worked by Carlos Ameghino.

The lengths of P_4 and the molars are considerably reduced by wear.

POLYACRODON Roth, 1899

Polyacrodon Roth, 1899, p. 382; 1927, pp. 248, 249; Simpson, 1936d, pp. 66, 74.

Parts = *Didolodus*, *Lambdaconus*, and *Megacrodon*, Ameghino, 1899, p. 12.

Decaconus Ameghino, 1901, p. 378; 1906, p. 470; Simpson, 1936d, pp. 66, 74.

Periacrodon Ameghino, 1904a, vol. 57, p. 334; 1906, p. 470; Roth, 1927, p. 247 [but continues to use *Polyacrodon*]; Simpson, 1936d, p. 74 [as synonym of *Decaconus*].

Oroacrodon Ameghino, 1904a, vol. 57, p. 335 [to replace *Polyacrodon* Roth, 1899, *nec Polyacrodus* Jaeckel, 1899]; 1906, p. 470; Schlosser, 1923, p. 525; Roth, 1927, p. 201 [but also uses *Polyacrodon*]; Simpson, 1936d, p. 74 [as synonym of *Polyacrodon*].

Type: *Polyacrodon ligatus* Roth, 1899.

Type of *Decaconus*: *Decaconus intricatus* Ameghino, 1901.

Type of *Periacrodon*: *Polyacrodon lanciformis* Roth, 1899.

Distribution: Musters formation, Patagonia.

Diagnosis: Litoptern upper molars with strong parastyle and mesostyle, metastyle very weak or absent, paracone and metacone subcrescentic or compressed conical, conules large, bunoid, and independent, large independent cingular hypocone, strong anterior and posterior cingulum cuspules.

Roth originally described *Polyacrodon* with two species, *P. lanciformis* and *P. ligatus*, in that order on the same page, without designation of type. Ameghino (1904a) maintained that *Polyacrodon* was preoccupied by *Polyacrodus* and proposed to substitute the new name *Oroacrodon*. In the same publication he removed *P. lanciformis* to a new genus, an action leaving only *P. ligatus* in *Polyacrodon-Oroacrodon* and hence fixing this as the type of those identical genera. In the meantime, Ameghino (1901) had described and named *Decaconus* as distinct from *Polyacrodon*. I have suggested (1936d) that *Polyacrodon* is a valid name, not being preoccupied by *Polyacrodus* under the International Rules, and that *Periacrodon* is synonymous with *Decaconus*. Since I now further believe that *Decaconus* is synonymous with *Polyacrodon* (and hence with *Oroacrodon*), this reduces all three of Ameghino's names to synonymy with *Polyacrodon* Roth.

In separating Roth's two species generically, Ameghino noted certain real differences between them, but he does not seem to have compared that which he called *Periacrodon* with his own prior genus *Decaconus*. They resemble each other to such a point that I cannot separate the types specifically.

The principal differences, aside from slight size distinction, between "*Periacrodon*" and "*Oroacrodon*," or in other words between Roth's *Polyacrodon lanciformis* and *P. ligatus*, are as follows:

P. lanciformis	*P. ligatus*
Parastyle slightly weaker	Parastyle prominent
Protoconule and metaconule distinct	Smaller
Hypocone internal	Hypocone slightly less internal
Definite cingulum cusp external to hypocone	Less definite
Internal cingulum continuous, cuspidate	Somewhat less continuous or cuspidate, rising to a point on the protocone

These are all rather slight differences of degree and not of kind, and even if they are supposed to occur on homologous teeth it is very doubtful whether they merit more than specific rank at best. In fact it seems highly probable that *Polyacrodon lanciformis* and the inseparable species *Decaconus intricatus* are based on isolated M^1, M^2, or both, while *Polyacrodon ligatus* is based on M^3. If this is true, they could well be not only the same genus but also the same species, a possibility enhanced by their occurrence together. I tentatively define them as species below, but can see no basis for retaining them as genera.

It is highly probable that *Polyacrodon* is the upper dentition of *Polymorphis*. They cover about the same size range, occlude well, and occur in about equal numbers at the same or closely approximated localities and horizons. The presence of distinct genera, such as

Xesmodon and *Heteroglyphis*, and the general doubt that still lies over this whole scrappy material and its intricate synonymy lead me, however, to retain the two genera as tentatively distinct. *Polyacrodon* is a genus, perhaps artificial, for upper molars and *Polymorphis* for lower teeth of animals surely closely related and probably synonymous in part or altogether. The two names were proposed in the same publication, *Polyacrodon* on a prior page but *Polymorphis* on a much better type.

The morphology of these various teeth may be described together, rather than under the imperfectly known or distinguished species. The only specimen with associated teeth is A.M.N.H. No. 29482, an upper jaw fragment with the posterior end of P^4, M^1 nearly complete but much worn and with the internal cingulum broken, and M^2 with most of the enamel broken off. P^4 has a strong metastyle and a posterointernal basin similar to the anterointernal basins of the molars. M^1 of this specimen has very strong parastyle and mesostyle but no metastyle. Paracone and metacone are subequal and crested anteroposteriorly. The conules are truncated but were evidently large, the protoconule probably somewhat the larger, and probably not definitely united to any neighboring cusps. The hypocone is large and almost directly posterior to the protocone. It passes externally into a posterior cingulum enclosing a small basin and bearing a cuspule, here worn but evidently small. There is a very strong anterior cingulum, forming a basin and bearing a relatively large cuspule immediately anterointernal to the protoconule. There was an internal cingulum but it is broken away.

The type of *P. lanciformis* is closely similar to the tooth just described but has the mesostyle relatively smaller, although still large, the posterior cingulum cuspule larger and more distinct, the hypocone slightly more internal. There is a strong internal cingulum, continuous with the anterior cingulum and completely circling the protocone but not the hypocone. It is broken up into definite small cuspules. The type of "*Decaconus intricatus*" is practically indistinguishable from this in any essential character of size or structure. The chief differences of *P. ligatus* have already been noted.

Polyacrodon ligatus Roth, 1899

Plate 13, figure 1; text figure 46

Polyacrodon ligatus ROTH, 1899, p. 383; SIMPSON, 1936d, pp. 66, 74.

=*Didolodus multicuspis*, AMEGHINO, 1899, p. 12.

Oroacrodon ligatus, AMEGHINO, 1904a, vol. 57, p. 335; 1904b, p. 204, figs. 273, 550.

TYPE: M.L.P. No. 12-2169. Isolated right upper molar. Roth Collection.

HYPODIGM: Type and, tentatively, A.M.N.H. No. 29481, unworn right upper molar.

HORIZON AND LOCALITY: Type from "Cretáceo superior de Lago Musters." Probably Musters formation of the Cerro del Humo, Chubut. Referred specimen from Musters level, south of Lake Colhué-Haupí.

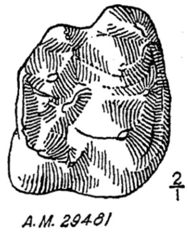

FIG. 46. *Polyacrodon ligatus* Roth. A.M.N.H. No. 29481, right upper molar. Crown view. ×2.

DIAGNOSIS: Isolated tooth smaller than others referred to genus, with prominent parastyle, small conules, hypocone not fully internal, posterior cingulum cusp weak, internal cingulum rising to a point on protocone not quite continuous, markedly cuspidate. Possibly M^3 of the same species as *P. lanciformis*. Length 8.5, width 10.7 mm.

A.M.N.H. No. 29481 closely resembles the type of this species but is a little larger, 9.7 by 12.2 mm., the conules are more distinct (perhaps only because less worn), and the hypocone is perhaps a trifle more prominent.

Polyacrodon lanciformis Roth, 1899

Plate 13, figure 2; text figure 47

Polyacrodon lanciformis ROTH, 1899, p. 383; 1927, p. 247; SIMPSON, 1936d, p. 66 [but as pertaining to *Decaconus*].

=*Lambdaconus suinus*, AMEGHINO, 1899, p. 12.

Periacrodon lanciformis, AMEGHINO, 1904a, vol. 57, p. 334; 1904b, p. 129, fig. 151; 1906, p. 343, fig. 175.

Decaconus lanciformis, SIMPSON, 1936d, p. 66.
Decaconus intricatus AMEGHINO, 1901, p. 378; 1904b, p. 126, figs. 146, 573; 1906, p. 302, fig. 104.

TYPE: M.L.P. No. 12-2170. Isolated left upper molar. Roth Collection.

TYPE OF *Decaconus intricatus:* M.A.C.N. No. 10897. Isolated right upper molar. Ameghino Collection.

HYPODIGM: The two types, as above, and, with some reserve, A.M.N.H. No. 29482, part of upper jaw with incomplete P^4–M^2.

HORIZON AND LOCALITY: "Cretáceo superior de Lago Musters." Probably Musters formation of the Cerro del Humo, Chubut. Type of "*Decaconus intricatus*" from *Astraponotus* fauna (i.e., Musters) but without other data. Referred A.M.N.H. No. 29482 from Musters formation at Cerro Blanco.

DIAGNOSIS: Isolated teeth somewhat larger than the type of *P. ligatus*, parastyle slightly weaker but still prominent, conules distinct, hypocone internal, posterior cingulum cusp distinct, internal cingulum continuous and cuspidate. Possibly includes M^{1-2} of *P. ligatus*.

M^1 of A.M.N.H. No. 29482, already referred to, seems to differ from the type of *P. lanciformis* in having the mesostyle more prominent, the posterior cingulum cusp weaker, and the internal cingulum weaker, but the latter is broken and the whole tooth is worn. It may also be that the type is M^2, a tooth too broken on our specimen to afford a good comparison.

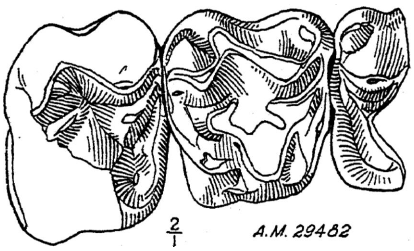

FIG. 47. *Polyacrodon lanciformis* Roth. A.M.N.H. No. 29482, right M^1 and parts of associated P^4 and M^2. Crown view. ×2.

The dimensions of M^1 of our specimen and of the two isolated types are given in table 23.

TABLE 23

Polyacrodon lanciformis

	L	W
M.L.P. No. 12-2170	10.5	14.5
M.A.C.N. No. 10897	10.5	14.0
A.M.N.H. No. 29482	11.7	*ca.* 13.5

XESMODON BERG, 1899

Glyphodon ROTH, 1899, p. 383 [*nec Glyphodon* Günther, 1858]; SIMPSON, 1936d, pp. 69, 73 [as synonym of *Xesmodon*].
Xesmodon BERG, 1899, p. 79 [to replace *Glyphodon*, preoccupied]; SIMPSON, 1936d, pp. 69, 73.

TYPE: *Glyphodon langi* Roth, 1899.

DISTRIBUTION: Musters, Patagonia.

DIAGNOSIS: Upper molars similar to *Didolodus* and to *Polyacrodon*, bunodont or nearly so, paracone and metacone slightly compressed cones, anterior cingulum present, hypocone cingular and large, conules both well developed and probably subequal. Distinguished chiefly by the probable absence of an external cingulum, very weak mesostyle, and subequal but weak parastyle and metastyle.

The dental material of the only known specimen surely referable to this genus is very imperfect, consisting only of the external parts of left M^2 and right M^3 and of most of left M^3, all considerably worn and rather obscure. These seem to establish definite differences in the outer molar wall from all other known Patagonian genera except *Paulogervaisia*. It is not, in fact, distinguishable from *Paulogervaisia* at present, but both genera are very inadequately known, and it is somewhat improbable that they are really synonymous. The inconclusive dental evidence thus tends to place *Xesmodon* in the Didolodontidae, but with much resemblance also to forms more probably litoptern.

Most of the skull is known, as described below, but in poor preservation. No skulls of contemporaneous or earlier sure litopterns or of any sure didolodontids are known, so that comparison can be only with later and, in any case, much more specialized litopterns and with North American condylarths. These two groups are indeed similar, and the most crucial points are not known in *Xesmodon.* The whole aspect is more primitive than in any known later litoptern skull, with the nasals apparently not at all retracted, the orbits open behind, and the general facial and cranial proportions condylarth-like. On the other hand the strong postorbital processes, prominent vascular foramina in the frontals, and, more vaguely and generally, the aspect of the skull as a whole do suggest the litopterns. The open orbits compare with *Theosodon,* but this is merely primitive, with respect to the proterotheres, and there seems to be nothing else especially macraucheniid.

The evidence of the unique skull is thus disappointingly vague. It could be either a condylarth or a very primitive litoptern, and if a litoptern it could be structurally ancestral either to proterotheres or to macraucheniids. For what it is worth, however, the existence of such an animal does tend to confirm the direct derivation of the litopterns from phenacodont-like condylarths.

Xesmodon langi (Roth, 1899)

Plate 13, figure 3

Glyphodon langi ROTH, 1899, p. 383.
= *Caliphrium simplex,* AMEGHINO, 1899, p. 12.
Xesmodon langi, SIMPSON, 1936d, pp. 69, 73.

TYPE: M.L.P. No. 12-1481. Most of skull, poorly preserved. Roth Collection.

HYPODIGM: Type only.

HORIZON AND LOCALITY: "Cretáceo superior [probably Musters formation] de Cañadón Colorado," central Chubut, Argentina.

DIAGNOSIS: Sole species surely referred to genus.

The known molar characters have been given. The alveoli are very obscure, but there appear to have been no large diastemata, and the canines were probably present but small.

The cranial and facial regions of the skull are approximately equal, the large orbits being near the middle of the skull. The premaxillae are not preserved, and their posterosuperior extensions were probably short. The emarginations between them and the nasals were surely shallow, and the nasals were long and extended nearly to the tip of the snout. They are constricted in the middle, much expanded anteriorly and slightly posteriorly. The outer form of the jugal-maxillary-lacrimal region is fairly well preserved on the right side, but after long examination I could not certainly identify the sutures and do not venture to interpret the structure of this region. The infraorbital canal may have been in part double internally, but it has a single facial opening.

The frontal region is flat and tabular and nearly equidimensional, the width slightly greater. There are two prominent vascular foramina near the middle of each frontal. The postorbital processes are long, sharp, and deflected, but there are no corresponding processes on the zygomata. The latter arise mostly opposite and in part posterior to M^3 and are simple, their posterior parts rather slender.

The palate is broad, its detailed structure obscured. The choanae are narrow and extend forward between the posterior parts of the last molars. The pterygoid crests fall to two projections, one about halfway to the beginning of the basicranial expansion, and one at the latter point, less developed, and at the end of the crests as such.

The cranium proper is of about equal breadth and length. The basioccipital-basisphenoid deflection is very slight. No cranial foramina are identifiable. From the roof of the choanae a broad groove on each side runs to the auditory region. There was no epitympanic sinus, at least in the notoungulate position, or, evidently, an ossified meatus, bulla (strictly speaking), or hypotympanic sinus. The meatus issued through a large, well-defined, open, bony notch. Anterior to this is a prominent blunt postglenoid process and posterior to it a well-developed posttympanic process (perhaps also involving a paroccipital process), compressed anteroexternal-posterointernally.

The occiput was perhaps broader than high, but it is crushed, and the lambdoid crest is

TABLE 24

SKULL OF *Xesmodon langi*

Estimated total length	*ca.*	190	mm.
Maximum width (across zygomata)	*ca.*	100	
Interorbital frontal width		55	
Length of orbit	*ca.*	35	
Width of palate between P^3	*ca.*	34	
Length of M^2		13.5	
Length of M^3		13.0	
Width of M^3		17	

broken. There was probably a high sagittal crest but it, too, is broken.

The principal dimensions are given in table 24.

?Xesmodon prolixus (Roth, 1899), new combination

Plate 13, figures 4–6

Megacrodon prolixus ROTH, 1899, p. 384; SIMPSON, 1936d, p. 73.

=*Lambdaconus suinus*, AMEGHINO, 1899, p. 12.

? *Megacrodon prolixum*, SIMPSON, 1936d, p. 66.

TYPE: M.L.P. No. 12-1743. Fragment of left lower jaw with P_{3-4}. Roth Collection.

HYPODIGM: Type only.

HORIZON AND LOCALITY: "Cretáceo superior de Lago Musters." Probably Musters formation of the Cerro del Humo, Chubut.

DIAGNOSIS: Lower premolars suggestive of *Polymorphis*, but trigonid not distinctly crescentic and paraconid apparently absent.

If, as now seems to be the case, the genotype of *Megacrodon* belongs in *Polymorphis*, this second supposed species of *Megacrodon* cannot be placed in either *Megacrodon* or *Polymorphis*. Nor does it appear to belong in any other genus in which P_{3-4} are known. "*Megacrodon*" *prolixus* and *Xesmodon langi* are of about the same age (although the specimens are not from the same locality), show analogous resemblance to condylarths on one hand and litopterns on the other, are of about the same size (and both slightly larger than any of their known probable allies from the same formation), and are both rare forms. This suffices for a very tentative reference of *prolixus* to *Xesmodon*. Obviously the reference is highly uncertain, but it is preferred to the alternative of erecting a new genus for this doubtful fragment.

These premolars are closely similar except that P_3 is more elongate. Both are considerably longer than wide and have the trigonid well elevated above the talonid. The trigonid consists essentially of subequal and nearly opposite protoconid and metaconid, each subcrescentic, their posterior crescent wings meeting and forming a transverse crest, the anterior wings descending to the midpoint of the front margin. There are here one or two small and obscure tubercles that close the trigonid and make it a small basin. The paraconid is otherwise absent. The talonid has one small median cusp and an anteroposterior crest, from the posterior end of which marginal crests pass externally and internally. There are anteroexternal and anterointernal cingula on the trigonid.

TABLE 25

?Xesmodon prolixus

P_3		P_4	
L	W	L	W
11.5	7.8	11.0	8.4

HETEROGLYPHIS ROTH, 1899

Heteroglyphis ROTH, 1899, p. 387; AMEGHINO, 1904b, p. 124; 1906, p. 470; SIMPSON, 1936d, pp. 66, 75.

=*Protheosodon*, AMEGHINO, 1899, p. 12.

TYPE: *Heteroglyphis dewoletzky* Roth, 1899.

DISTRIBUTION: Musters formation, Patagonia.

DIAGNOSIS: Upper molar with selenodont ectoloph, parastyle and mesostyle well developed, conules large and lophoid, protoconule nearly independent, metaconule strongly united to protocone and not to metacone, large anterointernal cusp, hypocone (if present) not united to protocone or metaconule.

It has not previously been noted that the posterior and posterointernal basal parts of the unique tooth on which this genus is based present a broken surface, so that a posterior cingulum and hypocone were probably present. Even in this mutilated condition, the tooth is very distinctive and the genus surely valid, although its affinities are not closely determinable. Among Casamayor genera, it resembles *Josepholeidya* and its allies, and is probably really related to that group, but it differs from all the Casamayor genera in having the protocone united to the metaconule and not (or less) to the protoconule, as well as in other details. The same connections, lophoid conule, and other features differ from *Polyacrodon* and *Xesmodon*, the only comparable Musters genera. In almost all the later proterotheres the protocone and protoconule tend to unite, a tendency opposite to that evidently developing in this genus, and in *Protheosodon* (a genus with which Ameghino erroneously equated *Heteroglyphis*) both the conules are nearly independent and definitely less crested. *Victorlemoinea* and the later undoubted macraucheniids differ still more markedly.

Heteroglyphis dewoletzky[1] Roth, 1899

Plate 13, figure 7

Heteroglyphis dewoletzky Roth, 1899, p. 387; Simpson, 1936d, p. 75.

Heteroglyphis devoletzkyi, Ameghino, 1904b, p. 124, figs. 143, 190, 526; Roth, 1927, pp. 201, 229.

Heteroglyphis dewoletzkyi, Roth, 1927, pl. 9, fig. 7.

Heteroglyphis devoletzky, Simpson, 1936d, p. 66 [misprint].

Type: M.L.P. No. 12-1462. Broken upper molar. Roth Collection.

Horizon and Locality: "Cretáceo superior de Lago Musters." Probably Musters formation of the Cerro del Humo, Chubut.

Diagnosis: Sole known species of genus. Approximate dimensions of type 11 by 13.5 mm.

INDETERMINATE POSSIBLE LIPTOPTERNS

EOLICAPHRIUM Ameghino, 1902

Eolicaphrium Ameghino, 1902a, p. 13; 1906, p. 467.

Type: *Eolicaphrium primarium* Ameghino.

Distribution: Casamayor, Patagonia.

Diagnosis: (*Fide* Ameghino.) Symphysis fused. Dentition complete. Incisors and canine in closed series, separated from cheek teeth by a diastema. I_1 with long crown, triangular point, median vertical external and internal carinae. Canine very small. P_1 two-rooted. P_2 twice as long as P_1.

Eolicaphrium primarium Ameghino, 1902

Eolicaphrium primarium Ameghino, 1902a, p. 13.

Type: Not found. Apparently a fragment of the lower jaw with I_1, I_3, and alveoli of I_2, C, and P_{1-2}.

Hypodigm: Type as described by Ameghino.

Horizon and Locality: (*Fide* Ameghino) upper part of Casamayor. No other data.

Diagnosis: (*Fide* Ameghino.) Unique species. Symphysis 30 mm. long, 19 mm. wide anteriorly and 30 mm. wide posteriorly. Diastema 11 mm. long. P_{1-2} together 16 mm. long.

The genus and species are practically indeterminate. Ameghino referred this form to the Proterotheriidae. There is no figure, and the description does not suffice for determination of affinities.

Paulogervaisia celata Ameghino, 1901, nomen vanum

Paulogervaisia celata Ameghino, 1901, p. 389.

Paulogervaisia coelata, Ameghino, 1902b, p. 43.

Type: M.A.C.N. No. 10947. Isolated tooth. Ameghino Collection.

Hypodigm: Type only.

Horizon and Locality: Musters formation, Patagonia. No exact data.

Diagnosis: Indeterminate.

The type is a triangular or pyriform, two-rooted tooth measuring 17.5 and 20 mm. in its principal dimensions. The coronal structure is completely obliterated by wear. The proportion and outline, all that one can judge by, are unlike those of any known tooth of *Paulogervaisia*, and that reference has little to support it. Any attempt at classification is futile, as the specimen is now indeterminate. More extensive comparative materials might rehabilitate it.

Lambdaconus elegans Roth, 1903, nomen vanum

Lambdaconus elegans Roth, 1903a, p. 153; Simpson, 1936d, p. 94 [as indeterminate].

Type: Not found. A mandible of a young animal changing its milk teeth. Roth described the canine, four premolars, and two molars.

Hypodigm: Type as described by Roth.

Horizon and Locality: "Cretáceo su-

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[1] This peculiar spelling of the trivial name is contrary to custom and etymology and has been variously emended, but it was evidently intentional in the first publication. I understand the Rules to permit a change in termination only in case of an evident *lapsus* or to make an adjectival trivial name agree in gender with the generic name, neither of which applies to the present case.

perior de Lago Musters." Probably Musters formation of the Cerro del Humo, Chubut.

DIAGNOSIS: Indeterminate at present.

The type of this species seems to have been a good specimen, and it will probably be determinate if it is rediscovered. Roth's description does not permit recognition of the species or of the genus, which almost surely was not *Lambdaconus*, and the specimen seems never to have been figured or cast. Except for the statement that "El cuarto premolar es igual al primer molar," which may refer to a milk tooth, Roth's description could apply to *Polymorphis lechei* or to species of several other genera.

PROACRODON ROTH, 1899, NOMEN VANUM

Proacrodon ROTH, 1899, p. 385; SIMPSON, 1936d, p. 93 [as indeterminate].

=*Trimerostephanos*, AMEGHINO, 1899, p. 12.

TYPE: *Proacrodon transformatus* Roth, 1899.

DISTRIBUTION: Probably Musters formation, Patagonia.

DIAGNOSIS: Indeterminate.

The sole specimen of this genus has also disappeared. It is described as a single lower molar, but was perhaps a premolar.[1] The anterior tubercles, protoconid and metaconid, are said to be ankylosed, forming a crest as in *Hyrachyus*, with a crest from the protoconid forming a crescent anteriorly, while the talonid is said to have a high crest in the form of a comma. The genus would perhaps be recognizable if the specimen were available, but the description could apply to various genera of this and other faunas. Ameghino (1899) equated *Proacrodon* with *Trimerostephanos* (a Deseado genus), which would be possible from Roth's description, but since Ameghino had not then seen the specimens and since his synonymies of Roth's genera and species in 1899 were all erroneous (as he later recognized for several of them), this is not reliable.

Proacrodon transformatus Roth, 1899, nomen vanum

Proacrodon transformatis ROTH, 1899, p. 385.

Probably *Trimerostephanos scabrus*, AMEGHINO, 1899, p. 12.

TYPE: Lost. A single lower molar or premolar.

HYPODIGM: Type as described by Roth.

HORIZON AND LOCALITY: Unknown. Probably Musters formation of Patagonia.

DIAGNOSIS: Indeterminate. Type said by Roth to measure 15 by 13 mm.

ORDER **NOTOUNGULATA** ROTH

DEFINITION: Skull with inflated osseous bulla and hypotympanic sinus. Well-developed epitympanic sinus in squamosal. Venous sinuses prominent in cerebral and otic regions and generally with prominent but variable cranial vascular foramina. Prominent vagina processus hyoidei and frequently a styliform process. Auditory meatus generally ossified and often crested. Skull as a whole becoming somewhat specialized in various lines, with limited nasal retraction and deepening face in correlation with hypsodonty, but in general persistently primitive and more or less condylarth-like. Orbit open. Zygoma strong and high posteriorly. Cranium proper remaining relatively small and usually pyriform. Toes hoofed, except in Homalodotheriidae. Feet primitively with five digits, usually with a tendency to become mesaxonic and reduced towards or to three (not fewer) functionally, but some aberrant types. Astragalus primitively somewhat condylarth-like and persistently with trochlea rather shallow, more dorsal than strictly proximal; distinct, constricted, oblique neck (shortening in graviportal types), head convex. Dentition primitively complete and a tendency to retain the full, closed series even in some relatively progressive lines, but several groups tend independently to acquire rodent-like incisors with some reduction of incisors, canines, and anterior premolars. Molars unreduced. Cheek teeth lophiodont. Lower molars with short, asymmetrical, simple trigonid crescent and long, more symmetrical talonid crescent. Entoconid forming a transverse crest within the talonid crescent, which may, in various lines, be further complicated by other crests and spurs. Upper molars with prominent

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[1] Roth sometimes called all the cheek teeth molars (as did Ameghino), although he distinguished the premolars in dental formulas and sometimes called them premolars in description. In the present case he was not explicit, but seems to imply a premolar.

ectoloph, long, oblique protoloph, and shorter, transverse metaloph. Accessory cuspules, cristae, crochet, antecrochet developing in the basin between the lophs, the exact pattern often becoming complex and characteristically different in the various lines of descent. Always some, but only very exceptionally advanced, molarization of premolars.

DISTRIBUTION: Paleocene to Pleistocene, South America. Paleocene, Asia. Eocene, North America. Pleistocene, Central America.

When Lydekker made one of the first general syntheses of South American fossil mammals in 1894, he placed the relatively few genera then known in four families: Pachyrucidae, Typotheriidae, Toxodontidae, and Homalodontotheriidae. The first three of these were placed in the Toxodontia and the last in the Astrapotheria, both classed as suborders of Ungulata. When Ameghino made his definitive classification in 1906, with the known genera enormously increased mainly through his own efforts, he did not recognize the unity of the group now called Notoungulata, even to the extent that Lydekker had done this in his emendation of Owen's Toxodontia. Ameghino referred a few genera now considered Notoungulata to Holarctic families but placed the great majority of them in 22 families distributed in the Prosimiae, Hyracoidea, Typotheria, Toxodontia, Hippoidea, Condylarthra, and Ancylopoda. Of these, only Typotheria and Toxodontia were native orders, the others being based in the first instance on fossil and living animals from other continents, the ancestors of which had, Ameghino believed, been found in Patagonia. Ameghino's Toxodontia included only the toxodonts in a strict sense, the single family Toxodontidae of Lydekker's and of modern less radical classifications. It is rather ironic that Ameghino, who contributed more than any other one man to knowledge of notoungulates, never recognized the existence of this group as such.

It was Roth (1903b) who first clearly distinguished the Notoungulata as a unit, essentially as it is now recognized, defining it on characters of the temporal, occipital, and, especially, auditory regions. He gave no complete list of included suborders and families, but he explicitly excluded the litopterns, astrapotheres, and all non-South American ungulates then known, and included the Toxodontidae, "Typotheriidae" (Mesotheriidae), "Homalodontotheriidae" (Homalodotheriidae), Notohippidae, Archaeohyracidae, Notopithecidae, and Notostylopidae, each of which families had been placed in a different order from the others by Ameghino. Roth's concepts of the affinities of some individual genera, especially in the earlier faunas, were mistaken, but his concept of the Notoungulata has been thoroughly justified by later study and requires no essential modification now.

Most later students recognized this group, either under Roth's name Notoungulata or Owen's Toxodontia, in the latter case emending the usage to include a much broader group than to toxodonts, strictly speaking. In most cases, however, general classifications have included in the same order other extinct South American groups here classified as ordinally separate. Thus Osborn (1910) made Notoungulata a superorder including Toxodontia, Litopterna, and Pyrotheria (i.e., all extinct South American ungulates), and in Toxodontia he placed Homalodotheria, Astrapotheria, Toxodontia *sensu stricto*, and Typotheria. In 1913 Scott used Toxodontia for what was essentially this group but also included the Pyrotheria. (In 1937 Scott accepted the definition of Notoungulata here adopted and essentially as proposed by Roth.) For the toxodonts, *sensu stricto*, Scott used the slightly altered spelling Toxodonta.

That the litopterns, astrapotheres, and pyrotheres should be excluded from the Notoungulata is, I think, sufficiently supported by the discussions of these groups in the present revision and by the previous literature on them. They were already sharply distinct in the Paleocene and Eocene. The astrapotheres do show some resemblance to notoungulates in the dentition, but there is reason to consider this probably convergent or parallel. The litopterns and astrapotheres particularly, and the pyrotheres possibly, may well have come from the same very remote stock as the notoungulates, but any common ancestor must have been so generalized that it would belong in the Condylarthra and not in a group of prototypal notoungulates.

Subordinal arrangement of the Notoungulata presents peculiar difficulties, and it can hardly be hoped that a durable system can yet be established. Nevertheless renewed work in recent years does suggest some radical emendations that seem surely to come closer to a natural arrangement.

The classical subdivision, already suggested but not yet clearly expressed by Lydekker, was trifold. The great majority of notoungulates were distributed in the Toxodontia (or Toxodonta) and the Typotheria, while *Homalodotherium* and some of Ameghino's Eocene forms were placed in a third group called Homalodotheria or Entelonychia. This arrangement was crystallized in Scott's work, the great Santa Cruz faunal revision and Scott's many other books and papers (prior to 1937), and was adopted without important exception by all students from 1906 (when Ameghino's generally rejected final classification appeared) to 1934. In 1934d, on the basis of renewed study of the early faunas that had not been known at first-hand to anyone else since Ameghino, I proposed retaining the three now classic groups but removing most of the Eocene groups from the Entelonychia and placing some of them in a primitive Suborder Notioprogonia. As proposed in Simpson, 1934d, the Order Notoungulata included the Suborders Notioprogonia, Entelonychia, Toxodonta, and Typotheria.

Since 1934 continuous study of the early faunas and, especially, work by Patterson on the Oligocene and Miocene faunas have suggested a more radical departure from the classic arrangement. This has already been embodied in Simpson, 1945, and is also supported by discussions of the various suborders given below. On the basis of the Eocene forms that had not acquired the striking specializations of *Homalodotherium*, and following Patterson's demonstration (1932, 1936) that *Homalodotherium* itself is only a toxodont with superficial aberrant limb characters, the Suborder Entelonychia is united with the Suborder Toxodonta. On the other hand study of the Musters (below) and later (Patterson, 1934b, 1936, and personal communication) hegetotheres shows that these are anciently and fundamentally separate from the typotheres in a strict sense (interatheres and mesotheres) and apparently merit subordinal distinction.

Thus the present evidence is that the known notoungulates may most naturally and conveniently be divided into these four suborders: Notioprogonia, Toxodonta, Typotheria, and Hegetotheria.

As in all South American faunas before the late Tertiary, notoungulates form the bulk of the known Paleocene and Eocene faunas, outnumbering any other one order both in taxonomic units and in individuals. The various groups are less divergent in the Eocene than in the Miocene, being apparently quite near their common origin in the earlier faunas, but they are more diverse. Of the 13 notoungulate families that I would recognize in South America (one other, Arctostylopidae, is Holarctic), nine occur in the Casamayor, Musters, or both. In the Santa Cruz there are only five families, Homalodotheriidae, Toxodontidae, Interatheriidae, Mesotheriidae, and Hegetotheriidae. Only the Toxodontidae, Mesotheriidae, and Hegetotheriidae survived at the end of the Tertiary. The primitive Suborder Notioprogonia is absent after the Musters. Each of the other three suborders survived into the Pleistocene, but by the end of the Tertiary each had been reduced to a single stereotyped family, each family including in the Pleistocene a single genus or a small group of closely related genera.

Thus in the Eocene the notoungulates were an exuberant group, with an unusually large number of different lines of descent or of differentiation. It will also be found that each population was then unusually variable. As time went on the number of surviving lines was progressively and sharply reduced. Each surviving line became relatively specialized and distinctive. By the early Miocene the basic specialization of surviving phyla was essentially complete, and thereafter the groups that continued were quite stereotyped, with only a minimum of phyletic progression.

The fact that the notoungulates were so extremely varied and variable in the Eocene and at the same time were relatively poorly differentiated into distinctive adaptive and morphological types makes the taxonomy of these early forms peculiarly difficult. In place of the clear-cut lines found from the Miocene on, there is an overabundant mass of genera with most confusing and intricate cross-resemblances. Evolution is here encountered in an explosive phase, and this puts a severe strain on the usual procedures and conventions of classification. At the same time it gives exceptional interest to the study of this phase.

Suborder **NOTIOPROGONIA** Simpson

Definition: A relatively generalized suborder of Notoungulata, including some very early divergent lines, superficially specialized but basically primitive. Dentition complete or with I_3^3 C_1^1 P_1^1 variously reduced. Incisors subequal or one pair, above and below, somewhat enlarged but rooted. Canines no larger than the adjacent teeth and sometimes reduced or even lost. All cheek teeth brachyodont, without cement. Upper premolars progressively complicated, but all triangular, or nearly so, with protocone at least on P^{2-4}, but no distinct hypocone. Upper molars transverse, with strong parastyle, well-formed ectoloph and oblique protoloph, but metaloph variable and often imperfect. Crochet present, anteroposterior when elongated, and generally free of ectoloph. Other secondary folds or crests slight or absent. M^{1-2} quadrate, with strong hypocones, nearly or quite equal to protocones. M^3 large but triangular, with hypocone small or unrecognizable as such. Lower premolars essentially bicrescentic, with subequal talonid and trigonid. Lower molars with very short trigonids and long talonids. Trigonids essentially a single transverse lophid, anterior wing reduced, paraconid inconspicuous and median or relatively external. Talonids with strong elongate crescentic lophid and simple transverse crested entoconid pillar, no secondary connections or crests. Rostrum, so far as known, short, deep, and rather narrow, with terminal nares. Zygomata arising opposite anterior molars. Cranium (in Notostylopidae, unknown in other forms but probably closely similar) triangular between squared zygomata, strong postorbital constriction, endocranial cast of same general type as in later typotheres but more primitive, and ear region of generalized notoungulate type, epitympanic sinus relatively small, porus low, ossified meatus short and nearly horizontal, tympanic crested, hypotympanic sinus large and globular, extending far ventral to basisphenoid, cranio-facial flexion slight. Mandible rather elongate and slender, tooth series nearly straight.

This suborder was proposed by me (Simpson, 1934d) to include the Arctostylopidae, Henricosborniidae (and Pantostylopidae), and Notostylopidae. Ameghino (1906) placed the Henricosborniidae in the Prosimiae, the Pantostylopidae in the Condylarthra, and the Notostylopidae in the Tillodonta. As usual, this apparently eccentric arrangement is based on real and important resemblances, although the implied interpretation of them cannot now be supported. In placing the Henricosborniidae in the Prosimiae, Ameghino was clearly influenced by their resemblance to the Notopithecidae, by him classified in that group. Both are primitive notoungulate groups and, although they lie along different lines of descent, this collocation was an essential recognition of the notoungulate character of the henricosborniids. Certain of the small forms, as brought out below, show a definite and suggestive approach towards the condylarths, and this other phase of their probable relationships, looking backward towards the ancestry rather than forward towards the descendants, was signalized by Ameghino in placing the Pantostylopidae (=Henricosborniidae) in the Condylarthra. Finally the notostylopids do show an adaptive convergence, of rather limited scope and surely not indicative of affinity, towards the tillodonts.

Other students have been all but unanimous in placing the Notostylopidae in the Entelonychia, although I am not aware that anyone but Ameghino has hitherto made any considerable study of them or given any detailed and accurate reasons for this position. The Arctostylopidae, from the time of their discovery, were always placed in the Entelonychia also, chiefly because of a real resemblance to notostylopids and because the Entelonychia were taken to include all notoungulates with relatively unspecialized teeth. The Henricosborniidae have generally been neglected, no student since Ameghino having any first-hand knowledge of them and his published data being very scanty. Scott placed *Henricosbornia* in the Archaeopithecidae and Typotheria, although the reason for this is not clear, and Schlosser followed him, while Osborn simply omitted his namesake from the classification.

When the whole mass of notoungulates was reviewed it was considered established, until recent studies showed that this exact grouping must be modified, that there are in the middle Tertiary to Pleistocene beds three main divisions: Toxodonta, Typotheria, and Entelonychia. These groups being considered firmly established, it was necessary to include in them as many of the earlier forms as seemed possibly assignable here, and in the absence of restudy it was thus quite proper to place the little known non-toxodonts, non-typotheres of the Casamayor in the Entelonychia.

Detailed study of these forms, however, shows that they are also decidedly non-entelonychians. The group Entelonychia (now considered a part of the Toxodonta) was based essentially on *Homalodotherium*, a specialized genus, and was broadened to include also forms, such as *Isotemnus*, that seem to be related to *Homalodotherium* but are much more primitive and show these specializations only in the most barely incipient form or not at all. Now as far as I have been able to determine, *Arctostylops*, *Henricosbornia*, *Notostylops*, and their respective kin do not have a single character which also appears in the so-called Entelonychia, early or later, and which does not occur in contemporaneous typotheres or toxodonts. Aside from the practical point that it would thus be completely impossible to retain and redefine the Entelonychia in such a way as to include these genera but to exclude typotheres, hegetotheres, and toxodonts, the retention of the classic arrangement would nvolve a very cumbersome and illogical elationship between taxonomy and phylogny. The Entelonychia would include not nly a series of closely related phyla which ulminate in some of the most aberrant of all otoungulates, but would also include several primitive phyla with no relationship to the others beyond also being notoungulates. This arrangement is neither horizontal nor vertical nor an acceptable compromise between the two.

These considerations, and others expressed more fully in Simpson, 1934d, or inherent in descriptions and discussions of the following pages, led to the erection of the Suborder Notioprogonia. This group is, in a sense, horizontal (which I do not consider as a drawback in such cases), since it includes at least three phyla which are united chiefly, but not exclusively, by the retention of primitive characters. It is natural, even phyletically, in that it includes lines which must have diverged, very shortly before their appearance in the present record, from a common ancestory and which did not, except through that ancestry and probably at a significantly more remote date, have anything to do with the other three suborders. Each of the three families now included here is divergent in a way peculiar to it, although none is really very specialized, even the Notostylopidae being basically a very primitive group. If they had survived each might well have given rise to a special later group as distinctive, as, say, the Toxodonta or Typotheria. But as far as known they did not survive and it would be manifestly absurd to follow such hypothetical considerations to their logical extreme, placing each family in its own suborder because they are somewhat divergent and because their common ancestry may, after all, have been that of the Notoungulata as a whole.

From another point of view and in a rather theoretical sense, the Notioprogonia do probably represent the structural, and might include the actual, ancestry of the Notoungulata, were it known. These families are in general very primitive, and a group defined to include them is characterized largely, but not entirely, by primitive features.

The Arctostylopidae are known only from Mongolia and North America. The presence of early and primitive notoungulates on those continents is of great zoogeographic interest and is discussed in connection with the origin of the South American fauna, but revision of the family is not pertinent here. The Henricosborniidae, most primitive of known notoungulates, occur only in the Río Chico and Casamayor. No notoungulates of such primitive stamp are found in the Musters or later formations, but even in the Río Chico they are conservative survivors rather than actual ancestors, because they were then already associated with somewhat (but not greatly) more specialized allies. The moderately divergent Notostylopidae also appeared in the Río Chico, were rather abundant in the Casamayor, and survived into the Musters but not later.

FAMILY **HENRICOSBORNIIDAE**
AMEGHINO, 1901

Henricosborniidae AMEGHINO, 1901.
Pantostylopidae AMEGHINO, 1901.
Selenoconidae AMEGHINO, 1902.

DEFINITION: (Incisors and canines unknown). Cheek teeth all very brachyodont. Upper premolars all triangular, with low, simple protocone, no hypocone or internal sulcus. M^{1-2} with subequal, distinct protocone and hypocone, simple oblique protoloph with vestigial protoconule and shorter, transverse metaloph, crochet strong to almost lacking, short, oblique but quite or nearly free of ectoloph, ectoloph with distinct paracone and metacone, mesostyle vague or absent. M^3 triangular and with very short metaloph, often not definitely crested or loph-like. P_{3-4} sub-molariform, rather simply bi-crescentic. Lower molars with oblique trigonid crest, metaconid higher than protoconid and slightly produced anteroexternal-posterointernally. Crest running straight anteriorly from protoconid, turning at right angles at the anteroexternal corner of the tooth. Talonid with simple external crescent with subequal hypoconulid and hypoconid, crescent meeting the trigonid near the midline (more, but not wholly, internal on P_4), hypoconulid median and projecting posteriorly. Entoconid distinct from talonid crescent, but relatively posterior in position and only very feebly crested transversely. All known forms relatively small in size.

DISTRIBUTION: Río Chico and Casamayor formations, Patagonia.

Ameghino (1906) distributed the genera here united as Henricosborniidae in three orders and four families, as follows:

Prosimiae
  Henricosborniidae [whole family]
  Hyopsodontidae [*Selenoconus*[1] only]
Condylarthra
  Pantostylopidae [whole family]
Perissodactyla
  Hyracotheriidae [*Prohyracotherium*]

Ameghino's definitions of the two principal groups, Henricosborniidae and Pantostylopidae, were different but not distinctive, including no contrasting characters. The impossibility of maintaining these genera in separate families, let alone orders, is demonstrated by the generic synonymies established below. *Selenoconus* and *Pantostylops* are synonyms of *Henricosbornia*, and so are three of the other four genera placed in the Pantostylopidae. *Peripantostylops* is valid but is clearly a close relative of *Henricosbornia* (and hence of its synonym *Pantostylops*, with which Ameghino did recognize a close relationship). *Prohyracotherium* is synonymous with *Henricosbornia*. Although Ameghino thus placed a single genus (and indeed species) in three different orders, the error involved should not be considered egregious or be harshly criticized. Its correction has been made possible only by greatly augmented collections, discovery of much more associated material, and the determination of the character and limits of variation in the group, quite impossible when Ameghino wrote.

The particular interest of this family is its primitive character. In the known parts, at least, the henricosborniids are clearly the most primitive known notoungulates, and they nearly fulfill all the theoretical requirements for a generalized type ancestral to all others known. The molar structure shows a marked similarity to small condylarths, such as *Asmithwoodwardia*, the essential difference being little more than the development of slightly more lophiodont teeth, a change which has often occurred within single phyletic lines and in a relatively short time.

Among the other notioprogonians the Arctostylopidae are distinctly more advanced in being still more lophiodont and in the

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[1] *Selenoconus* was first placed in the Phenacodontidae (1901) then made type of a family Selenoconidae (1902a) and finally referred to the Hyopsodontidae (1906).

peculiar trigonid specialization, no distinct trace of which is seen in the Henriocosborniidae. In other respects, such as the molarization of the premolars, the arctostylopids are not more progressive than the henricosborniids and may be more primitive. Evidently the two groups are divergent, and the henricosborniids are, as one would expect, decidedly closer to a generalized South American type. They closely resemble the notostylopids in many respects, but lack the specializations of the latter. As a practical matter, they may be distinguished from notostylopids by such details as the more definite metacone fold, shorter and more oblique crochet, and better separation of protocone and hypocone in the upper molars or the absence of the median trigonid cusp in the lower molars.

The henricosborniids also rather closely resemble the most primitive notoungulates of other suborders, particularly the Eocene Interatheriidae and the Oldfieldthomasiidae, and at first sight may even be confused with one of these families. Upon closer study, however, the resemblances seem to be almost entirely primitive and to coincide with the extent to which these other families have still retained ancestral characters. The principal characters by which henricosborniid upper molars can be separated in practice from those of the other two families mentioned are their lower crowns, weaker crochet, and absence of cristae. The lower molar crowns are also lower, wear never forms closed lakes on them, the point of attachment of the talonid crescent is slightly more external, the hypoconulid more median and more projecting, and the entoconid more posterior and less crested. The general form of the dentition, molarization of the premolars, and many other characters are very similar, and the modification required to convert the henricosbornid dentition into that of an Eocene interathere, oldfieldthomasiid, or isotemnid is relatively slight.

Ameghino named 10 genera that are now considered as Henricosborniidae. Our much more abundant and better material permits a fairly satisfactory solution of the problem of definition and synonymy. There are only three really distinct and well-defined generic types: *Henricosbornia*, *Othnielmarshia*, and *Peripantostylops*. *Postpithecus* is synonymous with *Othnielmarshia*, and the other six genera are synonymous with *Henricosbornia*.

The following list, in which the retained names are starred, shows the present disposal of Ameghino's genera:

**Henricosbornia* Ameghino, 1901 = *Henricosbornia*
**Othnielmarshia* Ameghino, 1901 = *Othnielmarshia*
Postpithecus Ameghino, 1901 = *Othnielmarshia*
Selenoconus Ameghino, 1901 = *Henricosbornia*
Pantostylops Ameghino, 1901 = *Henricosbornia*
Microstylops Ameghino, 1901 = *Henricosbornia*
Prohyracotherium Ameghino, 1902 = *Henricosbornia*
**Peripantostylops* Ameghino, 1904 = *Peripantostylops*
Hemistylops Ameghino, 1904 = *Henricosbornia*
Polystylops Ameghino, 1904 = *Henricosbornia*

Roth's genus *Monolophodon* also seems to be a synonym of *Henricosbornia*.

HENRICOSBORNIA AMEGHINO, 1901

Henricosbornia AMEGHINO, 1901, p. 357; 1904b, p. 89; 1906, p. 467; SCHLOSSER, 1923, p. 609; ROTH, 1927, pp. 235, 238; SCOTT, 1913, p. 462; 1937, p. 528; SIMPSON, 1937a, fig. 9B; 1937c, fig. 2.

Selenoconus AMEGHINO, 1901, p. 381; 1906, p. 467.

Pantostylops AMEGHINO, 1901, p. 423; 1906, p. 467; SCHLOSSER, 1923, p. 609.

Microstylops AMEGHINO, 1901, p. 426; 1906, p. 467.

Prohyracotherium AMEGHINO, 1902a, p. 15; 1904b, p. 107; 1906, p. 467.

Hemistylops AMEGHINO, 1904a, vol. 58, p. 38; 1906, p. 467.

Polystylops AMEGHINO, 1904a, vol. 58, p. 40; 1904b, p. 75; 1906, p. 467.

Monolophodon ROTH, 1903a, p. 143; SIMPSON, 1936d, p. 76.

TYPE: *Henricosbornia lophodonta* Ameghino.

TYPES OF SYNONYMS: *Selenoconus*: *S. centralis* Ameghino. *Pantostylops*: *P. typus* Ameghino. *Microstylops*: *M. clarus* Ameghino. *Prohyracotherium: P. patagonicum* Ameghino. *Hemistylops: Pantostylops incompletus* Ameghino. *Polystylops: P. progrediens* Ameghino. *Monolophodon: M. minutus* Roth.

DISTRIBUTION: Río Chico and Casamayor, Patagonia.

DIAGNOSIS. P^{3-4} with distinct paracone and metacone. M^{1-3} strongly transverse, with crochet generally weak, sometimes almost absent, mesostyle region gently convex, no external cingulum, strong metastyle on M^3. Hypoconid angulate and hypoconulid well differentiated on M_{1-2}. Entoconid well separated from hypoconulid on M_3.

Pantostylops was always placed in a different family from *Henricosbornia* by Ameghino, and he therefore never made an explicit comparison of them. The type of *Pantostylops typus* differs from that of *Henricosbornia lophodonta* in being unworn, but is otherwise almost identical in size and structure. The species, and hence also the genera, are indistinguishable.

Selenoconus was based on lower teeth. As they were placed in a different family, no direct comparison with *Henricosbornia* or any of its synonyms was made, and the definition contained nothing distinctive from that genus. When the family Selenoconidae was defined, it was contrasted only with the Phenacodontidae from which it is, of course, very distinct. In fact the type species and two others, *S. senex* and *spiculatus*, are quite indistinguishable from lower teeth now known surely to belong to *H. lophodonta*. A fourth species, *S. agilis*, is different and belongs to *Peripantostylops*.

Microstylops was defined by eight characters, seven of which did not distinguish it from *Henricosbornia* as defined by Ameghino. The eighth character, that of having a deep median basin without median tubercles (crochet), is distinctive from some specimens of *Henricosbornia* but, as will be shown below, is within its range not only of specific but also of individual variation.

Prohyracotherium was referred to the Hyracotheriidae and not compared with Henricosborniidae (or "Pantostylopidae"). When this comparison is made, the type upper teeth prove to differ from those of *Henricosbornia* only in slight details of size and proportion.

Hemistylops was based on an isolated last upper molar, and its definition is almost entirely on characters of M^3 in any henricosborniid, and included no real taxonomic distinction from *Henricosbornia lophodonta*. There are some morphological differences from the type of the latter, but these are now found to be within the known range of intraspecific variation.

Polystylops was chiefly distinguished by the presence of a (very feeble) mesostyle fold, absence of a separate posterointernal cusp, and presence of a crochet. All these characters also appear in *Henricosbornia*.

Monolophodon was referred by Roth to the Notostylopidae, but he did not explicitly cite distinctions from any of Ameghino's genera. The M^3 on which the genus was essentially based is quite surely a henricosborniid, not notostylopid, and it has no visible characters that exclude it from *Henricosbornia*. The species, "*M.*" *minutus*, is probably distinct.

The present arrangement of the Henricosborniidae is based mainly on a large number of specimens all collected from one horizon and locality in Cañadón Vaca by C. S. Williams and me. These include two specimens with associated upper and lower jaws, seven lower jaws, about 100 isolated upper molars and very numerous isolated premolars and lower teeth. We also collected some specimens, including one good upper and one good lower jaw, from other localities.

In order to provide a good objective basis for the consideration of variation, the last upper molars of the Cañadón Vaca sample were all sorted out, measured, and all their more obviously variable morphological characters observed and recorded. This sample is of completely homogeneous origin and, as far as conditions permit, is an entirely random selection; the only teeth rejected were those too broken to be measured accurately. M^3 was selected because it is abundantly represented (46 specimens) and is easy to identify. Among the lower teeth, there is a sufficiently large number of doubtful identifications to bias the sample. Among the upper teeth, it is impossible in every case to distinguish certainly between M^1 and M^2 (and perhaps also dm^4) or between P^3 and P^4, but M^3 can be surely distinguished. Furthermore M^3 seemed, on inspection, to be more widely variable than the others in morphology and at least as variable as any in size, and most of Ameghino's types are isolated M^3's.

The following are the principal characters recorded and studied for each tooth:

Length
Width
Ratio length: width
Presence or absence of external cingulum
Character of ectoloph wall between paracone and metacone folds
Strength of metacone fold
Presence and strength of metastyle fold
Strength and character of crochet
Attachment of metaloph to ectoloph
Height and length of metaloph
Presence, completeness, or absence of posterior cingulum
Presence, position, attachments, and size or absence of cingulum cusp
Character of other possible posterointernal cusps

The tabulated data at once revealed the presence of three separable groups with the following principal characters:

I. (5 specimens)
  Size small. Length 4.0–4.5 mm.
  Ratio length: width relatively large
  External cingulum absent
  Mesostyle region nearly flat, with a well-defined pit near the base of the crown
  Metastylar fold present but poorly differentiated
  Crochet strong
  Metaloph long
  Posterior cingulum present
  No accessory cusps
II. (33 specimens)
  Size intermediate. Length 4.4–5.5 mm.
  Relatively wider
  External cingulum absent
  Mesostyle region gently convex
  Metastylar fold strong
  Crochet weak
  Metaloph and posterointernal region highly variable; see below
III. (8 specimens)
  Size large. Length 5.5–6.1 mm.
  Length: width about as in II
  Sharp external cingulum
  Mesostyle region excavated
  Metastylar fold slight or absent, metacone far posterior
  Crochet very weak or absent
  Metaloph short
  Posterior cingulum present and forming a posterointernal cusp

Group I is readily recognizable as belonging to Ameghino's *Peripantostylops* and is further considered under that genus. It is so evidently distinct that it can properly be removed from the sample before further analysis is made. Group III is also quite distinct and can be removed. It proves to belong to Ameghino's *Othnielmarshia.*

The abundant group II contains evident specimens of Ameghino's *Henricosbornia*, but also of several other supposed genera. The principal variations within the group involve the crochet, metaloph, and posterointernal corner. The crochet is in some cases a fairly strong but short spur on the metaloph pointing towards, but not continuous with, a papilla in the central basin of the crown. In other cases the papilla is absent, and only the spur is seen. In others, even the spur is absent, or nearly so, although there seems always to be at least a thickening on the metaloph in this position. These three conditions are not clear-cut and distinct, but grade insensibly into each other.

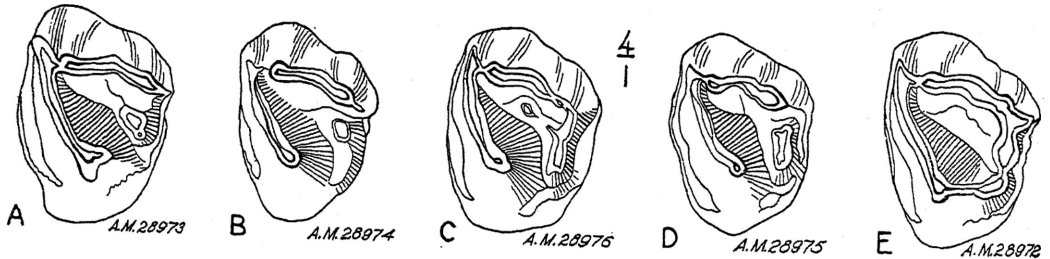

FIG. 48. *Henricosbornia lophodonta* Ameghino. Five major variants of M^3 among specimens found at the same horizon and locality in Cañadón Vaca. A–E. Typical examples of types 1–5, as described in the text. Crown views. ×4.

The posterior and posterointernal parts of the teeth are by far the most variable. The following are the outstanding types observed (see text fig. 48):

1. Metaloph represented only by a nearly circular, detached cusp. Posterior cingulum nearly or quite continuous, with a small cuspule posterointernal to the metaloph cusp. 10 specimens. Example: A.M.N.H. No. 28973
2. Similar to 1, but the cingulum cuspule tending to fuse with the metaloph so that the latter runs into the internal part of the cingulum. (In some cases this may be accentuated, or perhaps even caused, by wear.) 5 specimens. Example: A.M.N.H. No. 28974
3. Metaloph more elongate and tending to fuse with the ectoloph. Posterior cingulum complete, forming a distinct cuspule as in 1, but this usually more definite and more internal. (In two specimens the metaloph seems to continue into this cingulum cusp, but this is probably caused by wear in both cases.) 4 specimens. Example: A.M.N.H. No. 28976
4. Metaloph about as in 3, but cingulum with less tendency to form a cuspule. 3 specimens. Example: A.M.N.H. No. 28975
5. Similar to 3, but the posterointernal cuspule larger, somewhat attached to the protocone, and the cingulum circling its base. 2 specimens. Example: A.M.N.H. No. 28972

(The nine specimens not classified in this respect are too worn for these details to be distinguished with reasonable probability.)

As is also true of groups based on variations in the crochet (and others, less striking, not explicitly set forth here but carefully studied in reaching these conclusions), these groups are not constant within themselves and are not sharply defined. All the individuals of each group are different, and one group grades into the next by transition without any marked break. Neither in this nor in any other morphological character is there any discontinuity sufficiently marked to be of probable significance in a sample of this size.

The variations therefore do not in themselves give any means of separating the sample into different natural groups. Under these circumstances, the only way in which a separation could be effected would be by discovering significant associations between different characters. These possibilities were very thoroughly tested. The logical first attempt was to find a difference in size or proportions associated with some morphological type, a sort of association clearly shown by the *Peripantostylops* and *Othnielmarshia* specimens already removed from the sample as extraneous. No such association was found. On the contrary the size range of each morphological group, or of any combination of such groups, is as nearly identical with that of any other group or of the whole sample as it could well be if groups of these sizes were simply drawn at random from a homogeneous sample.

Comparison of the morphological groups themselves gave a similar result. There are a few features, such as the elongation of the metaloph and its union with the ectoloph, that are obviously dependent on each other. These are, of course, associated with each other, but the association is only apparent and not real, for such dependent characters should be regarded statistically as one attribute, not two. Aside from such cases, no significant association between attributes, either positive or negative, was found. For instance, the elongation of the metaloph is not necessarily accompanied by either the presence or absence of a cingulum cuspule, or by any particular condition of the crochet, or by any other character. All these characters vary independently.

Treatment of the numerical characters gives the statistical constants shown in table 26.

Grouped length and width distributions are given in table 27.

TABLE 26

Henricosbornia lophodonta

Variate	N	OR	M	σ	V
LM^3	33	4.4–5.5	5.0 ± .1	.30 ± .04	5.9 ± .7
WM^3	33	5.8–7.1	6.4 ± .1	.37 ± .05	5.7 ± .7
100 × LM^3:WM^3	33	70–85	78 ± 1	3.7 ± .5	—

TABLE 27

Henricosbornia lophodonta

L	W
4.3–4.5:3	5.7–5.9:4
4.6–4.8:7	6.0–6.2:7
4.9–5.1:13	6.3–6.5:11
5.2–5.4:9	6.6–6.8:7
5.5–5.7:1	6.9–7.1:4

None of these figures gives any suggestion of heterogeneity in the sample, but all are in strong agreement with the hypothesis that a single normally variable species is represented.

In résumé:

1. All the specimens of this sample are from one horizon and locality.
2. The numerical variates of the sample as a whole are normally distributed and are entirely consistent for a sample drawn from a single species or race.
3. The morphological variations show no clear-cut divisions, but in each case there is a relatively abundant central type grading insensibly into rarer divergent types.
4. The various morphological characters are not associated with each other or with any numerical character.

The only possible conclusion is that this sample does represent one species and that the variation shown is individual. Among other important consequences of the establishment of this fact is the synonymy of *Hemistylops* and *Polystylops* with *Henricosbornia*. They were based on last upper molars that do differ morphologically from those previously placed in *Henricosbornia*, but both these types occur in the present sample. The differences are thus shown to be neither generic nor specific, in themselves, but merely individual.

With M^3 thus satisfactorily sorted out, the other upper molars, M^1 and M^2 (the two being indistinguishable in most cases), were also measured and studied. They were found to fall also into three certainly distinct and natural groups, and these could be shown to correspond to the three major (generic) groups of M^3. Among other characters, these groups are distinguished as follows:

I. (5 specimens)
   Size small
   Length greater relative to width (teeth subquadrate)
   No external cingulum
   Mesostyle region flattened, with a small pit at the base of the crown
   Parastyle moderate
   Crochet strong

II. (45 specimens)
   Size intermediate
   Teeth relatively more transverse
   No external cingulum
   Mesostyle region gently convex
   Parastyle moderate
   Crochet weak, rarely absent or nearly so

III. (3 specimens)[1]
   Size large
   Proportions about as in II
   Sharp external cingulum
   Mesostyle region excavated
   Parastyle strong
   Crochet very weak

These are obviously the same as groups I, II, and III based on M^3. The association is further confirmed by specimens of *Peripantostylops* (group I) and of *Henricosbornia* (group II) with M^{1-3} of the same individual preserved.

The sample of M^1 and M^2, group II, also gives evidence of being derived from a single species. The variation is, indeed, considerably less than for M^3 in spite of the inclusion of two different teeth.[2] The variants that Ameghino named *Pantostylops*, *Microstylops*, and *Prohyracotherium* are all well within the

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[1] Theoretically it might be expected that isolated M^1 and M^2 together would be twice as numerous as isolated M^3. In fact the collection contains 46 isolated last molars (of all three species) and only 53 isolated first and second molars. The deviation from expectation is too great to be probably due entirely to chance, but is probably entirely explicable by the fact that M^1, particularly, and to a less extent M^2 become deeply worn on mature and old individuals, while M^3 is relatively unworn. This has a double selective effect: the more deeply worn teeth go to pieces readily and so are less likely to be collected, and they are more difficult to identify and so are less likely to be recognized. The fact that M^3 is more easily detached from the jaw may also have some influence; none of our three maxillae from Cañadón Vaca has this tooth.

[2] Since two teeth are included, it would be misleading to give statistical constants for this sample, but some have been calculated as an experiment and they show variation similar to that of M^3 in character and less in extent.

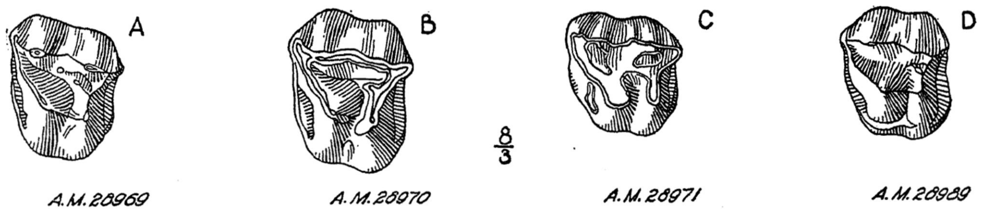

FIG. 49. *Henricosbornia lophodonta* Ameghino. Variant upper molars, other than M^3, among specimens found at the same horizon and locality in Cañadón Vaca. A. Moderate crochet, small cuspule in basin. B. Feeble crochet, no basin cusp. C. Well-developed crochet, protocone and hypocone not joined, crown unusually narrow (less transverse), perhaps a deciduous molar. D. Crochet almost absent, cingulum on protocone. Crown views. ×8/3.

range of this homogeneous sample morphologically, and those names are therefore synonymous with *Henricosbornia.*

MORPHOLOGY

The upper teeth of *Henricosbornia* are known especially from the following specimens:

M.A.C.N. No. 10808, type of *H. lophodonta,* right upper jaw with P^3–M^3, in possible association with right M_{1-2}. Ameghino Collection. No locality data

A.M.N.H. No. 28890, fragmentary skull with right P^1, broken P^3 and M^{1-2}, and left P^{1-4}, broken M^1, and M^2, associated with left P_3–M_2 and broken M_3. Found by G. G. Simpson in Cañadón Vaca

A.M.N.H. No. 28499, left upper jaw with P^4–M^2. Found by C. S. Williams in Cañadón Vaca

A.M.N.H. No. 28891, right upper jaw with P^4–M^1. Found by G. G. Simpson in Cañadón Vaca

And also the many separate teeth in the Scarritt Collection, discussed above, showing the nature of individual variation.

P^1 is a well-developed tooth, considerably longer than wide but with three roots. The ectoloph has distinct subequal paracone and metacone, and much smaller, subequal parastyle and metastyle. The protocone is a very small, low, but pointed cusp directly internal to the metacone. P^2 is known from only one specimen and is there poorly preserved. It seems to be closely similar to P^1 but is considerably wider.

P^{3-4}, abundantly represented in the collections, are closely similar except that P^4 is generally more transverse. Paracone and metacone are distinct but closely approximated and subequal, the paracone slightly larger; both have convex outer faces. Distinct parastyle and metastyle are present, but no mesostyle. The protocone is nearly median on the internal side, less posterior than on P^{1-2}. A low but continuous protoloph with a small protoconular swelling runs from the protocone to the parastyle. There is a very vague and rounded elevation running from the protocone to the metacone, and occasionally this has a slight thickening suggestive of a metaconule or rudimentary crochet. The crochet is otherwise absent, and the central basin is shallow and simple. There are anterior and posterior cingula, the latter often expanded so as to form a small posterointernal basin, but there is no posterointernal cusp. These two cingula are sometimes united across the protocone by an internal cingulum, especially on P^4, but this is a variable character.

The morphology of the upper molars has already been adequately discussed above.

Aside from the two specimens with associated upper and lower teeth, listed above,the lower dentition is known especially from the following specimens, all collected by the First Scarritt Expedition:

From Cañadón Vaca:

A.M.N.H. No. 28751, lower jaw with left I_3 or C, dm_2, and P_3–M_2 and right dm_2 and P_3

A.M.N.H. No. 28867, associated right P_4–M_3

A.M.N.H. No. 28837, right lower jaw with P_4–M_3

A.M.N.H. No. 28865, right lower jaw with P_3–M_2 and part of M_3

A.M.N.H. No. 28838, left lower jaw with P_2 and P_4–M_3

A.M.N.H. No. 28800, left lower jaw with P_4–M_2

A.M.N.H. No. 28866, right lower jaw with P_{3-4} and M_2

From south of Lago Colhué-Huapí:

A.M.N.H. No. 28702, back of lower jaw with right M_{1-3} and left M_{2-3}

It is not quite clear whether the M_{1-2} that Ameghino placed in *H. lophodonta* were actually associated with the type upper teeth or not. They may well have been, as they are similarly preserved and occlude perfectly. In any event they were correctly placed in that species, as is conclusively shown by our specimen A.M.N.H. No. 28890 in which upper and lower dentitions are certainly of the same individual, being found in occlusion.

Our immature lower jaw, A.M.N.H. No. 28751, has a still unerupted tooth which is probably I_3 but might be the canine. It is a semi-procumbent tooth with the labial face convex and the lingual face excavated. The apex is bifid. Dm_2, shown by the same specimen, resembles P_2 of A.M.N.H. No. 28838 save in being somewhat longer and wider, especially posteriorly. It is too worn to show much detail in the crown structure. This specimen shows something of the order of eruption. I_3 or C is still in the crypt, but its predecessor probably was lost. Dm_2 is still in place. P_3 is unerupted, but dm_3 is lost. P_4 is in place but quite unworn. M_1 is moderately, and M_2 slightly, worn. M_3 is not preserved, but partial alveoli on the left side suggest that it had been erupted. The probable order of eruption was, then:

M_1
M_2
P_4 and ?M_3
P_3
P_2

The symphyseal region is poorly preserved, but the tentative suggestion is that it had a graded arc of small, similar teeth, as in *Notopithecus* or *Oldfieldthomasia*, rather than being specialized, as in *Notostylops* or (in a different way) *Pleurostylodon*. The symphysis is narrow, sloping, and produced in a rather spout-like manner, as it is in almost all primitive notoungulates.

P_1 is unknown. P_2 is an elongate shearing tooth, its apex a single crest rising into a high median cusp and lower anterior and posterior cusps and modified by anterointernal, posteroexternal, and posterointernal (smaller and more posterior than the posteroexternal) excavations. P_3 and P_4 are similar to each other except that P_3 is more triangular, narrowing anteriorly. Each has an oblique anteroexternal-posterointernal trigonid crest, more or less excavated on the anterointernal side so as to be subcrescentic; this is individually variable, in some cases the crest being crescentic and almost as on the molars and in others, surely conspecific, almost straight. The main part of the crest bears two cusps. On P_3, when completely unworn, the protoconid is larger than the metaconid and on P_4 they are about equal (the metaconid is the larger of the two on the molars). Directly anterior to the protoconid, and on the same crest, is a very small anteroexternal cusp, presumably a vestige of the paraconid. The talonid bears a sharply crescentic crest on both teeth which abuts against the trigonid crest very slightly internal to the middle; although of such a minor character, this feature is apparently constant and is a good taxonomic distinction. The hypoconid is sharp (when unworn), but the hypoconulid is not very distinct, being merely the rather abrupt ending of the crest posteriorly at the midline. On P_4 there is a distinct, nearly conical entoconid directly internal to the hypoconulid. On P_3 this is only incipient and can barely be distinguished even on the completely unworn tooth.

The lower molar structure is adequately elucidated in the diagnosis and in the accompanying figures.

Few important cranial characters are known. The zygoma arises from a stout root above M^{2-3}, and the jugal lapped over this root to its anterior end and was thus large, although the extent to which it formed the orbital rim cannot be determined. The nasals are long and expanded posteriorly; they must nearly have touched the anterosuperior orbital rim. The parietals lapped forward laterally over the frontals, so that the latter were rather small and lozenge-shaped, much as in *Notostylops*.

The dental foramen is low, below the alveolar level, and the condyle is very high, far above the alveolar border, and is convex and elongate anteroexternal-posterointernally. The coronoid process is high, slender, and recurved. The angle is very large, broad, thin, and concave on the inner side. The horizontal ramus is of normal, primitive proportions with the posterior mental foramen small and beneath the anterior root of P_4 in the three adult specimens that show it and beneath the posterior part of P_3 in a juvenile specimen.

SPECIES

Ameghino identified 22 specimens as belonging to the various genera here united as *Henricosbornia*, and he placed these in 17 different species. Thirteen specimens (nine types and four referred specimens) are recorded as from "Oeste de Río Chico," and nine (eight types and one referred specimen) do not have any locality record. The specimens of unknown locality have the same general aspect as the others, and it is probable that most of them were also from "Oeste de Río Chico," although of course there can be no assurance of this. It is to some extent corroborated by our discovery of abundant representatives of the genus in Cañadón Vaca, which is west of the Río Chico. The genus does occur elsewhere, but is very rare at all other localities worked by us. There is a distinct possiblity that Carlos Ameghino found a pocket of henricosborniids, as we did, and that most or all of his specimens were from there. It may conceivably even have been the same locality as ours, although, as mentioned elsewhere, this is unlikely. On the other hand, the fact that the Ameghino specimens were described in three different years, and were therefore probably found on more than one expedition, to some extent reduces the probability that they were from one locality, although it does not make that impossible.

One type, that of *Henricosbornia lophodonta*, is a fine, thoroughly adequate specimen. One ("*Selenoconus centralis*") is a lower jaw with two teeth. The other 15 are all single teeth, seven either M^1 or M^2, six M^3, and two M_3. The comparable types are all really different in details of structure and in exact dimensions, and as in most of his work Ameghino accepted virtually every observable difference, however small, as of specific value or greater. From the viewpoint of modern knowledge and experience, it has become a truism that no two individuals of one species are exactly alike and hence that the existence of morphological differences does not in itself prove the presence of more than one species. The task of the reviser is to determine what degree and what kind of differences really do indicate properly phylogenetic and taxonomic distinctions.

The criteria must differ from one group to another. In one species a given character may be nearly constant and in another it may be highly variable, and the general variability of

TABLE 28

LENGTH OF M^1 OR M^2 OF *Henricosbornia lophodonta* AND SYNONYMS

	Cañadón Vaca Series	Ameghino Specimens	Ameghino's Designations
4.8	1		
4.9	3		
5.0	1	2	*Prohyracotherium matutinum* (type) *Prohyracotherium patagonicum* (referred)
5.1	1	1	*Henricosbornia lophodonta* (M^1 of type)
5.2	4		
5.3	5	1	*Prohyracotherium patagonicum* (type)
5.4	8	1	*Henricosbornia alouatina* (type)
5.5	10	4	*Henricosbornia lophodonta* (M^2 of type) *Microstylops monoconus* (type) *Pantostylops typus* (type and referred specimen)
5.6	2	1	*Microstylops clarus* (type)
5.7	4		
5.8	4		
5.9	3		
6.0	3		
6.1	1		

one species may be much greater than that of another. One of the safest aids in establishing a criterion is the availability of a series of specimens, surely or very probably of one species, the variability of which may be assumed to apply to other specimens of the same or, with proper caution, of closely related species. In the present case such a series is at hand, as described above. The evidence given by these specimens of variability in *Henricosbornia* may properly be applied to Ameghino's series of types to give some indication of the probability that they do really represent different species. In the absence of any possibility of obtaining a series of specimens surely from the type horizon and locality of any of Ameghino's species, it is necessary to hold that such of his types as fall in every respect within the limits of our series belong to one species and that the names based on these are synonyms.[1]

The principal morphological variations shown by the types of the 14 Casamayor species based on upper teeth are as follows:

	M^1 and M^2
Henricosbornia lophodonta *Henricosbornia alouatina*	Feeble mesostyle, simple, moderate crochet
Prohyracotherium patagonicum *Prohyracotherium matutinum*	Very weak mesostyle and crochet
Microstylops clarus	Crochet almost absent
Microstylops monoconus	Crochet weak, a rudimentary cusp in the basin
Pantostylops typus	Crochet and basin cusp distinct
Pantostylops completus	Crochet and basin cusp fused
	M^3
Henricosbornia lophodonta	Short metaloph, separate posterointernal cuspule, crochet moderate
Henricosbornia subconica *Polystylops amplus* *Hemistylops paucicuspidatus*	Elongate metaloph, slight or no posterointernal cuspule, crochet weak
Hemistylops incompletus *Hemistylops trigonostyloides*	Elongate metaloph, distinct posterointernal cuspule, crochet weak
Polystylops progrediens	Short metaloph, feeble posterointernal cuspule, short, distinct crochet

All these variations occur in various combinations in our Cañadón Vaca sample which has been shown to represent a single species. It therefore follows that they do not, in themselves, establish the validity of any of Ameghino's species. Nor do they occur in Ameghino's material in any combination that is unrepresented in our homogeneous samples, and the range of variation in his material does not appear to be greater in degree than in ours, or different in kind.[2]

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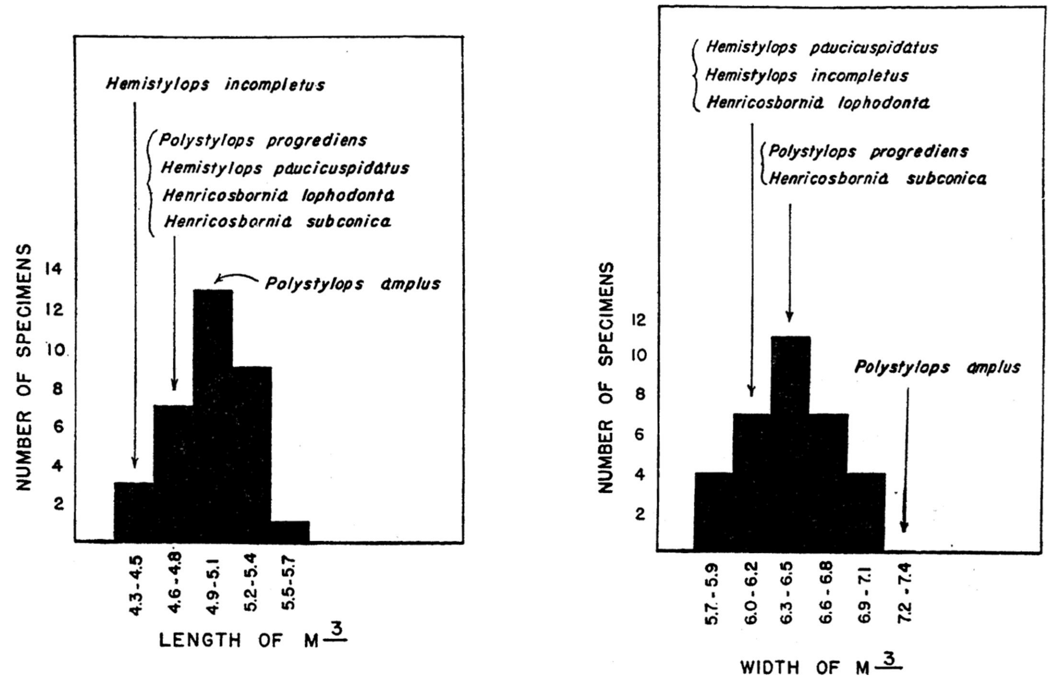
[1] This is a necessary procedure in the given circumstances and not a generalization. It does occasionally happen that distinct subspecies, or very rarely even species, have overlapping ranges for all their characters, and hence that a few individuals of one might be within the range of the other. In such cases these individuals cannot possibly be identified as such, but only as members of the group which, as a group, does have significant diagnostic characters. In the present case the Ameghino Collection is made up only of individuals and does not permit the formation of any group concept, the data on which alone such a concept could be objectively formed not being preserved or recoverable. Hence the possible units that might have been defined on wholly intergrading groups cannot here be recognized, nor is there any reason to hold tentatively to any names in hope of validating these later, for this cannot ever be done in this instance.

[2] Ameghino's type figures are slightly misleading, to the extent that they suggest a greater variety and more clear-cut distinctions than actually occur. They do not clearly indicate differences in wear, which radically change the aspect of the tooth; in some cases they fail to indicate the presence of broken surfaces; and in some instances they give more emphasis to the characters considered by Ameghino as diagnostic.

TABLE 29

LENGTH OF M_3 OF *Henricosbornia lophodonta* AND SYNONYMS

	Cañadón Vaca Series	Ameghino Specimens	Ameghino's Designations
4.4	2		
4.5	1	1	*Hemistylops incompletus* (type)
4.6			
4.7	5	2	*Hemistylops paucicuspidatus* (type) *Polystylops progrediens* (type)
4.8	2	2	*Henricosbornia lophodonta* (type) *Henricosbornia subconica* (type)
4.9	4		
5.0	6	1	*Polystylops amplus* (type)
5.1	3		
5.2	2		
5.3	2		
5.4	5		
5.5	1		



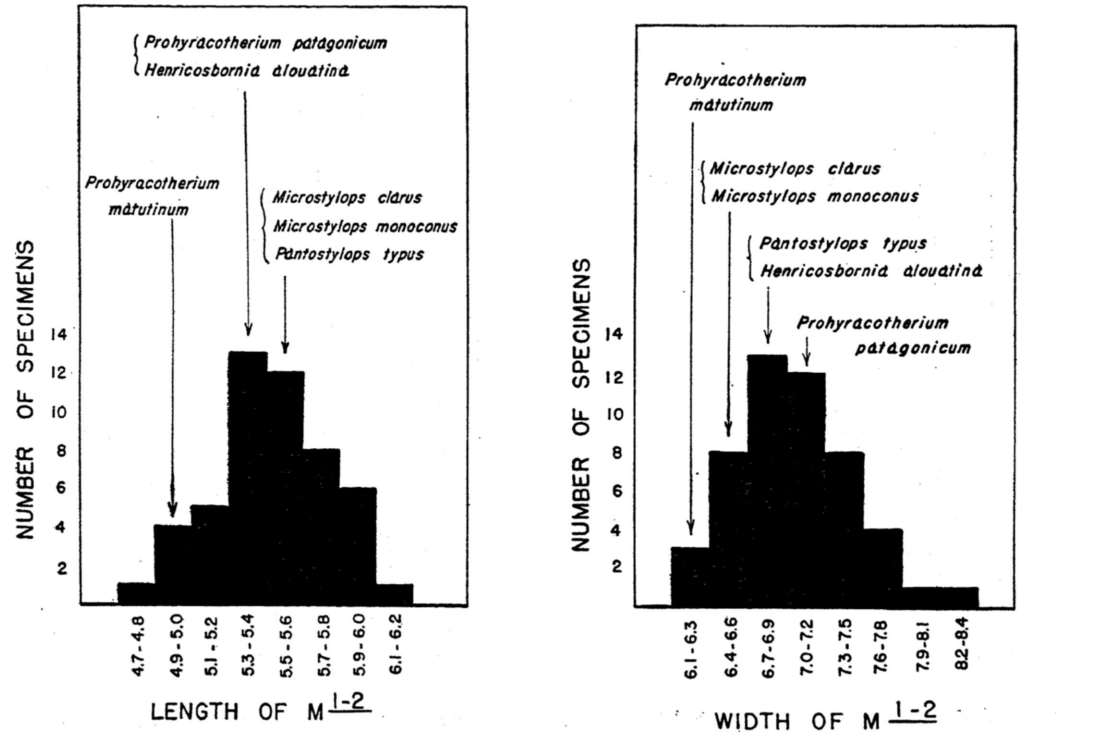
Henricosbornia lophodonta — Cañadon Vaca   Henricosbornia lophodonta – Cañadon Vaca

FIG. 50. *Henricosbornia lophodonta* Ameghino. Histograms of frequency distributions of the two dimensions of M^3 in the American Museum of Natural History sample from a single horizon and locality in Cañadón Vaca. The names and arrows above the histograms show the positions of types of Ameghino's species here considered synonymous with *H. lophodonta*. (These types are not included in the frequencies shown by the histograms.)

TABLE 30

Henricosbornia

		Cañadón Vaca Series	Ameghino Specimens	
			Whole Lot	Without *amplus*
LM^{1-2}	OR	4.8–6.1	5.0–5.6	
	M	5.5	5.3	
WM^{1-2}	OR	6.1–8.2	6.1–7.1	
	M	7.0	6.6	
LM^3	OR	4.4–5.5	4.5–5.0	4.5–4.8
	M	5.0	4.8	4.7
WM^3	OR	5.8–7.1	6.0–7.4	6.0–6.5
	M	6.4	6.4	6.2



Henricosbornia lophodonta - Cañadon Vaca   Henricosbornia lophodonta - Cañadon Vaca

FIG. 51. *Henricosbornia lophodonta* Ameghino. Histograms of frequency distributions of the two dimensions of M^1 and M^2 (combined) in American Museum of Natural History sample from a single horizon and locality in Cañadón Vaca. Above, positions of Ameghino's types of synonymous species, as in figure 50.

With a single exception, the dimensions of all of Ameghino's types are also within the range of the corresponding teeth of the Cañadón Vaca series.

This is shown by the distributions of the lengths of M^1 or M^2 (which cannot be distinguished as isolated teeth) and of M^3 (see tables 28 and 29 and text figs. 50–52).

The only exceptional specimen, in comparison with the Cañadón Vaca series, is the type of *Polystylops amplus*. Its length, as shown, is well within the Cañadón Vaca range and only slightly different from that of Ameghino's other types, but its width, 7.4, is slightly beyond the Cañadón Vaca range (5.8–7.1) and far beyond the range of the other types (6.0–6.5).

A general résumé of size relationships is given in table 30.

It is noteworthy that while the ranges of the Ameghino types are wholly included within those of the Cañadón Vaca series (except WM^3 of *P. amplus*), the means are in every case slightly smaller (except WM^3 if *P. amplus* is included). It is somewhat futile to speculate as to the meaning of this, and it would be invalid to attempt a statistical demonstration of its significance for the following reasons. In the first place, this statistical procedure is for the comparison of two

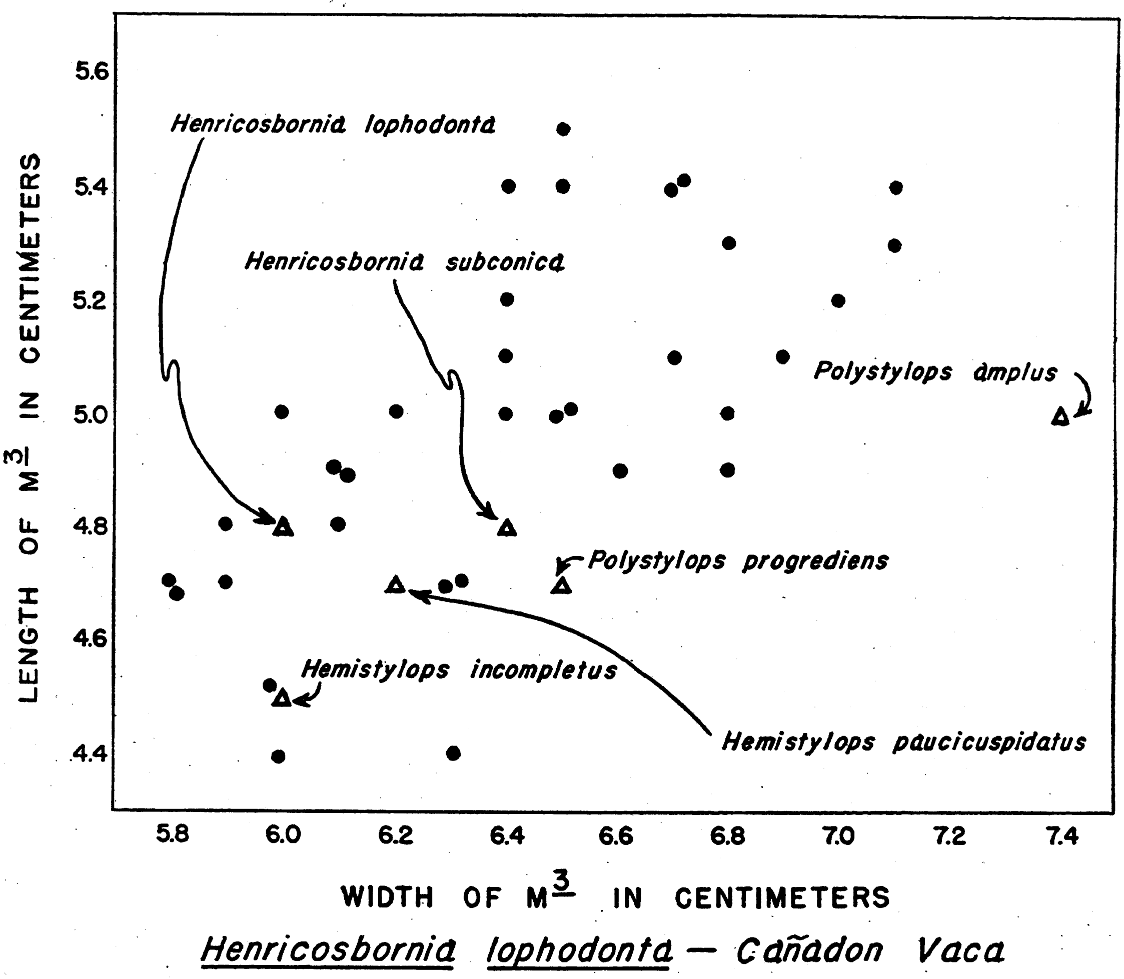


FIG. 52. *Henricosbornia lophodonta* Ameghino. Scatter diagram of length and width of American Museum sample of M^3 from a single horizon and locality in Cañadón Vaca (circles). Types of synonymous species based on M^3 are also shown (triangles).

samples, each from a single population, and if this condition is not fulfilled, the result is fallacious. In the present case, it is not a known fact, a reasonable probability, or a warranted hypothesis that the Ameghino specimens are drawn from a single population. They do not, in fact, constitute a sample in the statistical sense of the word. In the second place, even if it could be established that the difference in the means of the two groups is statistically significant, it would not follow that this difference has any biological, or at least taxonomic, significance. It could be entirely explained by a non-taxonomic hypothesis which is not open to proof or disproof, for instance by a preponderance of M^1 over M^2 in Ameghino's specimens and (or) of M^2 over M^1 in the Cañadón Vaca sample.[1]

In any event, it may be taken as established that all these species, with the sole possible exception of *P. amplus*, are synonymous. Even if the somewhat smaller average size of Ameghino's types should prove to be significant, or rather should have been significant (for this cannot now ever be proved), the complete inclusion of their variation in that of our homogeneous sample shows that the distinction would have been a very minor one, the taxonomic unit not greater than that of a local or temporal race.

The case of *P. amplus* is more dubious. It is outside the established range of variation, so should perhaps not be taken as a proved synonym, like the other 13 species, and yet its deviation is too small to prove conclusively that it is distinct. In comparison with the Cañadón Vaca sample of *H. lophodonta*, d/σ of its width is $+2.7$ and of its length:width index -2.7. Thus it could be, but probably is not, drawn from the same population. The species is left on record for the present, but is not adequately defined.

The types of the four species of *Selenoconus* are lower teeth. All include M_3, and all but *S. spiculatus* also include M_2, thus giving a good opportunity for comparison with the samples of *Henricosbornia lophodonta*. The morphological variation is relatively slight. The figure of *S. centralis* (Ameghino, 1906, fig. 73) shows the metaconids as if they were merely the ends of simple lophids, and not obliquely expanded or crested. This is incorrect, the metaconids being in fact exactly as in *Henricosbornia lophodonta*. The description of *S. senex* stated that the trigonid is more compressed anteroposteriorly than in *S. centralis*, the trigonid basined, and the hypoconulid partly fused with the hypoconid. The first of these characters I cannot confirm from the original specimens, and the other two are not distinctive from any specimens of *Henricosbornia*, or of *S. centralis*. The several morphological distinctions of *S. spiculatus* are certainly due to the unworn nature of the type tooth, and are not actual differences.

Our homogeneous Cañadón Vaca sample contains teeth surely identifiable as M_3 of the same species as the upper teeth already shown to belong to *Henricosbornia lophodonta*. The numerical characters of these are given in table 31.

Our referred specimen from Colhué-Huapí has length 6.3, width 4.0, and index 158, and is thus very near the Cañadón Vaca means. A comparison of the Ameghino types is given in table 32.

Selenoconus agilis is evidently distinct (it belongs in *Peripantostylops* and is discussed below), but the other three are all within the range of our sample of *H. lophodonta*. They are below average size, and might possibly represent a different subspecies, but this cannot be determined. They almost certainly do not differ specifically from *Henricosbornia lophodonta*, on this showing. The characters of M_2 fully confirm this for *S. centralis* and *senex* (this tooth not occurring in the *spiculatus* type). We have numerous isolated M_1 or M_2, but it is a crude comparison to set these against the known M_2 of the types. We have also five M_2's in the Cañadón Vaca sample that occur in jaws and are known to be such. They alone are used in the comparison given in table 33.

Again *S. agilis* is quite distinct, but *S. centralis* and *senex* are inseparable from *H. lophodonta*. Our Colhué-Huapí jaw has LM_2 5.6, WM_2 4.4, and $100\ LM_2/WM_2$ 127 and is thus very close to the other *H. lophodonta*

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[1] The few specimens in which these teeth can be definitely identified show that M^2 averages larger than M^1, but that their size ranges overlap extensively. Thus in one such specimen, M^1 measures 5.4 by 6.7 and in another specimen M^2 has exactly the same dimensions, but in a single individual, so far as shown, M^2 is always slightly larger than M^1.

TABLE 31

Henricosbornia lophodonta

Variate	N	OR	M	σ	V
LM_3	21	6.0–6.9	6.4 ± .1	.27 ± .04	4.2 ± .7
WM_3	21	3.7–4.6	4.1 ± .1	.26 ± .04	6.3 ± 1.0
100 LM_3/WM_3	21	144–179	158 ± 2	8.4 ± 1.3	—

TABLE 32

Henricosbornia lophodonta AND SYNONYMS

	LM_3	WM_3	100 LM_3/WM_3
Cañadón Vaca sample	OR: 6.0–6.9 M: 6.4	OR: 3.7–4.6 M: 4.1	OR: 144–179 M: 158
Type, *S. centralis*	6.0	4.0	150
Type, *S. senex*	6.1	*ca.* 4	*ca.* 152
Type, *S. spiculatus*	6.1	4.0	153
Type, *S. agilis*	5.7	3.1	184

TABLE 33

Henricosbornia lophodonta AND SYNONYMS

	LM_2	WM_2	100 LM_2/WM_2
Cañadón Vaca sample	OR: 5.0–5.9 M: 5.6	OR: 4.0–4.6 M: 4.3	OR: 123–138 M: 130
Type, *Henricosbornia lophodonta*	5.5	4.2	131
Type, *S. centralis*	5.5	4.3	128
Syntype, *S. senex*	5.8	4.4	132
Type, *S. agilis*	4.2	3.0	140

specimens in this tooth also. We also have a few fragmentary specimens from one or two other localities, but they are not very exactly identifiable.

Henricosbornia lophodonta Ameghino, 1901

Plate 14, figures 1–25; text figures 48–49, 53–55

Henricosbornia lophodonta AMEGHINO, 1901, p. 357; 1904b, p. 166, figs. 211, 401; 1904d, p. 75, fig. 67; CABRERA, 1935, p. 12; SIMPSON, 1937c, fig. 4.

Selenoconus centralis AMEGHINO, 1901, p. 381; 1906, p. 291, fig. 73.

Selenoconus senex AMEGHINO, 1901, p. 381.

Pantostylops typus AMEGHINO, 1901, p. 423; 1904b, p. 146, figs. 179, 486, 529; 1906, p. 321, fig. 139.

Pantostylops incompletus AMEGHINO, 1901, p. 423.

Hemistylops incompletus AMEGHINO, 1904a, vol. 58, p. 38; 1904b, p. 170, figs. 219, 506; 1906, p. 323; fig. 146; CABRERA, 1935, p. 14.

Microstylops clarus AMEGHINO, 1901, p. 426; 1904b, p. 170, figs. 218, 261, 332, 487, 528; 1906, p. 321, fig. 140.

Prohyracotherium patagonicum AMEGHINO, 1902a, p. 15; 1904b, p. 107, figs. 119, 309; 1906, p. 306, fig. 113b; CABRERA, 1935, p. 12.

Prohyracotherium matutinum AMEGHINO, 1902a, p. 16.

Selenoconus spiculatus AMEGHINO, 1902a, p. 20.

Pantostylops completus AMEGHINO, 1902a, p. 33; 1904b, p. 374, figs. 489, 502, 530.

Henricosbornia alouatina AMEGHINO, 1904a, vol. 56, p. 197; 1904b, p. 89, fig. 93.

Henricosbornia subconica AMEGHINO, 1904a, vol. 56, p. 198; 1904b, p. 167, fig. 212.

Hemistylops paucicuspidatus AMEGHINO, 1904a, vol. 58, p. 39; 1904b, p. 169, figs. 217, 505.

Hemistylops trigonostyloides AMEGHINO, 1904a, vol. 58, p. 39; 1904b, p. 386, fig. 507.

Polystylops progrediens AMEGHINO, 1904a, vol. 58, p. 40; 1904b, p. 75, figs. 73, 118, 503.

Microstylops monoconus AMEGHINO, 1904a, vol. 58, p. 41; 1904b, p. 404, fig. 527.

TYPE: M.A.C.N. No. 10808. Right maxillary fragment with P^3–M^3, and right lower jaw fragment, possibly associated and surely conspecific, with M_2 and broken M_1. No locality data.

TYPES OF SYNONYMS: *Selenoconus centralis*: M.A.C.N. No. 10797. Assciated left M_{2-3} (holotype or lectotype), also right M_3, right dm_4, and left M_3, not associated and not all surely conspecific. "Oeste de Río Chico."

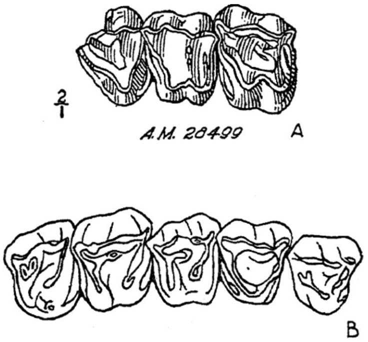

FIG. 53. *Henricosbornia lophodonta* Ameghino. A. A.M.N.H. No. 28499, left P^4–M^2. B. Diagrammatic reconstruction of P^3–M^3, not a portrait of an individual specimen but a composition based on available typical materials. Crown views. ×2.

Selenoconus senex: M.A.C.N. No. 10792. Isolated right M_1 or M_2, left M_1 or M_2, and left M_3, not associated. One of the isolated anterior molars and the M_3 are mentioned in the type description and are thus syntypes, but the M_3 was emphasized and is made lectotype. "Oeste de Río Chico."

Pantostylops typus: M.A.C.N. No. 10717. Left M^1 or M^2, right M^1 or M^2, and two broken upper molars, probably not associated. The left M^1 or M^2 was evidently the basis for the definition and is type or lectotype. "Oeste de Río Chico."

Hemistylops incompletus: M.A.C.N. No. 10707. Isolated left M^3. "Oeste de Río Chico."

Microstylops clarus: M.A.C.N. No. 10715. Isolated right M^1 or M^2. No locality data.

Prohyracotherium patagonicum: M.A.C.N. No. 10675. Isolated left M^1 or M^2. No locality data.

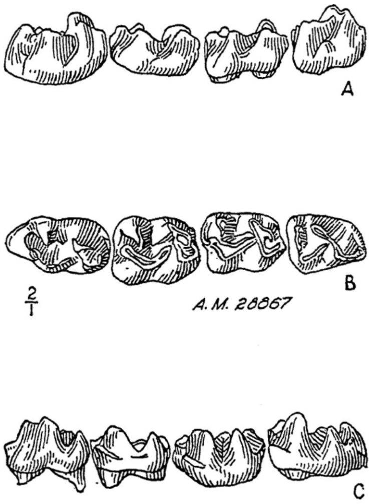

FIG. 54. *Henricosbornia lophodonta* Ameghino. A.M.N.H. No. 28867, right P_4–M_3. A. External view. B. Crown view. C. Internal view. ×2.

Prohyracotherium matutinum: M.A.C.N. No. 10676. Isolated left M^1 or M^2. No locality data.

Selenoconus spiculatus: M.A.C.N. No. 10795. Isolated right M_3. No locality data.

Pantostylops completus: M.A.C.N. No. 10716. Two isolated right upper molars, both lacking the ectoloph. The definition was evidently based on the slightly larger and less complete of the two, which is type or lectotype. No locality data.

Henricosbornia alouatina: M.A.C.N. No. 10810. Isolated left M^1 or M^2. "Oeste de Río Chico."

Henricosbornia subconica: M.A.C.N. No. 10809. Isolated left M^3. "Oeste de Río Chico."

Hemistylops paucicuspidatus: M.A.C.N. No. 10714. Isolated left M^3. No locality data.

Hemistylops trigonostyloides: M.A.C.N. No. 10710. Isolated broken right M^3. No locality data.

Polystylops progrediens: M.A.C.N. No. 10708. Isolated left M^3. "Oeste de Río Chico."

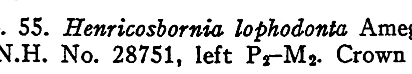

FIG. 55. *Henricosbornia lophodonta* Ameghino. A.M.N.H. No. 28751, left P_2–M_2. Crown view. ×2.

Microstylops monoconus: M.A.C.N. No. 10713. Isolated broken right M^1 or M^2. No locality data.

HYPODIGM: The above types and large series of referred specimens in the Museo Argentino de Ciencias Naturales and the American Museum of Natural History, the most important of which have been described or listed above.

HORIZON AND LOCALITY: Casamayor and probably Río Chico, Patagonia. Types of known origin all from "Oeste de Río Chico" as listed above. Referred specimens from Casamayor of Cañadón Vaca and south of Lago Colhué-Huapí. Other probably referable specimens from uppermost Río Chico, Bajo de la Palangana.

DIAGNOSIS: 100 LM^3/WM^3 in hypodigm 70–85. WM^3 in hypodigm 5.8–7.1 mm. WM_2 in hypodigm 4.0–4.6 mm. 100 LM_2/WM_2 in hypodigm 123–138. Metaconid strong, with sharply produced antero-external spur.

The characters and many of the dimensions of this species have been set forth above. The measurement of some individual specimens are given in tables 34 and 35.

A good specimen, A.M.N.H. No. 28968, right upper jaw with P^4–M^3 and part of P^3, and some fragments from the highest fossiliferous Río Chico horizon in the Bajo de la Palangana cannot be distinguished from *Henricosbornia lophodonta*—the most positive identification of a Casamayor species in the Río Chico, even at this upper level. Cabrera (1935) listed from this same horizon and locality three isolated teeth referred to *Henricosbornia lophodonta, Prohyracotherium patagonicum,* and *Hemistylops incompletus.* The last two species have been shown above to be synonyms of the first, and doubtless all Cabrera's specimens represent the same form as our upper jaw from this locality. (A distinct species occurs in an earlier level of the Río Chico; see below.)

Henricosbornia ampla (Ameghino, 1904), new combination

Plate 14, figure 26

Polystylops amplus AMEGHINO, 1904a, vol. 58, p. 41; 1904b, p. 385, fig. 504.

TYPE: M.A.C.N. No. 10709. Isolated left M^3.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayor, "Oeste de Río Chico," Patagonia.

DIAGNOSIS: Near *H. lophodonta* but WM^3 above observed range in the latter and 100 $LM^3/WM^3 = 68$, below observed range of *H. lophodonta.*

TABLE 34

Henricosbornia lophodonta

	P^3		P^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W	L	W
Type	5.0	*ca.* 5.0+	4.7	5.7	5.1	6.1	5.5	*ca.* 6.5+	4.8	*ca.* 6
A.M.N.H. No. 28890	4.9	5.8	4.8	6.2	5.2	6.3	5.5	6.7	—	—

TABLE 35

Henricosbornia lophodonta

	P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W
Type	—	—	—	—	—	—	5.5	4.2	—	—
A.M.N.H. No. 28890	5.1	2.8	5.0	3.4	5.3	3.9	5.9	4.3	—	—
A.M.N.H. No. 28867	—	—	5.1	3.9	5.6	4.1	5.9	4.6	6.8	3.8

Henricosbornia waitehor Simpson, 1935

Text figure 56

Henricosbornia waitehor SIMPSON, 1935a, p. 12, fig. 14.

TYPE: A.M.N.H. No. 28530. Left lower jaw with M_{1-2} and part of M_3.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Río Chico formation, Cañadón Hondo, Patagonia.

DIAGNOSIS: Similar to *H. lophodonta*, but lower molars absolutely and relatively narrower, metaconids weaker and less produced anteriorly. WM_1 3.7 mm. LM_2 5.5 mm. WM_2 3.8 mm. 100 LM_2/WM_2 145. All measurements of type only.

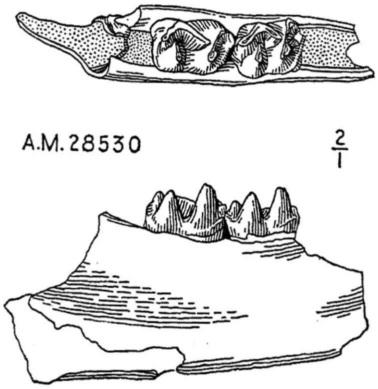

FIG. 56. *Henricosbornia waitehor* Simpson. Type, A.M.N.H. No. 28530, left lower jaw fragment with M_{1-2}. Crown and internal views. ×2.

This earliest form is not well known and the most distinctive parts are not preserved, but it is enough like *H. lophodona* for tentative reference to the same genus and sufficiently different to represent a distinct species beyond much question. It is likely that more complete dentitions or upper teeth will force generic separation, as few Casamayor genera occur at this considerably earlier horizon.

Henricosbornia minuta (Roth, 1903), new combination

Monolophodon minutus ROTH, 1903a, p. 143.
? *Polystylops minutus*, SIMPSON, 1934e, p. 13; 1936d, p. 69.

TYPE: M.L.P. No. 12-2174. Left M^3.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Río Chico formation, Gaiman, Chubut.

DIAGNOSIS: Type M^3 in size range of *H. lophodonta* but large and relatively narrow transversely. More symmetrical and triangular in outline than is usual in M^3 of *H. lophodonta.* Crochet apparently present but cutting off only a small corner of the central valley. Metacone fold fairly prominent, outer face of ectoloph between paracone and metacone long and somewhat excavated. Type measures 5.5 by 6.7 mm.

The type is worn and the diagnosis given above is by no means satisfactory, but it is improbable that this species is synonymous with any other yet named. Roth (1903a) said that he had an incisor, a canine, a premolar, and a molar from the upper dentition and an incisor and a premolar from the lower. Although all were found together, Roth himself doubted their being associated. Two anterior teeth and a left upper premolar are preserved as M.L.P. No. 12-2175, but their pertinence to this genus or species is so dubious that they do not merit description.

OTHNIELMARSHIA AMEGHINO, 1901

Othnielmarshia AMEGHINO, 1901, p. 358; 1904b, p. 110; 1906, p. 467; SCHLOSSER, 1923, p. 609.
Postpithecus AMEGHINO, 1901, p. 358; 1906, p. 467.

TYPE: *Othnielmarshia lacunifera* Ameghino 1901.

TYPE OF *Postpithecus*: *Postpithecus curvicrista* Ameghino, 1901.

DISTRIBUTION: Casamayor, Patagonia. Dubious in Río Chico.

DIAGNOSIS: M^{1-3} strongly transverse, with crochet very weak or absent, mesostyle region excavated, sharp external cingulum, little or no metastyle on M^3. Hypoconid less angulate and hypoconulid less distinct than in *Henricosbornia,* entoconid more conical and less sharply separated from hypoconulid.

Ameghino described *Othnielmarshia* and *Postpithecus* simultaneously, basing them respectively on upper and lower teeth of closely related animals of about the same size, evidently collected at the same time and the same place. These circumstances are susspicious, in themselves, for it at once comes to mind that they could well be upper and lower teeth of the same genus. The genus is rare, and actually associated upper and lower teeth have not yet been found, but the synonymy seems to be practically certain, on the following grounds:

1. All the known specimens of both genera are from one lot in the Ameghino Collection, from "Oeste de Río Chico," and one in the Scarritt Collection from Cañadón Vaca.
2. In both lots both *Othnielmarshia* and *Postpithecus* occur, in about equal numbers, although in both collections as a whole both genera are relatively very rare.
3. Aside from *Othnielmarshia*, there are no known upper teeth, in the hundreds available, that could belong with the lowers called *Postpithecus*, and aside from *Postpithecus* no known lower teeth could correspond to *Othnielmarshia.*
4. Upper teeth of *Othnielmarshia* and lower teeth of *Postpithecus* from the same horizon and locality are entirely harmonious in size and structure and they occlude well.

The genus is very poorly known. In the Ameghino Collection there are only five or six specimens that can be considered as surely of this genus, and in the Scarritt Collection there are 19, all of which are isolated teeth. These suffice to establish the genus as valid beyond any doubt, but they tell little of its character beyond the details of molar structure sufficiently brought out in the discussion of *Henricosbornia*, in the diagnoses, and in the figures.

Ameghino described one species of *Othnielmarshia* and two of *Postpithecus*. I suspect that these are all synonymous, or that two are, and that the third, if not synonymous, is extraneous to the whole group, but material is lacking to prove this. The available lower teeth from Cañadón Vaca almost certainly belong to the same species as the upper teeth from the same locality, placed in *O. lacunifera*, but there are only seven of these and they do not show whether the supposed species of "*Postpithecus*" are really within the range of *O. lacunifera* or not. All three species are therefore listed, but the last two are practically *nomina vana.*

Othnielmarshia lacunifera Ameghino, 1901

Plate 14, figures 27–29; text figure 57

Othnielmarshia lacunifera Ameghino, 1901, p. 358; 1904b, p. 110, figs. 123, 178; 1906, p. 292, fig. 78.

Type: M.A.C.N. No. 10807. A miscellaneous lot of teeth, not associated and perhaps not all conspecific, including a complete upper left M^1 or M^2 (figured specimen and now made lectotype), another left M^1 or M^2 broken, and a fragment of a right M^1 or M^2.

Hypodigm: Type and A.M.N.H. Nos. 28978 to 28985, inclusive, and 28988, eight lower and 12 upper molars, all isolated.

Horizon and Locality: Casamayor, Patagonia. Type labeled "Oeste de Río Chico."[1] Our series of referred specimens from Cañadón Vaca.

Diagnosis: Based primarily on the upper molars with the characters of the genus. Measurements given in tables 36 and 37.

The Cañadón Vaca sample of M^3 has the statistical constants given in table 36.

This tooth does not occur in the Ameghino Collection. We have only four specimens of

TABLE 36

Othnielmarshia lacunifera

Variate	N	OR	M	σ	V
LM^3	8	5.5–6.1	5.9 ± .1	.25 ± .06	4.3 ± 1.1
WM^3	8	6.9–7.6	7.3 ± .1	.23 ± .06	3.1 ± 1.1
$100\ LM^3/WM^3$	8	77–85	81 ± 1	2.5 ± .6	—

---

[1] There is another word on the label that might be "cuarcito." If so, the specimen might really be from the Upper Río Chico, or might be from one of the coarser tuffs of the Lower Casamayor, but this is all too uncertain for much consideration. Our specimens are definitely from the Casamayor.

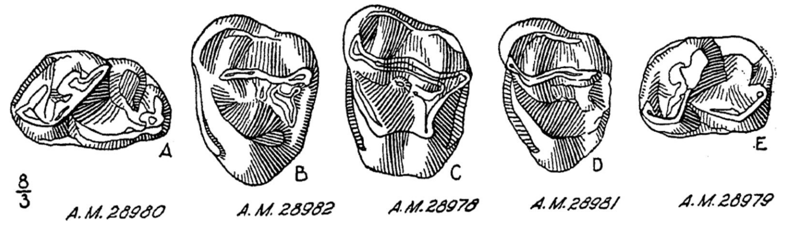

FIG. 57. *Othnielmarshia lacunifera* Ameghino. Isolated teeth from a single horizon and locality in Cañadón Vaca. A. A.M.N.H. No. 28980, left M_3. B. A.M.N.H. No. 28982, left M^3. C. A.M.N.H. No. 28978, left M^1 or M^2. D. A.M.N.H. No. 28981, left M^3. E. A.M.N.H. No. 28979, left M_1 or M_2. Crown views. ×8/3.

M^1 or M^2, which compare with one another and with the type as shown in table 37.

TABLE 37

Othnielmarshia lacunifera

	L	W	100 L/W
A.M.N.H. specimens	6.3 6.3 6.4 6.5	7.9 8.3 7.6 8.1	80 76 84 80
Type	6.1	8.0	76

The differences of the Cañadón Vaca specimens from the type are so slight as not to suggest any taxonomic difference. The morphological variation shown by all the various upper teeth is rather less than in *Henricosbornia lophodonta*, but this would be expected in view of the much smaller samples.

Othnielmarshia curvicrista (Ameghino, 1901), new combination

Plate 14, figures 30–31

Postpithecus curvicrista AMEGHINO, 1901, p. 358; 1906, p. 292, fig. 77.

TYPES: M.A.C.N. No. 10806. A number of isolated teeth, not associated and perhaps not all conspecific, including isolated left M_1 or M_2, isolated left M_3, left M_1 or M_2 in fragment of jaw, and right M_1 or M_2 in fragment of jaw. The isolated M_1 or M_2 and M_3 were later figured (Ameghino, 1906, fig. 77), but the type description was evidently based entirely on one tooth, a M_1 or M_2, and the measurements given are closer to those of the isolated M_1 or M_2 (not in jaw fragment) in the present lot of material. This is therefore probably the type, and may in any case be designated lectotype.

HYPODIGM: Essentially the lectotype only. Other referred specimens or syntypes are of doubtful reference to the species, if it is valid.

HORIZON AND LOCALITY: Casamayor, Patagonia. Type from "Oeste de Río Chico."

DIAGNOSIS: Probably equals *O. lacunifera*, but formally retained as based on lower teeth of this genus. Measurements are given in tables 38 and 39.

TABLE 38

MEASUREMENTS OF M_1 OR M_2 OF *Othnielmarshia*

	L	W
A.M.N.H., Cañadón Vaca specimens probably of *O. lacunifera*	5.7 6.3 6.6	4.8 4.8 5.3
Type of *O. curvicrista*	5.6	3.8
Figured specimen referred to *O. curvicrista* by Ameghino	6.3	4.1

TABLE 39

MEASUREMENTS OF M_3 OF *Othnielmarshia*

	L	W
A.M.N.H., Cañadón Vaca specimens referred to *O. lacunifera*	7.4 7.3 7.9 7.6	4.4 4.1 4.6 4.2
Figured specimen referred to *O. curvicrista* by Ameghino	7.5	4.1

It would appear that the Cañadón Vaca specimens of M_1 or M_2 are larger, or at least wider, then Ameghino's specimens, but the specimens are too few in any case to demonstrate that this is more than chance individual variation, and it may also be due simply to different homologies, as M_1 and M_2 cannot be distinguished in this material.

Ameghino's specimen of M_3 falls readily into our species in size, as it does also in structure.

Othnielmarshia reflexa (Ameghino, 1901), new combination

Plate 14, figures 32–35

Postpithecus reflexus AMEGHINO, 1901, p. 358; 1906, p. 292, fig. 76.

TYPE: M.A.C.N. No. 10803. Three fragmentary lower jaws, one with M_{1-2}, one with P_4–M_1, and one with P_{3-4}. They are not associated, and the last mentioned, at least, probably does not belong to this species, or indeed family. The type description was probably based entirely on the first specimen, with M_{1-2}, and this was also figured. It is therefore the type or lectotype.

HYPODIGM: Lectotype only. Referred specimens or syntypes doubtfully pertinent.

HORIZON AND LOCALITY: Casamayor, Patagonia. "Oeste de Río Chico."

DIAGNOSIS: Status very dubious. M_2 of type longer than any ?M_1 or ?M_2 referred to the other two nominal species. See table 40.

TABLE 40

Othnielmarshia reflexa

	P_4		M_1		M_2	
	L	W	L	W	L	W
Type or lectotype	—	—	6.4	4.5	7.1	5.1
Referred or syntype	4.7	*ca.* 4	6.3	4.1	—	—

The referred specimen is hardly separable from specimens referred to *O. lacunifera* and *O. curvicrista*. M_2 of the type is longer than other known lower M_1 or M_2 of the genus and is also unusually narrow relatively, the trigonid crest more oblique, and the twinning of the metaconid perhaps more advanced. All this is very vague, however. In the present state of knowledge, it is not impossible that this is merely a variant of *O. lacunifera*, and on the other hand it might not belong in this genus.[1]

Cf. **Othnielmarshia** sp.

Text figure 58

A jaw fragment with M_3 in the Feruglio Collection from the upper Río Chico level of the Bajo de la Palangana (cast, A.M.N.H. No. 27888) resembles *Othnielmarshia*, as previously reported in Simpson, 1935a (p. 13, fig. 15), where it was called "?*Postpithecus* sp." Since the original description of this specimen, the synonymy of *Postpithecus* with *Othnielmarshia* has been established, and examples of M_3 in this genus have been identified. The Río Chico specimen differs enough from these to suggest a distinct but probably allied genus, for which no name is proposed in view of the inadequacy of the evidence. The heel crest differs from that of *Othnielmarshia* in being single, without distinct cusps or transverse entoconid crest. The small spur or accessory cuspule on the metaconid, noted in Simpson, 1935a, also occurs in *Othnielmarshia*. The trigonid is relatively shorter in the Río Chico specimen than in *Othnielmarshia*.

FIG. 58. Cf. *Othnielmarshia* sp. A.M.N.H. No. 27888 (cast of a specimen in the Feruglio Collection), left M_3 from the uppermost Riochican. Crown view. ×2.

PERIPANTOSTYLOPS AMEGHINO, 1904

Peripantostylops AMEGHINO, 1904a, vol. 58, p. 37; 1906, p. 467.

TYPE: *Pantostylops minutus* Ameghino, 1901.

DISTRIBUTION: Casamayor, Patagonia. Dubious in Río Chico.

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[1] This (improbable) eventuality could not revive the name *Postpithecus*, as *P. curvicrista* is its type by original designation.

TABLE 41
Peripantostylops minutus

	P^3		P^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W	L	W
A.M.N.H. No. 28494	4.0	4.1	4.1	4.4	4.3	5.1	4.8	5.4	4.5	4.9

TABLE 42
Peripantostylops minutus

		M^3	
		L	W
5 specimens, M^3, from Cañadón Vaca, A.M.N.H. Nos. 28494, 28986	OR M	4.0–4.5 4.3	4.6–4.9 4.7

DIAGNOSIS: P^{3-4} with metacone very poorly differentiated or absent. M^{1-3} less transverse than in *Henricosbornia* or *Othnielmarshia*, crochet stronger, mesostyle region flattened (rarely somewhat convex) with a small pit at the base of the crown, no external cingulum, metastyle of M^3 poorly differentiated. Hypoconid generally less angulate and hypoconulid less separate than in either *Henricosbornia* or *Othnielmarshia*. Entoconid well separated on M_3.

The distinctive characters of this genus have already been rather fully brought out in comparison with other members of the family. Of the three valid genera, this seems to be the most primitive in several respects and is therefore of outstanding interest, although some features, such as the stronger crochet, are probably progressive.

Ameghino's conception of the genus was based on a single upper molar. He also referred to *Selenoconus*, the type of which is the lower dentition of *Henricosbornia lophodonta*, a small lower jaw fragment which he called *S. agilis*. Our discovery of associated upper and lower jaws shows that it was the lower dentition of *Peripantostylops minutus*. The genus is rare. Ameghino had only the two poor specimens noted, and our collection adds one fine specimen, nine surely identifiable isolated teeth, and a few more doubtful specimens.

Peripantostylops minutus (Ameghino, 1901)

Plate 14, figures 36–38; text figure 59

Pantostylops minutus AMEGHINO, 1901, p. 424.

Peripantostylops minutus, AMEGHINO, 1904a, vol. 58, p. 37; 1904b, p. 206, figs. 276, 488.

Selenoconus agilis AMEGHINO, 1901, p. 381; 1906, p. 291, fig. 72.

TYPE: M.A.C.N. No. 10711. Isolated right M^1 or M^2.

TYPE OF *Selenoconus agilis:* M.A.C.N. No. 10796. Part of the left lower jaw with M_{2-3} and broken M_1.

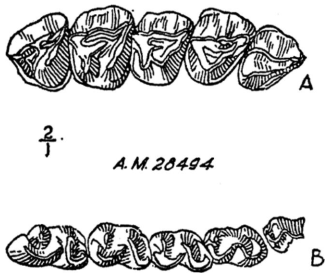

FIG. 59. *Peripantostylops minutus* (Ameghino). A.M.N.H. No. 28494, associated upper and lower dentitions. A. Right P^3–M^3. B. Right P_3 fragment and P_4–M_3. Crown views. ×2.

HYPODIGM: Types and the following: A.M.N.H. No. 28494, associated right upper and lower jaws with P^3–M^3 and P_3–M_3; A.M.N.H. Nos. 28986 and 28987, nine isolated upper molars.

TABLE 43
Peripantostylops minutus

		M^1 or M^2	
		L	W
7 specimens, M^1 or M^2, from Cañadón Vaca (including M^1 and M^2 of A.M.N.H. No. 28494), A.M.N.H. Nos. 28494, 28987	OR	3.9–4.8	4.8–5.5
	M	4.4	5.2
Type, *P. minutus*		4.5	5

TABLE 44
Peripantostylops minutus

	P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W
Type, "*Selenoconus agilis*"	—	—	—	—	4.2	3.0	5.7	3.1
A.M.N.H. No. 28494	4.2	2.5	4.1	2.7	4.3	2.7	5.3	2.9

Horizon and Locality: Casamayor, Patagonia. Types from "Oeste de Río Chico." Referred specimens from Cañadón Vaca.

Diagnosis: Sole species surely referred to genus. Simple crochet. Small. Measurements are given in tables 41–44.

Fig. 60. ?*Peripantostylops orehor* Simpson. Type, A.M.N.H. No. 28526, left M^2. Crown view. ×2.

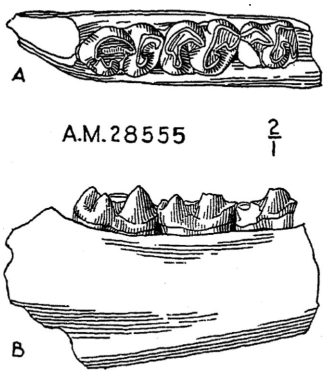

Fig. 61. ?*Peripantostylops orehor* Simpson. A.M.N.H. No. 28555, left lower jaw fragment with M_{1-3}. A. Crown view. B. Internal view. ×2.

?Peripantostylops orehor Simpson, 1935

Text figures 60–61

? *Peripantostylops orehor* Simpson, 1935a, p. 11, figs. 12, 13.

Type: A.M.N.H. No. 28526. Part of left maxilla with M^2.

Hypodigm: Type and A.M.N.H. No. 28555, part of left lower jaw with M_{1-3}.

Horizon and Locality: Río Chico formation, Cañadón Hondo, Chubut, Argentina.

Diagnosis: M_2 resembling that of *P. minutus* in relatively strong crochet, deep valley, etc., but larger, more transverse, and crochet weakly forked at end. Paratype lower teeth also slightly larger and relatively markedly more transverse, more strongly built, internal valleys less open, more distinct internal cingulum on metaconid.

TABLE 45
?*Peripantostylops orehor*

M^2		M_1		M_2		M_3	
L	W	L	W	L	W	L	W
4.8	6.8	4.2	3.3	5.1	3.8	5.6	3.6

This is probably a distinct genus, but it is difficult to define these small henricosborniids generically without better material than is yet available. The type and lower jaw are not associated, and there is inevitably some doubt as to their really being of the same species, but the characters are so harmonious and the occlusion so perfect that their tentative union is warranted.

FAMILY **NOTOSTYLOPIDAE** AMEGHINO, 1897

DEFINITION: Dental formula (4) $\frac{3\text{–}2\cdot1\text{–}0\cdot4\text{–}3\cdot3}{3\text{–}2\cdot1\text{–}0\cdot4\text{–}3\cdot3}$. I^3_3, C^1_1, and P^1_1 styliform and reduced, often absent, tending to leave a diastema anterior to the cheek dentition. I^1_2 enlarged but rooted. Cheek teeth brachyodont. Upper premolars triangular to subquadrate, P^4 often, and P^3 occasionally, with a vertical interval sulcus on the inner lobe, M^{1-2} quadrate, wider than long, with hypocone and larger protocone, united nearly to their apices but readily distinguishable and separated on inner face by one or more sharp vertical sulci. Protoloph simple, not completely confluent with ectoloph. Metaloph more confluent with ectoloph, giving off a long crochet (denticulate when unworn), which runs straight forward and ends freely near the protoloph. No cristae. P_{2-4} progressively more molariform, but with heel shorter and entoconid less separate from outer crest than on molars. Lower molars with oblique trigonid crest, when unworn with external, median, and internal apices; no other cusps on trigonid. Talonid with simple outer crescent and short, simple, transverse ectoconid crest; outer crest abutting against trigonid crest near median apex of latter.

Skull with short, narrow rostrum; nares terminal; orbit relatively anterior; broad, low cranium; generally strong sagittal and lambdoid crests.

DISTRIBUTION: Río Chico (?), Casamayor, and Musters formations, Patagonia.

This family has all the basic notoungulate characters well developed, but it is very distinctive and easily recognizable. Relatively complete specimens cannot be confused with anything else, and even isolated molars, if not too worn, are at once distinguished by the unique crochet of the upper molars and by the serially tricuspidate trigonid crests of the lowers.

Ameghino (1897a, p. 488) at once recognized the distinctive characters of *Notostylops*, and in his first publication on it he made it the type of a new, and unquestionably valid, family. In 1897 he maintained that this family was a collateral branch related to the Isotemnidae, a view since generally accepted with varying opinion as to the degree of relationship, but he also believed it to be ancestral to the North American tillodonts and placed it in the Tillodonta. Later (e.g., 1906, p. 348) he considered the Pantostylopidae, rather than the Isotemnidae, to be near the ancestry of the Notostylopidae, a view which now seems even more definite and correct, but he continued to stress the supposed tillodont affinities.

This is another very striking example of Ameghino's peculiar dualism in phylogeny. He saw two sorts of resemblances, admittedly real in each case: one to the "pantostylopids" (henricosborniids), primitive notoungulates, and the other to the tillodonts, and he accepted both as due to phyletic affinities. It now seems beyond dispute that the former is due to heritage, hence to real relationship, and the latter to habitus, hence to adaptive convergence. As has almost invariably happened, subsequent students have largely devoted themselves to attacking the erroneous part of Ameghino's conclusion, without properly examining or giving due weight and credit to the sound part of his work.

Later opinion need not be reviewed in detail, as it has been almost unanimous in recognizing the family Notostylopidae and referring it to the Entelonychia. The only important exception is Winge (1924, vol. 3, p. 38) who places both isotemnids and notostylopids as subfamilies of Typotheriidae. As far as regards the isotemnids, nothing can be said in favor of this view, which reveals Winge's lack of first-hand knowledge, but Winge was, I think, right as regards the Notostylopidae to the extent that they seem certainly to be as similar to the typotheres as to the true entelonychians, and in some respects definitely more similar. It does not, however, appear proper to place them in the Typotheria, from which they also have marked and apparently important differences.

These earlier opinions were all based on the work of Ameghino, since until recently

(Simpson, 1932e, 1933f; Patterson, 1932; Riggs and Patterson, 1935) no one had added any new morphological knowledge or revised that of Ameghino.

Ameghino placed 11 Casamayor genera in this family in his definitive classification (1906)—all his *-stylops* genera except *Prostylops* and the "Pantostylopidae." This number is certainly much too high. The genera are based principally on such characters as the presence or absence of various of the vestigial teeth, especially the canines and first premolars, on the length and characters of the diastema, on the degree of molarization of P^4, on the development of the sulci on the internal faces of the upper cheek teeth, etc. With a large series of specimens available for study, these characters all prove to be highly variable. The supposed generic characters in many cases do not have even specific value; in fact, in several instances opposite sides of the dentition of the same individual would have to be placed in different genera of Ameghino's classification. As defended below in more detail, the genera *Anastylops*, *Catastylops*, *Pliostylops*, *Entelostylops*, and *Isostylops* all appear to me to be based on characters of specific value at most and to be synonyms of *Notostylops*. *Eostylops* was based on milk teeth of *Notostylops* and is also a synonym. *Homalostylops*, while not very distinctive, may be retained as a separate genus, and *Acrostylops* is synonymous with it. *Tonostylops* is apparently valid, but its reference to this family is improbable and it is considered *incertae sedis* at present. *Coelostylops* is not a notostylopid but an isotemnid. The 11 Casamayoran genera previously referred to this family must therefore be reduced to the two closely related forms, *Notostylops* and *Homalostylops*, with *Coelostylops* and *Tonostylops* distinct from these but removed from this family. In addition to these *Edvardotrouessartia* is now placed in the Notostylopidae, where it constitutes a valid and distinctive genus. As explained in the discussion of this genus below, it seems clearly to be notostylopid, although this thought had never occurred to previous students and occurred to me only at the last minute of revising this manuscript. The genus was referred at first to the "Albertogaudryidae" and later to the Isotemnidae by Ameghino.

Ameghino did not refer any of Roth's genera from the Mustersan to the Notostylopidae, but in 1906 he listed "?*Notostylops*" in the Musters fauna. He does not seem to have named or described the material on which this was based, and I did not find it in his collection. Possibly it was a fragment of *Otronia*. In 1904a Ameghino placed *Otronia* Roth as a synonym of *Tychostylops* Ameghino, but probably without seeing Roth's material, as the two genera appear to be quite distinct.

In his original descriptions, Roth compared *Staurodon*, *Puelia*, *Otronia*, *Orthogenium*, and *Monolophodon* with *Notostylops*. Of these, *Staurodon* is a trigonostylopid, *Orthogenium* is probably of Deseado age and is not a notostylopid, *Monolophodon* is probably from the Río Chico group and is near or synonymous with *Henricosbornia*, and *Puelia*, as treated elsewhere in this memoir, is a rather dubious form without special resemblance to *Notostylops*. *Otronia* does appear to be a Musters notostylopid and is a valid genus, diagnosed below. Roth later said (1908) that he found *Notostylops* only in the *Pyrotherium* beds (Deseado) and not in those (by him called Upper Cretaceous) that he considered equivalent to Ameghino's *Notostylops* beds (Casamayor). I have not seen any specimens in the Roth Collection on which this statement could have been based, and it is surely erroneous as the much more extensive Ameghino, American Museum, and Chicago Museum collections, as well as several smaller collections, all show *Notostylops* to be abundant in the Casamayor and absent in the Deseado.

The scarcity or absence of notostylopids in the Río Chico is a striking negative character of that fauna. Even in the latest Río Chico faunule, where most of the genera and perhaps some species are the same as in the immediately following Casamayor, neither *Notostylops* nor a forerunner has yet been found. This is probably owing to difference of facies, and notostylopids are to be expected when more extensive Río Chico collections are made. In Cañadón Hondo the Río Chico has yielded two specimens, one unnamed and the other called *Seudenius cteronc*, that may perhaps be notostylopids but cannot be referred surely to this family.

In summary, the following genera are now recognized:

Notostylopidae
  Notostylops, Casamayoran
  Homalostylops, Casamayoran
  Edvardotrouessartia, Casamayoran
  Otronia, Mustersan
? Notostylopidae or *incertae sedis*
  Seudenius, Riochican
Incertae sedis, probably not Notostylopidae (description deferred to a later section of this revision)
  Tonostylops, Casamayoran

The morphology of the family is typified by *Notostylops*, described in detail below. Its relationships have been discussed above in connection with the suborder of which this is the best known family.

NOTOSTYLOPS Ameghino, 1897

Notostylops Ameghino, 1897a, p. 488; 1906, pp. 468, 470; Gaudry, 1904, pp. 13, 16, 20; 1906, p. 34, fig. 10; Scott, 1913, p. 462; 1937, p. 527; Schlosser, 1923, p. 615; Simpson, 1932e, p. 4; 1933f, p. 7, fig. 2; Patterson, 1934b, p. 105, fig. 21.

Anastylops Ameghino, 1897a, p. 490; 1906, p. 468.

Catastylops Ameghino, 1901, p. 421; 1904b, p. 18; 1906, p. 468; Schlosser, 1923, p. 615.

Pliostylops Ameghino, 1901, p. 421; 1906, p. 468; Schlosser, 1923, p. 615.

Eostylops Ameghino, 1901, p. 424; 1906, p. 468; Schlosser, 1923, p. 615.

Entelostylops Ameghino, 1901, p. 524; 1904b, p. 64; 1906, p. 468; Schlosser, 1923, p. 615.

Isostylops Ameghino, 1902a, p. 33; 1906, p. 468.

Type: *Notostylops murinus.*

Types of Synonyms: *Anastylops: A. vallatus. Catastylops: C. pendens. Pliostylops: P. magnificus. Eostylops: E. diversidens. Entelostylops: E. completus. Isostylops: I. fretus.*

Distribution: Casamayor of Patagonia.[1]

Diagnosis: Essentially with the characters of the family. I^3_3, C^1_1, and P^1_1 always vestigial and frequently lacking, with diastema between incisors and cheek teeth. Dentition highly differentiated. Species of moderate size. Cheek teeth crowns of moderate height. External folds and cingula of upper molars generally feeble.

The taxonomy of this group is complex and difficult. The abundance of material is accompanied by an abundance of names: seven supposed genera are now united here, and to these genera 23 supposed species have been referred. These species differ very little in size, are all of about the same age, and the majority of them are clearly synonyms.

GENERIC SYNONYMY

Anastylops vallatus was based on two upper premolars and an incisor, belonging to three different individuals. Because it seems to agree more nearly with Ameghino's intention, or later conception of the species, I have taken the smaller premolar as type (see below). In 1904, Ameghino referred the anterior half of a skull to this species, and based on it an extended definition of the genus, involving the following principal points:

1. Premolars with one external root instead of two.
2. Cheek tooth rows divergent anteriorly.
3. Palate 50 per cent wider than in *N. murinus* but no longer.
4. Premaxillae forming a pyramidal protuberance beneath the nares.
5. Palate very wide anterior to the cheek teeth.

None of these distinctions involves a valid difference:

1. This is not true of the types and does not, in my opinion, involve a valid taxonomic difference in any case in view of identity in every other respect.
2. The tooth rows are almost exactly parallel along their inner borders, as in all adult specimens of *Notostylops* which are uncrushed.
3. The palate of *N. murinus* is crushed. In one place its half width can be taken exactly, and is precisely the same as that of this palate of "*Anastylops.*"
4. This is true of all members of this family.
5. The width is about the same as in all uncrushed specimens of *Nostostylops.*

The two type cheek teeth of the genotype are both second upper premolars, and not of the same species, one being about 20 per cent larger and different morphologically. The smaller tooth, now the lectotype, agrees well enough with P^2 of the referred palate for the reference to be accepted as valid and the palate to be considered a neotype, but it is a

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[1] Ameghino, 1906, page 470, lists the genus questionably in the *Astraponotus* beds (Musters). As shown below, this later form is generically distinct.

curious fact that the only distinctive feature of that palate, the undivided root of P^2, is not shown by the actual types of the species. This palate agrees very closely with *Notostylops murinus*, differing only in the apparently unimportant feature of imperfect root division, and the lectotype agrees exactly with *N. murinus* even in this detail. It can only be concluded that *Anastylops vallatus* equals *Notostylops murinus* and that the genera of which these species are the types must hence also be synonymous.

Catastylops was founded on two characters: the presence of P^1 and the arrangement of the cheek teeth, inclined backward and overlapping. P^1 is variable. Two species referred by Ameghino himself to *Notostylops* have it, and Ameghino later referred species without P^1 to *Catastylops*. It is therefore obvious that he did not really consider its presence or absence as of generic value, in which he was surely correct, but relied wholly on the inclination and overlapping of the teeth as the generic distinction of *Catastylops*. This is also demonstrated by the fact that he later (1904b, pp. 18–19) emphasized this tooth arrangement in *Catastylops* as illustrative of a mechanical principle of importance in dental evolution. But this feature is not original. As so often happens in the Casamayor, in which severe distortion is the rule rather than the exception, the specimen is badly crushed, and in this case the crushing has taken the form of an oblique shear which has given the teeth this arrangement and has shattered both teeth and bone, although leaving most of the fragments cemented together. The genus is surely synonymous with *Notostylops*.

Pliostylops was defined as having C and P_1, with P_1–M_3 in continuous series and P_1 with a small anterior basal tubercle, the canine halfway between I_2 and P_1 and small, vertical, and conical. The type specimen of the genotype appears to be lost, but a specimen referred by Ameghino is not distinguishable from *Notostylops murinus*, and his definition contains nothing distinctive from specimens surely referable to *Notostylops*.

Eostylops was at first placed in the "Pantostylopidae" and was not compared directly with *Notostylops*. It looks very distinctive, but the individual is clearly young and for this and other reasons I suspected, when studying the Ameghino Collection, that these were milk teeth of *Notostylops*. The Chicago Museum specimens, revealing the upper milk dentition of the genus in detail, fully confirm this.

Entelostylops was likewise referred at first to the Pantostylopidae and was never directly contrasted with *Notostylops*. I can find no characters to separate the genera.

Isostylops was defined as having subquadrangular upper cheek teeth, the wearing surface devoid of fossettes or folds, the transverse crests barely indicated, the internal wall with a strong vertical sulcus, and the external wall with paracone and metacone folds and a hollow between them. The genus was based on isolated upper premolars which differ in no significant detail from those of Ameghino's "*Notostylops escaridus*" (an individual variant of *N. murinus*).

MORPHOLOGY

DENTITION

The dental formula varies from $\frac{2\cdot0\cdot3\cdot3}{2\cdot0\cdot3\cdot3}$ to $\frac{4\cdot1\cdot4\cdot3}{3\cdot1\cdot4\cdot3}$. I^{2-3}, C^1, P^1, I_1, I_3, C_1, and P_1 are in all cases small, styliform, vestigial teeth. I^2 and I_1 are never absent, so far as available material shows, but the others are highly variable in their occurrence. This seems in general to be of little significance; for instance, the type of *N. brachycephalus* had the canine on one side and not on the other. It is probable, however, that some species did tend to keep the teeth and others to lose them, and it is also probable, although based on less definite evidence, that even those forms which often have a reduced dentition in the adult had nearer the full number in the young. That the differences are not entirely due to age is shown, among other data, by the fact that C.N.H.M. No. P 13319, a very young individual of *N. murinus*, apparently has no milk or permanent canine, while A.M.N.H. No. 28634, a senile individual of *N. pendens*, has the complete dental formula.[1]

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[1] Schlosser (1923, pp. 614–615) gives the formula $\frac{3.1\text{–}0.4.3}{1.1\text{–}0.4\text{–}3.3}$ for the family and $\frac{3.1.3.3}{3.1.3.3}$ for the genus *Notostylops*. Even aside from the serious discrepancy between these two formulas, neither one is shown by any known specimens. He also errs in identifying the enlarged lower incisor as I_1. In general, Schlosser's study of the Casamayor collection in Munich seems to have been very superficial.

There is always a diastema in each jaw. The canine, if present, is in the middle of this. I^{1-3} and I_{2-3} are usually slightly spaced. I_1 and P_1 seem always to be closely applied to the adjacent tooth, I_2 and P_2, respectively, while P^1 may be closely applied to P^2 or slightly spaced. P_2^2–M_3^3 are always in tightly closed series.

UPPER DENTITION (TEXT FIGS. 62–64): I^1 is enlarged and strongly curved. The opposite incisors are directed towards each other so that their tips are in contact, although their roots are widely separated. The crown has a thick coating of enamel on the outer face, but there is only a thin film of enamel on the inner face, even when quite unworn. The edge is sharp, chisel-like, but rounded in contour. Wear is entirely on the inner, or more exactly, posterior surface and produces a nearly vertical facet which removes little of the heavy enamel. Even in very old individuals the tooth retains nearly the original form. The enamel is limited to the tip, and once the tooth is fully protruded it does not move significantly. The long, stout root is closed in the adult. The diameter of the central portion of the root is greater than that of the crown.

I^2, always present, is much smaller than I^1, with the root less curved and the crown more lanceolate. I^3, sometimes absent, is still smaller, with the root almost straight. All the incisors are distinctly procumbent, with the crown of I^1, but not I^{2-3}, somewhat recurved. Even in old individuals with I^1 well worn, I^{2-3} show very little wear and they clearly had no essential function.

A.M.N.H. No. 28956, a young adult of *N. murinus*, has four incisors on the right side and the normal three on the left. There is a diastema between I^1 and I^2, while I^{2-4} are in contact with each other. The three incisors of the other side are evenly spaced, or with a slightly greater gap between I^2 and I^3 than between I^1 and I^2. Right I^{2-4} form a graded series, being similar in form but decreasing in size from front to back. I^3 of the other side is about intermediate between I^3 and I^4 of this. It is impossible to say whether I^3 or I^4 is the supernumerary tooth; probably it is incorrect to think of this as a normal series with one intercalated tooth, and it should rather be considered as an anomalous series of three (that is, posterior to the surely normal I^1) instead of a normal series of two. The condition is not one of abnormal position of the canine: I^4 is distinctly in advance of the suture, and its form is that of an incisor and slightly, but distinctly, different from that of a *Notostylops* canine. Nor can it be concluded that a deciduous incisor has been retained, for I^{2-4} are about equally protruded and worn. The anomaly is interesting, but of course has little importance for the morphology of the genus beyond emphasizing the extreme variability in the region of these degenerate teeth.

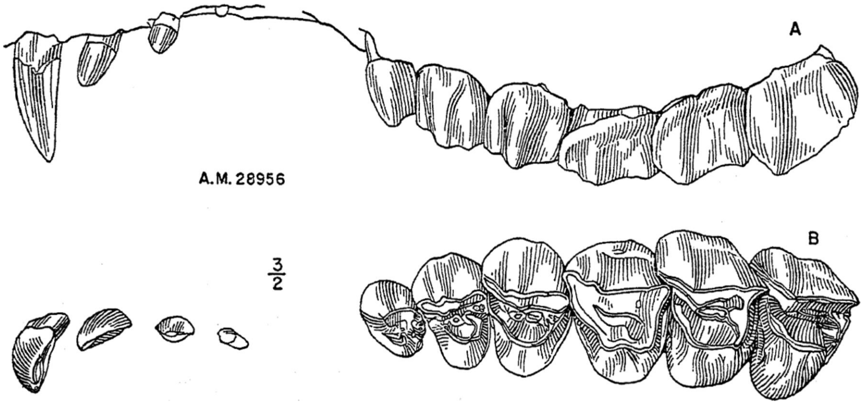

FIG. 62. *Notostylops murinus* Ameghino. A.M.N.H. No. 28956, left upper dentition. A. Lateral view. B. Crown view. ×3/2.

The upper canine is known only in A.M.N.H. No. 28614, although its alveolus is often preserved. It is rather like I^3 in size and form, but is implanted vertically and has the inner face slightly excavated and thinly coated with enamel.

P^1 is small and one-rooted when present

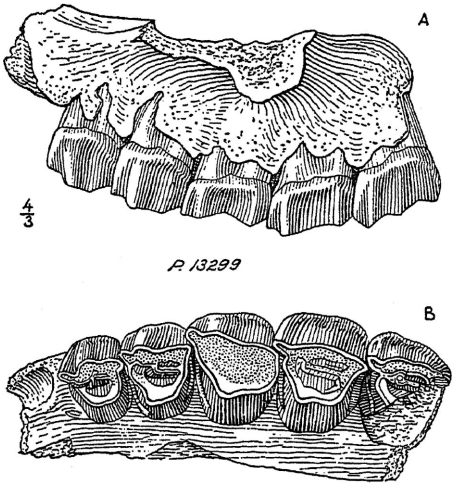

FIG. 63. *Nostostylops murinus* Ameghino. C.N.H.M. No. P 13299, maxillary fragment with left P^3–M^3. A. Lateral view. B. Crown view. ×4/3. After Riggs and Patterson.

and is frequently absent. It is lanceolate, with only one cusp, laterally compressed, and without any distinct trace of an internal heel.[1] This tooth is also functionless, and is almost completely unworn even in senile individuals.

P^2 is also well displayed by our material. It is apparently constantly present in this genus and consists of an outer wall and a somewhat lower internal heel. The wall has a stout cusp slightly anterior to the middle. Anterior to this there may be a small style, as on the following teeth, but this is here highly variable and often quite absent. The inner cusp, about intermediate between conical and crescentic form, is well separated from the outer wall, but there are two very feeble crests uniting them on the unworn tooth, one nearly median or slightly anterior, the other, rather nodular or discontinuous in some cases, along the posterior margin.

P^{3-4} differ from P^2 not only in being larger and more transverse, but also in the constant presence of a strong parastyle fold, the elongation of the ectoloph posterior to the paracone and development of a feeble metacone fold, and the more crescentic protocone and stronger transverse ridges. The anterior crest, homologue of the protoloph, is here fully anterior. Near its outer end it tends to develop a faint cuspule, protoconule, or in the species with more advanced premolars it may distinctly branch, one branch going to the base of the paracone and the other towards the parastyle[2]; the degree of union of protoloph and ectoloph varies. In the simpler forms, with unbranched protoloph, they are generally not united. In the others, both branches may be united, enclosing a deep hollow, or only one branch may unite with the ectoloph, or both may be free. The posterior crest, usually stronger, runs from the apex of the protocone to the posterior end of the ectoloph. From it there departs a spur which extends forward into the basin between the crests. It varies greatly in different species, sometimes only faintly suggested, and in other cases relatively as strong as on the molars. There is occasionally a tendency to division of the inner cusp on P^3, and this is common, but not invariable, on P^4. On P^4 and occasionally on P^3 there may be a sharp vertical sulcus on the inner face of the protocone. This tendency is in part a specific character. There is no internal cingulum, but a feeble external cingulum is sometimes present posterior to the paracone fold. A narrow poste-

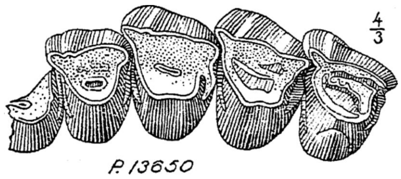

FIG. 64. *Notostylops murinus* Ameghino. C.N.H.M. No. P 13650, P^{4-3} and fragment of P^3. Crown view. ×4/3. After Riggs and Patterson.

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[1] Riggs and Patterson (1935) suggest that the supposed P^1 shown by Ameghino (1904b, fig. 534) and Gaudry (1904, fig. 15) is really dm^1. The crown of P^1 is not shown by any specimen of this genus in the Ameghino Collection and he figures only the alveolus. Our own specimens, three of which have P^1 of one or both sides well preserved, seem to agree with Gaudry's and in them this tooth is almost surely not dm^1. Two of the specimens, A.M.N.H. Nos. 28604 and 28634, with this tooth symmetrically developed on both sides, are old individuals with M^3 deeply worn, and on all three this tooth differs distinctly from dm^1 of this genus in morphology.

[2] I presume that this is the condition referred to by Riggs and Patterson (1935) when they say that "a ridge occupying the position of the ante-crochet is sometimes present."

rior cingulum, not basined and not distinctly cuspidate, is present on both P^3 and P^4, and a still less developed anterior cingulum is constantly present on P^4 but feeebler and sometimes almost imperceptible on P^3.

M^1 and M^2 are almost identical in structure. They are larger than the premolars, longer relative to the width, and more quadrate. The high, flattened outer wall, which makes an acute angle with the anterior border of the tooth, bears the parastyle and paracone ridges or folds anteriorly, separated by a sharp sulcus and usually relatively smaller and, in the case of the paracone fold, more sharply defined than on the premolars. The surface posterior to these is relatively longer than on the premolars and is nearly flat but may have another vertical swelling, very rarely a definite ridge and sometimes completely absent, which corresponds to the metacone. The inner side of the tooth is divided into two definite cusps, a larger and higher, anterior, subcrescentic protocone, and a smaller, posterior, more conical hypocone.[1] Although quite distinguishable, these are united nearly to their apices by a very short, nearly anteroposterior crest. On the inner face there occurs between these cusps a sharp vertical sulcus. This sulcus may be double, or even triple, but there are never additional apical cuspules corresponding to this multiple furrowing. From the protocone a sharp low crest passes externally along the anterior border of the tooth, ending in a small cuspule internal to the parastyle and paracone. This appears to be confluent with the ectoloph only when somewhat worn. From the hypocone a crest, somewhat shorter and more directly transverse than the protoloph, runs along the posterior border of the tooth and becomes nearly or fully confluent with the base of the ectoloph. From this a straight crochet runs forward across the basin of the tooth, ending near the protoloph, with which, however, it is never united. This peculiar secondary crest, long and well developed, quite independent of the ectoloph, and unaccompanied by cristae or antecrochet, is very characteristic of this family.[2] There are variable but usually distinct small horizontal anterior and posterior cingula. An internal cingulum cannot be said to be present as such, although the internal base may be swollen and rounded. A highly variable external cingulum is usually present, especially posterior to the paracone fold but sometimes crossing the base of that element.

M^3 is more triangular. There are one to three sulci on the posterointernal slope of the protocone, but they do not correspond to a definite division of the apex into two cusps. The metaloph is shorter than in the other molars. In some cases it extends nearly as far internally as the protocone, making the tooth only slightly less quadrate than M^{1-2}, but not ending in a similar high hypocone. In other cases this crest is very short, wedged between the protocone and ectoloph on the posterior border. The crochet is strong as on the other teeth.

P^2–M^3 normally have one inner and two outer roots, although the outer roots may be

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[1] Here, as elsewhere, I use the name "hypocone" for the major posterointernal cusp unless another established name (metaconule chiefly) is clearly applicable to it. Some students object to calling this cusp hypocone unless it arises from a cingulum and usually use the name "pseudhypocone" if it seems to originate by fission from the protocone or to grow upon the slope of the protocone or in any way other than from a pre-existing cingulum. This seems to be a distinction without a difference. It is fairly apparent that the hypocone has originated independently in various groups of mammals. Furthermore it may develop almost anywhere in this general region of the tooth, the exact locus depending, apparently, on mechanical factors in occlusion. Its happening to arise independently in two groups from a cingulum may not, in my opinion, involve any more true homology than if it arose in one from the cingulum and in another from the protocone. The conception of latent homogeny or predetermination is, in its present form, speculative or almost metaphysical and this possibility should not be discounted in a stable terminology. "Hypocone" may well be used as a topographic designation, with homology (as between major groups) a secondary consideration. The mode of origin of the hypocone, in this sense, in each group is, of course, a feature of importance.

[2] It is invariably present and with this general character, but varies greatly in prominence. As especially emphasized by Riggs and Patterson (1935), its summit when unworn may show a series of denticles. As these denticles are not always distinguishable, even on completely unworn teeth, and as in all cases they or their bases do in fact form a crest of this character, the crest, which may well be called a crochet for descriptive purposes, seems to me to be the essential structural element rather than the denticles as such. Whether in such a case denticles are primary and crest secondary, or the reverse, seems to be, if not quite indeterminate as a historical fact, a speculative and largely verbal argument of no importance.

imperfectly divided or even completely fused. Ameghino gave much importance to this feature, but it does not seem to correspond constantly to any other morphological distinctions and is known to be variable in mammals generally, so that it seems to me to be unimportant.

All the cheek teeth, but particularly the molars, have the inner face strongly inclined outward and the outer face, somewhat longer than the inner, strongly inclined inwards. The crowns are all low and the apical pattern is generally very shallow, even in proportion to the height of the crown. As a result, even relatively slight wear soon reduces these teeth to mere rims of enamel surrounding a central area of soft dentine without the deep loops and fossettes normal to herbivore teeth. Most of the *Notostylops* teeth found are in this condition. This seems highly inefficient, and the apparent germinal inability or slowness to develop a less wasteful masticatory apparatus may well have been an essential factor in the early extinction of this branch of the Notoungulata.

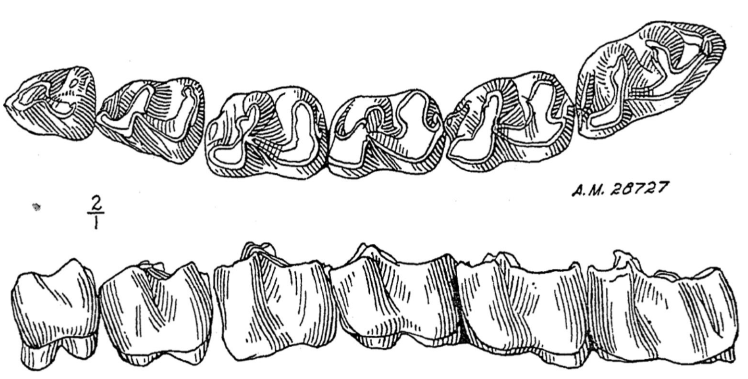

FIG. 65. *Notostylops murinus* Ameghino. A.M.N.H. No. 28727, left P_2–M_3. Crown and external views. ×2.

LOWER DENTITION (TEXT FIGS. 65–66): There are always two and often three lower incisors. I_1 has a very long straight root and a short, completely enameled, subspatulate crown. It is closely appressed against its fellow I_1 and the two are anterior to, or below, the second incisors rather than between them. I_2 is over twice as large as I_1. It, too, has a very long straight root nearly circular in section and a smaller and much shorter enameled crown. The unworn tip is asymmetrically spatulate, one side rounded and the other produced into a sharp edge which is not external, as would be expected, but median or internal. The tip is rounded in contour on the inner side and end, and angulate where it passes into the outer border of the tooth. The second incisors of opposite sides are often closely appressed at the alveoli, but may be slightly separated. All four incisors, I_{1-2} of both sides, act together against the posterior faces of the enlarged upper incisors, I^1. Their action is not really at all rodent-like, as they develop no chisel edge but have the tips truncate by wear approximately at right angles to the axis of the tooth. I_{1-2} are strongly procumbent, meeting I^1 at a right angle, but this varies somewhat with reference to the normally horizontal plane of the cheek teeth. They may be at as little as about 30 degrees to this plane, or as much as 45 degrees.

I_3, the canine, and P_1 are often absent, but several specimens show that they do occasionally occur, and we have one specimen, A.M.N.H. No. 28634, *N. pendens*, which shows the otherwise unknown crowns of the canine and P_1. I_3 is represented only by alveoli, which show it to have been a very minute and variable tooth closely crowded against the posterior or posteroexternal edge of I_2. The canine, when present, is a small, styliform, incisor-like tooth, sometimes as large as I_1 but usually smaller, and is placed immediately posterior to I_3. It is less procumbent than the incisors. The diastema in the lower jaw is between C and P_1 and is very short when both those teeth are present. The root of P_1, implanted vertically, is long, straight, swollen, and circular in section like the roots of the incisors, but the very small crown, completely enameled, is laterally compressed, the outer face convex, the inner with small vertical anterior and posterior excavations. There is one cusp, followed by a minute heel or angulation on the same longitudinal crest. The individual is fully adult, but P_1 is completely unworn.

P_2, always present, shows much individual and specific variation in size, proportions, and structure. In its simplest form it has an anterior cusp, nearly conical but so compressed as to have a short anteroexternal-posterointernal crest, and a heel nearly equal in size, only a little lower, with a V-shaped crest. In the next more progressive variant, i.e., more molariform, the crest of the trigonid is more pronounced and has an anterointernal sulcus, making it also V-shaped. Then this V-shaped trigonid crest may be complicated by a small anteroposterior spur, directed posteriorly from its posterointernal end. In its most complex form, P_2 resembles P_{3-4} except for being smaller and with the anterior end narrower. In general these various degrees of complexity are proportionate to the relative size of the tooth, individuals or species with relatively large P_2 having this tooth also more complex. P_2 generally has two roots, although these may be fused near the crown and distinct only at their ends.

P_{3-4} are always closely similar in structure. Trigonid and talonid are nearly equal in size, the trigonid slightly higher. The trigonid consists of a high sharp crest of complex form. The external part is sometimes anterointernal-posteroexternal in direction on P_3, while on P_4 and frequently also on P_3 it is almost straight anteroposterior, along the outer border of the tooth. From its anterior end a sharp spur falls away internally around the anterior side of the tooth. At its posterior end, the crest turns abruptly and crosses the tooth in an anteroexternal-posterointernal direction, ending in a fairly definite cusp near the middle of the inner side of the tooth. This transverse part of the trigonid crest is seldom perfectly straight but usually (as seen in less worn teeth) turns at a slight angle near the midline, the outer part being more directly transverse and the inner part more oblique, and where it turns the crest is a little swollen and may bear a tiny cusp-like apex when quite unworn. The talonid consists of a single crest and a more or less isolated cusp. The crest is crescentic or sickle-shaped and abuts against the middle portion of the transverse trigonid crest, whence it curves around the outer side of the heel to end in a cusp-like enlargement near the midline on the posterior margin. Directly internal or sometimes antero-

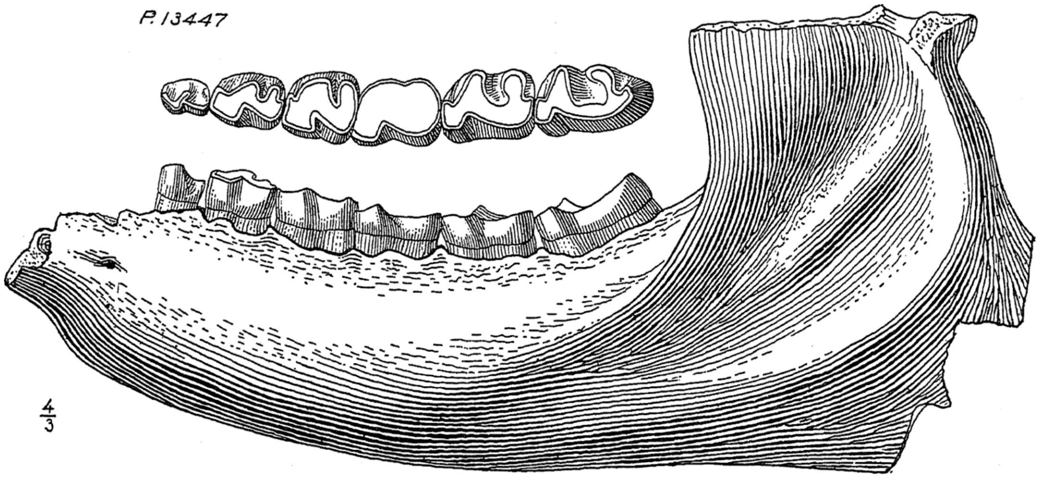

FIG. 66. *Notostylops murinus* Ameghino. C.N.H.M. No. P 13447, left lower jaw with P_2–M_3. Crown and lateral views. ×4/3. After Riggs and Patterson.

internal to this point is the entoconid, its base united to the external crescent by a transverse swelling of varying prominence, so that it usually appears independent when unworn but with wear either merges with the end of the crescent or seems to form a branch of the latter, depending on its exact position.

M_{1-2} are closely similar in structure and differ from P_{3-4} chiefly in having the trigonid shorter and the talonid larger. The trigonid is similar to that of P_{3-4} save in being more compressed anteroposteriorly and in having the oblique transverse crest straighter. As on the premolars, this bears a median cuspule visible when little worn. On the talonids, the external crescent does not so definitely end at, or slightly external to, the midline on the posterior border but continues as a falling, cingulum-like ledge posterior to the entoconid. The latter is relatively more anterior than is usually the case on P_{3-4} and more distinctly produced into the transverse crest so typical of all early notoungulates. With moderate wear, it does not form a mere continuation of the external crescent but a spur from it. Further wear makes them appear continuous.

The trigonid of M_3 is like that of M_{1-2}, but the talonid is much longer, the crescent extending far back and then almost to the internal side of the tooth where it ends in a distinct elevation. Sometimes a small closed basin is formed between this elevation and the entoconid. On unworn and little worn teeth there are frequently seen various cuspules and minor complications which probably are purely individual and adventitious. The tip of the entoconid may be bifid. Not infrequently there is a cuspule between the entoconid and hypoconulid, and in one case there is a cuspule in the basin anterior to the entoconid crest. In another specimen, completely unworn, there is a tiny cuspule low down near the midline on the anterior face of the tooth.

Deciduous Dentition: The deciduous dentition is represented chiefly by M.A.C.N. No. 10504, a lower jaw, and by C.N.H.M. Nos. P 13308 and P 13319, partial skulls. Apparently all the premolars were preceded by deciduous teeth, and it is possible that dm^1 was present even when no P^1 succeeded it.[1] Dm^1 is a small tooth with roots confluent except at the tips, with a compressed ectoloph accompanied by incipient parastyle, metacone, and protocone. It is thus more complex than P^1.

Dm^2 has a strong internal heel and is transitional to dm^{3-4}, but is more triangular and does not have the internal cusp divided. Dm^3 is still subtriangular but has the internal cusp divided by a vertical sulcus and has the outer wall definitely molar-like rather than premolar-like. Dm^4 is fully molariform, differing from the true molars in being smaller, slightly less transverse, and much lower crowned.

The material in hand suggests that M^1 was erupted long before the milk teeth were shed and M^2 also while all were in place, but that all the milk teeth were shed very soon after the eruption of M^2 and before that of M^3. This is all quite normal, and there is no suggestion of delayed replacement, of two replacements, or of the incorporation of any of the milk teeth in the permanent series.

Dm_1 and dm_2 are known only in deeply worn condition. They do not appear to have differed much from the corresponding premolars except that dm_2 is much longer than its successor and that it is relatively narrow and low crowned. Dm_3 (well preserved in A.M.N.H. No. 28734) likewise differs from its successor chiefly in being long, narrow, and low. Dm_4 (A.M.N.H. Nos. 28734, 28839, 28772, etc.), however, is markedly unlike P_4 and is fully molariform. It differs from M_1 only in being slightly smaller, relatively narrower, and with a lower crown. Regarding the lower milk teeth, see also *Homalostylops*, in one specimen of which these teeth are better preserved than in any of *Notostylops*.

Skull

Text figures 67–71

There is one fine skull of *N. murinus* and considerable parts of two others in the Ameghino Collection, as well as several palates, rostra, and lesser parts. The Chicago Museum has two skulls of *N. murinus*, one nearly complete, both juvenile. The American Museum has one nearly complete skull of *N. murinus*, three of *N. pendens*, and one, less

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[1] But, as previously pointed out, it is clear that an actual P^1 is frequently present, contrary to the suggestion of Riggs and Patterson.

complete, of *N. pigafettai.* The cranial morphology of the genus is thus very well shown, and only one or two of the most intricate details remain obscure.

The dentition of *Notostylops* is functionally more nearly analogous to that of *Adinotherium* than to that of *Homalodotherium* in the Santa Cruz beds, and the general appearance of the skull is also closer to *Adinotherium.* The skull of *Notostylops* is, however, much smaller in all the known species, little over half the size of *Adinotherium ovinum*, and is less massive and heavy throughout. In *Adinotherium* the postorbital region is scarcely longer than the antorbital, whereas in *Notostylops* the postorbital region is about two-fifths as long again as the antorbital, giving the effect of an unusually short rostrum and long braincase, with eyes far forward. The postorbital constriction is also markedly greater in *Nostotylops.*

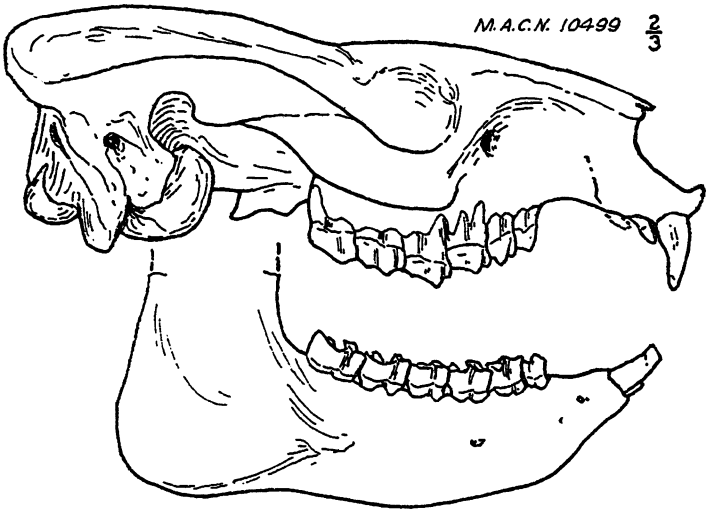

FIG. 67. *Notostylops murinus* Ameghino. M.A.C.N. No. 10499, skull (type of the synonym *N. brachycephalus*), and lower jaw, a composite from several specimens, not associated with the skull. Right lateral view. X2/3. After Simpson.

Viewed from above, the skull of *Notostylops* has a short, narrow rostrum expanding rapidly immediately anterior to the orbits into a quadrate oblong figure outlined by the zygomata and lambdoid crests. The width across the zygomata is about three times that of the rostrum. The frontal region is irregularly quadrate and about twice as wide as long. Immediately posterior to the postorbital processes there is a very sharp constriction. The roof of the cranium proper, formed chiefly by the squamosals and parietals, is markedly triangular by reason of its great posterior width across the zygomatic bases and strong anterior postorbital constriction. The length of this region is slightly less than the width. Posterolaterally this area is bounded by sharp upright crests continuing the upper border of the zygomata and running into the lambdoid crests, and posteriorly the strong lambdoid crests form an even sharper boundary, although they are less vertical and are inclined posteriorly. The sagittal crest (in adults) is very sharp and high and runs from the frontals to the occiput.

In lateral view the occiput, or at least its lateral edges, are seen to be inclined backward. The upper contour is gently convex along the sagittal crest and then nearly straight along the frontals and nasals. The frontals may be slightly convex, but are usually nearly plane and contain no extensive sinuses. The porus acusticus is placed below the level of the glenoid fossa and only slightly above the level of the alveolar border, a remarkably low position in comparison with *Adinotherium* or most later notoungulates. The zygoma has

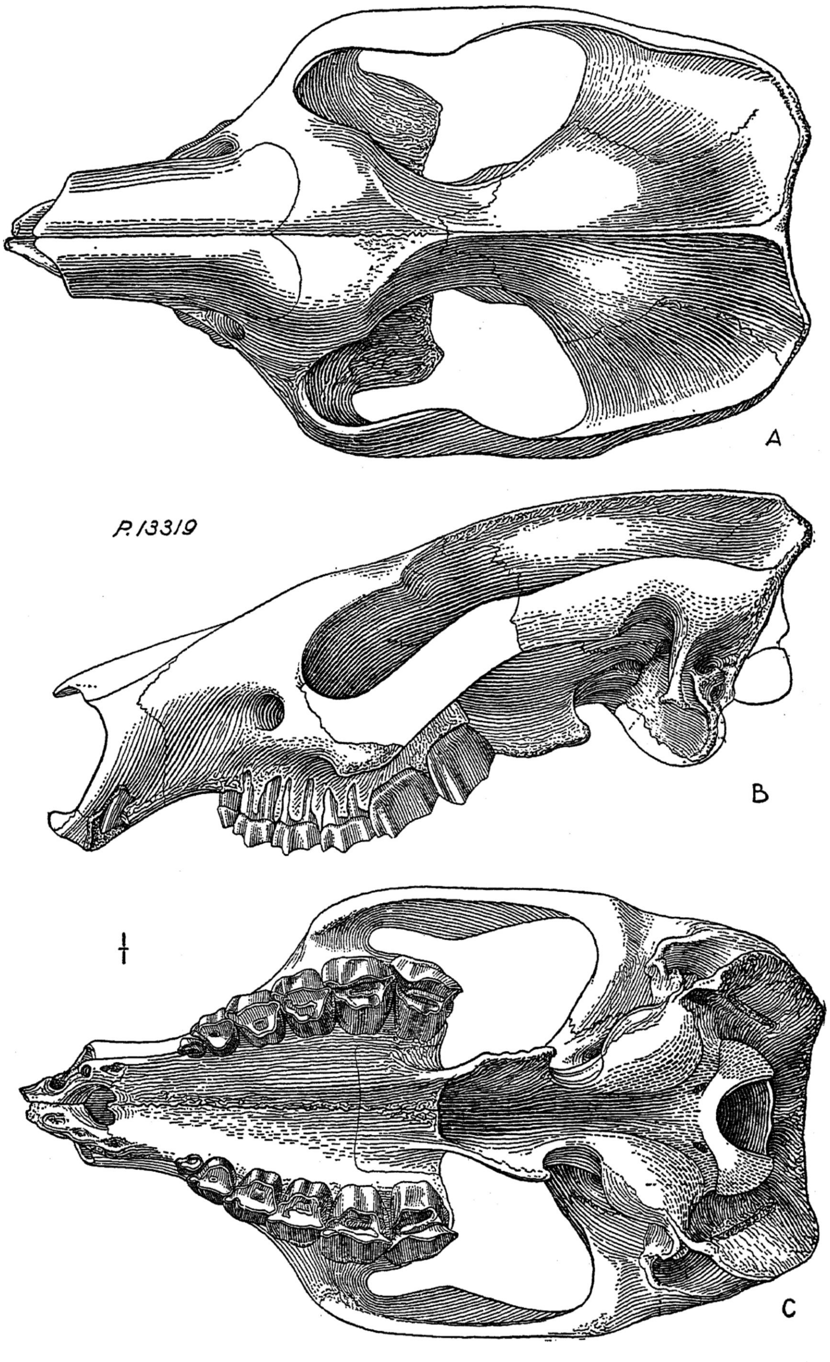

FIG. 68. *Notostylops murinus* Ameghino. C.N.H.M. No. P 13319, skull. A. Dorsal view. B. Left lateral view. C. Ventral view. ×1. After Riggs and Patterson, 1935.

the usual sigmoid curve but is relatively longer and more slender than in *Adinotherium* or in *Homalodotherium*. The rostrum is deep, the depth (when undistorted) considerably exceeding the width. The nasals are not retracted and the nares are fully terminal. In anterior view their outline is cordiform.

Skulls of different ages show in an interesting way some of the changes with growth. The following series (text fig. 69) is of *N. murinus:*

A. C.N.H.M. No. P 13308: milk teeth in place, M^1 erupted but unworn (M^2 missing, probably not erupted)
B. C.N.H.M. No. P 13319: milk teeth in place, M^1 slightly worn, M^2 erupted but unworn (M^3 missing, probably not erupted)
C. A.M.N.H. No. 28956: milk teeth lost, M^{1-2} worn, M^3 erupted but almost unworn

To this series might be added the type of *N. murinus*, a senile animal with all teeth deeply worn, but it is imperfect and shows nothing not better represented by C of the above series.

In *N. pendens* the following adolescent and adult stages are represented by skulls:

A. A.M.N.H. No. 28614: milk teeth lost, M^3 slightly worn
B. A.M.N.H. Nos. 28604, 28634: all permanent teeth well worn

The age changes in the skull are very marked, and successive stages would hardly be thought, offhand, to represent the same genus, were the teeth not available. With the additional factors that every known specimen is somewhat crushed and broken, and each in a different way, and that a series of any one age is not available for any one species, this makes it impossible to determine any specific characters in the skulls. Young and old *N. murinus* skulls, for instance, differ much more than do *N. murinus*, *N. pigafettai*, and *N. pendens* skulls of about the same age.

In stage A of the *N. murinus* series, the over-all dimensions of the skull are about three-fourths those of a stage-C skull. The proportions are, in some respects, quite different in the three known stages.

In stage A the braincase is relatively large, its width (exclusive of ear region and zygo-

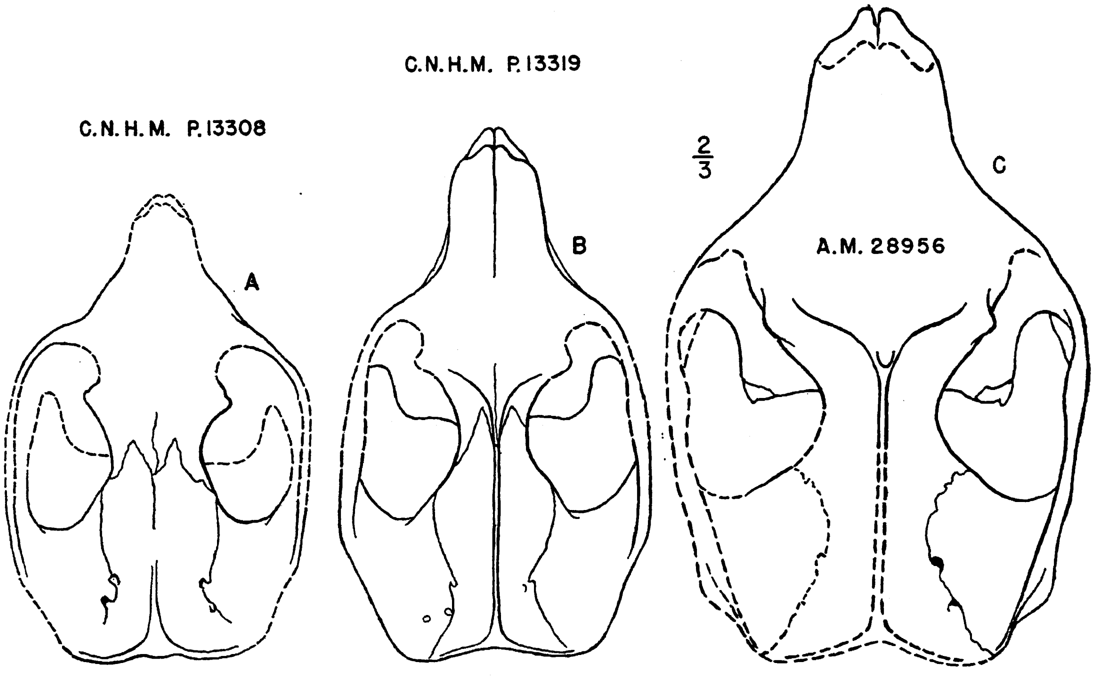

FIG. 69. *Notostylops murinus* Ameghino. Dorsal views of skulls of different ages, to show changes in size and proportions due to growth. A. Juvenile, all milk teeth retained, M^1 erupted but unworn. B. Advanced juvenile, milk teeth in place, M^1 worn, M^2 erupted. C. Adult, milk teeth replaced, M^3 erupted. ×2/3.

matic bases) scarcely less than in the adult stages. The length of the cranium is notably less in this juvenile individual, but this is in large part apparent only and owing to the feeble lambdoid crests. The width across the postorbital constriction is actually greater in stage A than in any later stage. This is doubtless in part owing to crushing, but there can be no doubt that the width here does not significantly increase with age and that the postorbital constriction thus becomes more and more marked, relatively large in the juvenile stages, and retains nearly the same size regardless of the growth of the skull as a whole. The sagittal crest is very feeble in stage A, being simple and distinct but low posterior to the cerebral expansion, but anterior to this bifurcating and becoming barely visible. As early as stage B it is single and prominent forward to the postorbital constriction, and in later stages it does not change its form or character but becomes even more prominent.

The sutures tend to become more firmly knit with age, but extensive fusion is not seen even in senile individuals, only a few sutures in the ear region and part of the parietal sagittal suture being obliterated.

The younger of the two known stages of *N. pendens* is already almost adult, and the only noteworthy change between this and the nearly senile skulls is a general increase in size, about 15 per cent in over-all dimensions.[1]

The following detailed description of skull structure applies to adult skulls regardless of species, unless otherwise noted.

The nasals are long, rather slender bones, of nearly uniform width throughout but expanded somewhat and about equally at anterior and posterior ends. Posteriorly they are nearly plane or are together slightly convex transversely. Anteriorly each is convex transversely, and there is a longitudinal dorsal groove at the midline between them. Anteriorly they project beyond the ascending rami of the premaxillae, and the end of each here is notched. Posteriorly a short pointed process of the frontals is inserted between them, and the frontals also extend on each side farther forward than the posterior end of the nasals, which are thus to some extent inserted into the frontals but much less so than in *Homalodotherium*, and somewhat less than in *Adinotherium*.

The premaxilla is a bone of moderate size with a lozenge-shaped facial expansion and ascending ramus. The anterior border of this part has sigmoid outline, following the root of I^1 in its lower part, at an angle of about 45 degrees to the dental border, and curving forward again at the upper end. It has a straight, strong suture with the nasal, 10 to 15 mm. in length. The posterosuperior corner is short and does not form a definite wedge between nasals and maxillae. The maxillary suture is simple and is at an angle of about 80 degrees to the incisive border. The premaxillary symphysis is short and apparently open throughout life. Above it, at the midline in the lower angle of the narial opening, the premaxillae are produced upward and forward into a small pyramidal process. Practically speaking there is no palatal process of the premaxillae, for they have no expansion in the more or less horizontal palate. Almost all of this part is taken up by the anterior palatal foramina, which are mainly between the second incisors. The premaxillae have no significant extension posterior to this on the palate.

The maxillae are very large and complex bones. The facial part is broad and simple, with a single infraorbital foramen of moderate size below the level of the orbit. This foramen is above dm^2 in stage A in *N. murinus*, above dm^3 in stage B, and above P^3 or P^4 in adults. There is a long maxillo-nasal suture and a shorter oblique maxillo-frontal suture, and the maxilla apparently just touches the anterosuperior rim of the orbit between the jugal and frontal. Within the orbit, the dental plate of the maxilla forms the whole orbital floor and internal aspect of the zygomatic root and forms most of the inferolateral orbital wall.

The zygomatic root is stout and is mainly opposite dm^4 in stage A, dm^4–M^1 in stage B, and M^2 in adults. It bears a pointed, downward-directed process, like that of *Interatherium* but much weaker, only incipient. The maxilla also extends back for some distance

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[1] The teeth of the older skulls are slightly larger, on the average, so that they are sexually or individually more robust individuals, but these differences are very small, only 2 or 3 per cent, and the increase in skull size is largely or wholly the result of age differences.

along the inner face of the zygoma, hidden by the jugal, with which it here has a vertical suture, in external view. The palatal process is large and forms most of the palate, which is strongly concave from side to side, although less so than in the later toxodonts. The inner borders of the opposite tooth rows are straight and nearly parallel or converge slightly anteriorly, but in harmony with the varying widths of the teeth, the outer borders are curved and more definitely convergent. Anteriorly, the palatal process of the maxilla extends to the anterior palatal foramen and is applied to the inner side of the premaxilla internal to I^3 (or the homologous region where this tooth does not occur) so that the premaxillae are not here inserted into the maxillae. Posteriorly there is the usual emargination for the palatines.

The palatal processes of the palatines are approximately rectangular and extend forward to about opposite the middle or anterior part of M^1. Each has a foramen near the anterolateral angle, and there may be other smaller foramina posterior to these. At these anterolateral angles the palatines are well removed (3–5 mm. on the palatal surface) from the alveoli, but the sutures diverge slightly posteriorly so that the palatine is closely applied to the alveolus of M^3 and the posterolateral notches or grooves are roofed by the palatines. The anterior margin of the choanae was opposite to M^3 in the adult, and apparently not at all posterior to that tooth even in the oldest individuals. The rounded median part of the margin is not elevated, but posterolaterally the rim is thickened and passes posteriorly into the vertical palatine plates. At their anterior end, the choanae are about half as wide as in the posterior part of the palate (between the teeth). From this part, the ascending plates diverge slightly (much less than in *Homalodotherium*) and also become higher and less vertical. The posterior parts of the divergent laminae are inclined at about 45 degrees, rather than being vertical. Near their midpoint, about halfway from the palate to the hamulus, they are thickened on the inner side, and immediately posterior to this the palatine is suturally separated from the pterygoid.

The palatine sutures in the orbital wall cannot be certainly made out in the available specimens, but this part of the bone was apparently well developed between the maxilla, lacrimal, frontal, orbitosphenoid, and alisphenoid-pterygoid, and there are indications of a large foramen, the internal orbital, near or at the angular junction with the horizontal suborbital plate of the maxilla, and another, very small, posterior to this and near the suture with the orbitosphenoid.

The orbitosphenoid sutures cannot be identified with much certainty on any of the specimens. This was probably a small element, roughly circular, and almost confined to the median wall of the anterior lacerate foramen and the immediately adjacent area. The endocranial beginning of the optic canal, within the cerebral fossa, is quite distinct from that of the anterior lacerate foramen, and probably these two would be distinct but closely approximated externally in undamaged skulls. In the actual specimens the optic foramen cannot be made out clearly.

The pterygoid and alisphenoid are generally indistinguishable, but in one specimen there is visible a probable suture between them. The pterygoid forms the hamulus and its insertion against the cranium. The hamulus is a large lamina of bone, pointed but not slender or hook-like. Medial to its posterior end is a very small and thin anteroposterior lamina of bone, probably also formed by the pterygoid.

From its (not certainly distinguishable) contact with the pterygoid, the alisphenoid extends backward, upward, and outward, coming in contact with the anterolateral margin of the bulla where it contains or bounds the nearly confluent foramen ovale, foramen lacerum medium, and Eustachian foramen. In this direction the alisphenoid reaches the extreme median edge of the glenoid fossa. Anterior to this the alisphenoid sends an ascending process upward and somewhat forward into the wall of the temporal fossa. This extension, likewise not delimited with perfect certainty, contains no foramina, but seems to be long and wide, extending to the junction of frontals and parietals high up on the braincase.

There is no foramen rotundum, and even within the endocranium V_2 follows the same path as V_1 and the associated nerves.

The lacrimal is a small bone, entirely intraorbital, with a relatively large foramen. Its lateral or inferolateral margin is strongly in contact with the jugal. The facial expansion, enlarged, probably secondarily, in a few notoungulates, is wholly lacking.

The dorsal surface of the frontal is nearly plane and is of rather small extent anteroposteriorly. Anteriorly the frontals have a pointed median projection between the nasals, and posteriorly a similar smaller but sharper projection between the parietals. Anterolaterally the frontal also extends to the posterior end of the nasal, to about the same distance or probably in one case even farther than at the midline. Here there is the strong maxillary contact. At the orbital border the frontal must nearly or quite touch the jugal, but this point is not perfectly preserved in any case.

The postorbital process is short and pointed. Sharp low crests run from the sagittal crest to the postorbital processes, but do not reach the ends of the latter. There is a small vascular foramen in the anterolateral part of each frontal, but no supraorbital foramen. From the anterolateral point of the parietal, the parietofrontal suture passes rapidly posteriorly and then almost directly downward on the cranial wall at the postorbital constriction. This descending plate is rather large and comes in contact, as usual, with alisphenoid, orbitosphenoid, palatine, and lacrimal. From the postorbital process a ridge runs obliquely downward and backward. There are no major foramina in the frontal, but on this ridge is a small vascular foramen directed very obliquely upward and forward, and just anterior to the ridge, at a higher level and nearly under the postorbital process, another very small perforation is visible in one specimen.

The parietals are long, narrow, simple bones. They narrow almost to a point anterior to the contact of the sagittal and lambdoid crests, but widen slightly again posterior to this. They are widest at about the midpoint of the cerebral lobes (although this is not the widest part of the cerebrum) and then narrrow again anteriorly. At the extreme anterior end the parietals form two slightly divergent, blunt processes overlapping the frontals anterior to the postorbital constriction. Large vascular foramina are usually present in both parietal and squamosal along or near their suture, but these are not very numerous in this genus and are variable. The parietals apparently take no part in the lambdoid crest, but form the entire sagittal crest, which, in the adult, runs along the midline for their whole length. The two parietals appear to be completely fused even in specimens with all other sutures open. The youngest specimen, stage A of *N. murinus*, has the posterior part of the suture wholly obliterated, but a possible trace of the anterior end remains, although this may be a crack. The shape of the parietals in this specimen is quite unlike that in the adult. They are as broad as in the adult but considerably shorter and are of more nearly equal width throughout, anterior and posterior ends, as exposed, being both relatively and absolutely wider than in the adults. As already mentioned, the sagittal crest is also much less developed at this age.

A nearly horizontal expansion of the squamosal forms a large posterolateral part of the cranial roof, although its exposure in the endocranial cavity is very slight. The glenoid surface, slightly convex anteroposteriorly, faces downward and slightly backward and is very elevated, even higher than the porus acusticus. Anterolateral to the cavity, at the zygomatic base, the squamosal is produced downward into a slight process. The postglenoid process is prominent and strongly compressed anteroposteriorly. Its inner end is closely applied to the external auditory meatus and hence is not a salient and distinct entity, but its outer end projects laterally beyond the meatus. There is a small foramen at the posteromedian angle of the glenoid fossa (probably the fissura glaseri) and a larger foramen (postglenoid venous foramen) on the posterior side of the postglenoid process, forming a vertical groove in it and between it and the outer end of the meatus.

Riggs and Patterson (1935) state that the jugal forms the entire zygoma and even enters into the glenoid surface to some extent, but the more extensive material available to me shows that this is not the case. The posterior half of the zygoma, approximately, is formed by the squamosal, and the squamoso-jugal suture is strongly oblique, nearly horizontal, and near the middle of the zygoma. A thin jugal process extends back beneath the squamosal nearly to the glenoid surface, but does not reach the latter. The anterior end of the free arch of the zygoma consists of the zygomatic process of the maxilla on the inner side and the jugal on the outer side, the suture being vertical and median in the zygoma. Passing forward onto the zygomatic root, the jugal becomes confined to the dorsal rim and to the internal face, the maxilla being largely exposed below it and forming the whole of the suborbital process. As a slender twisted plate, the jugal forms the actual rim of the orbit in its anteroinferior part, then continuing upward reaches the orbital rim but is chiefly intraorbital, and touches the lacrimal, where it ends.

The four occipital bones are fused. Above the transverse, oval foramen magnum a large triangular pit extends up the occiput. This is not very pronounced in the young skull (C.N.H.M. No. P 13319) where a median ridge is more visible, but in the adult this median ridge becomes quite subsidiary and the larger pit is very prominent, similar to the conditions in Toxodonta and some other notoungulates. The distinction signalized here by Riggs and Patterson (1935) and most of the other characters given by them as distinguishing *Notostylops* from *Homalodotherium* and *Adinotherium* in the occipital region are merely juvenile in *Notostylops* and not particularly distinctive in the adult. On each side of this depression, in the adult, a strong buttress passes outward and upward from the superolateral part of the foramen magnum, its outer end at the lambdoid crest above its bifurcation around the epitympanic inflation.

Below and lateral to this buttress is another depression. The occipital, presumably exoccipital, forms the medial rim of this and is emarginate, so that the triangular to lozenge-shaped lateral part of the occiput (as in notoungulates generally) is set into and not formed by the occipital elements. Below this the exoccipital is produced into a stout, ventrally directed paroccipital process.

The much disputed homologies of the bones in the lateral occipital region have been discussed by me elsewhere (1936a). From a comparison of several specimens, it appears that in *Notostylops* the condition is much as in *Oldfieldthomasia* and a number of other more or less primitive notoungulates. There are three elements here. The upper part is the pars epitympanica of the squamosal. In one case there is a possible suture between this and the squamosal proper, but probably this is only a crack. At the medial point of the emargination, depressed below the general occipital surface, is a foramen (mastoid foramen) and below and medial to this a small bone exposure, probably the periotic, true pars mastoidea. The inferolateral element, clearly separate from the pars epitympanica in two specimens and probably so in all, is the so-called posttemporal or posterior adventitious element. It is produced downward into an anteroposteriorly compressed, posttympanic process, which, when well preserved, is quite separate from the paroccipital process.

The basisphenoid receives the anterior end of the bulla in a posterolateral cusp, closely applied to the tympanic but not suturally united to it. It also has on each side a small elevated buttress against the anterior point of the bulla.

The ear region has been well described by Patterson (1932). The following description, based on much more extensive and better material, is in agreement with him except in a few details and adds a few observations not possible in his material. (See pl. 17.)

The very large tympanic contains a great hypotympanic sinus, or, in other words, forms a prominent inflated bulla of triangular shape. Anterointernally it comes to an acute angle or point, the internal side is almost straight and anteroposterior, and the long anteroexternal side, somewhat convex and swollen, runs from the anterior point to the postglenoid process. The posterior side is shortest and is almost directly transverse, but with considerable irregularity. The posteroexternal angle is produced into the auditory meatus. On its internal side the bulla is closely applied to basisphenoid, leaving no open fissure, but the union is one of plane contact and the bones separate readily.

The crista meati, generally sharp but not very high, begins near the posteroexternal corner of the bulla and runs outward and somewhat upward and backward to the ventral rim of the porus acusticus. The stylomastoid foramen, which faces more ventrally than laterally, is between the outer end of this crest and the posttympanic process. The deep vagina processus hyoidei is medial and slightly anterior to the stylomastoid foramen, posterior to the inner end of the crista meati, anterolateral to the paroccipital process, and anteromedial to the posttympanic process.

The meatus is short and more nearly horizontal than in most later notoungulates. Both postglenoid and posttympanic processes extend considerably farther laterally than does the bony meatus, thus forming a large acoustic notch at the medial side of which the porus appears. The general structure of the whole ear region was evidently almost exactly as in *Oldfieldthomasia.*

The posterior lacerate foramen is not conspicuous because it is in a depression closely hemmed by the bulla and the paroccipital processes, immediately medial to the latter. Posterior or slightly posteromedial to this, in the bridge of bone between it and the occipital condyle, is the condylar foramen, which is simple, although the hypoglossal canal, leading inward from it, branches in the bone and appears as a smaller dorsal and a larger ventral foramen in the endocranial cavity. There is no foramen or canal on the medial side of the bulla. Immediately lateral to its anteromedian angle is the foramen ovale. This is completely surrounded by the alisphenoid, but the posterior bar is very thin and readily broken or overlooked.

Posterior or slightly posterolateral to the foramen ovale is a fissure between the alisphenoid and tympanic. This runs upward and communicates with the cavum tympani above the hypotympanic sinus. Externally, a groove runs from it forward, downward, and medial into the lateral margin of the roof of the choanae. Clearly this canal is for the Eustachian tube.

There is another fissure on the median side of the glenoid surface, at the junction of the tympanic, squamosal, and alisphenoid (at its extreme posterolateral point). This probably communicates also with the cavum tympani, although I have been unable to demonstrate this conclusively. From its position and character, it seems probable that this is the fissura Glaseri, although this is not demonstrated.

Comparison of the foramina of *Notostylops* with those of *Hegetotherium* is instructive, excellent material of the latter genus permitting better knowledge of these details than for most notoungulates. Condylar, posterior lacerate, and stylomastoid foramina as well as the hyoidean vagina are similar in the two, the differences being in proportions and other superficial habitus characters. The postglenoid foramen of *Hegetotherium* is anterior, rather than posterior, to the postglenoid process, but this difference is apparently not so important as might appear. The foramina so identified are rather clearly homologous in the two genera, but in *Hegetotherium* the foramen has been displaced by the much stronger development of the ossified auditory meatus and its close union with the postglenoid process. *Hegetotherium* likewise has a very similar Eustachian foramen, and a possible Glaserian fissure medial to the glenoid fossa. The entocarotid enters a prominent foramen removed from the posterior lacerate, between the bulla and basioccipital, near the posteromedian corner of the former. This artery then runs forward in a short canal between tympanic, petrosal, and basioccipital and enters the cranial cavity through the internal foramen at the junction of petrosal, basioccipital, and basisphenoid. The foramen, functionally a median lacerate foramen, is more posterior than its usual probable homologue in most groups of mammals and is not visible externally.

In *Notostylops* there is little doubt that the entocarotid enters a canal the external aperture of which is confluent with the posterior lacerate foramen, or nearly so. The subsequent course of this canal and its point of entry into the cranial cavity have not been determined, but doubtless were as in *Oldfieldthomasia.*

The endocranium of *Notostylops* is fairly well known and has already been describe elsewhere (Simpson, 1933f). Its character will be summarized in a later section of this paper devoted to a comparative study of the notoungulate endocranium.

Mandible

The symphysis is fused, even in fairly young individuals. It generally extends back to the level of P_2 or even to P_3. Mental foramina are very irregular and variable. There may be only one, beneath the diastema, or as many as six or seven, scattered from the vicinity of I_2 to P_4. The horizontal ramus is generally shallow but stout. It varies much with age, being very slender in young individuals and rather massive in aged ones. In one or two cases (and more noticeably in some specimens of *Homalostylops*) it is unusually deep and thin transversely, which apparently is owing largely or wholly to crushing and plastic deformation post-mortem, especially of young jaws.

The post-dental region is short, the ascending ramus much higher than long, the coronoid slender and nearly vertical, slightly recurved. The sessile condyle is elevated well above the dental level. Its articular surface faces wholly upward, is transverse, is larger on the external than on the internal side, and is gently convex. A concave pocket is developed in the anterior face of the base of the coronoid, posteroexternal to M_3, and medial to this, directly posterior to M_3, is a well-defined internal process.

The angle is of herbivorous type, broad and flattened and expanded more posteriorly than ventrally. The dental foramen is near the alveolar level, posterior to the process alluded to in the last paragraph.

SPECIFIC TAXONOMY

As noted above, the seven genera now united under *Notostylops* included 23 species in Ameghino's taxonomic system. While this number seemed too high, any attempt to determine the synonymy and real specific limits appeared practically hopeless after long study of the types and other Ameghino specimens in 1931. A second attempt in 1933, with the additional material then available to me, also failed to bring any probable order into this remarkably confusing series. No two specimens are really alike, but in any particular dimensions or other characters the whole series seemed to intergrade indistinguishably, and at the same time the extremes are so very unlike that it seemed impossible for them to be conspecific. Finally in 1935, after I had closely studied well over 300 specimens of the genus, means were found to place the taxonomy on what appears to be a sound basis, to give distinctive definitions of the common, valid species, and to determine with reasonable probability the range of individual variation.

In the final approach to the problem the two main series of Scarritt expedition specimens of exactly known locality and level, about 30 specimens from south of Colhué-Huapí, and many isolated teeth and about 15 more complete specimens from Cañadón Vaca were taken as a point of departure. The Cañadón Vaca specimens are all from nearly the same level and seemed on inspection, corroborated by more detailed study, to be a homogeneous sample with the exception of one strongly aberrant individual, apparently a stray of another species. The Colhué-Huapí series is from five fairly distinct levels, but when the specimens were grouped by these levels and compared in detail there proved to be no consistent morphological differences associated with these age differences. The whole thickness of rocks from which they came, about 125 feet,[1] was apparently deposited with sufficient rapidity that no evolutionary or migratory changes occurred in the genus *Notostylops* at that place so far as can be determined from this sample.

The Colhué-Huapí and Cañadón Vaca series were then studied separately, and the exact characters and range of variation of each were determined and then were compared with each other. (See text figs. 72–73, pp. 201, 202.) From this work it appeared beyond any reasonable doubt that each of the two series was a homogeneous unit, definable as a species, and that they differed from each other in several definitely established ways. Three groups, of specific scope, were thus established: two, one each from Colhué-Huapí and Cañadón Vaca, well represented by good suites of specimens (including fine skulls of each), and a third, from Cañadón Vaca, represented by a single jaw that would not enter into either of the better known series.

Three specific groups thus being well established, without any reference to existing taxonomy, the type specimens (all of Ameghino) were compared one by one with these groups. The majority of Ameghino's types proved to be definitely within the range of our Colhué-Huapí series, a result not surprising since most of them were certainly from that locality and stratigraphic zone. It was concluded that these are synonyms and the old-

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[1] A single specimen, too imperfectly preserved for detailed comparisons, brings this to about 165 feet.

TABLE 46

COEFFICIENTS OF VARIATION IN TEETH OF *Notostylops*

Dimension	Sample of Heterogeneous Origin	A.M.N.H. Colhué-Huapí Series	Whole *N. murinus* Series
Length M_1	11.8	6.1	4.9
Length M_2	13.6	2.6	3.1
Length M_3	15.1	3.9	4.8
Length M^1	11.6	3.8	4.8
Length M^2	11.7	4.2	3.2

est name, *N. murinus*, was taken for this whole series. The various statistical constants and other characterizations, already calculated for our material alone, were then recalculated to include the Ameghino specimens considered members of this group. Another Ameghino type, of *N. pendens*, proved to be inseparable from the Cañadón Vaca series to which its name thus could be applied. Still another, that of *N. appressus*, rather more doubtfully but still with sufficient probability proved to be conspecific with the third and least known of the species in the Scarritt Collection. Only four of Ameghino's species referable to *Notostylops* were found, for various reasons (see below) to be such that neither their validity nor their synonymy could be established. They must be listed as dubious forms, the names having little or no present value. Three species originally placed in *Notostylops* or synonymous genera were found not to belong to this genus.

Finally, isolated specimens or smaller series from scattered localities were studied and compared with the established, valid species. They suggest some degree of geographic and geologic, racial and mutational variety, but with one exception were inadequate to demonstrate any specific difference from the three species already defined. One specimen, a skull from the Cerro del Humo, is clearly distinct from these three and from any of Ameghino's species (he did not have any material from that locality) and required a new name.

The coefficients of variation of certain tooth dimensions, without overemphasis on their value, furnish an interesting criterion of the propriety of the procedure followed. Their testimony is in harmony with that derived from all other considerations. In table 46, these coefficients are given first for a heterogeneous lot from all localities, excluding only manifestly extraneous specimens (such as those placed in *Homalostylops*), then for the American Museum sample from Colhué-Huapí, and then for the whole *murinus* series, adding to the last sample all the Ameghino types of species reduced to synonymy with *murinus*.

The heterogeneous large sample gives figures which are, on the whole, too high for a single race or species; one coefficient, not included here, was as high as 21.6, and the lowest was 9.8, which is high for most dimensions of a single species. The American Museum Colhué-Huapí series gives figures entirely consistent with a single species and considerably less than half as high as those for the unsorted sample. Addition of the Ameghino specimens does not markedly alter any of these last figures but tends to raise those that were low and to lower those that were high, giving figures still more consistent and still more in harmony with the hypothesis that the sample is of a single species, or even race. Each of these steps thus results in an improvement in the figures, and the validity of the final taxonomic arrangement seems well attested.

Although the original sorting of the specimens was by localities, and with some exceptions the final results of the detailed study show such division to be natural taxonomically, it does not necessarily follow that geographic distribution is the essential factor in the known specific differentiation of *Notostylops*. The field conditions are such that separation of samples by their geographic origin does or may also involve their separation into unified facies or into temporal subdivisions, both of which were doubtless important factors in the differentiation of the genus.

Ameghino's species and the present arrangement of them are as follows:

Notostylops murinus Ameghino, 1897	= *Notostylops murinus*
Notostylops bicinctus Ameghino, 1897	= *Notostylops bicinctus* (*nomen vanum*)
Notostylops parvus Ameghino, 1897	= *Homalostylops parvus*
Notostylops escaridus Ameghino, 1901	= *Notostylops murinus*
Notostylops complexus Ameghino, 1901	= *Notostylops murinus*
Notostylops irregularis Ameghino, 1901	= *Notostylops murinus*
Notostylops chicoensis Ameghino, 1902	= *Notostylops murinus*
Notostylops ampullaceus Ameghino, 1902	= *Notostylops murinus*
Notostylops aspectans Ameghino, 1902	= *Notostylops murinus*
Notostylops brachycephalus Ameghino, 1904	= *Notostylops murinus*
Notostylops promurinus Ameghino, 1904	= *Notostylops murinus*
Anastylops vallatus Ameghino, 1897	= *Notostylops murinus*
Catastylops pendens Ameghino, 1901	= *Notostylops pendens*
Catastylops deflexus Ameghino, 1904	= *Notostylops deflexus* (*nomen vanum*)
Pliostylops magnificus Ameghino, 1901	= *Notostylops murinus*
Eostylops diversidens Ameghino, 1901	= *Notostylops diversidens* (*nomen vanum*)
Eostylops obliquatus Ameghino, 1901	= (To Isotemnidae)
Entelostylops completus Ameghino, 1901	= *Notostylops murinus*
Entelostylops incolumis Ameghino, 1901	= *Homalostylops parvus*
Entelostylops tripartitus Ameghino, 1901	= *Notostylops murinus*
Entelostylops cestillus Ameghino, 1901	= *Notostylops cestillus* (*nomen vanum*)
Entelostylops appresus Ameghino, 1902	= *Notostylops appressus*
Isostylops fretus Ameghino, 1902	= *Notostylops murinus*
(Not present in Ameghino Collection)	*Notostylops pigafettai*

Notostylops murinus Ameghino, 1897

Plate 15, figures 1–12; plate 16, figures 1–9; text figures 62–69

Notstylops murinus Ameghino, 1897a, p. 489, figs. 67–70; 1898, p. 175; 1904b, p. 409, figs. 535, 536; Gaudry, 1904, pp. 16, 20, figs. 15, 25; Schlosser, 1923, p. 615, fig. 759c; Riggs and Paterson, 1935, p. 167, figs. 1, 2, pls. 1, 2.

Anastylops vallatus Ameghino, 1897a, p. 490; 1898, p. 175, 1904a, vol. 58, p. 248.

Notostylops escaridus Ameghino, 1901, p. 420; Simpson, 1932e, p. 5, fig. 3.

Notostylops complexus Ameghino, 1901, p. 420; 1904b, p. 408, fig. 533.

Notostylops irregularis Ameghino, 1901, p. 420.

Pliostylops magnificus Ameghino, 1901, p. 421.

Entelostylops completus Ameghino, 1901, p. 425; 1904b, p. 64, figs. 57, 277, 532.

Entelostylops tripartitus Ameghino, 1901, p. 425.

Entelostylops triplicatus, [in error], Schlosser, 1923, p. 615, fig. 759A and B.

Dimerostephanos chicoensis Ameghino, 1902a, p. 31.

Notostylops chicoensis Ameghino, 1902a, p. 31.

Notostylops ampullaceus Ameghino, 1902a, p. 32.

Notostylops aspectans Ameghino, 1902a, p. 32; Patterson, 1932, p. 9, fig. 2.

Isostylops fretus Ameghino, 1902a, p. 33; 1904b, p. 410, fig. 538.

Notostylops brachycephalus Ameghino, 1904a, vol. 58, p. 246; 1904b, p. 412, fig. 540; 1904d, p. 54, fig. 38; 1906, p. 346, fig. 179; Simpson, 1932e, p. 4, fig. 2; Scott, 1937, p. 528, fig. 334.

Notostylops promurinus Ameghino, 1904a, vol. 58, p. 247; 1904b, p. 408, fig. 534.

Syntypes: M.A.C.N. No. 10500, skull lacking occiput and basicranium, with median incisors, left P^{2-4} and M^3, and right P^2–M^3, all badly worn.

M.A.C.N. No. 10498, both sides of lower jaw with all teeth save the incisors and left P_2. I select this as lectotype, its teeth being more useful for comparison with those of other types than are those of the skull.

Types of Synonyms: *Anastylops vallatus:* M.A.C.N. No. 10469, two isolated upper premolars (the smaller of which is lectotype) and an incisor.

Notostylops escaridus: M.A.C.N. No. 10510, skull fragments with right incisor roots and all cheek teeth of both sides (lectotype). M.A.C.N. No. 10509, right lower jaw with P_2–M_3.

Notostylops complexus: The type description gives the length P^2–M^3, which could not be taken from any specimen labeled with this name by Ameghino, so that the type is evidently mislaid. M.A.C.N. No. 10532 includes left M^{1-3}, poorly preserved, also isolated left M^2 and left M^3 of two other individuals, all identified as of this species by Ameghino and hence representing his conception of it.

Notostylops irregularis: M.A.C.N. No. 10523, part of lower jaw with right I_{1-2} and P_2–M_1 and left I_2 and P_{2-3}.

Pliostylops magnificus: M.A.C.N. No. 10486, left P_4–M_3 and right anterior alveoli or roots through P_4.

Entelostylops completus: M.A.C.N. No. 10492, part of left upper jaw with P^4–M^3.

Entelostylops tripartitus: M.A.C.N. No. 10491, part of right upper jaw with roots and fragments of P^3–M^1 and inner walls of M^{2-3}.

Dimerostephanos chicoensis: M.A.C.N. No. 10647, right P_{3-4} (lectotype), right M_2, right P_{1-2}, left P_2, and left P_3, representing several different individuals.

Notostylops chicoensis: M.A.C.N. No. 10518, right M_{1-3}.

Notostylops ampullaceus: M.A.C.N. No. 10506, cranium (mostly preserved as a natural mold) and left lower jaw with P_3–M_3, right M_3, and distal end of a right humerus.

Notostylops aspectans: M.A.C.N. No. 10528, part of right maxilla with M^{2-3} and broken M^1, also part of right lower jaw with broken M_2.

Isostylops fretus: M.A.C.N. No. 10494, four isolated upper premolars, two of them broken.

Notostylops brachycephalus: M.A.C.N. No. 10499, a nearly perfect skull, with the dentition.

Notostylops promurinus: M.A.C.N. No. 10507, fragmentary left maxilla with P^2–M^3, the molars broken.

HYPODIGM: The types, as above, and a large series of other specimens of which the following are outstanding:

M.A.C.N. No. 10466, palate with complete dentition
C.N.H.M. No. P 13319, skull
C.N.H.M. No. P 13308, skull
C.N.H.M. No. P 13297, lower jaws with left P_2–M_1, and right P_3, M_{2-3}
A.M.N.H. No. 28956, skull
A.M.N.H. No. 28755, lower jaws with left P_3–M_1, and right P_3, M_1, M_3
A.M.N.H. No. 28746, left P^3–M^3

HORIZON AND LOCALITIES: Casamayor, Patagonia. The great bulk of the material is from south of Lago Colhué-Huapí, but scattered specimens are from north of the lake, the valley of the Río Chico, and elsewhere.

DIAGNOSIS: Ratio P^{2-4}: M^{1-3} (six specimens) mean $.73 \pm .02$. Length M_1 (13 specimens) mean $8.7 \pm .1$. (Other dimensions given below.) P^3 generally and P^4 always grooved on inner face.

Anastylops vallatus was based on two isolated upper premolars and an incisor. Later a palate, M.A.C.N. No. 10466, with complete dentition, was referred. This palate is surely of *N. murinus*, with which it agrees closely in every respect. The question of generic separation has been discussed above. The two isolated premolars are of different individuals and both appear to be P^2. One is slightly below average size for *N. murinus*, the other well above the average for that species, but both are within its known or probable range and neither differs significantly. The largest d/σ, for the length of the larger tooth, is 1.96, not clearly significant. The species is quite inseparable from *N. murinus*.

Notostylops escaridus was defined principally on these characters:

1. Larger than *N. murinus*
2. I^1 stronger, triangular
3. I^2 much smaller, placed against I^1
4. I^3 absent
5. External face of upper cheek teeth depressed, with vertical wrinkles
6. I_2 subcylindrical, tusk-like
7. Horizontal rami low and thick

Of these, characters 2, 3, 5, and 6 are not distinctive from any specimens of *N. murinus*, and 1, 4, and 7 are well within its range of variation. The types are included in the statistical analysis below, and all their characters enter perfectly into the distributions for *N. murinus*.

Notostylops complexus was defined by a description rather than an explicit comparison, and Ameghino's description seems to me to apply perfectly to many specimens of *N. murinus*. The available specimens are also inseparable from that species.

Notostylops irregularis was based principally on its small size and on the fact that P_2

is placed at an angle to P_3. It is smaller than most other specimens of *N. murinus*, but enters into the distributions of the latter as a normal small variant. The morphology also is well within the range of variation of *N. murinus*.

Pliostylops magnificus was defined on the presence of C_1 and P_1. As both these teeth are variable in *N. murinus* and may occur normally, this is not in itself a valid distinction, and there appears to be no other means of distinguishing the species.

Entelostylops completus was not compared with species of *Notostylops*. As shown above, the genera are inseparable, and it follows that the species is synonymous with *N. murinus*, as it shows no further distinctions.

Entelostylops tripartitus as defined had as its sole distinctive character the presence of two grooves on the internal faces of M^{2-3}. These cannot be seen clearly on the type of *N. murinus*, because it has these teeth too deeply worn, but certainly were normal for that species.

Dimerostephanos chicoensis was based on small fragments of several individuals. Because of their poor preservation, they were compared with isotemnids rather than notostylopids. When comparison is made with the latter, the specimens prove to be quite inseparable from *Notostylops murinus*. With reference of this species to *Notostylops*, this name and the next become homonyms, but since both are synonyms of *N. murinus* I see no point in proposing a new name on grounds of the homonymy.

Notostylops chicoensis (defined as a different species from that just discussed) was distinguished as a small species with high crowns and with the talonid pillar dividing the talonid basin into two fossettes. M_3 is below average size, but distinctly within the range of *N. murinus*, and the morphology does not appear to me to be distinctive. Despite its name, the type is labeled as from Colhué-Huapí. The preservation and matrix suggest a different level or locality from most specimens of *murinus*, but this is very inconclusive. The specimen does not agree so closely with any other locality or horizon group as it does with typical *N. murinus*.

Notostylops ampullaceus was defined as larger than *N. murinus* and with the mandible heavy anteriorly, although the latter character is not shown by a specimen referred to the species by Ameghino. All the characters are distinctly in the range of *N. murinus*, of which the type can be considered only as a somewhat robust variant. The type is from "Colhué-Huapí Norte." Were there a group of specimens from this locality it might be possible to define *ampullaceus* as a subspecies or race of *N. murinus*, but the single specimen is so close to the latter that the species can hardly be different, and it is, of course, impossible to anticipate what more data might reveal. A specimen referred by Ameghino is from Colhué-Huapí (i.e., south of the lake, at the type locality of *murinus*).

Notostylops aspectans is based essentially on M^{2-3}. M^3 is somewhat above average size, but both teeth are in every respect within the known range of *N. murinus*, so that there is no choice but to consider the species synonymous. The type is from "Oeste del Río Chico," and so might be expected to differ from *N. murinus*, but since it does not really show such difference, this *a priori* consideration does not permit retention of the species even tentatively. The difference from *N. pendens*, which is characteristic of the region west of the Río Chico, is definitely greater than from *N. murinus*.

Isostylops fretus was based on isolated upper premolars, worn and partly broken. The definition was based on the assumption that these teeth are, or include, molars, but they show no character outside the known range of premolars of *N. murinus*.

Notostylops brachycephalus was based on a splendid type, a nearly perfect skull. At first glance it appears quite distinct from the type of *N. murinus*, but on analysis most of the differences are due merely to differences in age and preservation. The true distinctions are slight and involve principally minor differences of size and proportions which all prove, on analysis, to be within the known and probable range of *murinus*, now that a large sample of the latter is available. The most variant character is the relatively large molar width, but this is not sufficiently aberrant to be of probable specific or even racial value. The type is included in the statistical data below and enters well into this taxonomically homogeneous sample.

Notostylops promurinus was defined as having P^1, upper molars without internal sulcus, and a crest (crochet) on the molars and P^{3-4}. P^1, vestigial in this specimen, is often present in *N. murinus*, and a similar crochet is universal in this family until removed by wear. As for the absence of the sulcus, the inner parts of the molars are broken on the specimen and were apparently restored by Ameghino's artist. The absence of a sulcus must have been inferred from its absence on the root, but in several other specimens the sulcus is absent on the root but present on the crown, so that this inference is unwarranted. No other differences from *murinus* are significant, and the species can be considered only a synonym.

Numerical data on *N. murinus* are given in tables 47 to 52.

The measurements on which statistical constants of *N. murinus* are based are taken from 32 specimens in the following collections:

Ameghino Collection, Buenos Aires
  13 specimens including the following types:
    Notostylops murinus
    Entelostylops completus
    Notostylops aspectans
    Notostylops brachycephalus
    Notostylops escaridus
    Notostylops irregularis
    Pliostylops magnificus
    Notostylops chicoensis
    Notostylops ampullaceus
  (Six other species are considered synonymous, but in each case, for various reasons, the measurements cannot well be used in the statistical analysis.)
Chicago Museum:
  6 specimens
American Museum, New York
  13 specimens

The lengths of M^1, M^2, and M^3 in the type skull of *N. murinus* are greatly and obviously reduced by wear to such a degree as not to be fairly comparable with those of average adult individuals. These measurements are therefore omitted from the analysis. Other measurements of the same specimen are less affected by its extreme age and are used.

All these specimens are known to be from the barranca south of Colhué-Huapí, with the following exceptions:

M.A.C.N. Nos. 10500, 10510, 10499, 10509, and 10523 are of unknown localities. From the matrix, preservation, and (approximate) times of collection it is probable that most or all are also from this locality.

M.A.C.N. No. 10528 (type *N. aspectans*) is labeled as from "Oeste del Río Chico," but almost certainly belongs to this species and not to the more typically Chico valley *N. pendens;* see page 192.

M.A.C.N. No. 10506 is from "Colhué-Huapí Norte."

C.N.H.M. No. P 13308 is from near Kilometro 145 of the Sarmiento Railroad, which is not far from the great barranca and is essentially part of the same deposit. (Only one tooth, M^1, of this specimen enters into the figures in any case and it has virtually no influence on the constants.)

The omissions from the specimens included in the statistics are of the following sorts:

1. Isolated specimens and small lots from distant localities, possibly not from the same or nearly the same stratigraphic position, and not surely of this species
2. Specimens which from crushing, extreme wear (removing all enamel), or breakage cannot be measured comparably or accurately
3. Specimens not including these teeth, and teeth of doubtful homologies
4. Specimens certainly not of this species (e.g., those from the same locality but belonging to *Homalostylops*)

These obviously necessary or advisable omissions make the sample essentially homogeneous, but cannot otherwise have biased it in any significant way.

HYPSODONTY: As a measure of this character, the index (100 height M^3)/(length M^3) may be used, higher values indicating greater hypsodonty. I can give only two fairly good values:

Nearly unworn specimen: 81
Slightly worn specimen: 77

The figure is, of course, rapidly reduced by wear.

Many other characters might be listed, and several others have been studied and discarded as less useful, but these seem to provide the best means of comparison and to be entirely adequate for the recognition and definition of species in this genus.

The revision of this group as far as it can be carried and the proposed basis for future tax-

TABLE 47

Notostylops murinus

	N	OR	M	σ	V
P_2					
L	5	3.8 – 5.4	4.7	$[\Sigma(d^2) = 1.39]$	—
W	5	3.0 – 4.2	3.5	$[\Sigma(d^2) = .87]$	—
P_3					
L	9	6.5 – 7.8	7.2 ±.1	.40 ±.09	5.5±1.3
W	9	4.9 – 5.9	5.5 ±.1	.37 ±.09	6.7±1.6
P_4					
L	13	7.0 – 8.7	7.8 ±.1	.45 ±.09	5.8±1.1
W	13	5.7 – 6.8	6.3 ±.1	.41 ±.08	6.5±1.3
M_1					
L	13	8.0 – 9.5	8.7 ±.1	.42 ±.08	4.9±1.0
W	12	5.3 – 6.6	6.1 ±.1	.45 ±.19	7.3±1.5
M_2					
L	12	8.6 – 9.6	9.4 ±.1	.30 ±.06	3.1± .6
W	13	5.9 – 6.9	6.4 ±.1	.29 ±.06	4.5± .9
M_3					
L	16	11.5 –13.7	12.4 ±.2	.59 ±.11	4.8± .8
W	15	5.7 – 7.0	6.3 ±.1	.40 ±.07	6.3±1.2
LP_4/LP_1	11	.80– 1.01	.90±.02	.057±.012	—
LM_1/LM_2	9	.84– 1.00	.94±.02	.046±.011	—

TABLE 48

Notostylops murinus

	N	OR	M	σ	V
P^2					
L	7	4.7 – 6.2	5.4 ±.2	.46 ±.12	8.6±2.3
W	7	6.0 – 7.6	7.0 ±.2	.57 ±.15	8.2±2.2
P^3					
L	9	6.9 – 8.2	7.6 ±.1	.40 ±.09	5.2±1.2
W	9	8.9 –11.1	10.0 ±.2	.63 ±.15	6.3±1.5
P^4					
L	9	7.6 – 8.7	8.1 ±.1	.36 ±.08	4.4±1.0
W	8	11.2 –12.8	11.8 ±.2	.58 ±.15	4.9±1.2
M^1					
L	11	8.5 –10.0	9.3 ±.1	.44 ±.09	4.8±1.0
W	11	11.2 –12.9	12.0 ±.2	.53 ±.11	4.4± .9
M^2					
L	11	9.6 –10.9	10.0 ±.1	.32 ±.07	3.2± .7
W	12	11.3 –13.9	12.4 ±.2	.78 ±.16	6.3±1.3
M^3					
L	9	9.3 –11.2	10.2 ±.2	.55 ±.13	5.4±1.3
W	9	10.5 –13.6	12.1 ±.3	.96 ±.23	7.9±1.9
LP^4/LM^1	8	.81– .98	.88±.02	.050±.012	—
LM^1/LM^2	9	.86– .99	.93±.01	.040±.009	—
P^2–M^3	7	41.8 –46.2	44.4 ±.5	1.45 ±.39	3.3± .9
P^{2-4}/M^{1-3}	6	.68– .78	.73±.02	.038±.011	—

onomy depend in large measure on the conclusion that this sample is drawn from a unit from the taxonomic point of view, that it does represent one species or race. It is, in fact, heterogeneous in some other respects. It presumably includes both males and females, since no way of distinguishing these has appeared, and it is probable that the sexes do differ in some way, even though this is not determinable from these data. The animals are not all contemporaneous, but must cover many generations during which some somatic changes must have occurred, although again these are not now determinable. Geographic locality is not absolutely the same for all, but the area covered is so small that no significant heterogeneity can be expected on this score. Finally, animals of different individual ages are included, from young with the permanent teeth unworn to aged with all the teeth deeply worn. This has a very marked effect on some dimensions, particularly the lengths of the molars. The most extreme fluctuations resulting from this cause have been eliminated by discarding length measurements of teeth in which no enamel remains on the anterior or posterior borders, but the available samples are not large enough to permit of grouping as to age and treating each age group as a unit. This would make each age group much more homogeneous, and variation must be expected to be greater because this could not be done.

In view of these factors making for fluctuation within a single species, the sample as a whole is remarkably constant, and certainly consistent in every way with pertinence to one race.

A first criterion is that of the actual distributions of variates: whether these are continuous within the limits of frequency errors imposed by the size of the sample and whether the corresponding curves rise to a single peak or in any case show two probably separable modes. On these tests, the curve corresponding to each variate measured proved to be completely indivisible. A typical example, for a dimension which shows variation above the average, is given in table 52.

Most of the distributions are even more compact and clearly unimodal. Although slightly asymmetrical (as any distribution of so small a sample is virtually certain to be)

TABLE 49

Notostylops murinus

	P_2–M_3
N	5
OR	47.1–51.5
M	49.2
Σ (d²)	10.92

TABLE 50

DENTAL FORMULAS IN *Notostylops murinus*

		No. of Specimens
Lower incisors	2	3
	3	0[a]
Lower canine	Absent	4
	Present	1
Lower premolars	3	7
	4	1
Upper incisors	4	1 side of 1
	3	3 and 1 side of 1
	2	1
Upper canine	Absent	3 and 1 side of each of 2 other
	Present	1 side on each of 2
Upper premolars	3	4
	4	3
Molars, upper and lower	3	All known specimens
Entire known dental formula		4–2.1–0.4–3.3 2.1–0.4–3.3

[a] It is highly probable that three lower incisors also occurred occasionally.

TABLE 51

GROOVING OF INNER FACES OF UPPER PREMOLARS IN NUMBERS OF SPECIMENS, *Notostylops murinus*

	Grooved	Not Grooved
P^3	9	3
P^4	14	0

TABLE 52

WIDTH OF M_3 OF *Notostylops murinus*

Measurement	Frequency
5.5–5.7	1
5.8–6.0	4
6.1–6.3	5
6.4–6.6	2
6.7–6.9	2
7.0–7.2	1

this distribution is not, in fact, skewed. Mean and mode are identical: 6.3.

The amount of variation shown is also fully consistent with a single species. Of the 23 coefficients of variation of linear dimensions calculated, the average is 5.6, lowest 3.1, and highest 8.6; all are sufficiently low to belong to one race, especially in view of the factors of nontaxonomic heterogeneity present, as mentioned above. Homologous figures for a single sex of a single race of man may average and range higher.

To translate these into figures more commonly used in earlier paleontology and still, perhaps, more readily visualized, the percentage by which the maximum observed value exceeds the minimum for each of these 23 dimensions was calculated. The average is 20 per cent, minimum 11 per cent, maximum 32 per cent. This, again, is not a large amount of variation for one species.[1]

The figures are, it is true, larger for P_2 (known in so few individuals that its statistical constants were not calculated). The largest known P_2 is 42 per cent longer and 40 per cent wider than the smallest. *A priori*, this might suggest heterogeneity, but the explanation is that P_2, which is reduced and is on the way to becoming functionless, is individually highly variable. In one individual the P_2 of one side is 18 per cent longer than that of the other side. When a difference of 18 per cent is thus not even indicative of individual difference, it is not surprising that a difference of 42 per cent can occur within the species.[2] Among the few individuals in which both sides are known, similar differences are common. Thus in another individual P^2 is 8 per cent wider on one side than on the other: the maximum difference for the whole species is 32 per cent. In still another the right P^4 is 10 per cent wider than the left: the maximum observed difference for the whole species is only 14 per cent.

With such remarkable variation in single individuals, the variation for the sample as a whole is strikingly low and its unity is well attested and the value of its characterization as a group rather than by the unsatisfactory method of selected types is apparent.

The differences in the dental formula, which might *a priori* be considered not only specific but also generic,[3] are shown to be unimportant taxonomically by similar occurrences. Of the few specimens in which the formula can be determined on both sides of the jaw or palate, it is different on the two sides in about half these specimens. When the difference between 4.0.4.3 and 3.1.4.3 (and furthermore with P^1 of one side large and that of the other tiny and lost during the life of the individal so that the definitive formula of the latter side was 3.1.3.3.) is not even individual, the observed differences in dental formula certainly do not demand specific separation. The fact that I_3, C^1_1, and P^1_1 are more often absent than present is, of course, characteristic of the species, even though none of these teeth (with the improbable exception of I_3) is invariably absent.

Notostylops pendens (Ameghino, 1901), new combination

Plate 18, figure 1; text figures 70, 71

Catastylops pendens AMEGHINO, 1901, p. 421; 1904b, p. 19, fig. 7.

TYPE: M.A.C.N. No. 10472. Badly crushed right maxilla with P^3–M^2. Ameghino Collection.

NEOTYPE: A.M.N.H. No. 28634. Skull and jaws with complete dentition. Collected by G. G. Simpson, 1930.

HYPODIGM: Type, neotype, and a large series of specimens, of which the following are outstanding:

---

[1] It will of course be borne in mind that this is a comparison of the largest and smallest known individuals of a species. If two groups of animals differed this much in their *means* they would certainly be distinct.

[2] If, as is sometimes maintained, a difference of 15 per cent is generally specific, this individual's right mandible belonged to one species and his left to another.

[3] Ameghino did, in fact, base both species and genera in this group principally on these differences, in which he was, of course, following well-established precedent.

A.M.N.H. No. 28604, skull and part of lower jaw
A.M.N.H. No. 28614, skull
A.M.N.H. No. 28603, left lower jaw with P_3–M_3

Horizon and Locality: Casamayor, type from "Oeste del Río Chico," neotype and referred specimens from Cañadón Vaca, Chubut, Argentina.

Diagnosis: Ratio P^{2-4}:M^{1-3} (three specimens) mean .59. Length M_1 (10 specimens) mean 8.1 ±.1. (Other dimensions given below.) P^3 and P^4 without internal grooves.

With the exception of much smaller individuals obviously allied to *Homalostylops* and of one strongly aberrant specimen, A.M.N.H. No. 28589 (placed in *N. appressus*), all our material from Cañadón Vaca seems to be of one species. This includes three skulls, one

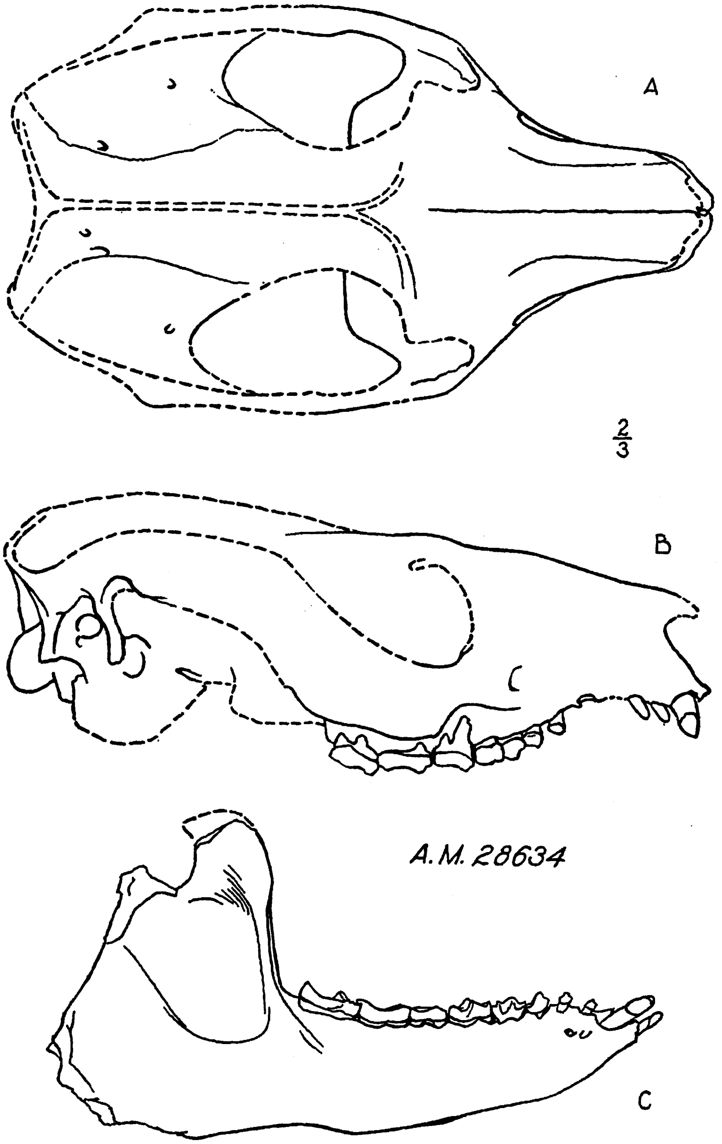

Fig. 70. *Notostylops pendens* (Ameghino). A.M.N.H. No. 28634, skull and jaws, neotype. A. Dorsal view of skull. B. Right lateral view of skull. C. Right lateral view of lower jaw. ×2/3.

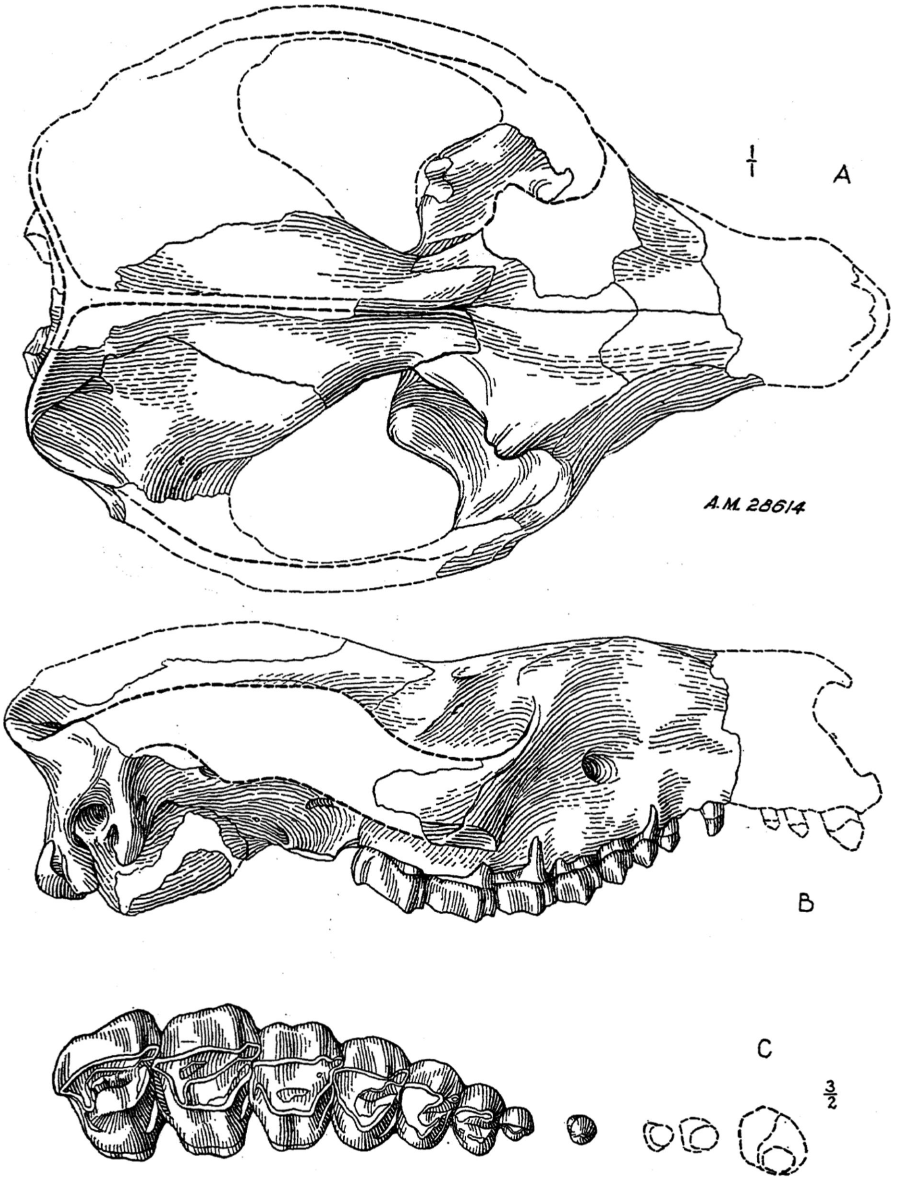

FIG. 71. *Notostylops pendens* Ameghino. A.M.N.H. No. 28614, incomplete skull. A. Dorsal view. ×1. B. Right lateral view. ×3/2. C. Crown view of right dentition. ×3/2.

with complete lower jaws, about 15 other partial jaws, and some 60 or 70 more fragmentary specimens or isolated teeth. The range, means, and other important characters of the different variates were worked out from this material. Although numerous, the isolated teeth were of little help. Except for M$_3^3$ they cannot all be certainly identified: there are, that is, some marginal specimens which might be either P_3 or P_4, others which might be either M^1 or M^2, etc. The omission of these doubtful teeth only, or their inclusion in the wrong category, would strongly bias the samples, and therefore all the isolated teeth except M$_3^3$ were omitted, leaving the samples much smaller but unbiased.

TABLE 53

Notostylops pendens

	P^3		P^4		M^1	
	L	W	L	W	L	W
M.A.C.N. No. 10472	4	8	6.7	10½	8½	12
Difference from mean Cañadón Vaca suite	−1.7	−.3	−.1	−.3	.1	−.1

The group thus characterized was found to be distinct from the Colhué-Huapí species, identified as *N. murinus*, and hence from most of Ameghino's species, the majority of which are synonyms of *N. murinus*.

Ameghino's *Catastylops pendens*, however, agrees in the principal characters which it shows, notably the presence of P^1 (perhaps more constant here than in *N. murinus*), the relatively small premolars, and absence of internal sulci on P^4. The type of *pendens* is so badly crushed that it cannot be measured accurately, but its approximate dimensions, compared with our suite, are given in table 53.

Except for the length of P^3, only very roughly ascertainable in the type in any event, the differences are negligible. There is a difference of only 0.1 mm. in the one measurement that is fairly accurate, length of P^4. Furthermore the type is from the vicinity of Cañadón Vaca, although probably not from that exact exposure. It seems fully permissible to conclude that these specimens are conspecific with the type of *pendens*, and in order to fix that name permanently and on a sounder basis, I name our best specimen as neotype. Since its measurements are manifestly inaccurate, the type is omitted from the statistical characterization in tables 54 and 55, but the neotype is, of course, included.

The synonymy of *Catastylops* with *Notostylops* is explained above. Comparison with *murinus*, showing that the ranges of almost all its characters overlap those of *pendens*

TABLE 54

Notostylops pendens

	N	OR	M	σ	V
P_2					
L	1	—	4.4	—	—
W	1	—	3.3	—	—
P_3					
L	4	5.8 - 6.1	6.0	$[\Sigma(d^2) = .05]$	—
W	4	3.8 - 4.5	4.4	$[\Sigma(d^2) = .39]$	—
P_4					
L	12	6.8 - 7.7	7.2 ± .1	.27 ±.05	3.7 ± .8
W	12	5.2 - 6.1	5.5 ± .1	.25 ±.05	4.5 ± .9
M_1					
L	10	7.4 - 8.5	8.1 ± .1	.32 ±.07	3.9 ± .9
W	9	5.2 - 6.3	5.6 ± .1	.31 ±.07	5.5 ±1.3
M_2					
L	11	9.2 -10.1	9.6 ± .1	.32 ±.07	3.3 ± .7
W	9	5.8 - 6.5	6.2 ± .1	.25 ±.06	4.1 ±1.0
M_3					
L	11	11.8 -13.8	12.9 ± .2	.51 ±.11	4.3 ± .9
W	10	6.0 - 6.7	6.3 ± .1	.21 ±.05	3.4 ± .8
LP_4/LM_1	4	.85- .92	.90	$[\Sigma(d^2) = .0030]$	—
LM_1/LM_2	6	.75- .85	.82 ± .01	.035 ± .010	—

TABLE 55

Notostylops pendens

	N	OR	M	σ	V
P^2					
L	3	4.3 – 4.4	4.4	$[\Sigma(d^2) = .01]$	—
W	3	6.6 – 6.7	6.7	$[\Sigma(d^2) = .01]$	—
P^3					
L	3	5.6 – 5.8	5.7	$[\Sigma(d^2) = .03]$	—
W	3	8.0 – 8.6	8.3	$[\Sigma(d^2) = .19]$	—
P^4					
L	3	6.8	6.8	—	—
W	3	10.2 –11.4	10.8	$[\Sigma(d^2) = .73]$	—
M^1					
L	3	8.1 – 8.7	8.4	$[\Sigma(d^2) = .18]$	—
W	3	11.2 –13.4	12.1	$[\Sigma(d^2) = 2.66]$	—
M^2					
L	5	9.8 –12.0	10.6	$[\Sigma(d^2) = 3.14]$	—
W	5	12.5 –13.8	13.4	$[\Sigma(d^2) = 1.15]$	—
M^3					
L	9	10.1 –12.7	10.7 ± .3	.77 ± .18	7.1 ± 1.6
W	9	11.8 –13.7	12.8 ± .2	.50 ± .12	3.9 ± 1.0
LP^4/LM^1	3	.78– .84	.81	$[\Sigma(d^2) = .0018]$	—
LM^1/LM^2	3	.83– .85	.84	$[\Sigma(d^2) = .0002]$	—
P^2–M^3	3	41.1 –42.6	41.8	$[\Sigma(d^2) = .93]$	—
P^{2-4}/M^{1-3}	3	.57– .62	.59	$[\Sigma(d^2) = .0013]$	—

(e.g., text figs. 72–73), offers further evidence against separating the genera.

Five specimens show important parts of the dental formula, and so far as determinable it is complete in all, that is: $\frac{3.1.4.3}{3.1.4.3}$. The number of specimens actually showing each tooth important in this connection is:

I_3 2
C_1 3
P_1 2 (probable but not certain in another)
I^3 1
C^1 2
P^1 3

TABLE 56

GROOVING OF PREMOLARS OF *Notostylops pendens*

		No. of Specimens
P^4	Grooved	0
	Not grooved	14[a]

[a] Isolated teeth surely P^4 are also counted. Unlike the dimensions, this leads to no bias, as the teeth doubtfully P^3 or P^4 are also all without grooves.

HYPSODONTY: Three reasonably good values for the index (on M^3) are available:

Nearly unworn: 70, 72
Slightly worn: 62

This sample is of more unified origin, geographically and stratigraphically, than is that of *N. murinus* for which the figures have been given, and this homogeneity is reflected in the statistical constants. Thus the average of the 10 V's calculated is only 4.4, maximum 7.1, while for *N. murinus* the average of the same V's is 5.7 and the maximum 7.9. The difference does not, however, suggest that the latter includes more than one species. It suggests, rather, that the Cañadón Vaca sample includes only one local racial or phyletic group within its species, while the *N. murinus* sample covers more ground and time.

Most of the continuous variates overlap those of *N. murinus* in their range, and even those that do not do so (length and width P_3, length P^2, length and width P^3, length P^4, length M^1/length M^2, and P^{2-4}/M^{1-3}) come so close that they might intergrade were the samples larger. Nevertheless, even in the intergrading characters, the two forms are distinguishable as the accompanying table (table 57) of values of t and P shows. (See Simpson and Roe, 1939.)

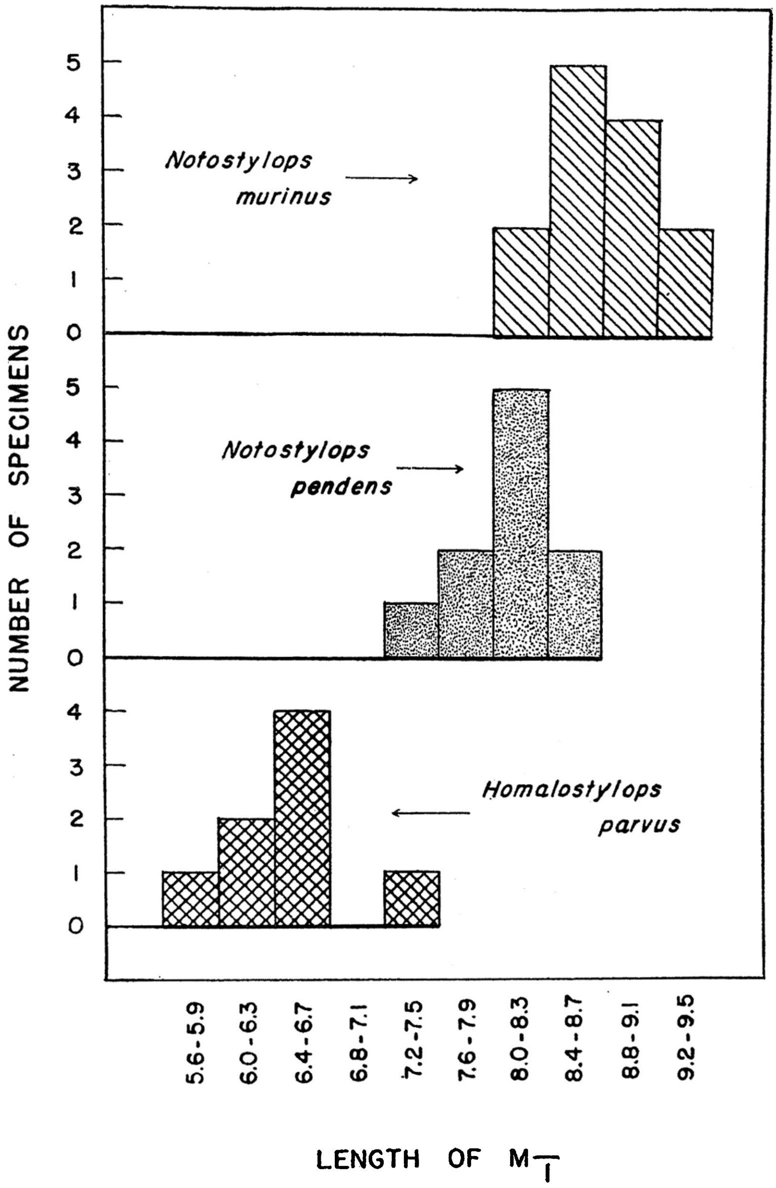

FIG. 72. Histograms of length of M_1 in the two common species of *Notostylops* and in *Homalostylops parvus*. See text, under the respective species, for specifications of samples and discussion.

The dimensions and ratios in which these groups differ significantly, P less than .01, are thus as shown in table 58, with the ratio of the mean in *N. pendens* to that in *N. murinus*.

Those in which the difference is probably, but not surely, significant, P between .01 and .05, are given in table 59.

The length of P^2 is particularly likely to prove significant. Its not being shown to be so as yet apparently results solely from the small size of the samples.

Notostylops appressus (Ameghino, 1902), new combination

Text figure 75

Entelostylops appresus[1] AMEGHINO, 1902a, p. 34.

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[1] So spelled. The name seems to occur only once in Ameghino's works, and it may be concluded with great

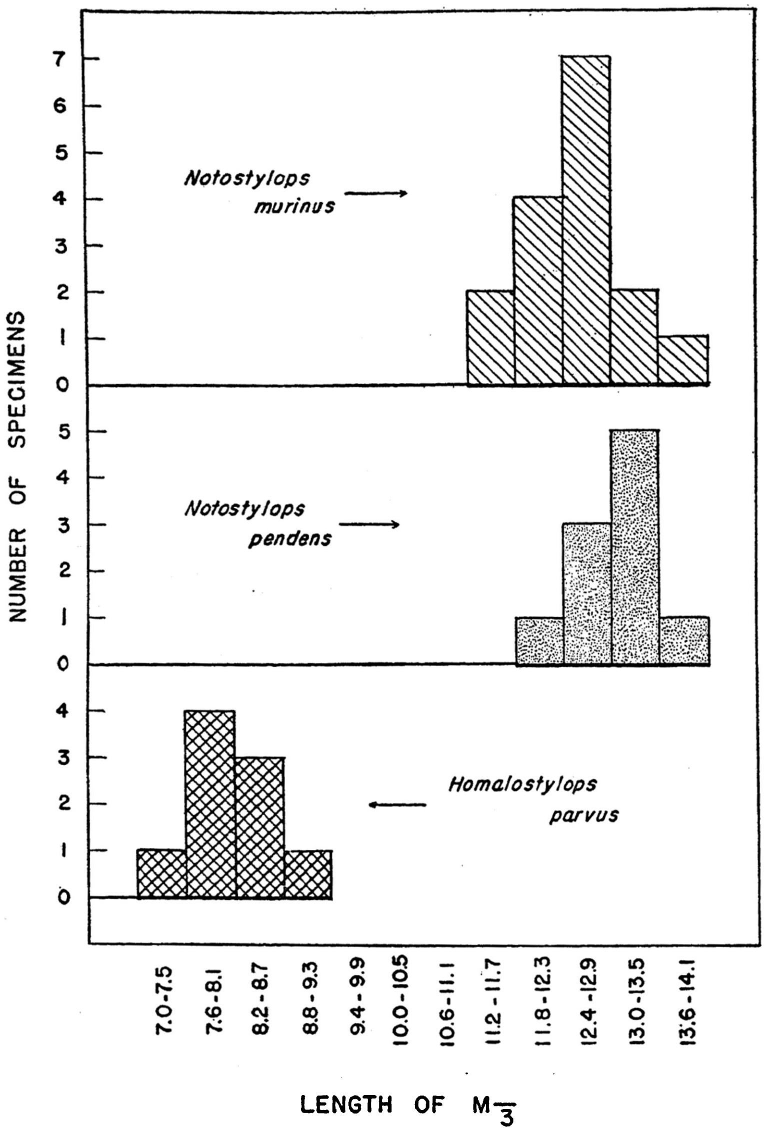

FIG. 73. Histograms of length of M_3 in three notostylopids. See also text figure 72.

TYPE: M.A.C.N. No. 10489. Four isolated upper teeth, probably P^2, P^3, M^1, and M^2, also an isolated M_3. Lectotype: the probable M^2.

NEOTYPE: A.M.N.H. No. 28589. Right lower jaw with P_3–M_1, M_3, and alveoli. Collected by C. S. Williams, 1930.

HYPODIGM: Essentially the types and neotype. Some other specimens are dubiously referred.

HORIZON AND LOCALITY: Casamayor. Type label apparently "R. Chico fr. yac. Pyroth.— f. notos. sup." (all but "R. Chico" obscure and not certainly correctly transcribed), that is, "Río Chico opposite *Pyrotherium* site [probably Cabeza Blanca of Loomis]—Upper *Notostylops* fauna." Neotype from Cañadón Vaca (also in valley of Río Chico, about 45 kilometers west of Cabeza Blanca). Possibly referable specimens from "Río Chico frente a Malaspina" (Ameghino)—which would be in the general area some 50 kilometers north-

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probability that this spelling is a misprint which should be corrected to read *appressus*.

TABLE 57

VALUES OF T AND P IN COMPARISON OF *Notostylops murinus* AND *N. pendens*

Variate	N_1+N_2	t	P		
			Less than .01	.01–.05	Greater than .05
LP_2	6	.46			X
WP_2	6	.39			X
LP_3	13	5.46	X		
WP_3	13	4.78	X		
LP_4	25	3.83	X		
WP_4	25	5.62	X		
LM_1	23	3.59	X		
WM_1	21	2.75		X	
LM_2	23	1.49			X
WM_2	22	.80			X
LM_3	27	2.34		X	
WM_3	25	0			X
LP_4/LM_1	15	0			X
LM_1/LM_2	15	5.89	X		
LP^2	10	3.33		X	
WP^2	10	.81			X
LP^3	12	7.46	X		
WP^3	12	4.13	X		
LP^4	12	5.75	X		
WP^4	11	2.38			X
LM^1	14	3.14	X		
WM^1	14	.17			X
LM^2	16	2.02			X
WM^2	17	2.97	X		
LM^3	18	1.50			X
WM^3	18	1.87			X
LP^4/LM^1	11	2.12			X
LM^1/LM^2	12	3.56	X		
$P^2–M^3$	10	2.69		X	
P^{2-4}/M^{1-3}	9	5.28	X		

TABLE 58

RATIOS OF MEANS IN *Notostylops pendens* TO THOSE IN *N. murinus*

Length P_3	.83
Width P_3	.80
Length P_4	.92
Width P_4	.86
Length M_1	.93
Length M_1/Length M_2	.87
Length P^3	.75
Width P^3	.83
Length P^4	.84
Length M^1	.90
Width M^2	1.08
Length M^1/Length M^2	.90
P^{2-4}/M^{1-3}	.81

northeast of Cabeza Blanca—and from immediately northeast of Pico Salamanca (Feruglio and the American Museum of Natural History collections), about 35 kilometers south-southeast of Cabeza Blanca.

DIAGNOSIS: An ill-defined and rather dubious species morphologically similar to *N. murinus* as far as known, but significantly smaller than that species or than *N. pendens*.

There are a few specimens from various scattered localities that are significantly smaller than *N. murinus* or *pendens* (and larger than *Homalostylops parvus*) in various dimensions and cannot belong to one of those species. They thus indicate the occurrence of

TABLE 59

RATIOS OF MEANS IN *Notostylops pendens* TO THOSE IN *N. murinus*

Width M_1	.92
Length M_3	1.04
Length P^2	.82
P^2–M^3	.94

at least one more species, but they are so few and fragmentary that they provide no firm basis for definition. The isolated teeth on which Ameghino defined *E. appressus* belong to this size group, and that name is available. On the basis of these very inadequate specimens, the name is practically a *nomen vanum*, but it seems warranted to assume that the specimens of this general size do represent one species, an assumption permitted by the few known facts and necessary if any meaning is to be attached to the name, and to designate the most characteristic specimen as neotype. This specimen occurs with *N. pendens* in Cañadón Vaca, but is so sharply distinct from that species (as shown in table 60) that it cannot enter into it. The occurrence of a single specimen of this smaller species with abundant *N. pendens* is explicable by various hypotheses, for instance that the two species occupied the same general region but in different ecological stations, this particular deposit happening to be in a spot occupied by *N. pendens* with only an occasional straggler or washed-in fragment of *N. appressus*.

FIG. 74. *Notostylops appressus* (Ameghino). A.M.N.H. No. 28589, right P_3–M_1 and M_3. Crown view. ×2.

M.A.C.N. No. 10526, from the Río Chico opposite Malaspina, was referred by Ameghino (MS label) to *N. bicinctus*, but it agrees better with *N. appressus*. One American Museum and one Feruglio specimen from the barranca northwest of Pico Salamanca also agree fairly well with this form and are tentatively referred to *N. appressus*. Some comparisons are given in table 60.

TABLE 60

COMPARISONS OF SPECIES OF *Notostylops*

	P^2		P^3		M^1		M^2	
	L	W	L	W	L	W	L	W
Types, *N. appressus*	4.7	5.8	5.8	8.5	8.1	9.7	8.5	10.0
Difference from means of *N. pendens*	+.3	−.9	+.1	+.2	−.3	−2.4	−2.1	−3.4
d/σ comparison with *N. murinus*	+1.5	−2.1	+2.8	+2.4	−2.7	−4.3	−4.7	−3.1

The isolated premolars are not certainly distinguishable from either *N. murinus* or *N. pendens*, but M^1 is probably, and M^2 is surely, so distinguishable. The latter is therefore made lectotype. There is no assurance that these teeth are really of one species.

Ratios to the means for *N. murinus* are given in table 61.

TABLE 61

RATIOS OF TYPES OF *Notostylops appressus* TO MEANS IN *N. murinus*

M^1		M^2	
L	W	L	W
.87	.81	.85	.81

Ratios for M_1 of the neotype are: length, .84, width, .82—an even closer agreement than would be expected on the hypothesis that the species are the same.

This is clearly distinct from the two species compared. The two Pico Salamanca referred specimens compare as shown in table 63.

TABLE 62

COMPARISONS OF SPECIES OF *Notostylops*

	P_3		P_4		M_1		M_3	
	L	W	L	W	L	W	L	W
Neotype, *N. appressus*	5.0	3.5	5.7	4.8	7.3	5.0	*ca.* 10.5	5.3
d/σ comparison with *N. murinus*	−5.5	−5.4	−4.7	−3.7	−3.3	−2.4	−3.2	−2.5
Same with *N. pendens*	—	—	−5.6	−2.8	−2.5	−1.9	−4.7	−4.8

TABLE 63

COMPARISONS OF REFERRED SPECIMENS OF *Notostylops appressus*

	M_1		M_2		LM_1/LM_2
	L	W	L	W	
Feruglio	7.0	4.7	7.7	—	.91
A.M.N.H.	—	—	7.8	5.3	—
d/σ with *N. murinus*	−4.0	−3.1	−5.7 −5.3	−3.8	− .7
Same with *N. pendens*	−3.2	−2.9	−5.9 −5.6	−3.6	+2.6

In the Feruglio specimen the length ratio is more as in *N. murinus*, and as far as the poor data from other specimens suggest, this may be generally true of the tooth length ratios in this species.

Notostylops pigafettai,[1] new species

Text figure 75

TYPE: A.M.N.H. No. 28758. Partial skull. Found by Justino Hernández, 1930.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayor formation, Cerro del Humo, north of Lago Colhué-Huapí, Chubut, Argentina.

DIAGNOSIS: About the size of *N. murinus*. Premolars larger absolutely than, and much larger relative to, molar series. P^3 and P^4 quadrate, with multiple internal grooves. M^3 reduced. P^1 absent (in type, perhaps variable).

This species differs from *N. murinus* in much the same way as the latter does from *N. pendens*. In fact the three species form a graded structural series in almost every respect, as is shown, among other things, by the representative measurements given in table 64.

TABLE 64

COMPARISONS OF SPECIES OF *Notostylops*

	Length P^2	Length M^3	P^{2-4}/M^{1-3}
N. pendens (mean)	4.4	10.7	.59
N. murinus (mean)	5.4	10.2	.73
N. pigafettai (type)	6.4	8.7	.93

The characteristic development of P^4 also forms a structural series. In *N. pendens* it is rounded-triangular, without internal grooves, in *N. murinus* triangular to subquadrate, with one internal groove, or occasionally two, and in *N. pigafettai* fully quadrate, with

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[1] For Antonio Pigafetta, Knight of Rhodes, companion and historian of Magellan's voyage, who visited Patagonia in 1520. His was the first European account of Patagonia. Shakespeare's "The tempest" has passages based on Pigafetta.

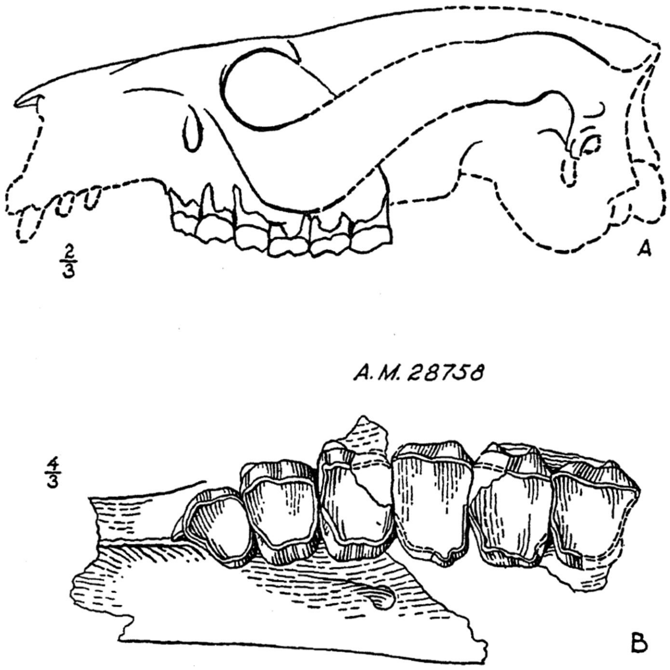

FIG. 75. *Notostylops pigafettai*, new species. Type, A.M.N.H. No. 28758, partial skull. A. Left lateral view. ×2/3. B. Occlusal view of left cheek teeth. ×4/3.

three internal grooves (in the type; doubtless somewhat variable, but the type is outside the range of variation of either of the other species). Probably hypsodonty was progressive, too, but the present type is too worn for accurate measurement. It was certainly more hypsodont than *N. pendens*.

It seems probable that *N. pendens* is the least and *N. pigafettai* the most specialized member of this series. Since no two species have been found superposed, and since the deposits in which they principally occur are isolated from each other, forming a large triangle about 60 kilometers on a side, it cannot be certainly established whether these differences in specialization correspond to differences in age, but it is entirely possible that they do. It is likewise impossible to determine whether the line is phyletic or not.

The type is the only specimen found at its

TABLE 65

Notostylops pigafettai COMPARED WITH OTHER SPECIES

	P^2		P^3		P^4		M^1		M^2		M^3		P^2–M^3	P^{2-4}/M^{1-3}
	L	W	L	W	L	W	L	W	L	W	L	W		
A.M.N.H. No. 28758	6.4	8.0	7.7	10.3	—	11.6	—	—	—	13.5	8.7	10.2	45.8	.93
d/σ comparison with *N. murinus*	+2.2	+1.8	+ .3	+ .5	—	+2.5	—	—	—	+1.4	−2.7	−2.0	+1.0	+5.3
Deviation from mean of *N. pendens*	+2.0	+1.3	+2.0	+2.0	—	+ .8	—	—	—	+ .1	−2.0 [d/σ= −2.6]	−2.8 [d/σ= −5.6]	+4.0	+ .34

locality, and none from other localities can be referred to the species at present. Specimens including molars only could probably not be distinguished from either of the other two species at present, but even isolated premolars would readily be so distinguished.

The principal dimensions and their comparison with those of *N. murinus* and *N. pendens* are as given in table 65.

NOTOSTYLOPS: NOMINA VANA

Here are included species that have been defined within the letter of the rules and that cannot be shown to be synonyms, but of which the definitions are now found to be doubtfully or not distinctive, and that cannot in fact be distinctively and usefully defined. The names are necessarily carried on the lists, but for any practical purpose they are empty or meaningless, and they do not apply to recognizable species. Some may be reinstated by later discovery, but in all cases this is improbable.

Notostylops cestillus (Ameghino, 1901), nomen vanum, new combination

Entelostylops cestillus AMEGHINO, 1901, p. 425.

TYPE: No material now in Ameghino Collection labeled as of this species. Type description mentions M^{1-3}.

HYPODIGM: Published data only.

HORIZON AND LOCALITY: Casamayor, Patagonia. No other data.

DIAGNOSIS: No distinctive characters known.

No material labeled or recognizable as of this species was found in the Ameghino Collection. The available descriptions do not distinguish the species from *N. murinus*, yet do not show it to be certainly a synonym. Unless the type is found, the species will never be recognizable and is a permanent *nomen vanum*.

Notostylops deflexus (Ameghino, 1904), nomen vanum

Plate 18, figure 2

Catastylops deflexus AMEGHINO, 1904a, vol. 58, p. 248.

TYPE: M.A.C.N. No. 10493. Left maxilla with P^{2-4} and alveoli or roots of M^{1-2}, badly preserved.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayor, south of Lago Colhué-Huapí, Patagonia.

DIAGNOSIS: No truly distinctive characters known. Cuspule on external cingulum of P^4.

The type is badly crushed, and the original definition failed to take this into account and also depended on characters of the alveoli made entirely unreliable by the crushing. Morphologically the preserved teeth are like those of *murinus*, except that on P^4 there is a strong cingulum on the posterior half of the outer face rising into a small cuspule; several specimens would be necessary to show that this is more than an individual anomaly.

The dimensions compare as shown in table 66.

In size the agreement with *N. pendens* is fairly close, although P^3 may be significantly wider. There is a sulcus on P^4, not observed on any specimen known to be of *N. pendens*. The only significant difference from *N. murinus* is the lesser length of P^{3-4}, which may possibly be affected by crushing. The teeth might conceivably belong to *N. appressus*, but their widths seem too great to make this reference probable. The real character and validity of the species are open to serious question.

TABLE 66

Notostylops deflexus COMPARED WITH OTHER SPECIES

	P^2		P^3		P^4	
	L	W	L	W	L	W
Type, *N. deflexus*	4.7	6.9	6.1	9.8	6.8	11.2
Difference from mean of *N. murinus*	− .7	− .1	−1.6	− .2	−1.3	− .6
d/σ	−1.5	− .2	−4.0	− .3	−3.6	−1.0
Difference from mean of *N. pendens*	+ .3	+ .2	+ .4	+1.5	0	+ .4

Notostylops bicinctus Ameghino, 1897, nomen vanum

Plate 18, figure 3

Notostylops bicinctus Ameghino, 1897a, p. 490; 1898, p. 175.

Type: M.A.C.N. No. 10512. Isolated left upper premolar.

Hypodigm: Type only.

Horizon and Locality: Casamayor, Patagonia. No other data.

Diagnosis: No distinctive characters known.

The single tooth on which this species was based was considered by Ameghino as P^2, but its size and proportions are such that it can hardly be anything but P^3 or P^4. It is compared with teeth of *N. murinus* and *N. pendens* in table 67.

TABLE 67

Notostylops bicinctus Compared with Other Species

	L	W
Type, *N. bicinctus*	6.6	9.8
Differences from mean of P^3 of *N. murinus*	−1.0	− .2
d/σ	−2.5	− .3
Differences from mean of P^4 of *N. pendens*	− .2	−1.0

The comparison is inconclusive. This could be either a P^3 of *N. murinus* or P^4 of *N. pendens*, in either case variant but not so much so as necessarily to be separated. Or it might be P^4 of *N. appressus*. Or it could be a distinct species, but is quite unrecognizable as such. The type is, in fact, indeterminable.

Notostylops diversidens (Ameghino, 1901), nomen vanum, new combination

Plate 18, figures 4–6

Eostylops diversidens Ameghino, 1901, p. 424.

Type: M.A.C.N. No. 10484. Various much broken jaw fragments with parts of upper and lower teeth, probably deciduous molars.

Hypodigm: Syntypes only.

Horizon and Locality: Casamayor, "Colhué-Huapí Norte," Patagonia.

Diagnosis: Not well comparable with other known species; no truly distinctive characters recognizable.

As noted above (generic synonymy), this species (and genus) is probably based on milk teeth. They are so poorly preserved that accurate measurements are impossible. The four milk teeth occupy about 23.5 mm., about the same as in *N. murinus*. The species could very well be synonymous, but the material is inadequate for a definitive conclusion.

Notostylops spp. div. s. innom.

Under this heading are discussed various lots of specimens from scattered localities, not surely referable to any named species and inadequate for certain definition. They are listed by localities.

A. Near Kilometer 145 of the Comodoro-Sarmiento Railway. Two specimens have the dimensions given in table 68.

These are almost certainly *N. murinus*. The only apparently significant difference, length of M$_2$, may well be due to wear and imperfect preservation.

B. Embayment of Bahía Solano.

Two specimens from this region have the dimensions given in table 69.

No significant difference from either *N. murinus* or *N. pendens* is shown, but the agreement with the latter is a little better. The specimens are inadequate for determination.

Also at Bahía Solano and near the same level was found a partial maxilla, with the tooth dimensions as given in table 70.

The small size is in agreement with the lower jaws from the same area and suggests the presence of a distinctive local or temporal race, but the possible distinctions are not sufficiently clear-cut for definition. These might possibly be robust specimens of *N. appressus*, but the agreement is not good and probabilities are against this.

C. Cañadón Lagarto. This cañadón is in the slope of the Pampa Castillo and runs into the Río Chico. The locality is east of that called Colhué-Huapí, south of Cañadón Vaca, and about equidistant from the two. In the Feruglio Collection are four measurable specimens from here (see table 71).

The specimens all happen to be a little be-

TABLE 68

COMPARISONS OF *Notostylops* SP.

	P_4			M_2		M_3	
	L	W		L	W	L	W
A.M.N.H. No. 28581	7.8	6.5		8.5	6.7	12.2	6.3
C.N.H.M. field no. 184Y	7.7	5.9		—	—	—	—
d/σ comparison with *N. murinus*	0 − .2	+ .5 −1.0		−3.0	+1.0	− .3	0

TABLE 69

COMPARISONS OF *Notostylops* SP.

	P_4		M_1			M_3		LP_4/LM_1
	L	W	L	W		L	W	
A.M.N.H. No. 28609	—	—	—	—		11.6	6.2	—
A.M.N.H. No. 28612	7.0	5.6	7.9	5.7		—	—	.89
d/σ comparison with *N. pendens*	− .7	+ .4	− .6	+ .3		−2.5	− .5	(not significant)
Same with *N. murinus*	−1.8	−1.7	−1.9	− .9		−1.4	− .3	−.2

TABLE 70

COMPARISONS OF *Notostylops* SP.

	P^4		M^1		M^2		LM^1/LM^2
	L	W	L	W	L	W	
A.M.N.H. No. 28901	7.5	10.6	8.3	11.1	9.0	12.1	.92
d/σ comparison with *N. murinus*	−1.7	−2.1	−2.3	−1.7	−3.1	− .4	−.3

TABLE 71

COMPARISONS OF *Notostylops* SP.

	P_3		P_4		M_1		M_3	
	L	W	L	W	L	W	L	W
Feruglio Collection	7.0	5.6	—	—	8.3	6.2	—	—
	—	—	7.6	5.7	8.3	5.5	—	—
	—	—	7.2	5.9	8.0	5.9	—	—
	—	—	—	—	—	—	11.2	5.4
d/σ comparison with *N. murinus*	− .5	+ .3			−1.0	+ .2		
			− .4	−1.5	−1.0	−1.3		
			−1.3	−1.0	−1.7	− .4		
							−2.0	−2.3

TABLE 72

Comparisons of *Notostylops* sp.

	P_2		P_3		P_4		M_1		M_2		M_3		LM_1/LM_2
	L	W	L	W	L	W	L	W	L	W	L	W	
C.N.H.M. No. P 13447	4.6	3.6	7.1	5.9	8.2	6.9	8.8	6.6	9.5	6.7	12.5	6.7	.93
C.N.H.M. No. P 13445	—	—	7.0	5.5	—	—	—	—	—	—	13.0	6.5	—

somewhat flattened, and not like that of *N. pendens*. The grooves on M^3 pinch off part of the internal slope of the protocone so that it almost forms a separate cusp, although this may be an individual aberration. The specimen is too close to *N. murinus* for its taxonomic separation to be attempted without further material, but a distinct race or subspecies is probably indicated.

E. Rinconada de Lopez. This locality is about 120 kilometers (about 75 miles) north of the type locality of *N. murinus*. In the American Museum there are numerous fragments of *Notostylops* from here, but they are poorly preserved. As a result of breakage, extreme wear, or the impossibility of determining homologies with complete certainty, only the measurements given in table 74 are available.

TABLE 74

COMPARISONS OF *Notostylops* SP.

	P_4		M_1	
	L	W	L	W
A.M.N.H. specimens from Rinconada de Lopez	7.8 —	6.1 —	8.9 8.5	— 5.4
d/σ comparison with *N. murinus*	0	−.5	+.5 −.5	— −1.6

No distinction from *N. murinus* is demonstrated.

HOMALOSTYLOPS AMEGHINO, 1901

Homalostylops AMEGHINO, 1901, p. 422; 1906, p. 468; SCHLOSSER, 1923, p. 615.

Acrostylops AMEGHINO, 1901, p. 421; 1906, p. 468.

TYPE: *Homalostylops rigeo* Ameghino.

TYPE OF SYNONYM: *Acrostylops pungiunculus* Ameghino.

DISTRIBUTION: Casamayor, Patagonia.

DIAGNOSIS: Closely similar to *Notostylops* but tooth series nearly or quite closed and rather evenly transitional. Species small. External folds and cingula of upper cheek teeth unusually strong.

Acrostylops was defined as lacking the canine but having P_1, the symphysis short, incisors nearly vertical, diastema very short, and size small. The type of the genotype is a crushed specimen and the characters of the symphysis and incisors, so far as unlike those of either *Notostylops* or *Homalostylops*, seem surely the result of deformation. The absence of the canine cannot be certainly affirmed, and would not necessarily be a generic character anyway as it is variable in *Notostylops* and probably also in *Homalostylops*. The genotype cannot be distinguished specifically from the genotype of *Homalostylops*.

The characters by which *Homalostylops* is distinguished from *Notostylops* are not, in themselves, of sure generic value. Except for its smaller size, not in itself generic, every character of *Homalostylops parvus* is closely approached by one or another variant or species of *Notostylops*. The genotypes are, however, strongly distinct species, and it seems probable that the genera are also separable. Even though the definition is unsatisfactory at present, *Homalostylops* may well be given the benefit of the doubt and retained.

As far as it is known, the dentition is so similar to that of *Notostylops* that no detailed description is necessary.

Homalostylops parvus (Ameghino, 1897), new combination

Plate 18, figures 7–10; plate 19, figures 1–9; text figures 76, 77

Notostylops parvus AMEGHINO, 1897a, p. 490; 1898, p. 175.

Homalostylops rigeo AMEGHINO, 1901, p. 422.

Acrostylops pungiunculus AMEGHINO, 1901, p. 421.

Entelostylops incolumis AMEGHINO, 1901, p. 425; 1904b, p. 208, figs. 278, 531.

TYPES: Four specimens are labeled as of this species in the Ameghino Collection, and it is not clear which, or how many, of them entered into the type description. The material included under the following two numbers almost surely did, and is collectively made lectotype. Although preserved as two separate lots, these probably are all parts of one individual, and certainly belong to one species:

M.A.C.N. No. 10527, right P^2–M^3 and left P^3–M^3

M.A.C.N. No. 10534, left P_3–M_3

TYPES OF SYNONYMS: *Homalostylops rigeo:* M.A.C.N. No. 10473 partial lower jaw with left P_3–M_2 and right P_{3-4}.

Acrostylops pungiunculus: M.A.C.N. No. 10468, partial lower jaw with right I_3 and P_1–M_3 and left I_2 and P_{3-4}.

Entelostylops incolumis: M.A.C.N. No. 10495, four isolated upper molars from two or more individuals. The original of Ameghino, 1904b, figures 278 and 531, is lectotype.

HYPODIGM: Types, as above, and the following:

M.A.C.N. No. 10520, left P^1–M^2
M.A.C.N. No. 10525, lower jaw with right P_2–M_1, M_3, and left M_1–M_2. (Some isolated teeth under this same number may not be of this species)
M.A.C.N. No. 10475, lower jaw with left P_1–M_1
M.A.C.N. No. 10470, lower jaw with left M_1–M_3
M.A.C.N. No. 10467, lower jaw with right and left P_1, P_3–M_3
A.M.N.H. No. 28599, lower jaw with right I_1 and left I_1, P_{1-2}, dm_{3-4}, M_{1-3}
A.M.N.H. No. 28959, left P^2–M^3
A.M.N.H. No. 28962, right P_4–M_2
A.M.N.H. No. 28587, right P_4–M_2
A.M.N.H. No. 28597, left P_4–M_2
A.M.N.H. No. 28743, M_{2-3}

HORIZON AND LOCALITY: Types and most other specimens from south of Lago Colhué-Huapí; referred specimens from same locality and Cañadón Vaca, Casamayor, Patagonia.

DIAGNOSIS: Size small. Sole definitely recognized species of genus.

The genus *Homalostylops* was distinguished by Ameghino as having the complete dental formula, and by inference this was the distinction between *H. rigeo* and *N. parvus*, but in fact the known specimens of the latter also indicate a complete dental formula as far as the parts are preserved. The sizes of the types of the two are closely similar, the morphology is indistinguishable, and the type localities are the same. The two are certainly synonymous, and of course the genotype must take the older name, *parvus*.

FIG. 76. *Homalostylops parvus* Ameghino. A.M.N.H. No. 28959, left P^2–M^3 (and roots of P^2). Crown view. ×2.

Given the fact that the supposed generic characters of *Acrostylops* are not valid, it follows that *A. pungiunculus* is indistinguishable from *parvus*, for there are no essential differences other than those mentioned in the discussion of the genus.

Entelostylops incolumis was based on several isolated upper teeth. They were not compared with "*Notostylops parvus*" or "*Homalostylops rigeo*," since they were originally referred to a different family. They agree in every respect with *H. parvus* and surely belong to that species.

Starting with a preliminary misapprehension in the family and generic sorting of his specimens, Ameghino, it thus appears, described the same species separately in four different genera.

Most of the known specimens, and all the types of this and synonymous species, are from the barranca south of Lago Colhué-Huapí.[1] The species is associated throughout this area with *Notostylops murinus*, which it rather closely resembles save for its much smaller size, more continuous dental series, and a few minor details.

The species has not been certainly identified elsewhere except at Cañadón Vaca, where a small form inseparable from this is associated with *Notostylops pendens*. These specimens include a partial jaw with P_3–M_2 and a number of isolated teeth, of which only the M_3's can be identified surely enough to be used in comparison. The jaw fragment is very close to those from Colhué-Huapí. The M_3's average noticeably shorter, but the difference is not shown by the few available specimens to be statistically significant. While the Cañadón Vaca specimens are necessarily and properly referred to *H. parvus*, there is a decided possibility that they may represent a different subspecies or race. They are omitted from the combined figures in table 75, and their dimensions are listed sepa-

[1] Their exact localities extend along the scarp for about 22 kilometers, but this is essentially a unit although the exposures are not completely continuous. There appear, from these and from associated specimens, to be no significant differences in age. One referred specimen in the Ameghino Collection has no locality label but is almost surely from here.

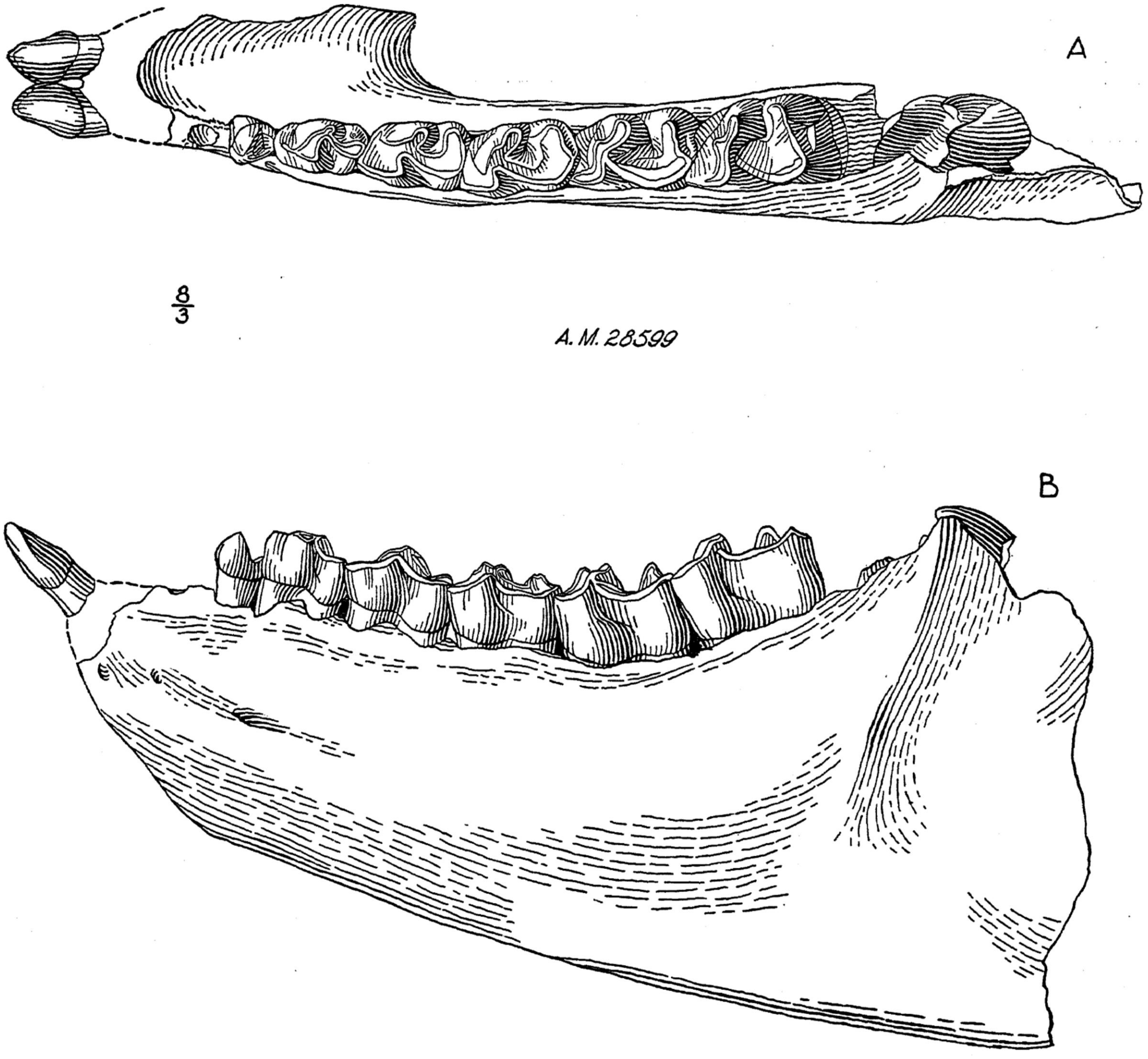

FIG. 77. *Homalostylops parvus* Ameghino. A.M.N.H. No. 28599, partial mandible with left and right I_1, and left P_{1-2}, dm_{3-4}, and M_{1-3}. A. Crown view. B. Lateral view. ×8/3.

rately, in order to provide relatively pure locality samples for future comparisons. Even combining the Colhué-Huapí and Cañadón Vaca specimens, the variation indicated does not pass probable specific limits, as shown by these combined figures for M_3 (table 75), the tooth in which the greatest difference is indicated.[1]

TABLE 75

Homalostylops parvus

	M_3	
	L	W
N	9	8
OR	7.2 –9.1	4.3 –4.8
M	8.1 ± .2	4.4 ± .06
σ	.54 ± .12	.16 ± .04
V	6.6 ±1.6	3.7 ± .9

In the known specimens, P_1^1 were always present. There are few really trustworthy

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[1] It is interesting that although Ameghino placed his specimens in two families, four genera, and four species, the most aberrant specimen in his collection, now M.A.-C.N. No. 10525, was referred by him to the original species, *parvus*. Omission of this specimen would reduce the variability of some dimensions markedly, but I think Ameghino's reference was correct.

TABLE 76

COLHUÉ-HUAPÍ SPECIMENS OF *Homalostylops parvus*

	N	OR	M	σ	V
P_1					
L	2	2.2	2.2	—	—
W	2	1.6	1.6	—	—
P_2					
L	3	4.0 –4.7	4.3	$[\Sigma(d^2) = .29]$	—
W	3	2.6 –3.2	2.9	$[\Sigma(d^2) = .19]$	—
P_3					
L	7	4.6 –5.5	5.2 ± .1	.28 ± .07	5.3 ± 1.4
W	7	3.7 –4.4	3.9 ± .1	.22 ± .06	5.5 ± 1.5
P_4					
L	8	4.9 –6.5	6.0 ± .2	.49 ± .12	8.2 ± 2.1
W	8	4.2 –5.1	4.6 ± .1	.25 ± .06	5.4 ± 1.3
M^1					
L	7	5.8 –7.2	6.5 ± .2	.41 ± .11	6.2 ± 1.7
W	8	4.0– 4.9	4.4 ± .1	.28 ± .07	6.4 ± 1.6
M_2					
L	6	6.3 –6.8	6.7 ± .1	.21 ± .06	3.1 ± .9
W	6	4.4 –5.0	4.6 ± .1	.20 ± .06	4.4 ± 1.3
M_3					
L	5	7.8 –9.1	8.4	$[\Sigma(d^2) = .94]$	—
W	4	4.3 –4.5	4.4	$[\Sigma(d^2) = .03]$	—
LP_4/LM_1	6	.88–1.03	.93 ± .02	.051 ± .015	—
LM_1/LM_2	5	.91– .99	.94	$[\Sigma(d^2) = .0094]$	—

TABLE 77

CAÑADÓN VACA SPECIMENS OF *Homalostylops parvus*

	P_4		M_1		M_2			M_3		LP_4/LM_1
	L	W	L	W	L	W		L	W	
A.M.N.H. No. 28587	5.3	4.1	5.7	4.4	6.5	4.8		—		.88
Other specimens								8.0	4.4	
								7.2	4.3	
								7.8	4.8	
								7.7	4.5	

data on the incisors or canines, but they were probably normally present.

All the specimens of P^4 show a groove on the internal face, as in *N. murinus* and not as in *N. pendens.*

Homalostylops interlissus Ameghino, 1901, nomen vanum

Plate 18, figure 11

Homalostylops interlissus AMEGHINO, 1901, p. 422.

TYPE: M.A.C.N. No. 10488. Two fragmentary symphyses without teeth.

HORIZON AND LOCALITY: Casamayor, "Colhué-Huapí Norte."

DIAGNOSIS: Indefinable.

This was placed in *Homalostylops* because the alveoli indicate, with some probability, the presence of I_3, C_1, and P_1. As shown above, this does not exclude possible reference to *Notostylops*. The size is greater than that of *H. parvus*, and probably about that of *N. murinus*. This might be a synonym of *N. murinus*, but the specimens are unrecognizable as to either genus or species, and the

TABLE 78

AVAILABLE UPPER JAWS OF *Homalostylops parvus*, ALL FROM COLHUÉ-HUAPÍ

	P^1		P^2		P^3		P^4		M^1		M^2		M^3		LP^4/LM^1	LM^1/LM^2	P^2–M^3	P^{2-4}/M^{1-3}
	L	W	L	W	L	W	L	W	L	W	L	W	L	W				
M.A.C.N. No. 10527	—	—	4.1	5.0	5.2	6.6	5.8	7.6	6.4	8.7	7.0	9.1	6.8	8.0	.91	.91	31.0	—
M.A.C.N. No. 10520	2.8	2.8	4.1	5.2	5.6	7.3	5.8	8.4	6.6	9.0	7.5	9.5	—	—	.88	.88	—	—
A.M.N.H. No. 28959	—	—	4.2	5.6	5.3	7.7	5.4	8.6	5.6	8.7	7.1	9.7	6.2	8.6	.96	.79	30.3	.76

name is, and probably must forever remain, a *nomen vanum.*

EDVARDOTROUESSARTIA AMEGHINO, 1901

Edvardotrouessartia AMEGHINO, 1901, p. 401; 1904b, p. 249; 1906, p. 468.

TYPE: *Edvardotrouessartia sola.*

DISTRIBUTION: Casamayor, Patagonia.

DIAGNOSIS: Lower dental series complete (with the possible exception of I_1), closed, crowded. Lower canine larger than I_3 or P_1. Premolars relatively simple. Cheek teeth somewhat higher crowned than in *Notostylops* or *Homalostylops.* Jaw deep and massive. Species much larger than any other referred to the family.

The discovery that *Edvardotrouessartia* is a notostylopid was one of the most completely unexpected results of this study. Its relatively enormous size and the rather high, massive, simple teeth, crowded together in continuous series, make it look so unlike *Notostylops* that the possibility of a family relationship simply did not occur to Ameghino, nor did it occur to me until this study was almost completed. Once this possibility was thought of, the reality of the relationship seemed almost obvious.[1]

The genus was originally based on a lower jaw with P_2–M_3 and was referred to the astrapothere group "Albertogaudryidae." The specimen is fundamentally unlike any astrapothere in the small size of the canine and unlike Casamayoran astrapotheres in the transverse entoconid column. The reasons for this reference were not clearly given, but I suspect that it was based on mistaking an alveolus or root fragment of I_2 for that of a canine, and probably also on the simple, subconical anterior premolars and on the relatively large size of the jaw. Three years later, Ameghino (1904b) transferred the genus to the Isotemnidae, without any comment on or explanation of the change. At that time he did not mention the type lower jaw (indeed he never mentioned this again, as far as I have found), but he discussed and figured two upper teeth under the name of this genus and species. Upper teeth had not been mentioned in the original description, and these specimens

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[1] This is a rather interesting example of a psychological factor's impeding scientific research. With the materials available, it would hardly have occurred to anyone to compare *Edvardotrouessartia* with *Notostylops* except as a desperate last recourse. I had, in fact, gone over the genus thoroughly twice and was doing so for a third time, still baffled by its differences from the supposedly allied isotemnids, when the idea that it might be a notostylopid suddenly came to me with the force of a startling inspiration. I then immediately saw that this is its correct place, and now find it rather hard to understand why I did not see this at once and why Ameghino did not see it long before. This example helps to explain most of Ameghino's references of species and genera to wrong groups: he started the comparison with certain genera on some superficial basis, such as size in the case of *Edvardotrouessartia*, and this so firmly fixed the species or genus in a certain psychological setting that any other became difficult or virtually impossible. This is all the more likely, and of course completely excusable, in dealing with such a very large fauna with so many diverse but confusingly similar families and genera. It is quite likely that future students will still find examples of this failing in the present revision.

were clearly found or identified at a later date and were not associated with the type. Ameghino's basis for the reference is unknown, but it was perhaps merely that these upper teeth are of approximately the right size to occlude with the type lower teeth. The referred upper teeth, which have been lost or mislaid since 1904, seem from the figures then published to belong to a true isotemnid; in fact they are probably of *Isotemnus* itself, and perhaps *I. primitivus*. It is virtually certain that they have nothing to do with *Edvardotrouessartia*.

The type lower jaw was photographed by Scott, and he published a lithograph made from his photograph (Scott, 1928a, pl. 35, fig. 2). He did not describe or discuss the specimen, but his figuring it in a comparative series of astrapotheres would seem to imply endorsement of Ameghino's first opinion that it is an astrapothere. This opinion, quickly abandoned by Ameghino himself, is certainly incorrect, as noted above. Romer (1945) listed *Edvardotrouessartia* as a homalodotheriid, without discussion. This was doubtless based on Ameghino's reference of the genus to the Isotemnidae. As far as I know, no one but Ameghino, Scott, and Romer has so much as mentioned the genus.

The type lower jaw has been lost or mislaid and is now known only by Ameghino's brief, unillustrated diagnosis, by Scott's photograph (a print of which was kindly supplied for my use and is reproduced here), and by the lithograph based on the latter. Fortunately we found another specimen, A.M.N.H. No. 28654, which can be positively identified as *E. sola* and which makes it possible to redefine the genus and to determine its affinities. Scott's photograph permits determination of this new specimen, but by itself the photograph could not possibly have led to a correct determination of affinities in spite of the fact that the type specimen was much more nearly complete than ours. Without Scott's photograph and with only Ameghino's diagnosis it would have been entirely impossible to identify our specimen as *Edvardotrouessartia* or as *E. sola*.

Our specimen includes a fragment of the symphysis, with the root of I_2 and alveoli for I_3–P_1 and with P_2 complete. The presence and size of I_1 cannot be surely determined on this specimen, but possible alveolar traces hint that it was present and small. I_2 was a large, procumbent, long-rooted tooth, a character typical of the Notostylopidae. I_3 was relatively very small, and its alveolus is crowded between the labial parts of the much larger alveoli for I_2 and C. The canine alveolus is oval in section and is smaller than that of I_2 but larger than the alveoli for I_3 and P_1. Ameghino (1901) spoke of the canine of the type as small and not triangular, a statement evidently made in comparison with astrapotheres. Scott's photograph suggests that it is unlikely that the canine alveolus was preserved in this specimen. It may have been broken between the time of Ameghino's description and that of Scott's photograph, but it seems probable that Ameghino's statement was based on a terminal portion of the root or alveolus of I_2 and that this natural error was involved in his first impression that the genus is an astrapothere.

P_1 is represented by a single small alveolus.

P_2 has two roots confluent at the base of the crown but long and diverging below. The base of the crown is almost circular, and the crown itself is a modified cone. An anterior superficial ridge from the crest divides below and passes into an anteroexternal cingulum, not passing around the outer face of the base, and an anterointernal cingulum continued across the inner face and into the heel. A stronger but curved and irregular posterior crest from the apex runs down to the single apex of the heel, which is very short and more like a posterior cingulum than a real talonid. From its apex a strong crest passes down and internally into the internal cingulum. This crest is irregularly cuspidate.

In Scott's photograph, P_3 is seen to have a talonid, still small but more normal than on P_2 and with a more definite external groove between it and the trigonid. The trigonid has, besides the main apex, a small anterior blade. The crown is broken on P_3 of our specimen, but it shows that both trigonid and talonid internal valleys are very poorly developed and near their respective ends of the tooth.

P_4 is well preserved in our specimen. The talonid is relatively small but has the usual crescentic crest, with a poorly differentiated, relatively marginal (posterior) entoconid. The trigonid has a strong, transverse, antero-

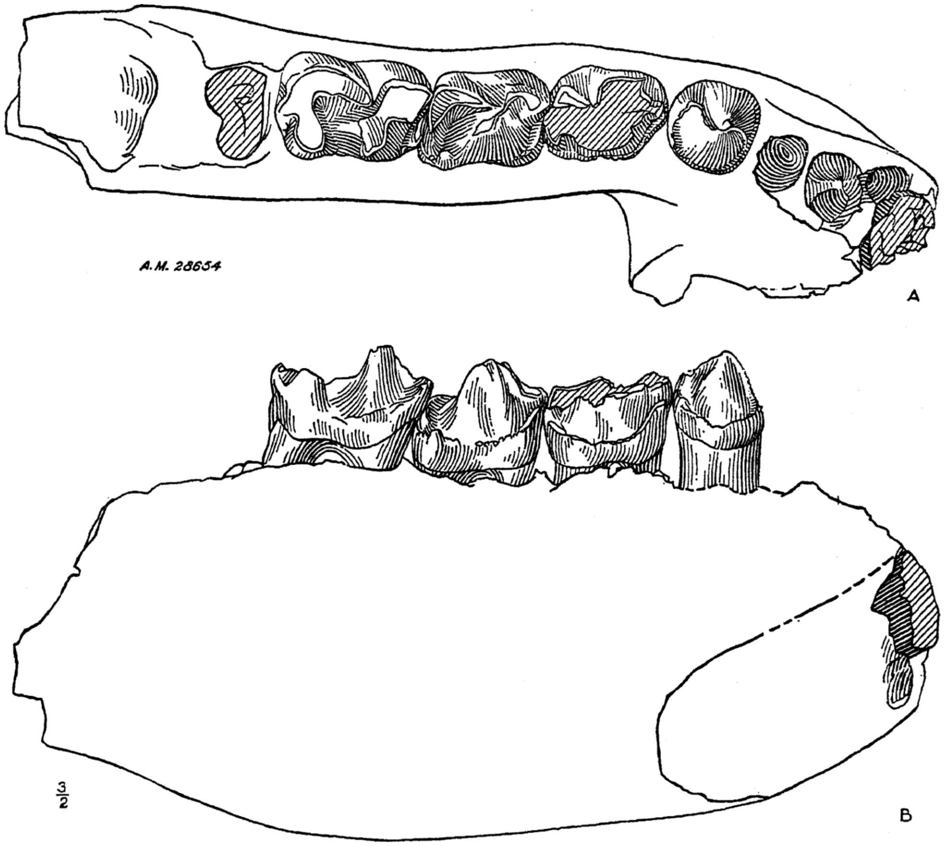

FIG. 78. *Edvardotrouessartia sola* Ameghino. A.M.N.H. No. 28654, partial lower jaw with left P_2–M_1 and alveoli of anterior teeth. The drawing is a composition from three fragments that belong to one individual but do not make actual contact, as explained in the text. P_2 and M_1 are reversed from the other ramus. The cross-hatched area on P_3 is broken, not worn. A. Crown view. B. Internal view. ×3/2.

external-posterointernal crest, highest in the middle, where it has a poorly differentiated cuspule similar to that at each end of the crest. A shorter crest extends almost directly anteriorly from the protoconid along the outer side of the tooth and ends in a distinct but poorly defined paraconid. There are no accessory crests or cuspules on the internal side of the trigonid. The basic structure of this whole tooth is typically notostylopid, and its details are unlike those of any known isotemnid.

M_1 may be briefly described as a much enlarged and slightly more hypsodont version of M_1 in *Notostylops*. Its pattern is that basic for all notoungulates, virtually devoid of any specialization or peculiarity within the group except for the notostylopid tendency to form a median cuspule on the trigonid crest. To the extent that isotemnids also have primitive notoungulate lower molars, there is a resemblance to that family, but *Edvardotrouessartia* lacks the one distinctive feature of the isotemnid lower molar, the presence of an accessory cuspule on or near the metaconid.

M_{2-3} are not preserved in our specimen. Ameghino remarks that there is a high, narrow, transversely elongate entoconid ("tubercule postérieur interne") on all three molars, but this is true of all Casamayoran (and most later) notoungulates. Scott's photograph shows only the outer sides of M_{2-3} and gives no helpful additional information except that the hypoconulid of M_3 seems to be fairly well differentiated.

In our specimen the symphysis is massive, its lower contour smoothly rounded, and the horizontal ramus is also stout. The photograph of the type suggests the same characters. In our specimen the lower border has an upward curve below M_2. This region is broken in the type, as shown in Scott's photograph.[1]

Edvardotrouessartia sola Ameghino, 1901

Plate 18, figure 12; text figure 78

Edvardotrouessartia sola Ameghino, 1901, p. 401; 1904b, p. 249, figs. 334, 388, 389 [these figures are not of the type and not of this genus or species]; Scott, 1928a, pl. 35, fig. 2 [this is the type].

Type: A right lower jaw with P_2–M_3, now lost or mislaid.

Hypodigm: A.M.N.H. No. 28654, partial lower jaw with right P_2 and M_1, left P_3–M_1 (P_3 and M_1 broken), and alveoli or root fragments of right I_1–P_1.[2] Also published data and Scott's photograph of the type.

Horizon and Locality: Casamayoran, Patagonia. No other data for type. A.M.N.H. No. 28654 is from Cañadón Vaca.

Diagnosis: Sole known species of genus. Measurements given below.

There is a batch of six isolated teeth in the Ameghino Collection, M.A.C.N. No. 10599, labeled as of this species, but it includes neither the type nor either of the specimens erroneously referred to the species in 1904. These teeth do not seem to be of *Edvardotrouessartia* and need not be considered here. Perhaps the label was misplaced.

Ameghino (1901) gave the length P_2–M_2 as 74 mm. in the type. This is apparently a misprint for P_2–M_3. Neither measurement can be made on our specimen, but I estimate that on it P_2–M_2 would be not over 60 mm. and P_2–M_3 would be about 75 mm. Scott's photograph and lithograph of the type are said to be "slightly less than natural size," and in them length P_2–M_2 is about 55 mm. and P_2–M_3 about 70 mm., consistent with the inference that the original measurements were about 60, or slightly less, and 75, respectively.

Ameghino gave the depth of the ramus below M_1 as 38 mm., possibly an estimate, because the lower border is broken here, as shown in Scott's photograph. This dimension has been somewhat reduced by crushing in our specimen and is 33 mm. as the specimen is preserved. It was probably about 35 mm. or a little more before crushing. The tooth measurements of our specimen are given in table 79.

TABLE 79

Edvardotrouessartia sola

P_2		P_3		P_4		M_1	
L	W	L	W	L	W	L	W
7.4	7.5	9.9	8.9	10.7	8.6	13.1	9.6

OTRONIA Roth, 1901

Otronia Roth, 1901, p. 255; Simpson, 1936d, p. 76.

Othronia [error or invalid emendation], Ameghino, 1904a, vol. 58, p. 243 [as synonym of *Tychostylops*].

Type: *Otronia mühlbergi* Roth, 1901.

Distribution: Musters formation, Patagonia.

Diagnosis: An advanced notostylopid. P^1_1 absent and large diastemata present. P_2 very small, one-rooted; upper and lower premolar series short in comparison with the molars. Molar crowns higher than in *Notostylops*. Hypoconulid of M_3 projecting far posteriorly and distinguished from rest of talonid crescent. P^{3-4} strongly transverse, without internal sulci. Protocone and hypocone relatively well separated on M^2. Mandible shallow anteriorly and deep posteriorly.

Otronia is a relatively rare genus. There are three specimens in the Roth Collection, and Roth may have had some others (see below). We found only three isolated teeth, and I have not recognized any remains of the genus in the Ameghino Collection.

On the whole this genus is more progressive than is *Notostylops*. With the possible excep-

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[1] Ameghino gave a measurement of the depth of the ramus under M_1, which could not be taken on the specimen as photographed by Scott. This may have been an estimate, or the specimen may have been broken after it was measured.

[2] This specimen consists of three separate fragments, no two of which make actual contact. It is, however, certain that all belong to one individual.

tion of I$^3_3$, the dental reduction is as great as in the extreme variants of *Notostylops*. The height of cheek tooth crowns can be exactly measured on only one specimen, but was greater than in *Notostylops*. The reduction of the premolars with respect to the molars also appears to be a specialization, although it is opposite to the sequence suggested by the structural series *Notostylops pendens-N. murinus-N. pigafettai*. These species have the value of P$^{2-4}$/M$^{1-3}$ .59, .73, and .93, respectively. It is not exactly determinable in *Otronia mühlbergi* but is about .55. The absence of sulci on P$^{3-4}$ is also unlike *N. murinus* or *N. pigafettai* and is probably primitive. The lack of reduction of M^3 also suggests a different line from those species of *Notostylops*, as do the relatively well-developed I^3 and the possible presence of a vestigial I$_3$, this latter very doubtful, however. M^3 is evidently more specialized in the crochet in *Otronia*, and *O. mühlbergi* is much larger than any species of *Notostylops*. *Otronia* could well be derived from such a form as *Notostylops pendens*, with pronounced specialization which, however, was along a different line from *N. murinus* and *N. pigafettai*. The somewhat more hypsodont teeth and the differentiated hypoconulid of M$_3$ are resemblances to *Edvardotrouessartia*, but that genus is otherwise quite unlike *Otronia* and almost certainly not ancestral to the latter.

As the last of the known notostylopids, *Otronia* is of great interest. Its very distinctive and relatively specialized character helps to confirm the evidence that it was, indeed, derived from the Musters.

Otronia mühlbergi Roth, 1901

Plate 19, figures 10–12; text figure 79

Otronia mühlbergi Roth, 1901, p. 255.
Otronia mühlbergi, Simpson, 1936d, p. 76.

Type: Not surely identified. Roth's description involves a lower jaw with the horizontal ramus from the incisive alveoli through M$_3$ (at least) and with the crown of M$_1$ (at least), and mentions upper molars without further specification. M.L.P. No. 12-1731, a right lower jaw with I$_2$, P$_4$, and M$_{2-3}$, may possibly be the type lower jaw, but only if "M$_1$" in Roth's description is a misprint. In any case it was identified by Roth and is an important specimen that may be designated as neotype, if it is not the type.

Hypodigm: Type or neotype, as above, and the following:

M.L.P. No. 12-1730, partial skull
M.L.P. No. 12-2283, left premaxilla with I$^{1-3}$
A.M.N.H. Nos. 29484–6, three isolated molars

Horizon and Locality: "Cretáceo superior de Lago Musters," probably Musters formation of the Cerro del Humo, Chubut. American Museum specimens from Cerro del Humo.

Diagnosis: Sole species referred to genus. Measurements below.

In addition to the neotype, or possibly type, listed above, there is in the Roth Collection a partial skull, M.L.P. No. 12-1730, with left P^2, P^4, and M$^{2-3}$, and right P$^{3-4}$ and M$^{2-3}$. It is possible that Roth's remark on upper molars in the type description[1] was based on this specimen, but this is improbable. The specimen (as I saw it) was not labeled by or for Roth, and it would be extraordinary if Roth had before him this fine specimen and said nothing more about it. The specimen is now confidently referred to this species, but it is not the same individual as the lower jaw mentioned above. There is also a left premaxilla with I$^{1-3}$, M.L.P. No. 12-2283, which was not classified by Roth but probably belongs here. No other specimens were seen in the collection, and the basis for Roth's measurements of M$_1$ (or for his mention of upper molars) is not established. All three specimens bear the same data as to provenience.

I$^{1-3}$ are all strongly procumbent. I^1 is much enlarged and has the root somewhat compressed transversely but the spatulate or chisel-like enameled crown compressed labiolingually, convex on the outer side and excavated on the inner. I$^{2-3}$ are both well developed, subequal, about half the size of I^1 and with less spatulate crown.

The canine was probably absent. This is not certainly established, but there was a diastema in the upper dentition. P^1 is absent.

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[1] He says only that "En los molares superiores se parece en la forma más al *Archaeopithecus Rogeri* que al *Notostylops*," which is not strictly true, of this specimen at least.

P^2, deeply worn in the only specimen showing it, is a very small oval or subtriangular tooth. P^{3-4}, also too worn for the coronal details to be made out, are strongly transverse and resemble those of the simplest type in *Notostylops*, small and with no internal sulci. M^1 is unknown. M^2 has about the same outline as in *Notostylops* but evidently had a higher crown and a deeper fossa, which has not been obliterated by advanced wear. The protocone and hypocone, although united basally, are more separate than is usual in *Notostylops*. The hypocone is much smaller than the protocone. M^3 is large and subquadrate. The metaloph region is reduced, but the hypocone is nearly as internal as the protocone.

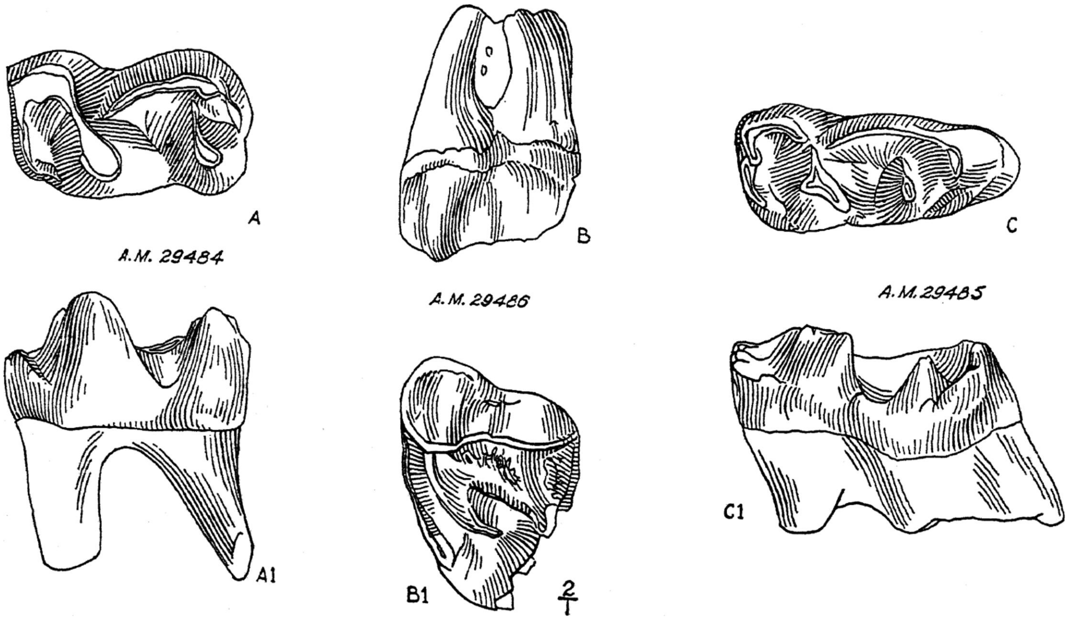

FIG. 79. *Otronia mühlbergi* Roth. Three isolated molars. A. A.M.N.H. No. 29484, right M_2. Crown view. A1. Same. Internal view. B. A.M.N.H. No. 29486, left M^3, with posterointernal part broken. External view. B1. Same. Crown view. C. A.M.N.H. No. 29485, right M_3. Crown view. C1. Same. Internal view. All ×2.

A.M.N.H. No. 29486, from the Cerro del Humo, is an isolated, somewhat broken left M^3 apparently of this species and of interest as being less worn than Roth's specimen. The outer face has higher relief than in *Notostylops pendens* or *N. murinus*, especially in the prominence of the paracone fold and the posterior swelling of its base, a peculiarity perhaps in part individual. The most important feature is that the coronal enamel was evidently thin, and the crochet region is occupied by an irregular mass clearly papillate when unworn and wearing into a surface with numerous very small folds and lakes, the whole reaching both protoloph and ectoloph in the stage of wear here presented. In *Notostylops* the crochet is papillate and is sometimes a continuous crest and sometimes a simple linear series of small cuspules. The condition in *Otronia* is evidently a specialization in which this papillate structure has lost its purely linear arrangement and has expanded into an irregular mass. This may, of course, have had a more crested apex when unworn. The enamel of the paracone apex is barely worn through, and the height of the enamel on the ectoloph at this point divided by the ectoloph length is .77, while in an analogously worn M^3 of *Notostylops pendens* it is .61, confirming the more hypsodont nature of *Otronia*. The posterointernal corner of the tooth is broken, and the rest is closely similar to *Notostylops* except as already noted.

I_1 appears to have been absent, but this may be caused only by imperfect preserva-

TABLE 80

Otronia mühlbergi, M.L.P. No. 12-1730

	P^2		P^3		P^4			M^2		M^3	
	L	W	L	W	L	W		L	W	L	W
Right side	—	—	7.6	10.7	8.8	4.4		12.2	16.2	12.7	16.9
Left side	6.0	6.9	—	—	9.0	4.0		12.5	17.0	12.7	16.6

tion. I_2 is enlarged and is similar to that of *Notostylops*. There is an embayment on the posterior side of the alveolus of I_2 that suggests an alveolus for a vestigial I_3. This is uncertain, however, and if ever present the tooth was probably lost before death. The lower canine and P_1 are absent. From their alveoli, P_2 was a very small, single-rooted tooth, and P_3 was somewhat larger. P_4, of which the crown is preserved, is relatively shorter, broader, and higher than in *Notostylops* but otherwise similar. The worn M_{2-3} of the neotype also resemble *Notostylops* except for the higher crowns, but M_3 is somewhat more elongate and with the hypoconulid more distinct.

A.M.N.H. No. 29484 is a less worn isolated right M_2 from the Cerro del Humo, probably of this species. It is larger and higher than in *Notostylops* and also has the anterior trigonid crest better developed. A.M.N.H. No. 29485, from the same horizon and locality, is a nearly unworn isolated right M_3 which also has the anterior trigonid wing stronger than in *Notostylops*, and here the main trigonid crest is more oblique. The entoconid is more purely transverse, without the tendency usual in *Notostylops* to expand along the inner margin and it is farther removed from the hypoconulid, which projects, as already noted, and tends to form a vague third lobe. Enamel height below the protoconid divided by the basal length of the tooth is .55, while in a comparable specimen of *Notostylops murinus* it is .49.

The skull fragment is not very characteristic beyond showing a general resemblance to *Notostylops*. The zygomatic roots are slightly more posterior, mostly opposite M^{2-3}. The palate and choanae may be relatively narrower and the whole skull somewhat more elongate, but this is uncertain.

As Roth pointed out, the marked increase in depth of the horizontal ramus from front to back is distinctive, but the difference from *Notostylops* is not great. The symphysis extends to the posterior end of P_2. There are mental foramina beneath the diastema and M_1.

Measurements are given in tables 80 to 82. The measurements of the upper teeth of the two sides were taken at the same time in the same way and the differences shown are real, again emphasizing the valueless nature of species based on small differences of size and proportion between single specimens.

TABLE 81

Otronia mühlbergi, M.L.P. No. 12-1731

Length of diastema (between alveoli)	8
Approximate length P_2–M_3	66
Maximum diameter of crown of I_2	7

TABLE 82

Otronia mühlbergi, M.L.P. No. 12-1731

P_4		M_2		M_3	
L	W	L	W	L	W
9.5	7.2	14.0	9.7	18.2	9.0

?NOTOSTYLOPIDAE INCERTAE SEDIS

Here will be described the Río Chico forms that may, very doubtfully, represent the notostylopids in that early formation.

SEUDENIUS SIMPSON, 1935

Seudenius SIMPSON, 1935a, p. 14.

TYPE: *Seudenius cteronc* Simpson.

DISTRIBUTION: Río Chico formation, Patagonia.

DIAGNOSIS: A primitive notoungulate with extremely low-crowned teeth. P^{3-4} very short and wide, P^3 with convex outer wall and small, separate, parastyle fold. Protocone of P^4 attached to protoloph but not to metaloph. Small posterointernal cingulum but no hypocone on P^4. M^1 quadrate, with fairly prominent metacone fold and slightly basined external cingulum between this and paracone fold. M^2 trapezoidal, metacone fold absent or very weak, external cingulum distinct, hypocone small and not strongly united to protocone. Valleys of P^3–M^2 not forming closed fossettes, or these obliterated immediately by wear.

There are three specimens of this peculiar genus in the collection, but all are very imperfect. They show that the genus is very distinctive, but do not permit any close determination of affinities. There are resemblances to three different families (and suborders), but in no case is the resemblance close enough to demonstrate special relationship. There is some resemblance to the most primitive isotemnids, such as *Maxschlosseria*,[1] but the simpler premolars, very low crowns, and absence or very early obliteration of closed fossettes are distinctly non-isotemnid characters. There is also some resemblance to the larger henricosborniids, but here, too, the very simple and transverse premolars are different from those of any known genus, as are also the ectoloph wall of M^1 and, especially, M^2, and also the proportions of protocone to hypocone on M^2. The species is also much larger than any known henricosborniid. Finally, there is a strong suggestion of the more primitive notostylopids, especially *Homalostylops parvus*, which is of about the same size, but the crowns are still lower in *Seudenius*, P^4 is still simpler than in *Homalostylops*, the lack of a protocone-metaloph connection on the premolars is distinctive, and there are other minor differences. Presumably *Seudenius* belongs to one of these three groups, perhaps with slightly greater probability to the last, but the discovery of completely unworn molars or of the anterior dentition is necessary to determine the question.

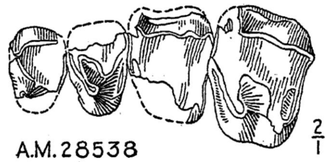

FIG. 80. *Seudenius cteronc* Simpson. Type, A.M.N.H. No. 28538, left P^3–M^2. Crown view. ×2. After Simpson.

Seudenius cteronc Simpson, 1935

Text figure 80

Seudenius cteronc SIMPSON, 1935a, p. 15, fig. 16.

TYPE: A.M.N.H. No. 28538. Part of left maxilla with P^3–M^2, somewhat broken.

HYPODIGM: Type and A.M.N.H. Nos. 28540 and 28550, badly eroded fragments of upper jaws.

HORIZON AND LOCALITY: Río Chico formation, Cañadón Hondo, Chubut, Argentina.

DIAGNOSIS: Sole known species of the genus. P^3 length 3.9 mm.; M^2 length 7.2, width 9.1 mm.

GEN. ET SP. INDET.

A.M.N.H. No. 28556, from the Río Chico beds in Cañadón Hondo, is an isolated upper molar, probably M^2, which is unlike any other known to me but is too doubtful in character to warrant more than a passing note. A little larger than *Henricosbornia lophodonta*, it differs in the flattened ectoloph posterior to the paracone fold, in the small and subordinate hypocone, and in the flattened inner wall without a definite groove between protocone and hypocone. These are all notostylopid characters. On the other hand its very small size (length 6.1, width 7.7 mm.), slight but continuous and oblique crochet basally united with the ectoloph, and relatively low crown are all unlike any known notostylopid. Comparison with *Seudenius cteronc* cannot be very detailed, but the crown is relatively a little higher, and the species is considerably smaller.

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[1] Which, however, is aberrant and not surely isotemnid.

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PLATES 2–19

NOTE: On all plates, unless otherwise credited, photographs of M.A.C.N. specimens were specially taken for this work by the staff of the Museo Argentino de Ciencias Naturales through the courtesy of Dr. M. Doello-Jurado. Photographs of M.L.P. specimens are from the files of the Museo de La Plata and were provided by that museum through Dr. Angel Cabrera.

PLATE 2

MARSUPIALIA

1–6. *Caroloameghinia mater* Ameghino.

1. Ameghino specimen (not found in collection) M^{1-4}. Crown view. Photograph by Scott. ×1, approximately.

2. Ameghino specimen (not found in collection), lower jaw with canine and P_1–M_2. External view. Photograph by Scott. ×1, approximately.

3. M.A.C.N. No. 10348, neotype, lower jaw with P_2–M_4. Somewhat oblique crown-internal view. Photograph by Scott. ×1, approximately.

4. A.M.N.H. No. 28441, isolated upper molar. Crown view. ×6.

5. Ameghino specimen (not identified in collection), M_{3-4}. Crown view. ×5. After Ameghino.

6. Type (not found in collection), lower jaw with C–M_4. External view. ×3. After Ameghino.

7. *Procladosictis anomala* Ameghino. Type, M.A.C.N. No. 10327, right P^3–M^3. External, crown, and internal views (the internal view inverted). ×3/2. After Ameghino.

8. *Polydolops thomasi thomasi* (Ameghino). Type, M.A.C.N. No. 10338, right upper jaw with P^3–M^3. Internal view. ×1.

9. *Polydolops thomasi crassus* (Ameghino). Type, M.A.C.N. No. 10349, left lower jaw with M_{1-4}. External view. ×1.

10. *Eudolops caroli-ameghinoi* (Ameghino). Type, M.A.C.N. No. 10334, left lower jaw with M_{1-4}. Internal view. ×1.

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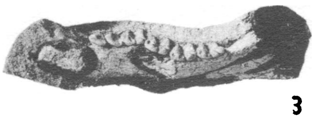

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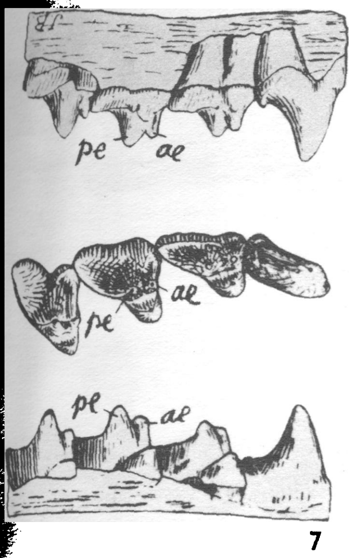

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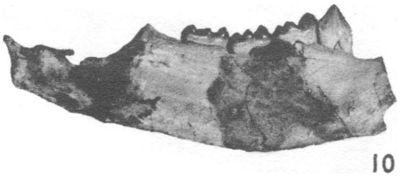

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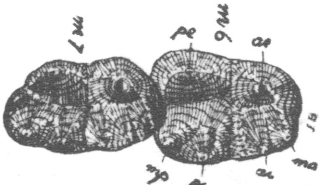

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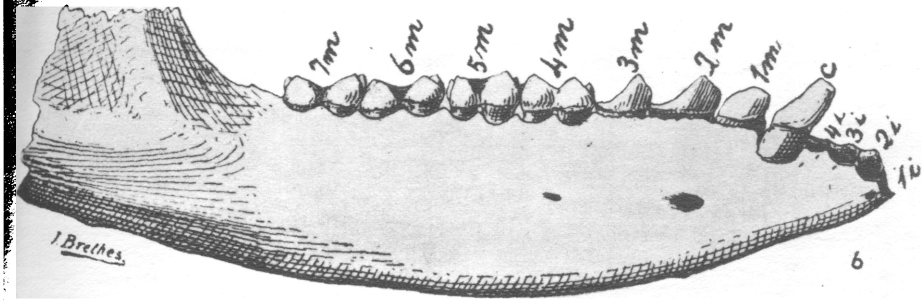

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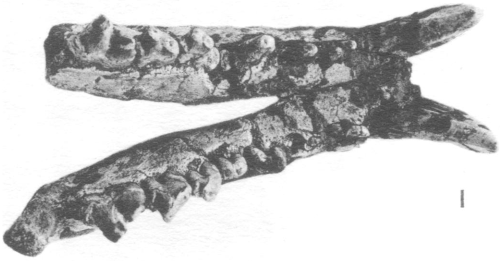
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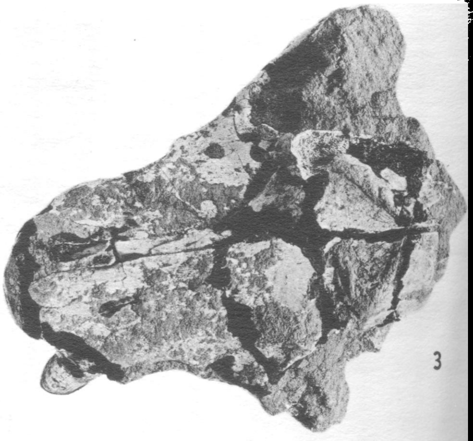
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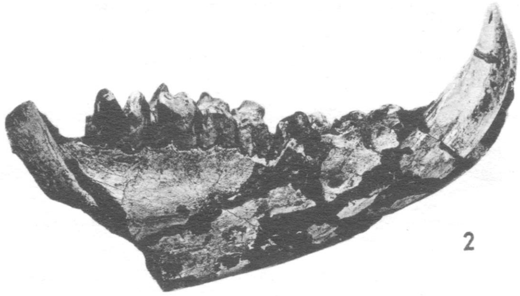
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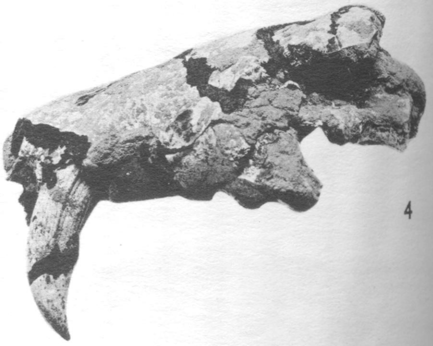
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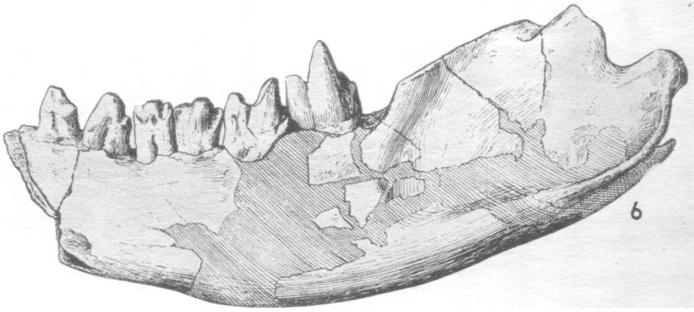
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PLATE 3

BORHYAENIDAE

1–5. *Arminiheringia auceta* Ameghino.

1. Type, M.A.C.N. No. 10970, lower jaw. Crown view. ×3/8.

2. Same. Right lateral view. ×3/8.

3. Type, M.A.C.N. No. 10972 (probably same individual as 10970), anterior part of skull. Dorsal view. ×3/8.

4. Same. Left lateral view. ×3/8.

5. Same. Palatal view. ×3/8.

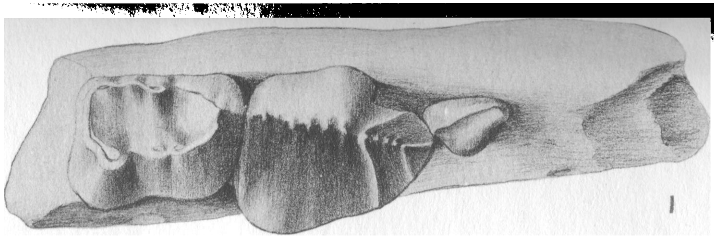
6. *Pharsophorus lacerans* Ameghino. M.L.P. No. 11-114 (type of *Plesiofelis schlosseri* Roth), left lower jaw with P_2–M_3. External view. ×1/2. After Cabrera.

7. *Pharsophorus cretaceus* (Roth). Type, M.L.P. (catalogue number not given), jaw fragment with left M_4. External view. ×1/2. After Cabrera.

PLATE 4

Polydolops thomasi AMEGHINO

1. *Polydolops thomasi thomasi* (Ameghino). A.M.N.H. No. 28444, right lower jaw with P_3–M_2. Crown view. ×6.
2. Same. External view. ×6.
3. *Polydolops thomasi mara* Simpson. Type, A.M.N.H. No. 28921, left lower jaw with M_{1-3}. Crown view. ×9/2.
4. Same. External view. ×9/2.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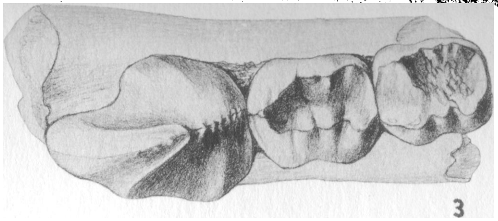
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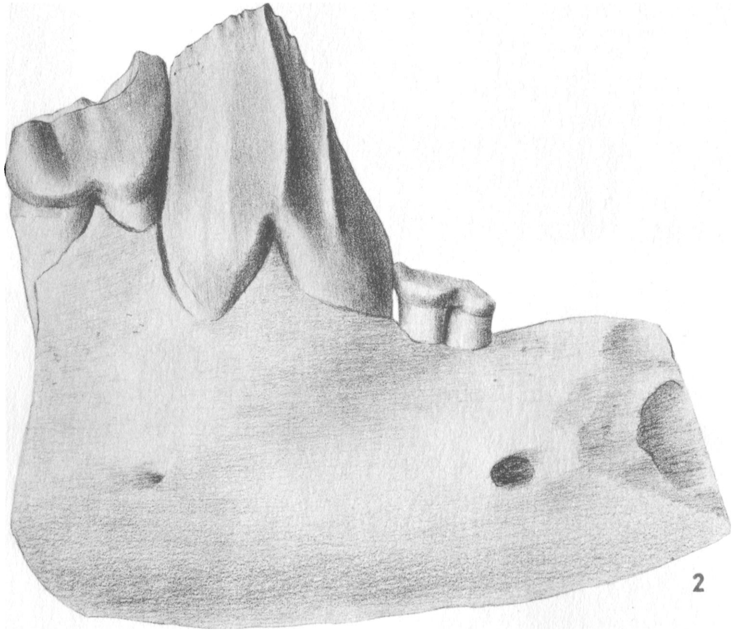
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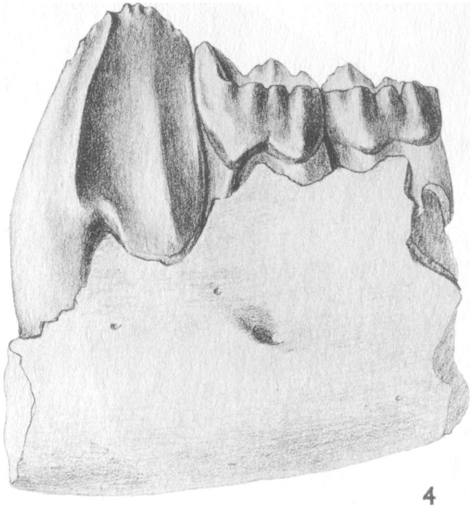
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PLATE 5

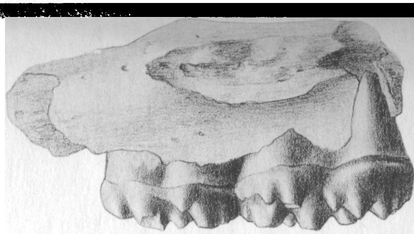
Polydolops

1. *Polydolops thomasi paahi* Simpson. Type, A.M.N.H. No. 28434, right lower jaw with M_{1-3}. Crown view. ×6.
2. Same. Internal view. ×6.
3. ?*Polydolops kamektsen* Simpson. Type, A.M.N.H. No. 28525, right lower jaw fragment with M_3. Crown view. ×6.
4. Same. External view. ×6.

PLATE 6

POLYDOLOPIDAE

1. *Polydolops bocurhor* Simpson. Type, A.M.N.H. No. 28427, right M^{2-3}. External view. ×6.
2. Same. Crown view. ×6.
3. *Polydolops thomasi* Ameghino. A.M.N.H. No. 28440, part of left upper jaw with M^{1-4}. External view. ×6.
4. Same. Crown view. ×6.
5. *Amphidolops serrula* Ameghino. A.M.N.H. No. 28929, part of left upper jaw with M^{2-3}. Crown view. ×9/2.
6. *Seumadia yapa* Simpson. Type, A.M.N.H. No. 28431, isolated M^4. Crown view. ×6.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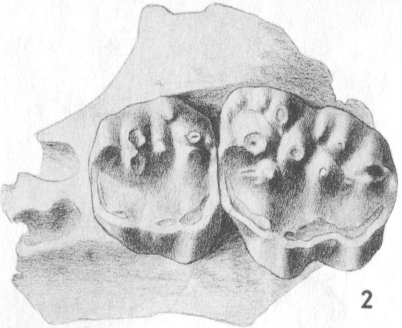
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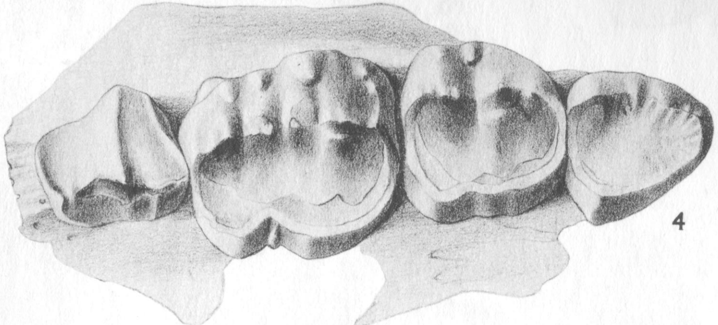
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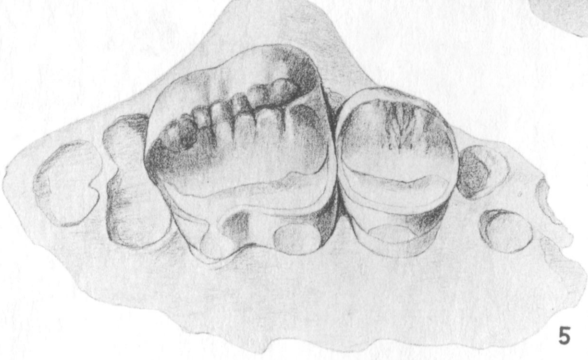
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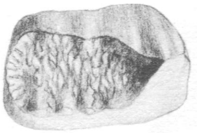

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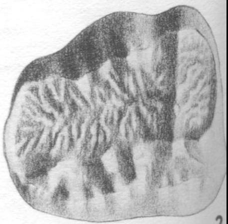

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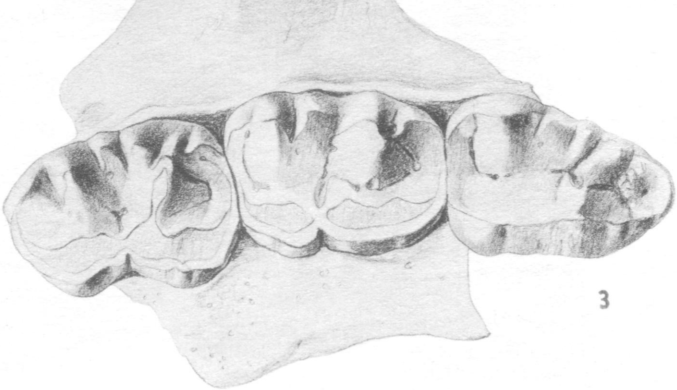

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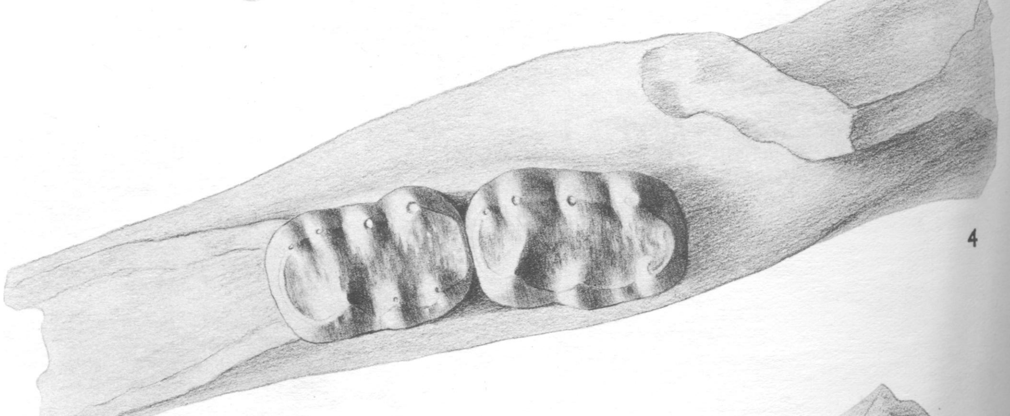

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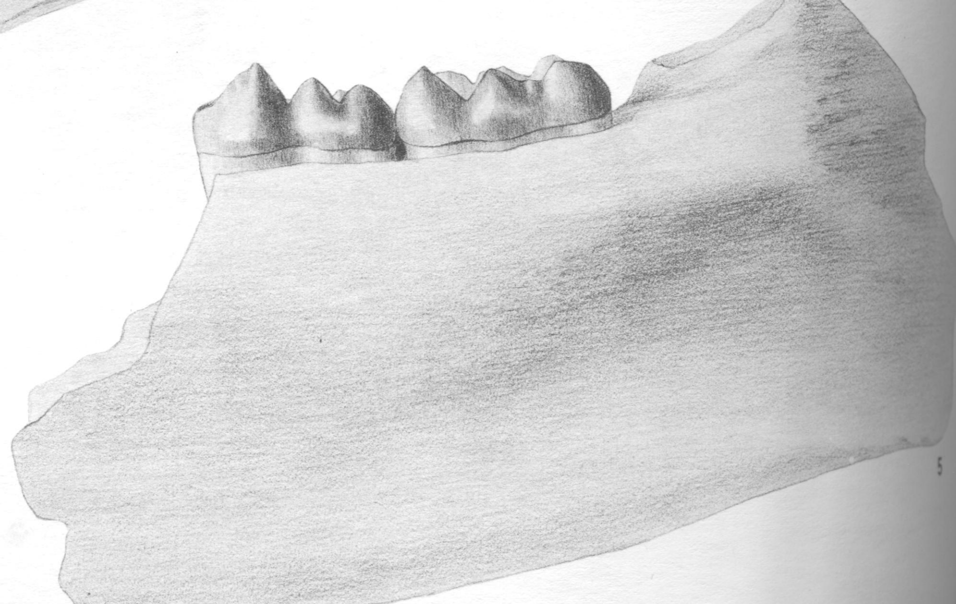

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PLATE 7

POLYDOLOPIDAE

1. *Amphidolops serrula* Ameghino. A.M.N.H. No. 28922, isolated M_2. Crown view. ×9/2.

2. *Amphidolops serrula* Ameghino. A.M.N.H. No. 28438, isolated M^2. Crown view. ×6.

3. *Eudolops tetragonus* Ameghino. A.M.N.H. No. 28932, palatal fragment with left M^{2-4}. Crown view. ×9/2.

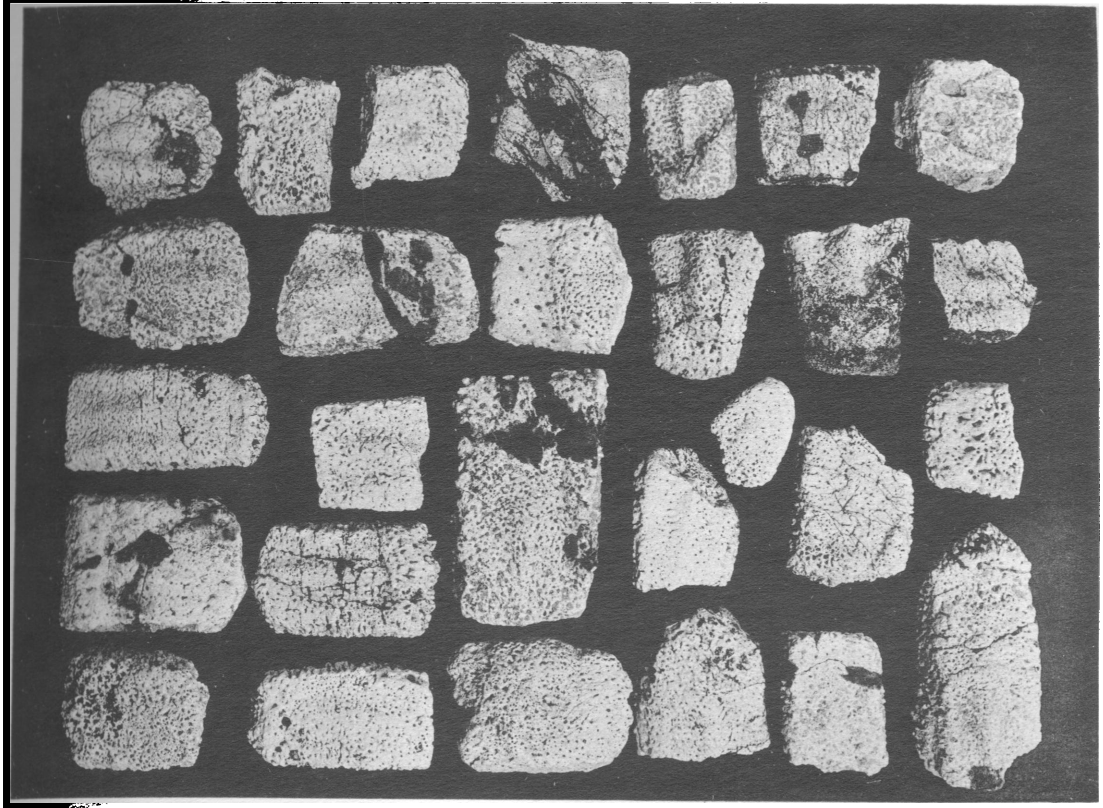
4. *Eudolops caroli-ameghinoi* Ameghino. A.M.N.H. No. 28435, right lower jaw with M_{3-4}. Crown view. ×9/2.

5. Same. Internal view. ×9/2.

PLATE 8

XENARTHRAN SCUTES

1. *Machlydotherium asperum* Ameghino. Type, M.A.C.N. No. 10951, 28 probably associated scutes. ×2/3.
2. *Pseudeutatus clypeus* Ameghino. Type, M.A.C.N. No. 10959, isolated buckler scute. ×4/3.
3. *Pseudeutatus depictus* (Ameghino). Syntype, M.A.C.N. No. 10961, isolated buckler scute. ×4/3.
4. *Pseudeutatus depictus* (Ameghino). Lectotype, M.A.C.N. No. 10961, isolated buckler scute. ×4/3.
5. *Pseudeutatus cuneiformis* (Ameghino). Type, M.A.C.N. No. 10956, isolated buckler scute. ×4/3.
6. *Lomaphorelus depstus* Ameghino. Type, M.A.C.N. No. 10950, isolated scute. ×4/3.



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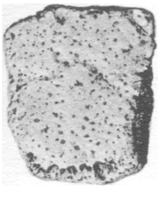

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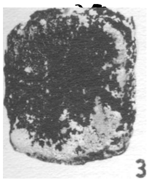

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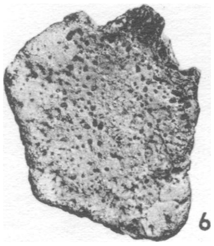

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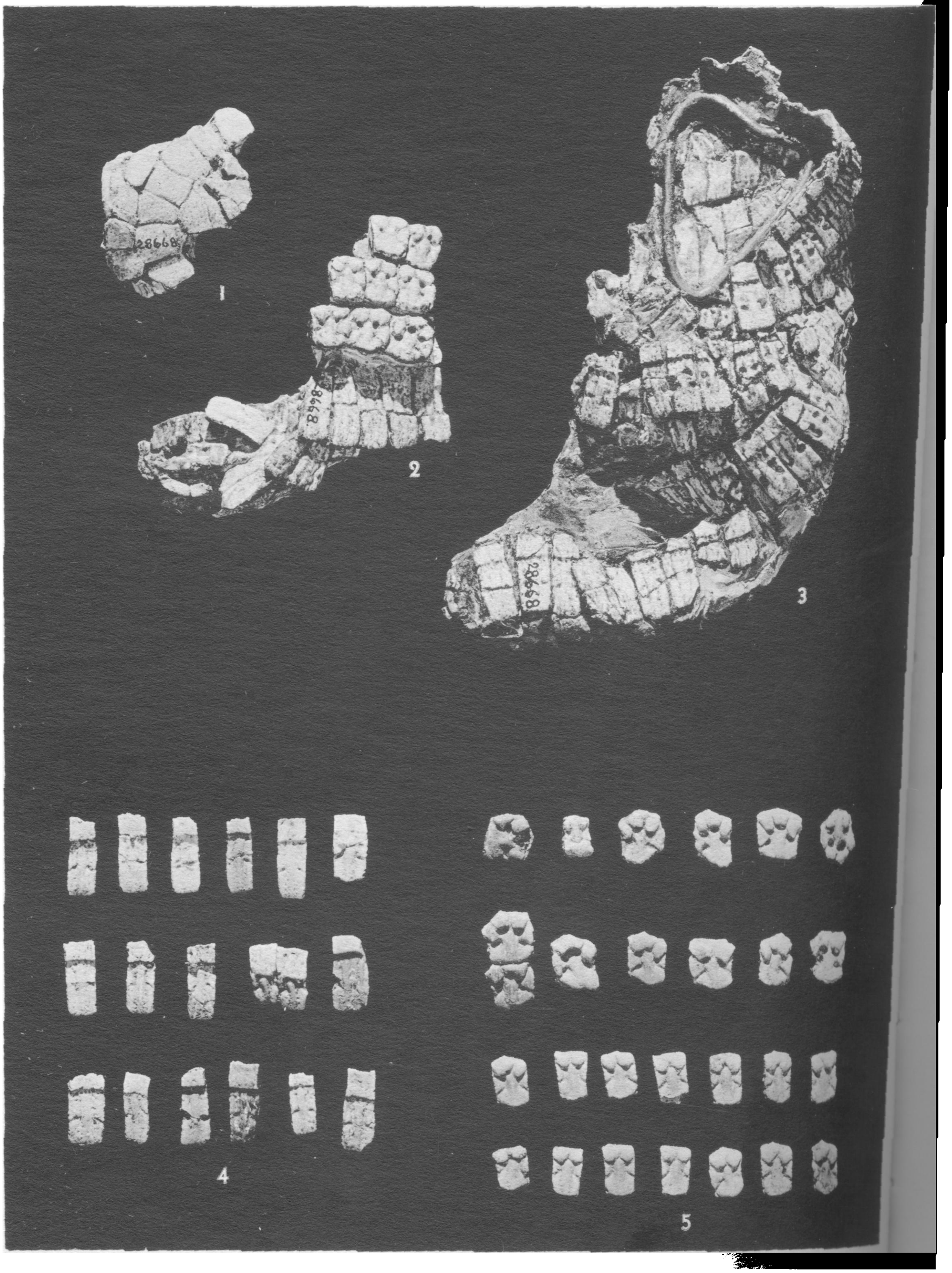
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PLATE 9

Utaetus buccatus AMEGHINO

A.M.N.H. No. 28668, scutes of one individual (associated with partial skeleton).
1. Part of casque.
2. Group including buckler and band scutes.
3. Group of band scutes.
4. Separate band scutes.
5. Separate buckler scutes.

All ×4/3, approximately.

PLATE 10

CONDYLARTHRA

1–8. *Didolodus multicuspis* Ameghino.

1. Type, M.A.C.N. No. 10690, left upper jaw with P^2–M^3. External view. ×1.

2. Same. Crown view. ×5/6. Photograph by Scott.

3. M.A.C.N. No. 10689, right P_2–M_3 (type of the synonym *D. crassicuspis*). Crown view. ×5/6.

4. M.A.C.N. No. 10733, isolated, broken right M^2 (type of the synonym *D. dispar*). Crown view. ×6/5.

5. M.A.C.N. No. 10730, isolated left M^1 (type of the synonym *Lonchoconus lanceolatus*). Crown view. ×6/5.

6. M.A.C.N. No. 10736, right M_3 (syntype of the synonym *D. colligatus*.) Crown view. ×6.5.

7. M.A.C.N. No. 10736 (as above), left P_4. Crown view. ×6/5.

8. M.A.C.N. No. 10736 (as above), left M_3. Crown view. ×6/5.

9. *Argyrolambda conidens* Ameghino. Type (not found in collection; no catalogue number). Right upper molar. Crown view. ×3. After Ameghino.

10. *Paulogervaisia inusta* Ameghino. Type, M.A.C.N. No. 10664, isolated right M_3. Crown view. ×6/5.

11. *Paulogervaisia mamma* (Ameghino). Syntype, M.A.C.N. No. 10719, part of right lower jaw with P_3–M_2. External view. ×1.

12. Same. Crown view. ×5/6.

13. *Paulogervaisia mamma* (Ameghino). Lectotype, M.A.C.N. No. 10719, left upper jaw fragment with broken M^{2-3}. Crown view. ×5/6.

14. *Paulogervaisia mamma* (Ameghino). Syntype, M.A.C.N. No. 10719, isolated right M^2(?). Crown view. ×5/6.

15. *Paulogervaisia porca* (Ameghino). Type, M.A.C.N. No. 10721, right upper jaw fragment with M^3 and part of M.^{2} Crown view. ×6/5.

16. *Proectocion argentinus* Ameghino. Type, M.A.C.N. No. 10673, right M^3. Crown view. ×6/5.

17. *Proectocion precisus* Ameghino. Type, M.A.C.N. No. 10679, right upper jaw fragment with P^4–M^3. Crown view. ×6/5.

18. Same. ×4. After Ameghino.


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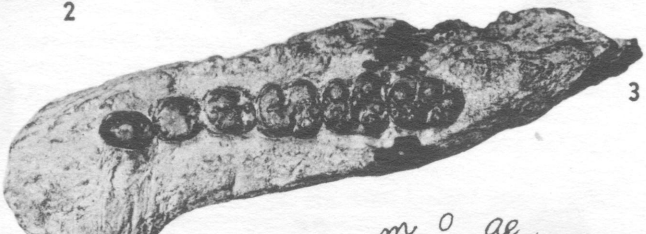
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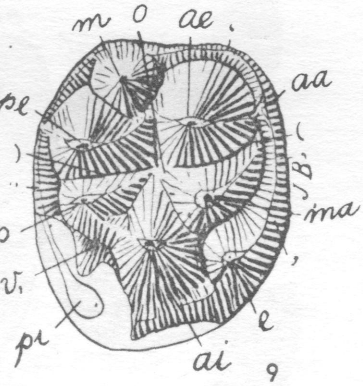

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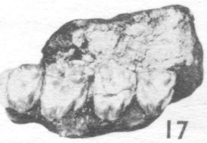
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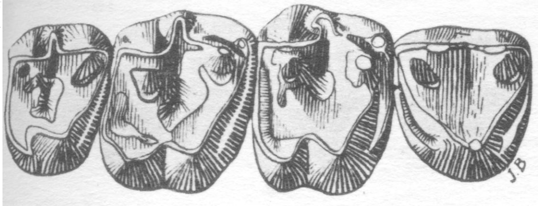

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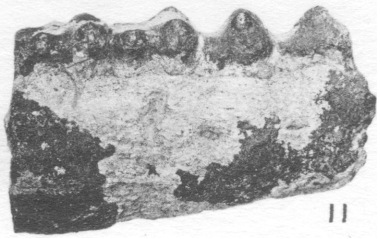
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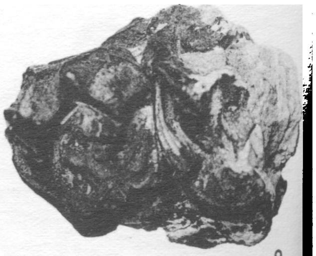
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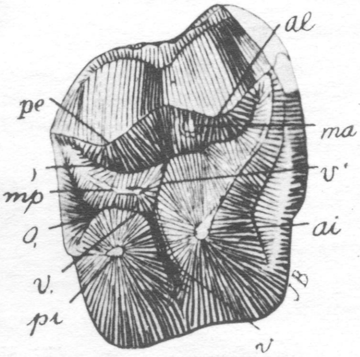

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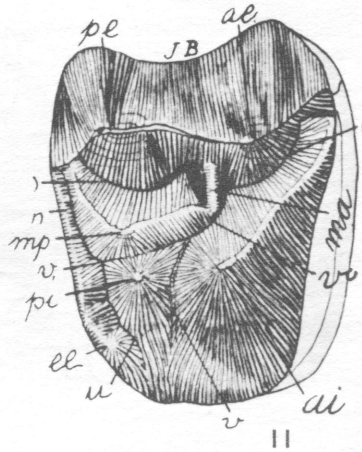

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PLATE 11

Condylarthra and Litopterna

1. *Enneoconus parvidens* Ameghino. Type, M.A.C.N. No. 10726. Crown view. ×6/5.
2. *Asmithwoodwardia subtrigona* Ameghino. Syntype (not lectotype), M.A.C.N. No. 10723, left lower molar. Crown view. ×6/5.
3. *Ernestokokenia nitida* Ameghino. Type, M.A.C.N. No. 10735, left M_2. Crown view. ×6.5.
4. *Ernestokokenia nitida* Ameghino. M.A.C.N. No. 10722, left M_1 (type of the synonym *E. marginata*). Crown view. ×6/5.
5. *Ernestokokenia patagonica* (Ameghino). Type, M.A.C.N. No. 10687, right upper molar (M^2?). Crown view. ×6/5.
6. *Ernestokokenia trigonalis* (Ameghino). Type, M.A.C.N. No. 10688, left upper molar (M^1 or M^2). Crown view. ×6/5.
7. *Archaeohyracotherium mediale* (Ameghino). Type, M.A.C.N. No. 10677, left upper molar. ×6/5.
8. *Victorlemoinea labyrinthica* Ameghino. Type, M.A.C.N. No. 10671, left P^4 and part of M^1. Crown view. ×6/5.
9. *Victorlemoinea emarginata* Ameghino. Type, M.A.C.N. No. 10672, right M^1 and part of M^2. Crown view. ×6/5.
10. ?*Victorlemoinea longidens* (Ameghino). Lectotype, M.A.C.N. No. 10670, right lower jaw fragment with M_1 and trigonid of M_2. External view. ×6/5.
11. *Rutimeyeria conulifera* Ameghino. Type, M.A.C.N. No. 12013, right upper molar. Crown view. ×8. After Ameghino.
12. *Amilnedwardsia brevicula* Ameghino. Type, M.A.C.N. No. 12011, right upper molar. Crown view. ×6. After Ameghino.
13. *Josepholeidya adunca* Ameghino. Type, M.A.C.N. No. 10702, left upper molar. Crown view. ×6/5.
14. *Josepholeidya deculca* Ameghino. Type, M.A.C.N. No. 10682, left upper molar. Crown view. ×6/5.
15. *Ricardolydekkeria praerupta* Ameghino. Type, M.A.C.N. No. 10701, right upper cheek tooth. Crown view. ×6/5.
16. *Ricardolydekkeria profunda* Ameghino. Lectotype, M.A.C.N. No. 10706, incomplete right upper cheek tooth. Crown view. ×6/5.
17. *Ricardolydekkeria cinctula* Ameghino. Type, M.A.C.N. No. 10705, right upper cheek tooth. Crown view. ×6/5.
18. *Guilielmofloweria plicata* Ameghino. Type, M.A.C.N. No. 10703, left upper cheek tooth. Crown view. ×6/5.
19. *Anisolambda fissidens* Ameghino. Syntype, M.A.C.N. No. 10668, right M_{1-3}. Crown view. ×6/5.
20. *Anisolambda fissidens* Ameghino. Syntype, M.A.C.N. No. 10668, left M_{1-2}. Crown view. ×6/5.
21. *Anisolambda fissidens* Ameghino. Lectotype, M.A.C.N. No. 10668, right M_{1-3}. Crown view. Slightly less than ×1. Photograph from Scott.

PLATE 12

LITOPTERNA

1. *Polymorphis lechei* Roth. Type, M.L.P. No. 12-2168, symphysis and left lower jaw with left I_1–M_3 and right I_{1-3}. Crown view. ×10/7.
2. *Polymorphis planus* (Roth). Type, M.L.P. No. 12-1732, symphysis and left lower jaw with M_3. Crown view. ×6/7.
3. *Polymorphis alius* (Ameghino). Type, M.A.C.N. No. 10893, lower jaw with left P_2–M_1 and right P_2–M_3. Right lateral view. ×1.
4. Same. Crown view. ×1.


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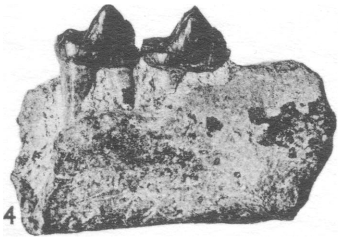
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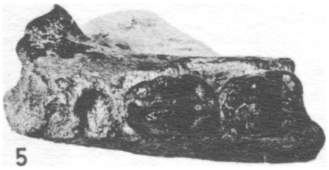
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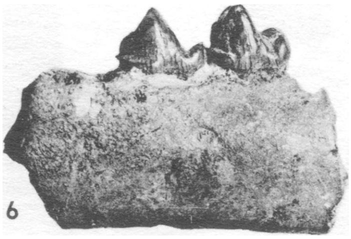
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PLATE 13

LITOPTERNA

1. *Polyacrodon ligatus* Roth. Type, M.L.P. No. 12-2169, right upper molar. Crown view. ×1.

2. *Polyacrodon lanciformis* Roth. Type, M.L.P. No. 12-2170, left upper molar. Crown view. ×1.

3. *Xesmodon langi* (Roth). Type, M.L.P. No. 12-1481, skull. Dorsal view. ×2/3.

4–6. ?*Xesmodon prolixus* (Roth). Type, M.L.P. No. 12-1743, left lower jaw fragment with P_{3-4}. ×1.

4. Internal view.
5. Crown view.
6. External view.

7. *Heteroglyphis dewoletzky* Roth. Type, M.L.P. No. 12-1462, incomplete left upper molar. Crown view. ×1.

PLATE 14

HENRICOSBORNIIDAE

1–25. *Henricosbornia lophodonta* Ameghino.

1, 2. Type, M.A.C.N. No. 10808, right P^3–M^3. 1. External view. 2. Crown view. ×3/2.

3, 4. Right M_{1-2}, possibly associated with type, M.A.C.N. No. 10808. 3. External view. 4. Crown view. ×3/2.

5. M.A.C.N. No. 10797, left M_{2-3} (lectotype of the synonym *Selenoconus centralis*). Slightly oblique crown view.

6. M.A.C.N. No. 10797, right M_3, probably incorrectly associated with specimen shown in 5. Crown view.

7. M.A.C.N. No. 10792, left M_3 (lectotype of the synonym *Selenoconus senex*). Crown view.

8. M.A.C.N. No. 10792, left M_1 or M_2, probably incorrectly associated with specimen shown in 7. Crown view.

9. M.A.C.N. No. 10792, right M_1 or M_2, probably incorrectly associated with specimens shown in 7 and 8.

10. M.A.C.N. No. 10717, left M^1 or M^2 (lectotype of the synonym *Pantostylops typus*).

11. M.A.C.N. No. 10717, broken upper molar, probably incorrectly associated with specimens shown in 10, 12, and 13.

12. M.A.C.N. No. 10717, incomplete upper molar, probably incorrectly associated with specimens shown in 10, 11, and 13.

13. M.A.C.N. No. 10717, right M^1 or M^2, probably incorrectly associated with specimens shown in 10–12.

14. M.A.C.N. No. 10707, left M^3 (type of the synonym *Hemistylops incompletus*).

15. M.A.C.N. No. 10715, right M^1 or M^2 (type of the synonym *Microstylops clarus*).

16. M.A.C.N. No. 10675, left M^1 or M^2 (type of the synonym *Prohyracotherium patagonicum*).

17. M.A.C.N. No. 10676, left M^1 or M^2 (type of the synonym *Prohyracotherium matutinum*).

18. M.A.C.N. No. 10716, right M^1 or M^2 lacking the ectoloph (lectotype of the synonym *Pantostylops completus*).

19. M.A.C.N. No. 10716, right M^1 or M^2, incomplete externally, probably incorrectly associated with specimen shown in 18.

20. M.A.C.N. No. 10810, left M^1 or M^2 (type of the synonym *Henricosbornia alouatina*).

21. M.A.C.N. No. 10809, left M^3 (type of the synonym *Henricosbornia subconica*).

22. M.A.C.N. No. 10714, left M^3 (type of the synonym *Hemistylops paucicuspidatus*).

23. M.A.C.N. No. 10710, broken right M^3 (type of the synonym *Hemistylops trigonostyloides*).

24. M.A.C.N. No. 10708, left M^3 (type of the synonym *Polystylops progrediens*).

25. M.A.C.N. No. 10713, broken right M^1 or M^2 (type of the synonym *Microstylops monoconus*).

26. *Henricosbornia ampla* (Ameghino). Type, M.A.C.N. No. 10709, left M^3.

27. *Othnielmarshia lacunifera* Ameghino, type, M.A.C.N. No. 10807, left M^1 or M^2.

28. *Othnielmarshia lacunifera* Ameghino, M.A.C.N. No. 10807, left M^1 or M^2, probably incorrectly associated with the specimens shown in 27 and 29.

29. *Othnielmarshia lacunifera* Ameghino, M.A.C.N. No. 10807, upper molar fragment, probably incorrectly associated with the specimens shown in 27 and 28.

30. *Othnielmarshia curvicrista* (Ameghino), type, M.A.C.N. No. 10806, left M_1 or M_2.

31. *Othnielmarshia curvicrista* (Ameghino), M.A.C.N. No. 10806, left M_3, probably incorrectly associated with the specimen shown in 30.

32, 33. *Othnielmarshia reflexa* (Ameghino), type, M.A.C.N. No. 10803, right lower jaw fragment with M_{1-2}. 33. Internal view. ×3/2.

34, 35. *Othnielmarshia reflexa* (Ameghino), M.A.C.N. No. 10803, left lower jaw fragment with P_4–M_1, probably incorrectly associated with the specimen shown in 32 and 33. 35. Internal view. ×3/2.

36. *Peripantostylops minutus* (Ameghino), type, M.A.C.N. No. 10711, right M^1 or M^2.

37, 38. *Peripantostylops minutus* (Ameghino), M.A.C.N. No. 10796, left lower jaw fragment with M_{1-3} (type of synonym *Selenoconus agilis*). 38. Internal view. ×3/2.

Except as otherwise noted, all figures are crown views. ×6/5.


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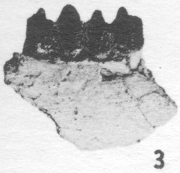
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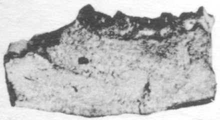
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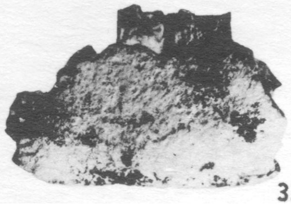
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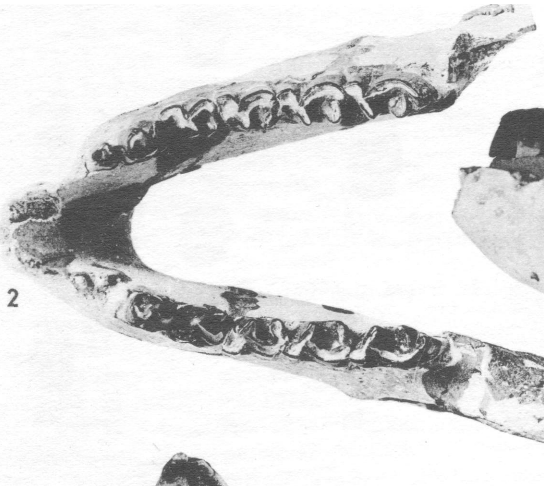
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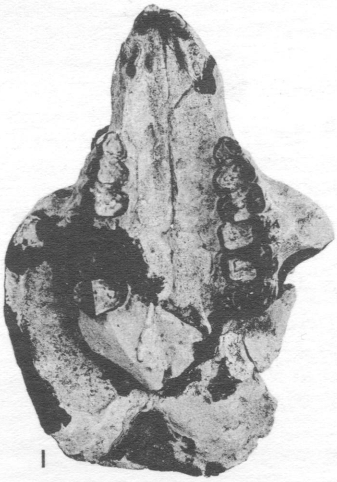
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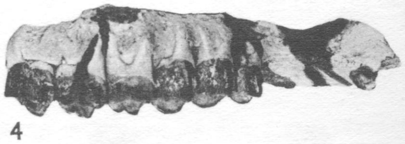
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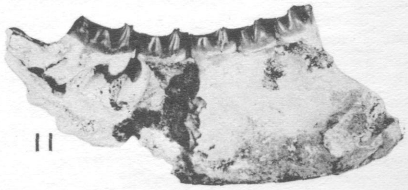
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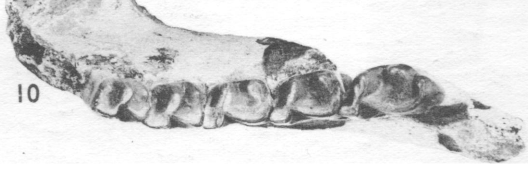
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PLATE 16

Notostylops murinus AMEGHINO

1. M.A.C.N. No. 10499, nearly complete skull (type of the synonym *N. brachycephalus*). Palatal view. ×1.
2. Same as 1. Dorsal view. ×½.
3. Same as 1 and 2. Right lateral view. ×½.
4. M.A.C.N. No. 10466, palate with complete dentition. Palatal view. ×3/4.
5. M.A.C.N. No. 10507, maxillary fragment with incomplete left P^2–M^3 (type of the synonym *N. promurinus*). Crown view. ×5/6.
6. M.A.C.N. No. 10491, maxillary fragment with roots and parts of crown of right P^3–M^3 (type of the synonym *Entelostylops tripartitus*). Crown view. ×5/6.
7. M.A.C.N. No. 10528, maxillary fragment with right M^{2-3} and roots of P^{3-4} (type of the synonym *N. aspectans*). Crown view. ×5/6.
8. M.A.C.N. No. 10469, isolated upper premolar (lectotype of synonym *Anastylops vallatus*). Crown view. ×5/4.
9. M.A.C.N. No. 10469, isolated upper premolar (syntype of the synonym *Anastylops vallatus*). Crown view. ×5/4.

PLATE 15

Notostylops murinus AMEGHINO

1. Syntype, M.A.C.N. No. 10500, skull, lacking occiput and basicranium. ×½.
2. Lectotype, M.A.C.N. No. 10498, lower jaw with all teeth but incisors and left P_2. Crown view. ×1.
3. Same as 2. Left lateral view. ×2/3.
4. M.A.C.N. No. 10510, right upper jaw with all cheek teeth (part of lectotype of the synonym *N. escaridus*). Lateral view. ×2/3.
5. Same as 4. Crown view. ×1.
6. M.A.C.N. No. 10509, right lower jaw with cheek teeth (syntype of the synonym *N. escaridus*). Crown view. ×1.
7. M.A.C.N. No. 10532, poorly preserved left M^{1-3} (referred by Ameghino to the synonym *N. complexus*). Crown view. ×5/6.
8. M.A.C.N. No. 10486, jaw fragment with left P_4–M_2 (part of type of the synonym *Pliostylops magnificus*). Crown view. ×5/6.
9. M.A.C.N. No. 10492, maxillary fragment with left P^{4-3} (type of the synonym *Entelostylops completus*). Crown view. ×5/6.
10. M.A.C.N. No. 10506, left lower jaw with P_3–M_3 (part of type of the synonym *N. ampullaceus*). Crown view. ×1.
11. Same as 10. Internal view. ×2/3.
12. Same individual as 10–11, natural internal mold of cranium. Dorsal view. ×2/3.

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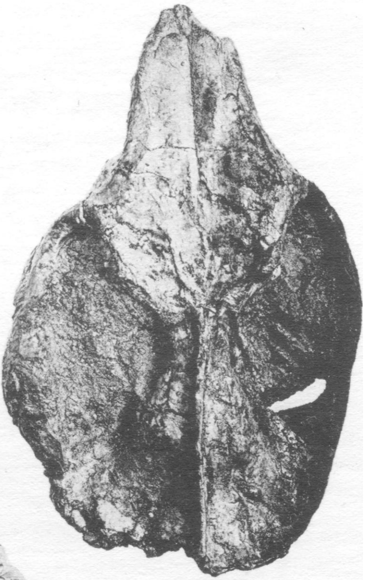

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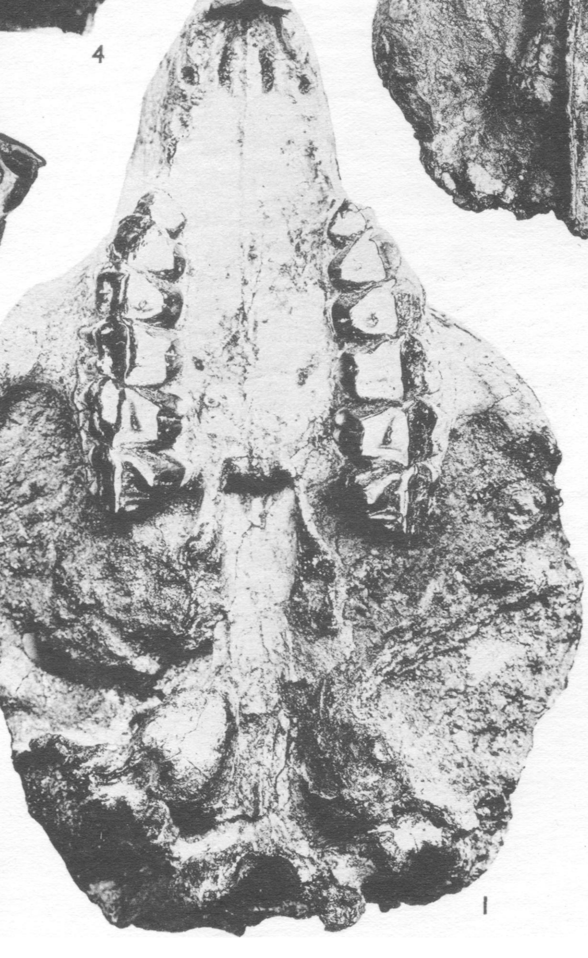

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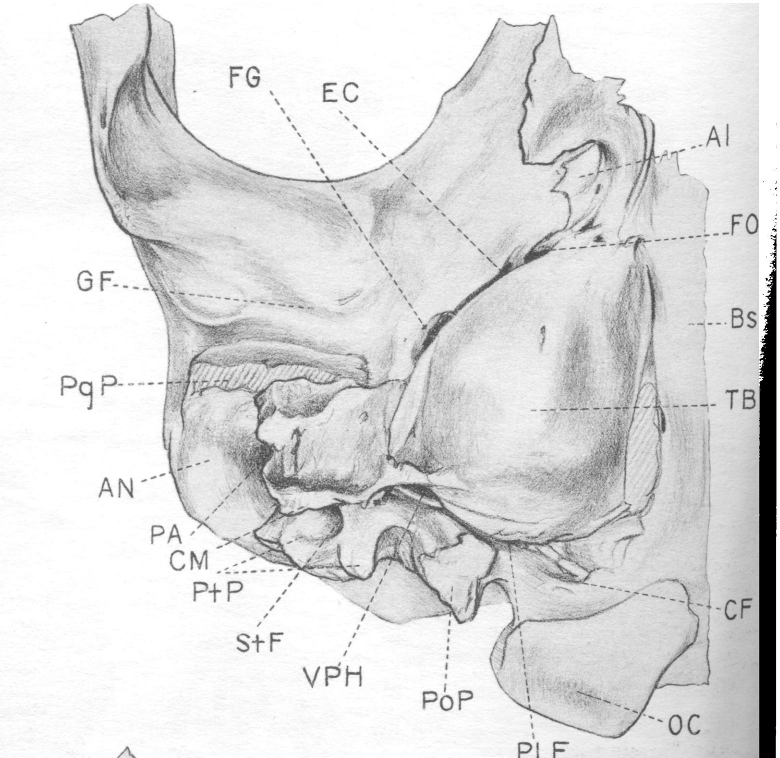
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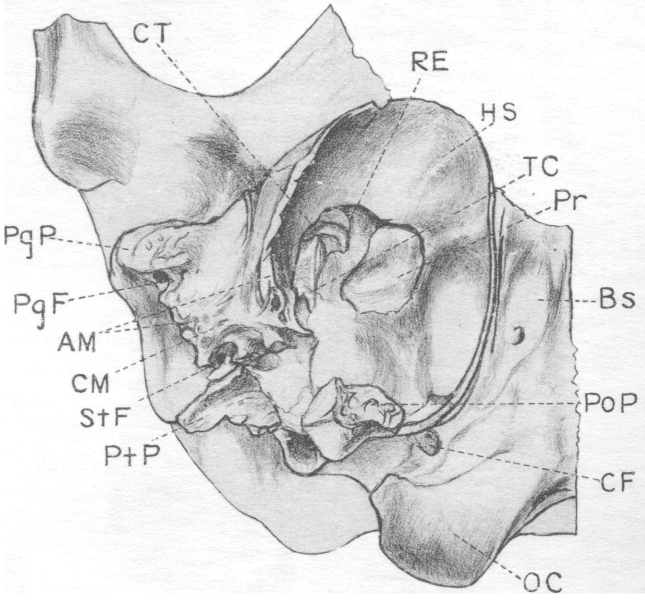
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PLATE 17

Notostylops, VENTRAL VIEWS OF RIGHT AUDITORY REGION

1. *Notostylops murinus* Ameghino. A.M.N.H. No. 28956, with bulla entire. ×2.

2. *Notostylops pendens* (Ameghino). A.M.N.H. No. 28634, with bulla broken, revealing the middle ear. ×2.

Both specimens are somewhat crushed in different ways, and distortion is not corrected in the drawings.

Abbreviations: Al, alisphenoid; AM, auditory meatus; AN, acoustic notch; Bs, basisphenoid; CF, condylar foramen; CM, crista meati; CT, crista tympanica; EC, Eustachian canal; FG, fissura glaseri; FO, foramen ovale; GF, glenoid fossa; HS, hypotympanic sinus; OC, occipital condyle; PA, porus acusticus; PgF, postglenoid foramen; PgP, postglenoid process; PLF, posterior lacerate foramen; PoP, paroccipital process; Pr, promontorium of the petrosal; PtP, posttympanic process; RE, recessus epitympanicus; StF, stylomastoid foramen; TB, tympanic bulla; TC, tympanic cavity; VPH, vagina processus hyoidei.

PLATE 18

Notostylopidae

1. *Notostylops pendens* (Ameghino). Type, M.A.C.N. No. 10472, maxillary fragment with right P^3–M^2, poorly preserved. Crown view. ×5/6.

2. *Notostylops deflexus* (Ameghino). Type, M.A.C.N. No. 10493, maxillary fragment with left P^{2-4}. Crown view. ×5/6.

3. *Notostylops bicinctus* Ameghino. Type, M.A.C.N. No. 10512, isolated left upper premolar. Crown view. ×4/5.

4–6. *Notostylops diversidens* (Ameghino). Syntypes, M.A.C.N. No. 10484.

4. Fragment of left maxilla with deciduous molars. Crown view. ×2/3.

5. Fragment of maxilla with deciduous molars. Crown view. ×2/3.

6. Fragment of left mandible with deciduous molar. Crown view. ×2/3.

7–10. *Homalostylops parvus* Ameghino.

7. M.A.C.N. No. 10468, partial lower jaw with right I_3 and P_1–M_3 and left I_2 and P_{3-4} (type of the synonym *Acrostylops pungiunculus*). Crown view. ×1.

8. M.A.C.N. No. 10473, partial lower jaw with left P_3–M_2 and right P_{3-4} (type of the synonym *H. rigeo*). Crown view. ×5/6.

9. M.A.C.N. No. 10467, partial lower jaw with P_1 and P_3–M_3 of both sides. Crown view. ×1.

10. Lectotype, M.A.C.N. No. 10534, partial left ramus with P_3–M_3 (possibly same individual as M.A.C.N. No. 10527, see pl. 19, fig. 7). Crown view. ×5/6.

11. *Homalostylops interlissus* Ameghino. Type, M.A.C.N. No. 10488, fragmentary mandibular symphysis with crowns of teeth lost. Dorsal view. ×2/3.

12. *Edvardotrouessartia sola* Ameghino. Type (specimen lost or mislaid and not catalogued; the number in the photograph is Scott's negative number, not the number of the specimen), partial right ramus with P_2–M_3. Lateral view. ×1, approximately. Photograph from W. B. Scott.

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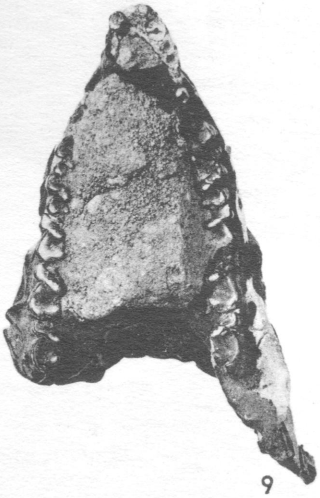

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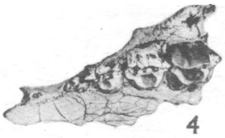

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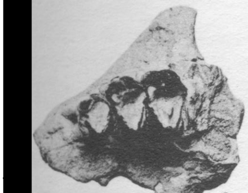

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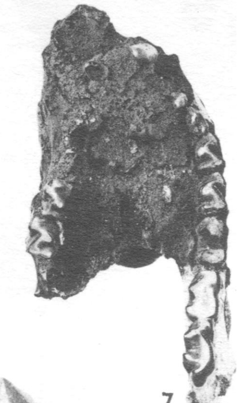

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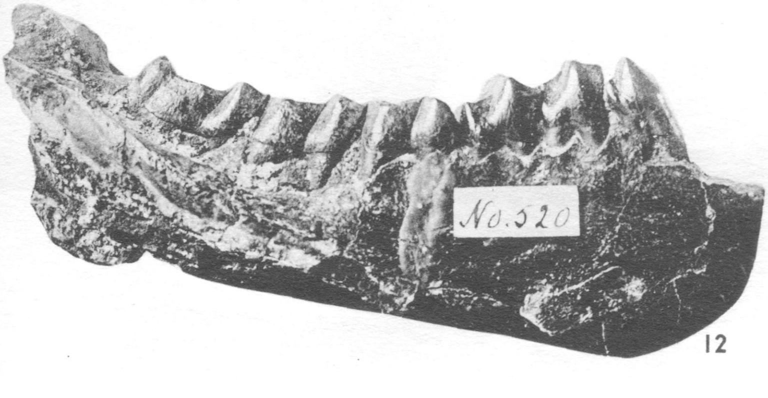

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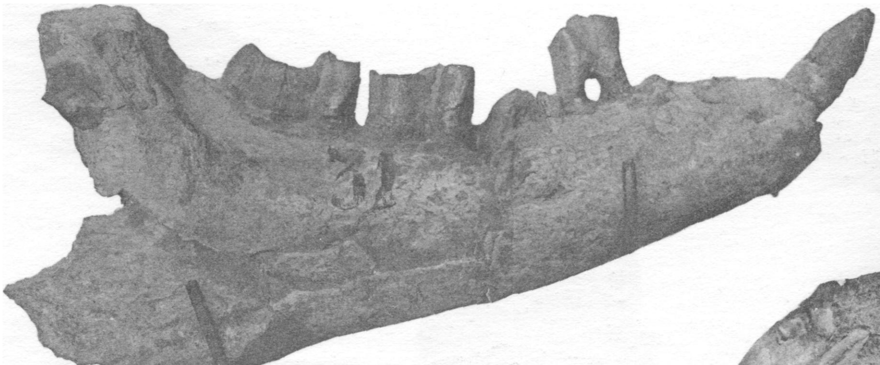

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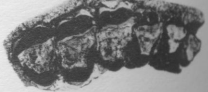

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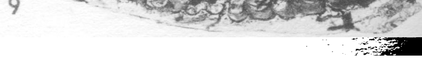

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PLATE 19

Notostylopidae

1–9. *Homalostylops parvus* (Ameghino).

1–4. M.A.C.N. No. 10495, four isolated right upper molars (syntypes of the synonym *Entelostylops incolumis*). Crown views. ×4/3.

5. M.A.C.N. No. 10520, maxillary fragment with left P^1–M^2. Crown view. ×5/6.

6. M.A.C.N. No. 10525, partial right ramus with P_2–M_1 and M_3. Crown view. ×5/6.

7. Lectotype, M.A.C.N. No. 10527, maxillary fragment with right P^2–M^3 (possibly same individual as M.A.C.N. No. 10534; see pl. 18, fig. 10). Crown view. ×1.

8. M.A.C.N. No. 10575, partial left ramus with P_3–M_1. Crown view. ×5/6.

9. M.A.C.N. No. 10470, symphysis and partial left ramus with M_{1-3}. Crown view. ×1.

10–12. *Otronia mühlbergi* Roth.

10. Type or neotype, M.L.P. No. 12-1731, partial right ramus with I_2, P_4, and M_{2-3}. Lateral view. ×1.

11. M.L.P. No. 12-2283, left premaxilla with I^{1-3}. Lateral view. ×1.

12. M.L.P. No. 12-1730, partial skull. Palatal view. ×1.