THE BEGINNING OF THE AGE OF MAMMALS IN SOUTH AMERICA

PART 2

GEORGE GAYLORD SIMPSON

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 137 NEW YORK : 1967

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PART 2. SYSTEMATICS: NOTOUNGULATA, CONCLUDED (TYPOTHERIA, HEGETOTHERIA, TOXODONTA, NOTOUNGULATA INCERTAE SEDIS); *ASTRAPOTHERIA; TRIGONOSTYLOPOIDEA; PYROTHERIA; XENUNGULATA; MAMMALIA* INCERTAE SEDIS

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OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 137 NEW YORK : 1967

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Volume 137, pages 1–260, text figures 1–54, plates 1–46,
tables 1–79

Issued December 29, 1967

Price: $25.00 a copy

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INTRODUCTION TO PART 2

The present publication completes the systematic revision of the Riochican, Casamayoran, and Mustersan mammalian faunas of Patagonia, within the scope planned in 1930. The first part, systematics through Notioprogonia, was published in 1948 (Simpson, 1948). A projected third part, stratigraphy and narrative of the Scarritt Expeditions to Patagonia, is still deferred as such. A popular account of the first expedition was published long since (Simpson, 1934a) and has recently been reissued in modified form (Simpson, 1965). In both parts of this memoir locality and stage have been given for specimens collected by those expeditions. All those specimens are also precisely placed on measured stratigraphic sections, which remain in manuscript but are available to qualified, interested parties in the archives of the American Museum of Natural History.

The major acknowledgments up to that date were given in the Preface to Part 1 (Simpson, 1948, pp. 5–7). Some additions must now gratefully be made. The late Dra. Noemí Cattoi assisted in locating and studying a number of Ameghino's types not found during my original study of that collection. Sr. G. J. Scaglia placed in my hands for study a small but interesting Casamayoran collection. Dr. Rosendo Pascual has checked some points about the Roth Collection and has discussed some problems with me. Professor Bryan Patterson has continued to contribute wisdom and knowledge. Professor C. Arambourg and the Abbé R. Lavocat enabled me to study pertinent specimens in Paris. Dr. Carlos de Paula Couto facilitated study of the Itaborai fauna, which is not included here but knowledge of which was essential for the interpretation of some Patagonian taxa. Mr. Chester Tarka has made drawings and photographs that are here new illustrations of specimens in the American Museum. (Sources of other illustrations were acknowledged in Part 1.) Mrs. Mary James has typed and, in part, copy-edited and checked the manuscript. The Department of Vertebrate Paleontology of the American Museum of Natural History, under the chairmanship, successively, of Dr. Edwin H. Colbert and Dr. Bobb Schaeffer, has continued to facilitate and, in part, support this work, although I left that staff in 1959. Since 1959 the Museum of Comparative Zoology, Drs. A. S. Romer and E. Mayr, successive directors, has provided extensive additional support and research facilities, largely from the endowment of the late Alexander Agassiz.

It is sad to report that many who helped earlier stages of this work are now deceased. This study may be considered as involving a memorial tribute to them. Among them are Horace S. Scarritt, Walter W. Holmes, Childs Frick, M. Doello-Jurado, Lucas Kraglievich, Ángel Cabrera, Carlos Ameghino, Egidio Feruglio, Albert Thomson, Carl Sorensen, George Olsen, John C. Germann, E. S. Riggs, and Noemí Cattoi.

In regard to the illustrations, photographs of specimens in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" were especially taken for this work by the staff of that institution through the courtesy of the late Dr. M. Doello-Jurado and, for the fewer specimens noted in the text as having been more recently located, of the late Dra. Noemí Cattoi. Photographs of the specimens in the Museo de La Plata are from the files of that museum. Most of them were made for the late Sr. Santiago Roth, and prints were provided for the present work by the late Dr. Ángel Cabrera. Photographs of specimens in the Muséum National d'Histoire Naturelle in Paris were provided through the courtesy of Prof. C. Arambourg and the Abbé R. Lavocat. Most of the illustrations of the specimens in the American Museum of Natural History were made by Mr. Chester Tarka especially for my work and were provided through the courtesy of Dr. Edwin H. Colbert and Dr. Bobb Schaeffer. Mr. Tarka also assembled all the plates and text figures and supervised their clarification and differential enlargement. Miss Ruth Tyler has meticulously edited the manuscript and seen it through the press.

Collections involved and the abbreviations used for them are as follows:

A.M.N.H., the American Museum of Natural History: Mostly the collections made by the Scarritt expeditions in 1930–1931 and 1933–

1934 under my leadership but also a number of smaller lots variously acquired through the years.

C.N.H.M., Field Museum of Natural History, Chicago, Illinois (formerly the Chicago Natural History Museum): Collections made by E. S. Riggs in 1922–1924.

M.A.C.N., Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina: Reference here is almost entirely to the great and basic Ameghino Collection. In addition to a few small odd lots, this museum also has a Casamayoran collection made by Alejandro Bordas. Dra. Cattoi and I planned to publish a joint study of this collection, and I made a preliminary study of it, but Dra. Cattoi was unable to continue. The specimens, apparently including some new taxa but of orthodox Casamayoran aspect, are not included in the present publication.

M.H.N., Muséum National d'Histoire Naturelle, Paris, France: Reference is to the small but important and classic Tournouër Collection. The catalogue numbers are not general for that museum but were applied *ad hoc* to identified specimens in this collection.

M.L.P., Museo de La Plata, La Plata, Argentina: Reference is to the Roth Collection. Currently this museum under Rosendo Pascual is acquiring important new early Tertiary collections from Patagonia. These are not included in my studies. They may be expected to provide the next stride forward in knowledge of these faunas.

The following small collections have also been involved in my studies to some extent but are not given abbreviations:

Paleontological collections of the University, Munich, Germany: Under an agreement with Zittel, the Ameghinos sent a number of Patagonian specimens to Munich, and some of these were studied and illustrated by Schlosser (1923). I studied them in 1927 and based one paper mostly on them (Simpson, 1928), but they are not explicitly included in the stated hypodigms of the present publication. Almost all of these specimens were destroyed during Hitler's war.

University of Padua, Italy: A small but interesting collection made by the late Egidio Feruglio while working in Argentina for the Yacimientos Petrolíferos Fiscales. Some of these specimens are explicitly included in the present work but are here identified by the catalogue numbers of casts in the American Museum of Natural History.

Museo Municipal . . . de Mar del Plata, Argentina: A small collection made by G. J. Scaglia and associates. It contains one important specimen, type of *Scaglia kraglievichorum*, included in this study.

All measurements are given in millimeters and the indication "mm." is not given in the tables. The now universally adopted designations of teeth are used: I^{1-3}_{1-3} C^{1}_{1} P^{1-4}_{1-4} M^{1-3}_{1-3} for the full placental formula. Other abbreviations in the tables (slightly modified from Part 1) are as follows:

L, length
W, width
N, number of specimens in sample
$\underline{O}$R, range observed in sample
$\overline{X}$, arithmetic mean of designated variate (X) in sample
s, square root of sample variance (estimate of standard deviation)
V, sample estimate of coefficient of variation
±, stands before standard errors
d, difference between two values being compared, usually, and unless otherwise stated, between an individual measurement and a sample mean

ADDITIONS AND EMENDATIONS TO PART 1

SINCE PART 1 (Simpson, 1948) of this study was published, some modifications and amplifications of its subjects have become possible.

The most important addition to knowledge has been the discovery and description of the Riochican fauna from São José de Itaborai near Rio de Janeiro in Brazil (Paulo Couto, 1950, 1952a–1952d, 1954, 1958, 1961, 1962). That fauna, still not completely published, is incomparably richer than the known Riochican of Patagonia. Its systematic description is excluded from the present memoir, but account is taken of its bearing on the interpretation of the Patagonian faunas.

When my basic study of the Ameghino Collection was made, I was unable to locate a few specimens, especially types and including some particularly dubious species and genera. After that, the late Dra. Noemí Cattoi resorted and re-installed the collection in new quarters, and she found most of the missing specimens. Notes on them are here given, insofar as they bear on observations published in Part 1.

After Part 1 was published, I was able for the first time to study the Tournouër Collection of Casamayoran mammals. A Spanish version of that study has been published elsewhere (Simpson, 1964). A corresponding English version, with suitable modification, is incorporated in this work.

ORDER **MARSUPIALIA**

FAMILY **DIDELPHIDAE** GRAY, 1821

This family, present but very rare in Patagonian early Cenozoic collections, is abundant and highly diversified in the Itaborai fauna (Riochican in age) of Brazil (Paula Couto, 1962). The following Patagonian species has been described since the publication of Part 1.

?**Coona gaudryi** Simpson, 1964

Text figure 1

TYPE: M.H.N. Tournouër Collection No. 1, two lower jaw fragments, probably associated, one with right M_{1-2} (probably) and one with left P_4 and M_2 (probably). If these fragments should prove to be of different individuals, that from the right side is to be taken as the type.

HYPODIGM: Type only.

KNOWN DISTRIBUTION: Casamayoran of Colhué-Huapí, Chubut, Argentina.

DIAGNOSIS: Generally similar to *Coona pattersoni* Simpson, 1938, but only about two-thirds as large as that species. Anterior and posterior cingula on lower molars almost absent.

Ideodelphys microscopicus Ameghino, 1902, the only supposed Casamayoran didelphid named prior to 1938, was based on a fragment of a lower jaw without teeth. It is essentially indeterminate and must reasonably be ignored. *Coona pattersoni* is the only really determinable Casamayoran didelphid hitherto described. Comparison with the present specimen is somewhat indirect, as probable M_{1-2} in this specimen must be compared with M_{3-4} of *C. pattersoni*. In both, the talonid is distinctly wider than the trigonid, the trigonid is moderately elevated and not definitely compressed, the paraconid is slightly

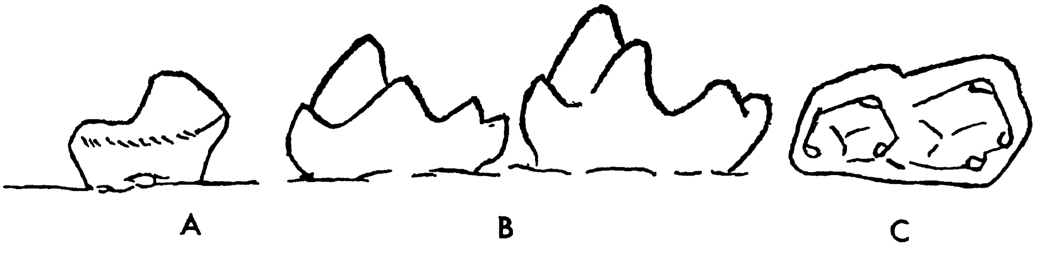

FIG. 1. ?*Coona gaudryi* Simpson, M.H.N. Tournouër Collection No. 1, type. A. Left premolar, probably P_2, lingual view. B. Right M_{1-2}, lingual view. C. right M_2, crown view. The dimensions are given in table 1.

TABLE 1

MEASUREMENTS OF SPECIES REFERRED TO *Coona*

		C. pattersoni, Type	*?C. gaudryi*, Type[a]
P_2			
	L	—	1.4
	W	—	0.9
M_1			
	AL[b]	2.2	1.3
	L	—	1.5
	W	—	1.0
M_2			
	AL	2.3	1.3
	L	—	1.8
	W	—	1.0
M_3			
	AL	2.3	—
	L	2.6	—
	W	1.7	—

[a] The depth of the mandibular ramus on the internal side below P_2? is 2.7 mm.

[b] Length on alveolar rims.

higher than the entoconid, the metaconid is between the paraconid and protoconid in height, and the hypoconulid is small and near the entoconid. The comparison suggests close relationship and does not warrant generic separation, although generic identity is not proved. The size difference is great enough to make specific identity highly improbable. *Coona pattersoni* has strong molar cingula and *?C. gaudryi* only traces.

The didelphids from the Riochican (?Paleocene) of Itaborai, Brazil, are older geologically than *?C. gaudryi*. The species are clearly distinct. The genera resemble *?C. gaudryi* only to the extent that some of them resemble *Coona*, which has priority.

Measurements are given in table 1.

FAMILY **CAROLOAMEGHINIIDAE** AMEGHINO, 1901

Caroloameghinia mater Ameghino, 1901

When Part 1 was written, the type of this species had not been found, and a neotype, M.A.C.N. No. 10348, was designated. Cattoi subsequently found the type and catalogued it as M.A.C.N. No. A55-13. When described and figured by Ameghino (1901; 1902b, figs. 4–6), the type had the canine and all the cheek teeth. When relocated, the crowns of M_{3-4} had been broken off and lost. The type is thus less adequate than the neotype, but the type is specifically identifiable, and the neotype designation is hereby withdrawn.[1] The two specimens are certainly conspecific, and the species concept based on the neotype designation is confirmed by the type.

Under No. 2, the Tournouër Collection in Paris includes four unassociated teeth: (a) slightly broken right M_1; (b) right M_2 or M_3; (c) left M_2 or M_3; and (d) left M_4 in a fragment of jaw. All closely resemble the teeth of neotypical *C. mater* (see Simpson, 1948) in size and structure. The measurements are: (a), length, *ca.* 3.8, width, 2.2; (b), length, 3.7, width, 2.7; (c), length, 3.8, width, 3.2; (d), length, 4.0, width, 2.5. The widths given for (a), (b), and (c) are across the talonid, wider in those teeth. Their trigonid widths are 1.8, 2.2, and 2.4, respectively. On (d) the trigonid is slightly wider, the talonid measuring 2.3 in width.

FAMILY **POLYDOLOPIDAE** AMEGHINO, 1897

Remarkably good specimens of this family have been described by Paula Couto (1952a) from the Itaborai fauna in Brazil. These earlier and somewhat more primitive forms show that M_4 is absent from the Casamayoran genera and that the shearing teeth are P_3^3, contrary to my previous opinion (Simpson, 1948). The shearing teeth are thus probably not homologous in the Polydolopidae and the Abderitinae. There is, however, no serious reason to question the pertinence of both groups to the Caenolestoidea and their relationship at that level.

Polydolops thomasi Ameghino, 1897

M.H.N. Tournouër Collection No. 3 is a fragmentary left lower jaw of this species, with M_3 preserved and measuring 3.8 in length and 3.1 in width. In addition to the two usual internal talonid cusps, there is a third, accessory, cuspule. The specimen is labeled "Couche inf," i.e., "lower bed," and is thus from a relatively low level at Tournouër's "Cerro Negro" locality, or the Casa-

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[1] Under the current International Code (Stoll and others, 1964), Article 75(f), "If, after the designation of a neotype, original type-material is found to exist, the case is to be referred to the Commission." In the present case, that complex, time-consuming, and costly procedure would be absurd. This is certainly the type, and it is certainly conspecific with the former neotype.

mayoran of Colhué-Huapí. Although there is no exact basis for comparing Tournouër's levels with ours, it is noteworthy that the type of *P. thomasi paahi* is also from a low level in that exposure and that it compares very closely with this Tournouër specimen, even to the presence of three internal talonid cuspules on M_3. (See Simpson, 1948.) It is not, however, established that the subspecies of *P. thomasi* can be clearly distinguished on the basis of M_3 alone.

M_3 of the Tournouër specimen measures 3.8 by 3.1 mm.

TAXA DUBIOUSLY OR INCORRECTLY REFERRED TO THE MARSUPIALIA

PROGARZONIA Ameghino, 1904

Progarzonia notostylopense Ameghino, 1904

The type of this species, which is the type of the genus, has been found by Cattoi and catalogued as M.A.C.N. No. A55-14. It is a fragment of left lower jaw with a single, two-rooted premolar, 2.5 mm. in length. This agrees with Ameghino's description (1904a), and the animal may be a caenolestid, but in my opinion it is not adequately identifiable at any taxonomic level below the class.

?Promysops primarius Ameghino, 1902

The type of this supposed species has also now been found and is M.A.C.N. No. A55-10. Ameghino's figures (1906, fig. 209) are accurate. As previously concluded (Simpson, 1948, p. 50), this specimen does not belong to *Promysops*, which is a synonym of *Eudolops*. The specimen is not identifiable, and the specific name is a *nomen vanum*.

Family **ODONTOMYSOPIDAE** Ameghino, 1902

ODONTOMYSOPS Ameghino, 1902

Odontomysops spiniferus Ameghino, 1902

Plate 1, figures 1–3

Ameghino's family, genus, and species, referred to the Allotheria (= Multituberculata), were based on three specimens, recently relocated by Cattoi and catalogued as M.A.C.N. Nos. A55-2a, A55-2b, and A55-2c. M.A.C.N. No. A55-2a is a poorly preserved, subconical tooth, a canine or perhaps a large incisor. M.A.C.N. No. A55-2b is an anterior fragment of a left lower ramus, with a large anterior alveolus and badly broken and worn traces of three or more cheek teeth, each probably two-rooted. M.A.C.N. No. A55-2c is the small lower jaw fragment with a partly erupted tooth as figured by Ameghino (1903a, fig. 13). Ameghino's definitions of the supposed family and genus were based on all three specimens: for the supposed upper incisor on M.A.C.N. No. A55-2a; for the symphysis, supposed lower incisor (actually an alveolus of doubtful homology), anterior cheek teeth (actually alveoli only), and depth of ramus on M.A.C.N. No. A55-2b; for the supposedly following larger cheek tooth on M.A.C.N. No. A55-2c. In fact the three specimens certainly belong to three different individuals and probably to different genera or, indeed, families. In my opinion none of the three specimens is identifiable, and the familial, generic, and specific names are all *nomina vana*.

Order **EDENTATA**

Superfamily **MEGALONYCHOIDEA** Simpson, 1931

PROPLATYARTHRUS Ameghino, 1905

Proplatyarthrus longipes Ameghino, 1905

The type of this species, now M.A.C.N. No. A55-9, is another of the formerly mislaid specimens relocated by Cattoi. Ameghino's figure (1905a, fig. 69) is accurate, and the specimen certainly represents a ground sloth and probably a megalonychid.

Ameghino (1905a, p. 59) said that this specimen was from the highest part of the *Astraponotus* beds, i.e., the Musters formation, and I (Simpson, 1948, p. 70) mentioned the possibility that it had drifted down from an overlying Deseadan deposit. The specimen itself, which is of clean, white bone, is in fact more like usual Deseadan fossils than like most of those from the Mustersan. This is not conclusive, but I suspect all the more strongly that the specimen is post-Mustersan. It is probably identifiable to genus, at least, so that further collecting should eventually settle the problem.

TAXA INCORRECTLY REFERRED TO THE EDENTATA

Family **PROTOBRADYIDAE** Ameghino, 1902

PROTOBRADYS Ameghino, 1902

Protobradys harmonicus Ameghino, 1902

Plate 1, figures 4, 5

The rediscovery of the type of this species, now M.A.C.N. No. A10330, is especially gratifying. It was supposedly the earliest known sloth, and Ameghino (1902a, p. 49) has ascribed to it some quite peculiar charactersitics but had not provided a figure or a fully comprehensible description.

The field label is: "R[ío] Chico frente a Malaspina. Notostylops [i.e., Casamayoran]."

The specimen is a fragment of a left maxilla, with alveoli. As Ameghino stated, there are five successive alveoli, the second larger than the others. However, there is no apparent basis for Ameghino's statements that milk teeth occurred, that there were rudimentary anterior teeth, that the palate widened anteriorly, or that the zygoma lacked a descending process. There was a diastema anterior to the first preserved alveolus. The large second alveolus is subtriangular, vaguely tripartite, with a separate anteroexternal socket, and it probably lodged a cheek tooth with three perhaps imperfectly separated roots. Medial to the third and fourth serial alveoli there is the edge of another, larger alveolus not noticed by Ameghino. That alveolus and the third and fourth of the series were probably for one three-rooted tooth. The fifth serial alveolus was in all likelihood for the anterolabial root of a likewise three-rooted tooth.

The other supposed tooth mentioned by Ameghino as of this group but not species is M.A.C.N. No. A10331, which is not an edentate tooth but an eroded fragment of a root of a tooth of some other, but unidentifiable, order.

The type specimen cannot possibly represent a sloth or an edentate of any sort. It is otherwise unidentifiable. Familial, generic, and specific names are all *nomina vana.*

ORDER **CONDYLARTHRA**

FAMILY **DIDOLODONTIDAE** SCOTT, 1913

Didolodus ?multicuspis Ameghino, 1897

Plate 1, figure 6

M.H.N. Tournouër Collection No. 4 includes a fragment of the right mandibular ramus with P_{2-4} and a lower right M_3, apparently of the same species but not surely of the same individual. P_{3-4} are in every respect closely similar to those teeth in previously described specimens of *D. multicuspis* (see Simpson, 1948), but P_2 is distinctly smaller than the only one hitherto described, and it may be more molariform. It is, however, somewhat broken. The measurements are: P_2, length, 6.5, width, —; P_3, length, 7.7, width, 6.2; P_4, length, 7.6, width, 6.4.

The M_3 preserved with those premolars but not necessarily associated with them is 12.3 mm. in length, whereas five specimens previously referred to *D. multicuspis* range from 10.0 to 10.9. It is improbable that so large a molar belongs to the same individual or perhaps even species as the premolars just discussed. It may belong to *Paulogervaisia mamma*, but M_3 is not surely known in that species, and the present molar is poorly preserved.

Didolodus cf. **minor** Simpson, 1948

Plate 1, figure 7

M.H.N. Tournouër Collection No. 5 is a left lower jaw fragment with P_{2-3}. These teeth closely resemble those referred to *Didolodus* but are distinctly smaller than those in *D. multicuspis.* They are of a size appropriate for *D. minor*, in which the lower premolars are (otherwise?) unknown. If this possible specific reference were confirmed, it would contradict the suggestion (Simpson, 1948, p. 104) that *D. minor* is geographically segregated from *D. multicuspis*, for No. 5 is from a region, at least, if not a level, where *D. multicuspis* also occurs. The basis for specific identification is, however, too shaky to warrant a firm conclusion. P_2 is 6.2 mm. in length and 4.5 in width, and P_3 measures 6.5 by 5.0. With these teeth are a loose P_4 and a likewise loose, deeply worn M_1. These are also smaller than *D. multicuspis*, and they may be associated.

Didolodus conidens (Ameghino, 1904)

Argyrolambda conidens AMEGHINO, 1904a, vol. 57, p. 338; 1904b, p. 395, fig. 516; 1906, p. 298, fig. 94. SIMPSON, 1948, p. 104.

Argyrolambda conulifera AMEGHINO, 1904b, p. 123, fig. 140. *Lapsus* for *A. conidens.*

TYPE: M.A.C.N. No. A55-8, completely unworn crown cap of a right upper molar, probably M^1, roots not yet formed.

HYPODIGM: Type only.

DIAGNOSIS: Probably synonymous with

Didolodus multicuspis, but protostyle perhaps somewhat stronger. Dimensions of upper molar 8.3 by 10 mm.

This is another type supposed lost but relocated by Cattoi.

Ameghino's figure, also reproduced by me (Simpson, 1948, pl. 10, fig. 9) is accurate except for a slight exaggeration of the protostyle. The protostyle really is somewhat larger than is usual in *Didolodus multicuspis*, but the species are probably synonymous. In any case, generic separation is unwarranted, and *Argyrolambda* Ameghino, 1904, should be added to the synonymy of *Didolodus* Ameghino, 1897.

Ameghino's label with the specimen calls it "*conulifera*," and Ameghino also once used that specific name in print (1904b, p. 123), but *conidens* is also used in the same publication and in others both earlier and later.

Ernestokokenia spp.

Plate 1, figures 8–10

Only isolated molars of this genus had been made known from Casamayoran beds until my paper on the Tournouër Collection (Simpson, 1964). No two of the isolated molars are quite alike, but all are rather closely similar (Simpson, 1948). Their association into natural species and a reconstruction of the tooth series were not possible. The Tournouër Collection includes six teeth of this genus and thus adds considerably to the available materials. These specimens merit some discussion, even though they tend more to complicate than to simplify attempts to sort out possible species. It is inadvisable to give them specific designations at present.

Ameghino (1901) at first referred upper molars of this genus to the North American Torrejonian (middle Paleocene) genus "*Euprotogonia*" (= *Tetraclaenodon*), which they do resemble although generically distinct as Ameghino later established. Gaudry (1904) accepted this reference and also compared other Casamayoran forms with non-South American genera. He believed correctly that South American mammals became more and more distinctive from (in our terms) Casamayoran to Santacrucian, but he did not fully appreciate the extent to which they had already diverged in the Casamayoran.

M.H.N. Tournouër Collection No. 6 includes two right upper molars figured by Gaudry (1904, fig. 2) as "*Protogonia* (*Euprotogonia*) *patagonica*." The two were figured together as M^{1-2}, but the legend correctly stated that they are not from the same individual. The figure is fairly accurate, but simplifies details and shows the teeth reversed, as if they were from the left side. The two teeth are virtually identical in structure but differ slightly in size and proportions, one measuring 6.9 by 8.8 mm. and the other 6.4 by 8.9 mm. They are either first or second molars. Both have a basal cuspule between the paracone and the metacone on the buccal face, followed by a series of denticles across the base of the metacone. There is a slight swelling, but no distinct basal cingulum, across the buccal face of the paracone. There is a small basal cuspule on the lingual side between protocone and hypocone.

M.H.N. Tournouër Collection No. 7 includes two lower molars, also not associated, figured by Gaudry (1904, fig. 8). One, measuring 6.9 by 6.5 mm., is probably M_1 but possibly M_2 as Gaudry thought. The other, 7.9 by 5.0 mm., with an elongated talonid, is M_3. The M_3 is smaller and relatively narrower than the one previously figured by me (Simpson, 1948, fig. 31) and referred to *E. nitida.* The M_1 or M_2 is about as long as the type of *E. marginata* (probably = *E. nitida*) and shorter than the type of *E. nitida*, which is probably M_2, but wider than either. The paraconid is vestigial on both these teeth. The M_1 or M_2 has a cuspule anterior to the entoconid, not shown in Gaudry's figure.

M.H.N. Tournouër Collection No. 8 includes two teeth, probably P_4 and M_1, possibly of one individual. The probable M_1 is almost exactly like the M_1 or M_2 under No. 7 but is smaller (6.1 by 5.3 mm.) and has a more angulate crest in the paraconid region without, however, a true paraconid. P_4 has hitherto been known among didolodontids only in *Didolodus* itself. The present specimen, if correctly identified as P_4, differs markedly from that of *Didolodus* in being more elongate and slender, with the paraconid less distinct and more median, the one strong talonid cusp external, without an external talonid basin, but with a distinct internal basin bounded posteriorly by a sharp crest falling away rapidly from the external talonid cusp. This tooth measures 6.8 by 4.6 mm. The field data on the label are "Cerro Negro 1905.15"—different from those on any other specimens in the Tournouër Collection.

ORDER LITOPTERNA

FAMILY PROTEROTHERIIDAE AMEGHINO, 1887

Josepholeidya sp.

Plate 1, figure 11

M.H.N. Tournouër Collection No. 9 is a lot of four isolated upper molars. Three of these are referable to *Josepholeidya*, and of these two are the originals of figure 1 in Gaudry (1904) by whom they were identified, probably correctly, as unassociated M^2 and M^3. In line with his belief that this early fauna had relationships with Europe and North America, Gaudry considered *Josepholeidya* synonymous with the late Paleocene to early Eocene primate *Plesiadapis*, surely in error. In Gaudry (1906, fig. 1) an outline drawing of the same M^2 as in Gaudry (1904, fig. 1) was labeled simply as *Plesiadapis*, with no indication that it is in fact a Casamayoran specimen from Patagonia and not a real *Plesiadapis* from the Cernaysian of France.

Those teeth are well represented in Gaudry's figure except that the figure does not show that the anteroexternal part of the M^3 is missing and has been restored (probably nearly correctly) by the artist. The figured M^2 measures 9.0 by 12.4 mm. and M^3 about 8.5 by 12 mm. The greatest peculiarity of these teeth, within this highly variable genus, is that both the figured M^2 and another under the same number have an unusually strong cingulum around the lingual face of the protocone and several accessory cuspules in this region.

?Ricardolydekkeria sp.

Plate 1, figure 12

The fourth specimen included under M.H.N. Tournouër Collection No. 9 is another upper molar, considerably worn but probably belonging to *Ricardolydekkeria* rather than *Josepholeidya*. It measures 8.8 by 12.9 mm. and thus is rather short and wide, suggestive of *Ricardolydekkeria cinctula*, which is, however, more likely to be a form dependent on position in the tooth series than a true species, that is, a taxon as a populational unit.

Ricardolydekkeria lunulata (Amerghino, 1904)

As discussed previously (Simpson, 1948, p. 128), this species is the type of *Heterolambda* but seems to me inseparable from *Ricardolydekkeria* and doubtfully separable from *R. praerupta*. The type had been mislaid, and my earlier study was based on an excellent sulphur cast. The type, found by Cattoi, is M.A.C.N. No. A55-4. It measures 8.9 by 9.6 mm., and the metaconule has a sharp anterior wing. Otherwise there is nothing to add to conclusions based on the cast.

Anisolambda nodulosa Roth, 1904, ***nomen vanum***

Text figure 2

This species was omitted from my earlier study of the Roth Collection (Simpson, 1936d) and from Part 1 of this memoir (Simpson, 1948) because it was stated by Roth (1904, p. 156) to be from the "Formación terciaria inferior." By that designation Roth meant Ameghino's *Pyrotherium* beds, our Deseadan, not included in my detailed studies. (Roth agreed with Ameghino in referring the *Notostylops* and *Astraponotus* beds, our Casamayoran and Mustersan, to the late Cretaceous, "Formación cretacea superior.") *Anisolambda nodulosa* was one of a number of supposedly Deseadan mammals from "Cañadón Blanco (Territorio de Chubut)," a locality unknown to other collectors or to maps. Bryan Patterson (personal communication) has found that specimens so listed or labeled as "T.i.C.B." are certainly a mixture in which Casamayoran, Mustersan, and Deseadan are all represented. Scraps referable to *Notostylops* are included, and this fact is doubtless the basis for Roth's (1908)

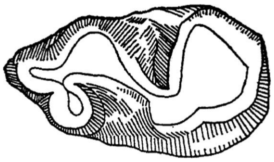

FIG. 2. *"Anisolambda" nodulosa* Roth, type, left M$_3$, crown view. In the Museo de La Plata, not catalogued. Drawing by M. T. Cabrera for B. Patterson. ×3.

statement that he found *Notostylops* only in the *Pyrotherium* beds, an absurdity that baffled me (Simpson, 1936d, p. 76) when I restudied Roth's earlier materials.

The most important of Roth's pre-Deseadan specimens from "Cañadón Blanco" are those he called *Eurystomus stehlini* and *Lonkus rugei*, here considered synonymous with the Mustersan species *Eomorphippus obscurus* and discussed under that name on another page of this Part 2 (p. 184).

Anisolambda is not surely known from any stage but the Casamayoran, and if Roth's generic reference were correct his supposed species would probably be from that level. The type, in the Museo de La Plata, is an isolated, deeply worn M_3. It probably belongs among the most primitive, condylarth-like Proterotheriidae, but it is not really identifiable as to either genus or species. Distinctions from *Anisolambda fissidens* were said by Roth to be smaller size (11 by 7 mm.) and absence of a cingulum. Those are also the supposedly distinctive characters of *Anisolambda amel* Simpson, but, in fact, Roth's specimen is nearer to *A. fissidens* in size and is not known to be of the same genus or the same age as *A. amel.* Both in size and in what little is preserved of structure, the type of *Anisolambda nodulosa* is close to *Polymorphis planus* Roth, itself a possible synonym of *P. lechei* Roth, both from the Mustersan. It is thus quite likely that the generic reference of *Anisolambda nodulosa* is wrong and that it is from the Mustersan and not the Casamayoran. (The original reference to the Deseadan is extremely improbable.) In any case, the name may best be considered a *nomen vanum* and forgotten.

ORDER **NOTOUNGULATA**

FAMILY **NOTOSTYLOPIDAE** AMEGHINO, 1897

Notostylops murinus Ameghino, 1897

M.H.N. Tournouër Collection No. 27 is a crushed but nearly complete cranium with the left part of facial skull except the anterior end, left P^2–M^3. It was figured in Gaudry (1904, fig. 15).

P^1 was present and is represented by a small, single alveolus. As Gaudry noted, the crown of P^1 in his figure was taken from a "Cerro Negro" (Colhué-Huapí) specimen. Although not noted, P^2 has been restored; it is broken in the specimen. The figure is somewhat generalized and fails to show a slight groove on the lingual face of P_4, but is otherwise accurate. The size and morphology are within the established range of *Notostylops murinus* (see Simpson, 1948), except that the length of P^3 is slightly below the previously known range. However, it is not below the statistically probable range for the species. The measurements of these teeth are: P^2, length, *ca.* 5, width, *ca.* 7; P^3, length, 6.6, width, 9.0; P^4, length, 8.2, width, 11.3; M^1, length, 9.1, width, 12.6; M^2, length, 10.4, width, 12.6; M^3, length, 9.4, width, 12.0.

Notostylops cf. murinus Ameghino, 1897

M.H.N. Tournouër Collection No. 28 is a palate with part of the face and with badly broken left P^1 and well-preserved left P^2–M^3 and right P^3–M^3. There is no groove on the lingual face of P^4. Such a groove is invariably present in specimens surely referable to *N. murinus*, but is absent from one or two specimens that may be mere variants in that species. P^4 of this Tournouër specimen is smaller, and M^1 is wider, than otherwise known in *N. murinus* (see Simpson, 1948, table 48), but within the possible range. The measurements of the teeth in M.H.N. Tournouër Collection No. 28 are: P^2, length 5.0, width, 6.7; P^3, length, 7.0, width, 9.9; P^4, length, 7.3, width, 10.8; M^1, length, 8.9, width, 13.2; M^2, length, 9.7, width, 13.3; M^3, length, 9.8, width, 11.8.

M.H.N. Tournouër Collection No. 11 includes a number of isolated teeth and jaw fragments and also a partial right lower jaw with P_4–M_3. The widths of P_4–M_2 are larger than in my previous sample of *N. murinus* (Simpson, 1948, table 47), but the differences are doubtfully significant or not significant statistically. Measurements are given in table 2.

Homalostylops parvus (Ameghino, 1897)

The Tournouër Collection includes four partial lower jaws of this elegant little notostylopid. The morphology is just that previously described for the species (Simpson, 1948) and, although some measurements differ slightly, they are well within the probable specific range (see table 2).

TABLE 2

Homalostylops parvus, TOURNOUËR COLLECTION

Specimen No.	P_2		P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W	L	W
12	4.1	3.1	5.0	4.2	5.6	5.2	6.1	4.6	—	—	—	—
13	—	—	—	—	6.3	4.3	5.7	4.5	7.1	5.3	—	—
14	—	—	5.4	4.0	5.8	5.1	6.2	4.6	6.6	4.9	8.7	4.6
15	4.5	2.3	4.8	3.6	5.9	4.6	6.0	4.2	6.3	4.6	8.0	4.1

Edvardotrouessartia sola Ameghino, 1901

Previous discussion of this genus and species (Simpson, 1948) was based on Ameghino's publications, on a photograph of the type of the species, and on a referred specimen found by me. The type had not been located in the Ameghino Collection. Now Cattoi has found a lot of specimens, M.A.C.N. No. A55-7, labeled by Ameghino as belonging to this species and as from "Este de Río Chico Notostylops," i.e., Casamayoran. Included are a right lower jaw fragment with M_{2-3}, a broken left M_3 of a different individual, and a fragment of a right maxilla with P^4–M^1 of still a third individual. The last-mentioned specimen is apparently the original of Ameghino (1904b, figs. 388 and 389), although P^4 and M^1 are there figured as separate. As previously noted (Simpson, 1948, p. 218), those figured teeth are mislabeled and do not belong to the same family, genus, or species as *Edvardotrouessartia sola*. They, as well as the other two specimens under M.A.C.N. No. A55-7, are Isotemnidae, not otherwise precisely identified. The type of *Edvardotrouessartia sola* is still missing.

SYSTEMATICS, PART 2

ORDER **NOTOUNGULATA** (CONCLUDED)

SUBORDER **TYPOTHERIA** ZITTEL, 1893

DEFINITION: Dentition primitively complete and closed, but with a strong tendency to reduce or lose lateral incisors, canines, and anterior premolars and to develop a diastema in this region. Incisors primitive in Archaeopithecidae but in all other groups early becoming scalpriform and, in later forms one pair of upper incisors, at least, becoming gliriform. Canines, when present, small and incisiform. Cheek teeth brachydont in earliest and most primitive forms, but with accelerated tendency toward hypsodonty even in the early faunas and by Deseadan time all hypsodont and most rootless. Upper molar patterns varied and not fundamentally different from those of Toxodonta but all apparently departing from a basic pattern that was relatively complex for its time, with well-developed protoloph, metaloph, ectoloph, posterior cingulum, often also an entoloph, and two cristae, a crochet and in some cases an antecrochet variously developed and connected, the first crista normally united to the protoloph. Nasals long and not retracted, even in advanced forms. Zygoma and its anterior root expanded, rodent-like in habitus, but muscle attachments not extending onto muzzle or into infraorbital foramen. Septum in the bulla vestigial or absent, hypotympanic sinus tending to fill with cancellous bone from medial wall in later forms, styliform process usually present at anterior end of bulla, but may be lost, internal carotid traversing bulla. Brain unprogressive, retaining triangular or pyriform contour and linear arrangement even in relatively large and late forms. Clavicles retained. Limbs primitive in general, the only apparent specializations being that they tend to become moderately slender and elongate, the feet digitigrade, and one digit in some cases lost. The animals small to medium in size and characterized in a broad way by rather strong convergent habitus resemblance to the rodents or, even more, the lagomorphs.

DISTRIBUTION: Riochican to Pampean, South America.

This group was originally based on the latest and most specialized genus, *Mesotherium* (= "*Typotherium*"), and the earlier interatheres and hegetotheres were referred to it because, although unlike *Mesotherium* in many other ways, they share its rodent-like habitus. Ameghino (e.g., 1906) accepted this grouping for the mid-Tertiary and later forms, placing in the Typotheria the three families "Typotheriidae" (= Mesotheriidae), Hegetotheriidae, and "Protypotheriidae" (= Interatheriidae). The Hegetotheriidae were traced by him to the Mustersan, and the "Protypotheriidae" to the Deseadan. He also added, in Deseadan and Casamayoran, the "Eutrachytheriidae," now considered early Mesotheriidae. The Casamayor genera placed in this family were based on astragali and are extremely dubious, so that the mesotheres (typical typotheres) are not now surely recognized before the Deseadan. Ameghino did not place any other Casamayoran forms in the Typotheria. The Archaeopithecidae and "Notopithecidae" (= Notopithecinae, a subfamily of the Interatheriidae) were called "Prosimiae" and the "Acoelodidae" (= Oldfieldthomasiidae) were placed in the Hyracoidea.

Although the collocation of Interatheriidae and Mesotheriidae in the Typotheria cannot be considered wholly certain, it has not been very seriously challenged and is retained here and by all other recent authors. This placing for the Hegetotheriidae has, however, been cogently questioned by Patterson (especially 1936), and I (Simpson, 1945) tentatively removed them to a separate suborder, Hegetotheria (see below). They are not further considered in this section.

With recognition that the "Eutrachytheriidae" are early Mesotheriidae and the "Notopithecidae" early Interatheriidae, the remaining question is where to place the Oldfieldthomasiidae, Archaeopithecidae, and Archaeohyracidae. Scott (1913) placed all three in the Typotheria, and Schlosser (1923) did the same, with somewhat greater detail. On this authority, such has been the usual course by recent students, but this has been somewhat an act of faith rather than of knowledge, because no real restudy of the families was involved. Even Schlosser, who did have some good specimens at hand, had a decidedly inadequate view of the problem. He placed the very different Henricosborniidae in the Archaeopithecidae and subordinated to this family the more numerous and distinctive Oldfieldthomasiidae ("Acoelodidae"), to which he referred *Eohyrax*, although that genus seems well placed in the Archaeohyracidae, as Ameghino had shown.

In my first studies on these early faunas I concluded that the Archaeopithecidae could not be distinguished from the "Notopithecidae" on the basis of cheek teeth, all that was then known of the former family, and I queried whether the Archaeohyracidae and "Acoelodidae" were typotheres or toxodonts (Simpson, 1934d). It later appeared that the Archaeopithecidae, as shown by new materials collected by us, must be separated from the "Notopithecidae," because they lack the incisor and zygoma specializations of the Interatheriidae, to which the "Notopithecidae" are now referred. Later I tentatively placed the three families in question (Oldfieldthomasiidae, Archaeopithecidae, Archaeohyracidae) in the Toxodonta (Simpson, 1945, written in 1942). I am now still rather tentatively reversing part of this decision and returning the Oldfieldthomasiidae and Archaeopithecidae to the Typotheria. The Archaeohyracidae are now placed in the Hegetotheria with somewhat more confidence on the basis of Patterson's still unpublished studies of the much better known Deseadan forms.

This vacillation and the fact that the present arrangement is not advanced with strong conviction reflect the confusing nature of these early faunas, when all families were so near a common origin that they closely and confusingly resemble one another in many ways, and when the phyletic and subordinal differences so marked in later times were only incipient. These three families resemble early toxodonts (Isotemnidae) more than they do later typotheres or hegetotheres. It is improbable that they are directly ancestral to later, undoubted typotheres or hegetotheres, at least in the known forms. Therefore it would be permissible taxonomy to broaden the Toxodonta at the base and include in it a horizontal grouping of forms differentiating at a level higher than the Notioprogonia but not yet clearly specialized along the lines of later Tertiary suborders. Such action would imply that the typotheres and hegetotheres might (verbally) be derived from early toxodonts, which was the basis of my tentative arrangement published in 1945.

On the other hand, although the Oldfieldthomasiidae are very similar to the Isotemnidae and probably quite close to the latter as regards horizontal grouping or a common ancestry, they have diverged and have some early specialization which seems to be distinctly in the direction of the Archaeopithecidae. The Oldfieldthomasiidae seem to be very close also to that family, especially when attention is focused on progressive rather than on primitive characters. The Archaeopithecidae in turn seem to be close to the Interatheriidae. The Notopithecinae, early Interatheriidae, are considerably more like the Archaeopithecidae than like later Interatheriidae, even though they have, and the Archaeopithecidae lack, the basic interatheriid incisor and zygoma specializations. The Interatheriidae could well be derived from the Archaeopithecidae, although not from the known forms of the latter because these are contemporaneous with true Interatheriidae.

The earliest Archaeohyracidae are also very like the Oldfieldthomasiidae and Archaeopithecidae, but are more progressive than these. Their progressive characters suggest the Mesotheriidae, largely owing to parallelism. The last and most mesothere-like archaeohyracid is contemporaneous with but distinct from the earliest unquestionable true mesothere, and, as already mentioned, the Deseadan archaeohyracids have been found by Patterson to have probably diagnostic hegetothere characters.

The families included in the Typotheria, under this modified concept of that suborder, are thus as follows, in approximate order of increasing basic specialization:

Oldfieldthomasiidae
Archaeopithecidae
Interatheriidae
Mesotheriidae

Family OLDFIELDTHOMASIIDAE
Simpson, 1945

(Acoelodidae Ameghino, 1901. [Doubtfully equal to this family; see text below.])

Definition: Notoungulates of primitive type, skull of generalized proto-toxodont stamp, dentition also primitive, but with characteristic complication of the upper molar pattern. Dentition, $\frac{3}{3}\frac{1}{1}\frac{4}{4}\frac{3}{3}$, brachydont, in closed series, rather evenly transitional, but premolars not fully molariform. No incisors markedly enlarged. Canines incisiform. Upper premolars triangular, usually without internal sulcus. M^{1-2} moderately to strongly transverse. Coronal pattern similar to that of Notopithecidae and Archaeopithecidae: protocone and hypocone distinct but joined nearly to apices, never fully separate; three constant fossettes, one large and internal, two small, anteroexternal and posteroexternal, in some cases also a median external fossette; strong parastyle and paracone folds on external wall, usually weaker metacone fold, in some cases also distinct mesostyle and metastyle folds. Lower premolars more or less compressed transversely. Lower molars of very simple notoungulate type: metaconid little expanded and without accessory cuspule; no closed trigonid basin; talonid fossettes lacking or transitory; entoconid pillar-like, not expanded, and not fully fused with external crescent; hypoconulid distinguishable in crescent, strongly so on M_3. Nares anterior, snout long, nasals slender. Orbit medial, lacrimal foramen immediately internal to rim, with prominent tubercle. Well-developed postorbital processes. Jugal normal, large, reaching lacrimal. Epitympanic and tympanic sinuses moderately and about equally inflated. No septum in tympanic. Mandible slender.

Distribution: Riochican, Casamayoran, and Mustersan of Patagonia.

The definition given is based primarily on *Oldfieldthomasia* but does not exclude the other genera tentatively placed in the family. When these other genera are better known, it may be found that some of the stated characters are not common to all members of the family. The definition as now given does distinguish this group from all others known, but in some respects the distinctions are perhaps trivial and none too clear-cut, especially as regards the Archaeopithecidae on one hand and the Isotemnidae on the other.

This family is essentially that called Acoelodidae by Ameghino. I have retained Ameghino's names whenever possible, but in this case it would have been highly misleading to do so and would not have promoted stable nomenclature. Ameghino's conception of the family was based almost entirely on *Oldfieldthomasia*, not on *Acoelodus*. Indeed, it is doubtful whether *Acoelodus* really belongs to this family. As shown below, that genus is in general of extremely dubious status and is almost a *nomen vanum*, although it might be rehabilitated and its proper position established by future discovery. In the meantime *Oldfieldthomasia* is a relatively well-known, sharply defined genus which does, in fact, typify this family.

Ameghino reported the Acoelodidae from the Casamayoran only, and referred to it *Acoelodus*, *Oldfieldthomasia*, *Paracoelodus*, and *Anchistrum*. As previously noted, *Acoelodus* is a dubious form, and *Oldfieldthomasia* is the real basis for this family. *Paracoelodus* probably belongs here, but it is apparently a synonym of *Maxschlosseria*, which Ameghino placed in the Isotemnidae. *Ultrapithecus*, referred to the Archaeopithecidae by Ameghino, is evidently closely related to *Maxschlosseria* and may also be placed in the Oldfieldthomasiidae. *Anchistrum* seems to me to be an isotemnid. Another Casamayoran genus, *Paginula*, referred to the Isotemnidae by Ameghino, is of dubious affinities, but it resembles the Oldfieldthomasiidae a little more than it does the Notopithecinae or Isotemnidae and is tentatively placed in the Oldfieldthomasiidae. Thus the Casamayoran genera now recognized in the family are *Oldfieldthomasia*, *Ultrapithecus*, and *Maxschlosseria*, with *Acoelodus* and *Paginula* more doubtfully referred. In preliminary studies for this memoir, I found that unidentified specimens in the Roth Collection represent a possible Mustersan oldfieldthomasiid, which I named *Tsamnichoria*, and the Riochican collections also contain a probable member of this family, named *Kibenikhoria* in my preliminary description of that faunal stage.

TABLE 3

Comparison of Five Genera of Oldfieldthomasiidae

Kibenikhoria	*Oldfieldthomasia*	*Ultrapithecus*	*Maxschlosseria*	*Tsamnichoria*
P¹ two-rooted, longer than wide	P¹ two-rooted, longer than wide	P¹ one-rooted, wider than long	P¹ one-rooted (?), longer than wide	(Unknown)
No internal groove on upper premolars	No internal groove on upper premolars	Feeble grooves on P^{3-4}, which are somewhat quadrate	No internal grooves on upper premolars	Internal grooves on P^{2-4}, P^4 markedly quadrate
Metacone fold absent from premolars, distinct on molars	Metacone fold well developed on both molars and premolars	Metacone fold absent from premolars, weak on molars	Metacone fold absent from premolars, weak on molars	Metacone fold feeble on premolars, distinct on molars
No mesostyle, deep basal pocket	Strong mesostyle on molars	Mesostyle rudimentary or absent, region flat, no pocket	Mesostyle rudimentary or absent, region flat, no pocket	Mesostyle rudimentary, no pocket
No median external fossette in known wear stages	A median external fossette, deeply united to main (inner) fossette, even with advanced wear	No median external fossette in known wear stages	No median external fossette in known wear stages	No median external fossette in known wear stages
Anteroexternal fossette poorly distinguished from main fossette	Anteroexternal fossette shallow, but well distinguished from main fossette	Anteroexternal fossette poorly distinguished	Anteroexternal fossette poorly distinguished	Anteroexternal fossette poorly distinguished

With the omission of the more doubtful *Acoelodus* and *Paginula*, the five genera here tentatively grouped as Oldfieldthomasiidae can be distinguished as shown in table 3.

There are other minor distinctions, discussed under the several genera. The markedly more complex molars distinguish *Oldfieldthomasia* rather sharply from the other four genera, which are so much alike in this respect that isolated molars can hardly be distinguished generically. This fact casts some doubt on whether the group is, after all, natural and whether *Oldfieldthomasia* is not the unique representative of one group while the other genera are archaeopithecids, isotemnids, or a separate group in themselves. Such is a distinct possibility, but there is a certain stamp of similarity to *Oldfieldthomasia*, and of difference from archaeopithecids and isotemnids, in the dentitions as a whole. The tentative union of all five genera in this family seems convenient and conservative pending more detailed knowledge, especially of the skulls.

KIBENIKHORIA SIMPSON, 1935

Kibenikhoria SIMPSON, 1935a, p. 16.

TYPE: *Kibenikhoria get.*

DISTRIBUTION: "*Kibenikhoria* faunule," Riochican of Cañadón Hondo.

DIAGNOSIS: P^1 two-rooted, longer than wide. P^2 simple, not developing a closed fossette unless possibly in the last stages of wear. P^{1-3} relatively less transverse than in *Ultrapithecus*. No internal groove on upper premolars. Metacone fold absent from premolars but distinct on molars. No mesostyle, this region with a small, deep basal pocket on molars. Coronal pattern of molars similar to that of *Maxschlosseria* or *Ultrapithecus*. Brachydont, but crowns relatively high for this fauna.

Contrary to my first opinion, I think that this genus may be closer to *Maxschlosseria* than to *Ultrapithecus*, but these genera are, in any case, so similar that this point is unimportant. On the other hand, the tendency toward higher crowns at this early date might suggest a trend in the direction of the Archaeopithecidae, which also have closely similar dentitions.

The diagnosis of the genus is based on the upper teeth, but isolated lower teeth or jaw fragments with two or three teeth which are almost surely of *Kibenikhoria* also occur in the collection. They seem to be highly variable, probably owing to the different wear stages and to the fact that most of them are broken or crushed. As in the upper teeth, the crowns are higher than in other members of this fauna. The hypoconulid is small and appears as a small spur. The entoconid forms a large and plump tranverse crest, and the valley between this and the expanded metaconid is deep and narrow. The hypoconid crescent abuts against the middle of the protolophid, from which its apex is free, although the bases are completely fused. The metaconid is simple even when only slightly worn.

There are also several symphyses, without tooth crowns, in the collection, which probably belong to this genus, to judge from their abundance, size, and general character. They are long and slender, I_1 to C all strongly procumbent and arranged in a narrow parabola, the roots increasing constantly in size from I_1 to C.

Kibenikhoria get Simpson, 1935

Text figure 3

Kibenikhoria get SIMPSON, 1935a, p. 19, figs. 18–19; 1937a, fig. 9c.

TYPE: A.M.N.H. No. 28542, part of left maxilla with P^2–M^1 and roots of P^1.

HYPODIGM: A series of specimens, all from the type horizon and locality, among which the following are the most important: type, as above; A.M.N.H. No. 28563, part of right maxilla with P^2–M^3; A.M.N.H. No. 29103, left M^{2-3}; A.M.N.H. No. 28544, right M_{1-2}; A.M.N.H. No. 28548, left M_3; A.M.N.H. No. 28543, left M_3; A.M.N.H. No. 28552, symphysis, without teeth.

HORIZON AND LOCALITY: "*Kibenikhoria* faunule," Riochican of Cañadón Hondo, Patagonia.

DIAGNOSIS: Sole known species of genus. Measurements of the type are: P^2, length, 5.2, width, 6.3; P^3, length, —, width, 7.1; P^4, length, 5.5, width, 8.3; M^1, length, 6.3, width, 8.3.

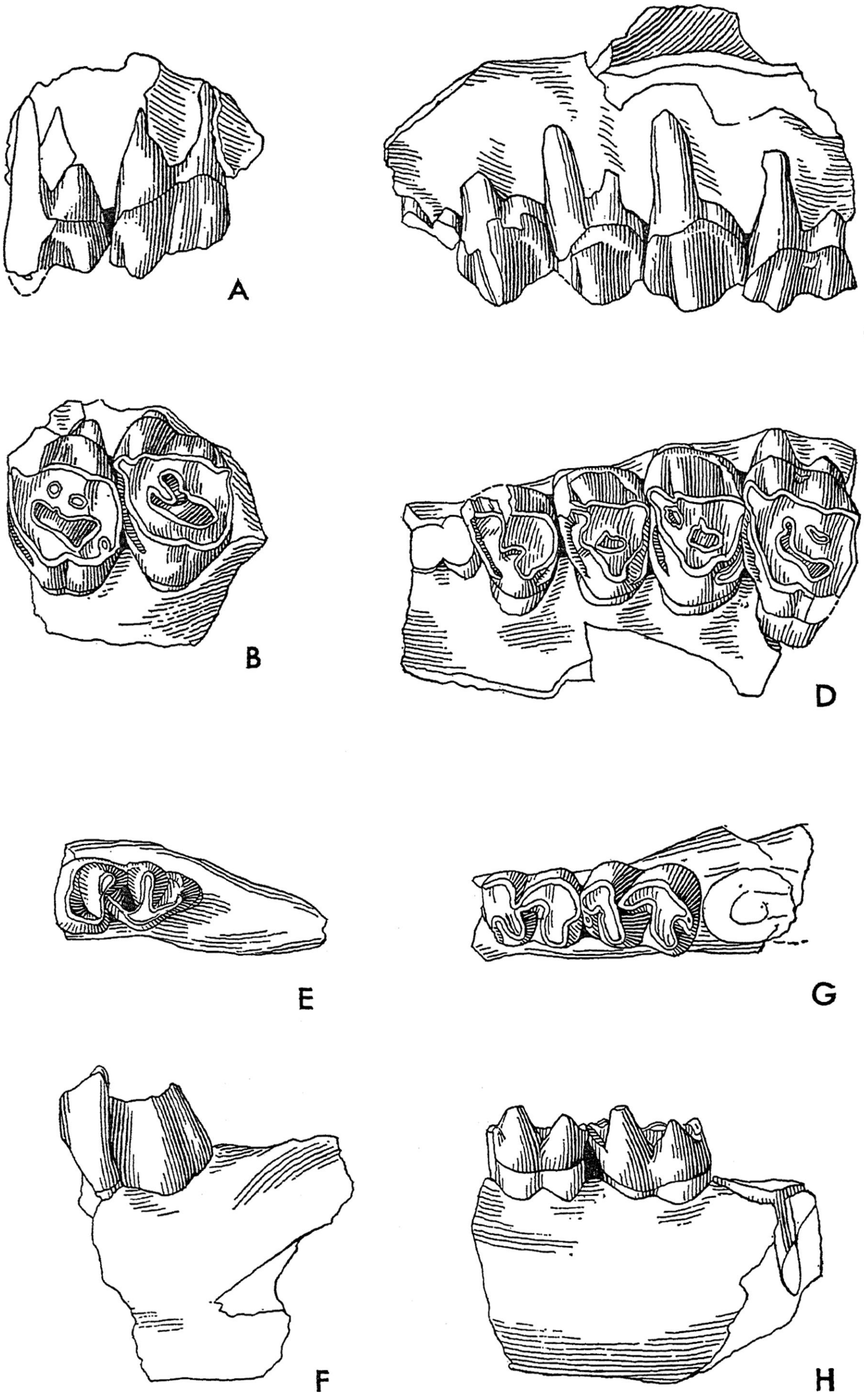

FIG. 3. *Kibenikhoria get* Simpson. A–D. Upper cheek teeth. A, B. A.M.N.H. No. 29103, left M^{2-3}. A. Buccal view. B. Crown view. C, D. A.M.N.H. No. 28542, type, left P^{2}–M^{1}. C. Buccal view. D. Crown view. E–H. Lower cheek teeth. E, F. A.M.N.H. No. 28548, left M_{3}. E. Crown view. F. Buccal view. G, H. A.M.N.H. No. 28544, right M_{1-2}. G. Crown view. H. Buccal view. All ×2.5.

OLDFIELDTHOMASIA AMEGHINO, 1901

Oldfieldthomasia AMEGHINO, 1901, p. 366; 1904b, p. 45; 1906, p. 467. SCHLOSSER, 1923, p. 609, fig. 754. ROTH, 1927, p. 248. SIMPSON, 1932e, p. 7, fig. 5; 1936a, p. 3, figs. 1–9. SCOTT, 1937a, p. 516.

TYPE: *Oldfieldthomasia furcata* (= *O. debilitata*).

DISTRIBUTION: Casamayor, Patagonia.

DIAGNOSIS: With the characters given for the family. P^1 two-rooted, longer than wide. No internal groove on upper premolars. Metacone fold strong on both premolars and molars, strong mesostyle on molars. Anteroexternal and posteroexternal fossettes on molars both well separated from main, internal fossette. A median external fossette deeply united with main fossette.

Ameghino named 11 species in *Oldfieldthomasia*, but later removed one to a new genus, *Paracoelodus*. I would remove another species, *O. septa*, to that genus, or rather to *Maxschlosseria*, with which it is synonymous, but would refer *Acoelodus debilitatus* to *Oldfieldthomasia*, so that 10 of Ameghino's species are placed in this genus. One of these is well defined, *O. debilitata;* six seem certainly to be synonyms; and the other three are retained, but their characters are not well known and they are not clearly or certainly definable. Despite the abundance and variability of remains of *Oldfieldthomasia*, no other generic name seems to have been based on them.

As regards the upper teeth, at least, *Oldfieldthomasia* is so distinctive that it can hardly be confused with any other genus. It is one of the commoner fossils at most Casamayoran localities and makes an excellent guide fossil in the field.

The morphology is discussed in connection with the one well-known species, *O. debilitata*.

Oldfieldthomasia debilitata (Ameghino, 1901)

Plates 2–6; text figures 4–16

Acoelodus debilitatus AMEGHINO, 1901, p. 365.

Oldfieldthomasia debilitata: SIMPSON, 1932e, p. 7, fig. 4. SCOTT, 1937a, p. 517, fig. 327.

Oldfieldthomasia furcata AMEGHINO, 1901, p. 366; 1906, p. 308, fig. 117.

Oldfieldthomasia cuneata AMEGHINO, 1901, p. 366; 1904b, p. 47, figs. 42, 72, 125.

Oldfieldthomasia cingulata AMEGHINO, 1901, p. 366; 1904b, p. 86, figs. 88–89; 1904d, p. 60, fig. 45.

Oldfieldthomasia conifera AMEGHINO, 1901, p. 367.

Oldfieldthomasia plicata AMEGHINO, 1904a, vol. 56, p. 199; 1904b, p. 209, fig. 279.

TYPE: M.A.C.N. No. 10376, skull with nearly complete but deeply worn dentition. No locality data.

TYPES OF SYNONYMS: Of *O. furcata*, M.A.C.N. No. 10748, left maxilla with P^1–M^3, M^3 broken,[1] from Colhué-Huapí; of *O. cuneata*, M.A.C.N. No. 10762, right maxilla with P^1–M^3, from Colhué-Huapí; of *O. cingulata*, M.A.C.N. No. 10772, badly preserved skull with deeply worn right P^2–M^3 and left P^4–M^3, from Colhué-Huapí; of *O. conifera*, M.A.C.N. No. 10757, part of left maxilla with P^4–M^3, from Colhué-Huapí; of *O. plicata*, M.A.C.N. No. 10764, isolated right dm^4 (type or lectotype), also left M^{2-3} and broken M^1, not associated, from Colhué-Huapí.

HYPODIGM: The types, as above, and large series of specimens, especially in the Ameghino Collection in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" and the Scarritt Collection in the American Museum of Natural History, among them the following: M.A.C.N. No. 10765, anterior part of skull with right P^{2-4} and left P^2–M^3, from Colhué-Huapí; M.A.C.N. No. 10400, most of a skull, badly preserved, with parts of left P^2–M^3 and right P^1–M^3, without locality data; M.A.C.N. No. 10761, right P^4–M^3, from Colhué-Huapí, figured as *O. cingulata* by Ameghino (1904b, figs. 88–89); M.A.C.N. No. 10749, four unassociated lower jaw fragments: left P_2–M_1, left M_{2-3}, right P_2–M_3, and left P_{2-4}, from Colhué-Huapí; M.A.C.N. No. 10744, left lower jaw with M_{2-3}, from west of the Río Chico; M.A.C.N. No. 10750, three lower jaw fragments, not associated: left M_{2-3}, left P_2–M_1, and right M_{1-2}, from Colhué-Huapí; A.M.N.H. No. 28680, associated right I^{2-3} and P^1–M^3, left I^{2-3}, right M_{2-3}, and left P_{2-4} and M_{2-3}, Colhué-Huapí; A.M.N.H.

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[1] Part of the definition, referring to the cranium, could not have been based on this or any other specimen labeled as of this species now in the collection. These characters must have been based on an unlabeled or lost specimen or on inference. There is no doubt that M.A.C.N. No. 10748 is the chief if not the only original type.

No. 28780, part of left upper jaw with I^2–P^3 and associated natural endocranial cast, Colhué-Huapí; A.M.N.H. No. 28632, poor cranium and associated left P^1–M^2, Colhué-Huapí; A.M.N.H. No. 28691, facial skull with left dm^1–M^3 and right dm^1–M^2, Colhué-Huapí; A.M.N.H. No. 28896, badly preserved skull, but top of cranium and left zygoma well preserved, Colhué-Huapí; A.M.-N.H. No. 28600, well-preserved cranium (one-half serial sectioned), Cerro Blanco; A.M.N.H. No. 28678, right dm^{1-4}, M^{1-2}; A.M.N.H. No. 28730, part of lower jaw with left P_1–M_2 and right I_1–C, Colhué-Huapí; A.M.N.H. No. 28963, lower jaw with left P_3–M_3 and right P_2–M_2, Colhué-Huapí; C.N.H.M. (not catalogued, field no. 191c), associated fragments with left P_4–M_3 and right P_4–M_3.

HORIZON AND LOCALITY: Casamayor, Patagonia. Types of known provenience and most referred specimens from south of Colhué-Huapí.

DIAGNOSIS: The only well-known species of the genus. Mean dimensions of M^1 in Ameghino sample, 6.90 by 9.73 mm.; of M^2, 7.55 by 10.61.

TAXONOMY

This species was referred by Ameghino to *Acoelodus*, probably in the belief that it had no mesostyle, since this is the most striking difference between the two genera as Ameghino conceived of them. The specimen otherwise conforms with Ameghino's conception of *Oldfieldthomasia* and not of *Acoelodus*. The mesostyle disappears in very worn *Oldfieldthomasia* molars, and vestiges of it are present on this old specimen on M^{2-3}, so that there is no doubt that it really belongs to *Oldfieldthomasia*. *Oldfieldthomasia furcata* was based on a less worn specimen and also one in which perhaps an anomaly and certainly an erroneous reconstruction (as shown in the description of the dentition, below) led to wrong identification of the anterior cheek teeth.

Oldfieldthomasia cuneata was differentiated from *O. furcata* as having P^1 smaller than P^2, the external folds stronger, and the parastyle fold prolonged anteriorly. The first character is really normal for *O. furcata*, the supposed difference arising from erroneous identification of teeth in that species. The other two characters are functions of age, this type being younger. In a comparable stage of wear it would be almost exactly like the type of *O. furcata*.

Oldfieldthomasia cingulata was supposed to have the external folds stronger than in *cuneata* and an external cingulum on all upper cheek teeth and an internal cingulum on the molars. The first character is barely noticeable and surely well within the range of individual variation. The external cingulum is weak and is not the same on the two sides of this individual, which differ about as much as either side does from individuals referred to *furcata* or *cuneata* by Ameghino. There is no internal cingulum on M^1, and it is variable on M^{2-3}. A specimen referred to *cingulata* by Ameghino does not have strong external folds or cingula, so that his conception of the species cannot have agreed entirely with the published diagnosis. I do not detect any structural or size characters not clearly within the range of the large series of *debilitata* now available.

Oldfieldthomasia conifera was described without differential diagnosis. The type specimen is poorly preserved but almost unworn, and the description and characters are those of an unworn *debilitata*. All the apparent differences would disappear were the teeth worn to the levels of the other types.

Oldfieldthomasia plicata was based on a single tooth considered as M^1. On this basis it would be distinctive in being lower-crowned and less transverse. None of the other characters in Ameghino's description are unlike those of *O. debilitata* in a similar stage of wear. The agreement with dm^4 of *O. debilitata* is so close that the only reasonable assumption is that the tooth is dm^4 and the species a synonym.

As regards size, it is necessary to allow for marked variation, as is conclusively shown by the fact that measurements on opposite sides of the same individual seldom agree exactly and differ by as much as 0.9 mm., or 10 per cent, by careful measurements made at the same time in the same way. Extremes of wear stages are also represented and strongly affect the length measurements. Our series of upper teeth does not give more than five values for any one variate, but combined with

TABLE 4

STATISTICAL DATA FOR UPPER TEETH OF COMBINED SAMPLES OF *Oldfieldthomasia debilitata*

Variate	N	R	$\bar{X}$	s	V
LP^2	10	6.0– 7.6	6.66±.14	.44±.10	6.6±1.5
WP^2	9	5.7– 6.7	6.24±.12	.35±.08	5.7±1.3
LP^3	9	5.9– 6.8	6.49±.10	.29±.07	4.5±1.1
WP^3	9	7.1– 8.2	7.67±.11	.34±.08	4.4±1.0
LP^4	10	5.9– 7.1	6.64±.12	.38±.08	5.7±1.3
WP^4	11	8.3–10.5	9.13±.16	.55±.12	6.0±1.3
LM^1	11	6.4– 7.8	6.90±.11	.36±.08	5.3±1.1
WM^1	12	9.2–10.1	9.73±.08	.29±.06	2.9±0.6
LM^2	11	6.9– 8.3	7.55±.11	.38±.08	5.1±1.1
WM^2	11	9.8–11.0	10.61±.10	.34±.07	3.2±0.7
LM^3	11	6.7– 8.1	7.39±.13	.42±.09	5.5±1.2
WM^3	10	9.5–10.5	9.98±.09	.28±.06	2.8±0.6

the Ameghino Collection it gives a good idea of the variation of the species. The figures in table 4 include six Scarritt specimens, all from the richest horizon south of Colhué-Huapí, and eight Ameghino specimens, including the types of *Acoelodus debilitatus*, *Oldfieldthomasia furcata*, *O. cuneata*, *O. cingulata*, and *O. conifera*, and specimens referred to *O. cuneata*, *O. cingulata*, and *Acoelodus oppositus*.[1] All except the type of *Acoelodus debilitatus* are labeled as from south of Colhué-Huapí, and that specimen was probably from there also, although the data are lost.

It is possible that minor temporal mutations are present in this combined sample, which may represent more than one precise horizon, although our samples suggest no significant difference between specimens of different horizons at this locality. That such differences may be present is suggested by the fact that the Scarritt specimens average slightly smaller than those of Ameghino in most dimensions, although the difference is not statistically significant. The constants and the distributions are, however, entirely consistent with pertinence to a single species. The measurements that are most reliable and least affected by wear, widths of molars, are indeed remarkably little variable. The greatest coefficient of variation, 6.6±1.5, is not unusually large, and the corresponding maximum percentage difference is 27 per cent, which is not remarkable as the greatest difference in a species in which homologous measurements on different sides of a single individual have been observed to differ by 10 per cent. None of Ameghino's types in this genus are or include lower jaws. There are numerous lower jaws in his collection, and he correctly identified most of these as belonging to *Oldfieldthomasia debilitata* or synonyms, although a few that seem clearly also to belong here were referred to *Acoelodus oppositus*.

We have 19 partial lower jaws with teeth from three different horizons south of Colhué-Huapí. Comparison of groups from the separate horizons revealed no constant or significant differences, although the whole sample, as would be expected, varies more than any of the included samples from a single horizon. The variation does not, in any case, exceed that usual for a single species, nor is any means of separating the whole sample into lesser taxonomic units suggested. The principal statistical data for the Scarritt sample from this locality are given in table 5.

The Ameghino lower jaws from this locality are all within the range of ours except for the following: one specimen has LP_4 5.6; one has LM_2 7.6; and two have WM_2 5.6.

These would not, however, greatly alter the constants given.

The value of V for LM_1 is raised by the great changes in this dimension due to wear. The whole sample happens to include two completely unworn specimens of this tooth,

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[1] Probably the label of this specimen, M.A.C.N. No. 10400, was misplaced, for it is very unlikely that Ameghino really referred to *A. oppositus* a specimen so unlike his conception of that species.

TABLE 5

STATISTICAL DATA FOR LOWER TEETH[a] OF *Oldfieldthomasia debilitata*

Variate	*N*	R	X	s	V
LP_3	3	6.1–7.1	6.50	—	—
	6	5.9–7.1	6.38±.15	.38±.11	5.9±1.7
WP_3	3	3.2–3.8	3.53	—	—
	6	3.2–3.8	3.60±.09	.23±.07	6.4±1.9
LP_4	7	5.8–6.7	6.19±.11	.30±.08	4.9±1.3
	11	5.8–7.0	6.29±.11	.37±.08	5.8±1.2
WP_4	7	3.9–4.6	4.24±.08	.22±.06	5.2±1.4
	11	3.9–5.0	4.37±.09	.30±.06	6.9±1.5
LM_1	8	5.6–6.7	6.11±.15	.41±.10	6.7±1.7
	15	5.6–7.3	6.39±.14	.56±.10	8.7±1.6
WM_1	7	4.3–5.1	4.69±.09	.25±.07	5.3±1.4
	14	4.3–5.2	4.81±.07	.26±.05	5.4±1.0
LM_2	6	6.6–7.1	6.88±.06	.16±.05	2.3±0.7
	11	6.5–7.3	6.94±.07	.24±.05	3.4±0.7
WM_2	7	4.6–5.3	4.96±.09	.24±.07	4.9±1.3
	12	4.6–5.4	5.03±.08	.28±.06	5.6±1.1
LM_3	6	8.3–9.2	8.82±.14	.34±.10	3.9±1.1
	10	8.3–9.8	9.04±.13	.43±.10	4.7±1.1
WM_3	6	4.4–5.4	4.88±.13	.31±.09	6.4±1.9
	10	4.4–5.4	5.03±.10	.32±.07	6.4±1.4

[a] For each tooth the upper value is for a sample from a single horizon and the lower for the whole sample from Colhué-Huapí.

and their high values for length increase the coefficient of variation markedly but do not in fact increase the biological variability of the species which would be more nearly represented by a coefficient of six or less. The samples are not large enough for separation into age groups, and this fact must be kept in mind in dealing with the data derived from them.

There are a number of odd specimens from scattered localities that seem to belong to this species or to varieties of it. Comparisons of the more important of these with our whole Colhué-Huapí sample are given in table 6, the values entered being d/s.

A.M.N.H. No. 28873, which has an unusually weak mesostyle fold, in addition to being relatively little transverse, may not belong to this species, but the other specimens rather clearly do. They show that it may occur almost anywhere in the area of the Casamayor beds, but it has so far been rare elsewhere than south of Colhué-Huapí.

DENTITION

The dentition is complete and in closed series. Only the lower canine may be very slightly spaced; otherwise the teeth are crowded and overlap, with a reversal of the direction of overlap definitely on P^1 and vaguely on P_1.

The type of the genotype (*O. furcata*), M.A.C.N. No. 10748, was interpreted by Ameghino as having I^3–M^3, which would make the canine and P^{1-2} much more progressive than in any other specimen referred to the genus. In fact the premaxillo-maxillary suture is anterior to the first tooth preserved, which is therefore the canine, and the premolar series includes five teeth as the specimen is preserved. The first two teeth are morphologically like P^{1-3} of normal specimens and the last two like P^{3-4}. The third tooth resembles P^3, and in this specimen virtually duplicates the fourth. The specimen is crushed in this region, and the apparent two third premolars are very crowded and pushed out of line. The specimen has been repaired with "mastic,"[1] so that the real character is

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[1] "Mástico," prepared by mixing plaster and hot melted beeswax, used in the preparation of most of Ameghino's specimens. It conceals many points of importance, much impairs the appearance of the specimens, and has frequently been instrumental in their deteriora-

TABLE 6

VALUES OF D/S FOR SCATTERED SINGLE SPECIMENS OF *Oldfieldthomasia* IN COMPARISON WITH THE COLHUÉ-HUAPÍ SAMPLE OF *O. debilitata*

		C.N.H.M. Field No. 191c, Estancia Procaccia	C.N.H.M. No. 13440, Punta Casamayor	A.M.N.H. No. 28836, Cerro Blanco	A.M.N.H. No. 28873, Cabeza Blanca
P_4					
	L	0.8	—	—	—
	W	0.8	—	—	—
M_1					
	L	0.4	—	—	—
	W	2.3	—	—	—
M_2					
	L	1.9	0.3	—	—
	W	2.0	0.3	—	—
M_3					
	L	0.6	−0.8	—	—
	W	0.8	−0.4	—	—
M^1					
	L	—	—	1.4	—
	W	—	—	−0.5	—
M^2					
	L	—	—	0.4	0.1
	W	—	—	1.7	−2.9

not clear. A photograph by Scott shows the tooth now third as absent and, in its place, broken alveoli clearly full of original matrix. It is thus clear that the tooth now in this position does not belong to the specimen but was inserted artificially. It is possible that this was an anomalous individual with five premolars, the third not really known, but it is much more probable that it had only four and that the third was crushed out of place and its broken alveoli filled with matrix at the time of burial. In any case this is not the normal structure of the genus.

The upper incisors are all compressed transversely, convex on the outer surface and concave on the inner with a vertical column, corresponding with the asymmetrical apex, flanked by two grooves. I^1 is larger than the other two, and I^3 slightly longer than I^2, but the differentiation is not pronounced. The canine is incisiform and is intermediate between I^1 and I^3 in size.

P^1 is longer than broad and has a simple ectoloph with rudimentary metacone and a small, distinct, posterointernal protocone.

P^{2-4}, like all the cheek teeth, are lower-crowned than in *Acropithecus* (an archaeopithecid, the dentition of which is described in detail on pages below and used as a standard of comparison for these closely similar families), but are otherwise similar. The most pronounced peculiarities are their less transverse proportions, with P^2 longer than broad and the others likewise relatively narrow, and the strong metacone folds, which are approximately equal to the paracone folds in shape and in prominence. The anteroexternal fossette is not closed on P^2 and may be feeble to distinct on P^3. On P^4 the fully developed "face" pattern occurs, the middle wear stages with isolated anteroexternal and posteroexternal fossettes and an elongate internal or main fossa with a central external spur. The walls of the latter are generally folded in a relatively complex and highly variable pattern. The posterior cingulum is large but less complex and less projecting internally than in *Acropithecus*, and the anterior cingulum is more constant, P^{3-4} being more symmetrical. An internal groove may be indicated on P^4, but is weak and inconstant. P^4 in some cases, but not invariably, has a feeble mesostyle fold.

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tion rather than preservation, because it tends to break up or pull away with age, taking bits of the specimen with it.

TABLE 7

MEASUREMENTS OF INDIVIDUAL SPECIMENS OF *Oldfieldthomasia debilitata*

		M.A.C.N. No. 10376[a]	A.M.N.H. No. 28680	A.M.N.H. No. 28691	M.A.C.N. No. 10749C	A.M.N.H. No. 28793
Maximum diameters of crowns						
	I^1	6.0	—	—	—	—
	I^2	3.9	—	—	—	—
	I^3	5.4	—	—	—	—
	C	5.9	—	—	—	—
P^1						
	L	6.0	—	—	—	—
	W	4.0	—	—	—	—
P^2						
	L	7.6	6.3	—	—	—
	W	6.4	5.9	—	—	—
P^3						
	L	6.4	6.4	—	—	—
	W	7.9	7.5	—	—	—
P^4						
	L	7.1	6.5	—	—	—
	W	10.5	8.3	—	—	—
M^1						
	L	6.7	6.4	—	—	—
	W	10.0	9.6	—	—	—
M^2						
	L	7.9	7.3	—	—	—
	W	11.0	10.5			
M^3						
	L	7.5	6.9	—	—	—
	W	10.5	9.9	—	—	—
dm^1						
	L	—	—	5.3	—	—
	W	—	—	4.3	—	—
dm^2						
	L	—	—	6.9	—	—
	W	—	—	5.9	—	—
dm^3						
	L	—	—	6.7	—	—
	W	—	—	7.0	—	—
dm^4						
	L	—	—	6.9	—	—
	W	—	—	7.9	—	—
P_2						
	L	—	5.9	—	5.7	—
	W	—	2.9	—	3.2	—
P_3						
	L	—	6.3	—	6.2	—
	W	—	3.6	—	3.6	—
P_4						
	L	—	6.0	—	6.2	—
	W	—	4.4	—	4.3	—
M_1						
	L	—	6.1	—	6.2	—
	W	—	4.8	—	4.7	—

TABLE 7—(*Continued*)

		M.A.C.N. No. 10376[a]	A.M.N.H. No. 28680	A.M.N.H. No. 28691	M.A.C.N. No. 10749C	A.M.N.H. No. 28793
M_2						
	L	—	7.0	—	6.8	—
	W	—	5.3	—	5.6	—
M_3						
	L	—	8.9	—	9.1	—
	W	—	4.9	—	5.1	—
dm_3						
	L	—	—	—	—	7.8
	W	—	—	—	—	3.7
dm_4						
	L	—	—	—	—	7.7
	W	—	—	—	—	4.3

[a] This is a senile individual. Measurements were taken on the right side. Those of the left all differ slightly, and the width of P^4 is there 9.6.

The upper molars are essentially of the same pattern as that in *Acropithecus*, with the "face" pattern as on P^4 but more expanded. The high posterior cingulum is simple and has a shallow fossa, and the low anterior cingulum is constant. The large protocone and somewhat smaller hypocone are united nearly to their apices, but the groove between and below them is very pronounced and forms a deep invagination or even a closed fossa. The outstanding generic character is the presence of five distinct external folds on the ectoloph. These are individually variable, and also vary at different wear levels, but usually near the apex the mesostyle fold is sharpest and most salient, the paracone fold is larger and almost or quite equally salient but less sharp, the parastyle fold is less salient than either of these but as sharp as the mesostyle fold, the metacone fold is similar to that of the paracone but less salient or sharp, and the metastyle fold is small and feeble. Toward the base the parastyle and metastyle folds merge with those of the adjacent cones, and still farther from the apex the mesostyle fold merges with that of the metacone or simply dies out. M^3 differs but little from M^{1-2} but is more oval with the posterior cusps reduced as usual.

The only unworn tooth available to me is an M^2 with a hypsodonty index of 100.

The lower incisors and canine are almost exactly similar to those of the interatheriid *Notopithecus*, and the description of them for that genus elsewhere in this publication can be applied without important additions to this. The lower cheek teeth, also, are structurally almost identical with those of *Notopithecus*, despite their much larger size, and hardly require independent description. They are also very similar to those of *Acropithecus*, but are relatively more slender and, as a rule, slightly less complex and without closed fossettes, although occasional specimens form a very transient anteromedian talonid fossette. Unlike *Notopithecus*, but like *Acropithecus*, there is normally a vertical external groove setting off the hypoconulid from the hypoconid on M_3.

The deciduous cheek teeth are likewise analogous to those of *Notopithecus*. They are all lower-crowned and less transverse than are the premolars. Dm^3 has the inner lobe feebly divided, and dm^4 is fully molariform. In the lower jaw only dm_{3-4} are known. They are almost exactly like those of *Notopithecus*, except for their greater size.

Statistical constants for most of the cheek teeth have already been given. Measurements of important individual specimens are given in table 7.

SKULL

In general aspect the skull is about like that of other primitive notoungulates, such as *Notostylops* or *Notopithecus*, but the orbits are very large and near or slightly posterior to the middle of the skull, the cranium is less

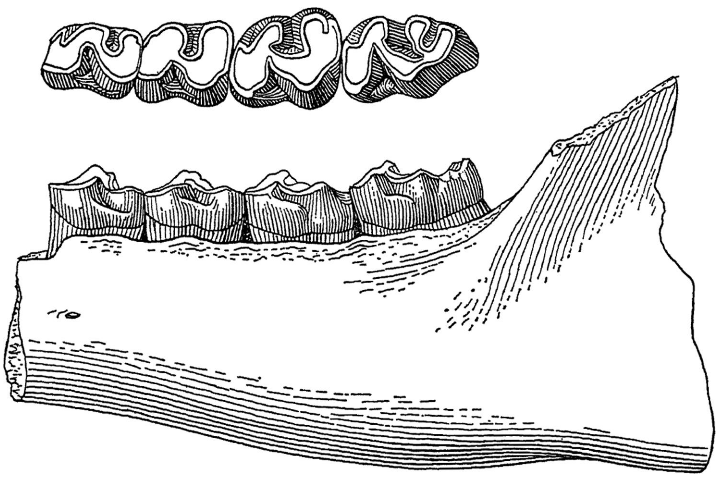

FIG. 4. *Oldfieldthomasia debilitata* Ameghino, C.N.H.M. Field No. 191, left lower jaw with P_4–M_3, crown and buccal views. ×2.

elongate than in *Notopithecus*, at least, and the postobital constriction is less. The relatively long muzzle seems to have been shallow in the available specimens, possibly owing to crushing in each case.

The nasals are not complete in any specimen, but were long and slender, not at all retracted. Their suture against the frontal is not clearly shown, but may have been nearly straight and near the level of the anterior orbital rim. The premaxilla is slender, extended, and triangular, with moderate palatal processes and small anterior palatal foramina separated by a stout median bar.

The facial part of the maxilla is not excavated even to the slight degree seen in, for example, *Adinotherium*. The infraorbital canal is rather long, and the small circular foramen is above dm^3 in juvenile, and P^{3-4} in adult, specimens. The zygoma arises mainly opposite M^2, also in part M^1 in juveniles and M^3 in adults. It arises simply, much as in the

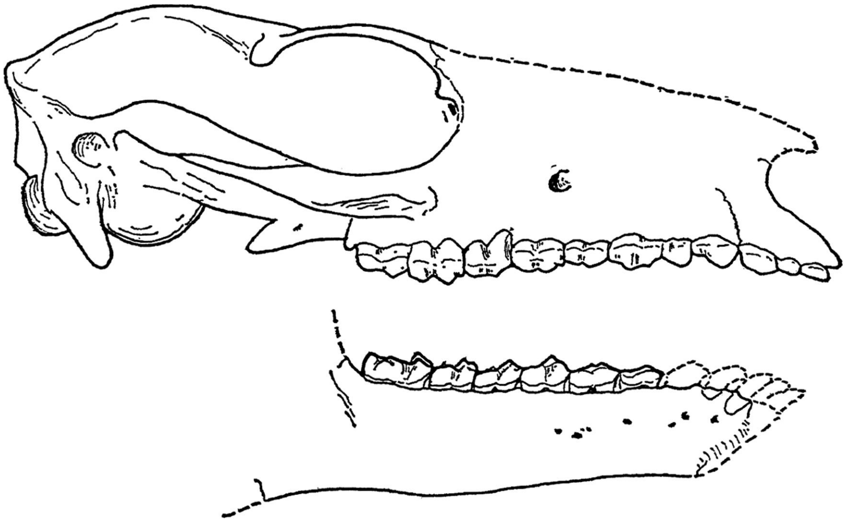

FIG. 5. *Oldfieldthomasia debilitata* Ameghino, reconstruction of skull, M.A.C.N. No. 10376, and jaws, composite, right lateral view. ×1.

more primitive later toxodonts, and quite devoid of any of the diverse specializations seen in various typotheres. It is still less expanded than in *Acropithecus*. The maxilla forms the internal face (only) of the anterior part of the zygoma, which is slender, simple, and without a postorbital process. The jugal is large and primitive, forming most of the lateral aspect of the zygoma, nearly or quite reaching the glenoid surface and sending a splint forward and upward to form the orbital rim and come in contact with the lacrimal. The lacrimal foramen is on the orbital rim, but there is only a small exposure of the lacrimal bone on the face.

The palatine has its lateral suture near but not at the alveolar border and extends forward to about the level of the posterior part of P^4. There are deep posterolateral notches in the palatines, and expanded winglike processes on each side of the choanae, but the structure of the pterygoid region is not clearly known, nor is that of the interorbital wall.

There are large, flat, supraorbital processes developed principally on the frontals but buttressed by the anteroexternal ends of the parietals. The cranial roof has the same structure as that in *Notostylops* and in *Notopithecus*, although relatively wider than in those genera.

The structure of the cranium is known principally from A.M.N.H. No. 28600, one-half of which was studied by serial sections. The data have mostly been published elsewhere (Simpson, 1936a), but the principal features are given here also in order to include these important general features of the early notoungulate skull in the present comprehensive review of these early South American faunas.

For study the cranium was first sawed vertically along the midline. The left half was preserved for surface morphology and orientation, and the right half was embedded in plaster (hardened with gum and shellac) and sectioned serially. A series of parasagittal sections at intervals of 0.4 mm. was taken. Sectioning was begun at the most lateral point, and recording started when sufficient bone of the ear region was exposed to be in an area of distinctive preserved morphology. The sections from this point are numbered serially from 1 to 54, covering a thickness of 21.2 mm. Section 1 is 24.6 mm. from the midline of the skull, and section 54 is 3.4 mm. from the midline. Subsequent cuts revealed nothing of interest, being beyond the ear region and all foramina and in the uniform and simple basicranial axis.

Bone Elements: The only elements in the cranial roof (anterior to the supraoccipital) are the squamosal and the parietal, which are here readily distinguishable in the sections and in the unsectioned half of the skull.

The sutures in the anteroinferior region are more confusing, the sutural lines being very complex and often nearly in the plane of the sections, which greatly obscures them, but after close study, with transparencies, it appears that there are here, anterior to and above the bulla, four different elements. One is continuous with the basisphenoid medially, extends laterally below the sphenorbital fissure, forms a strip along the anterolateral edge of the bulla, including the anterior rim of the foramen lacerum medium, and finally disappears in the somewhat confused region anterior to the lateral corner of the bulla. This clearly must be the alisphenoid.

A second element forms the upper rim of the sphenorbital fissure and the vertical cranial wall anterior to this and extends laterally for a short distance, about to section 40. This I take to be the orbitosphenoid. A still more anterior element, poorly developed in the sections because the anterior break barely includes its posterior end, appears anterior to and above the orbitosphenoid, with a clear suture against the latter (section 45) and against the parietal (section 40), and disappears at about the same point laterally (about section 38). This is probably the posterolateral edge of the frontal.

Overlapping and, at its extreme medial end, partly inserted into the alisphenoid, first appearing definitely in about section 39 (in going through the sections from the midline outward), is another element which becomes larger laterally until it excludes the alisphenoid from contact with the parietal and in the area anterior to the glenoid surface forms the whole inferolateral wall of the cerebral cavity. With the lateral disappearance of the parietal, the element in question is seen to be continuous with the dorsal part of the

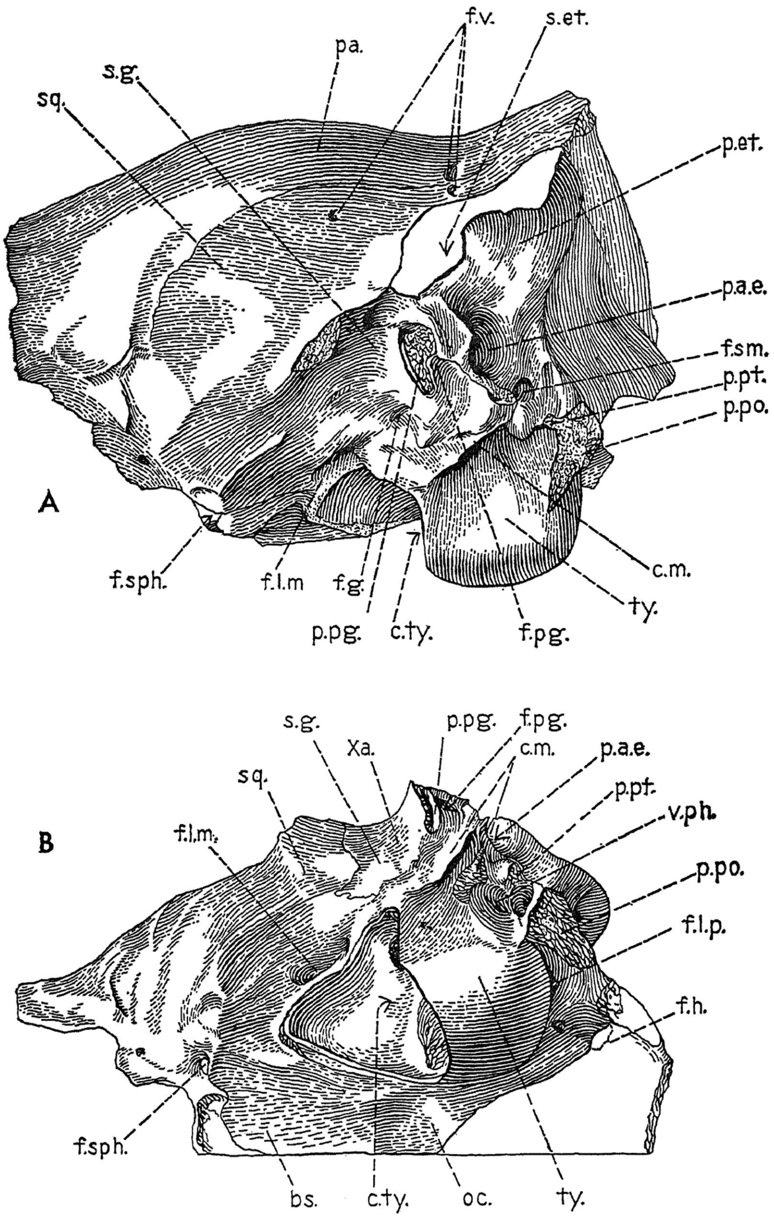

FIG. 6. *Oldfieldthomasia debilitata* Ameghino, A.M.N.H. No. 28600, left half of cranium. A. Lateral view. B. Ventral view. ×2.

Abbreviations: bs., basisphenoid bone; c. m., crista meatus; c. ty., tympanic cavity (revealed by breaking away of part of bulla); f. g., fissura Glaseri; f. h., hypoglossal foramen; f. l. m., foramen lacerum medium; f. l. p., foramen lacerum posterius; f. pg., postglenoid foramen; f. sm., stylomastoid foramen; f. sph., sphenorbital foramen; f. v., venous foramina; oc., (fused elements of) occipital bone; pa., parietal bone; p. a. e., porus acusticus externus; p. et., pars epitympanicus of squamosal; p. pg., (broken base of) postglenoid process; p. po., (broken base of) paroccipital process; p. pt., (broken base of) posttympanic process; s. et., (opening to) epitympanic sinus (through break in specimen); s. g., glenoid surface; sq., squamosal bone; ty., tympanic bone, forming bulla; v. p. h., vagina processus hyoidei; Xa., "anterior adventitious element."

squamosal and is, of course, part of that bone.

The individuality of the periotic and its extent are not in any doubt. There are only two sections (26 and 27) in which there is any possible question as to its outline, and here only because it rapidly expands posteriorly, with the lateral boundary of this extension nearly in the plane of the section so that it is not clearly shown.

The occipital elements are completely fused with each other without any trace of division, so that they are simply labeled "occipital" in the sections and other figures. The only place in which this compound occipital is not clearly separated from the adjacent bones is in the median ventral axis, where the basioccipital is completely fused with the basisphenoid, although the presence of a slight ridge and the relationships to the endocranium show where this division occurred.

It is regarding the elements of the ear region that there has been the greatest question. These are very poorly understood, and unfortunately the present specimen is not sufficiently well preserved nor are its sutures sufficiently clear at every point for a complete solution of this intricate problem. It does, however, provide many data, some of which are of particular interest and value.

The occipital sutures are very obscure, as usual, but can be almost certainly and fully determined in the sections. By a method of projection from the latter, a reconstructed posterior view of the essential portion of the occiput can be made. Five suturally separate bones are in this view: (1) the occipital (its elements completely fused); (2) the squamosal, enclosing the epitympanic sinus; (3) the tympanic (forming the bulla and part of the meatus, not extending onto the occiput proper); (4) the periotic, or its pars mastoidea; and (5) the "adventitious bone," marked Xp.

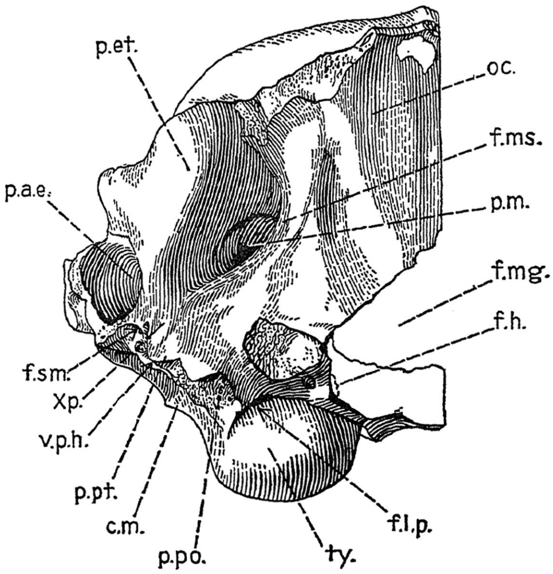

FIG. 7. *Oldfieldthomasia debilitata* Ameghino, A.M.N.H. No. 28600, left half of cranium, posterior view. ×2.

Abbreviations: c. m., crista meatus; f. h., hypoglossal foramen; f. l. p., foramen lacerum posterius; f. mg., foramen magnum; f. ms., mastoid foramen; f. sm., stylomastoid foramen; oc., (fused elements of) occipital bone; p. a. e., porus acusticus externus; p. et., pars epitympanica of squamosal bone; p. m., pars mastoidea of periotic bone; p. po., (broken base of) paroccipital process; p. pt., (broken base of) posttympanic process; ty., tympanic bone, forming bulla; v. p. h., vagina processus hyoidei; Xp., "posterior adventitious element."

The wall of the epitympanic sinus, although somewhat broken (especially in the lateral part), appears to be a single bone and is surely separate from any of the elements below it. There are some cracks above which may suggest, in single sections, that a suture against the squamous part of the squamosal is present, but in no case is this clearly a suture, and, studying the whole series of sections, I believe that it is very improbable that a suture is present at all in this specimen. The epitympanic sinus appears to be an inflation of the squamosal proper, well distinguished topographically but not a distinct osseous element. Roth (1903) based his belief that the epitympanic walls, and in some cases subjacent parts as well, form a separate element in notoungulates on the very rare supposed presence of a suture against the squamosal. Apparently he believed himself actually to have observed this suture in only two cases, and these are open to question, since there is a strong possibility that the supposed suture is merely a crack. As far as I know, no subsequent student has recorded a suture in this region, all (see especially Sinclair, 1909; Scott, 1912a, 1912b; Patterson, 1932) indicating the epitympanic wall (whatever they

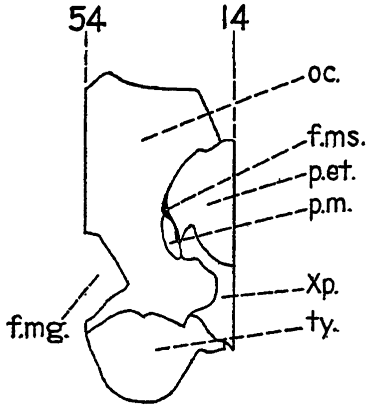

FIG. 8. *Oldfieldthomasia debilitata* Ameghino, A.M.N.H. No. 28600, part of right half of occiput reconstructed from serial sections 14 to 54. ×1.25.

Abbreviations: f. mg., foramen magnum; f. ms., mastoid foramen; oc., (fused elements of) occipital bone; p. et., pars epitympanica of squamosal bone; p. m., pars mastoidea of periotic bone; ty., tympanic bone, forming bulla; Xp., "posterior adventitious element."

call it) as fused with the (rest of the) squamosal. Without denying the possibility of sutural separation, I think it is fair to say that none is demonstrated, and the epitympanic wall may at least provisionally be considered as part of the squamosal, for which I have proposed the name pars epitympanica.

The true mastoid, which is very clearly shown by the sections to have nothing to do with the pars epitympanica of the squamosal, or with the crista meatus of the tympanic, or with the "adventitious bone," must be represented by the posterior projection of the periotic which in this genus and many (but not all) other notoungulates has a small occipital exposure.

It is the "adventitious bone," Xp, that remains extremely dubious, not as to its individuality, which is demonstrated, but as to its identity. Although it shows some apparent tendency to fuse with the tympanic in this skull, and in others studied seems to be completely so fused (being, for instance, considered part of the tympanic by Roth, 1903, as I interpret his paper, although he certainly overlooked no possible sutures in his material), there is in several sections (e.g., 17) a clear suture which cannot possibly be a crack. Even though the suture is apparently lost by fusion in other regions, its certain presence in any part is sufficient demonstration of the separate individuality of the bones in question. Its separation from the (ex)occipital is still more certain, as the latter simply overlies it without forming a sutural connection (e.g., section 20). Separation from the pars epitympanica is not clear in all sections, probably because of the imperfection of the specimen, but is in some (e.g., section 20), and this suture clearly developed on the occiput has been distinguished externally in a number of different genera.

The only apparent true connection of this bone is seen in sections 20–22, in which it passes without a visible break into a bridge of bone above the medial end of the external auditory meatus, immediately lateral to the epitympanic recess, and is in this way united with an element developed in the postglenoid process, anterior to the tympanic. Such a union does not necessarily prove that these are the same bone, as fusion of really separate elements in the few crucial sections could well occur, but it demands new evidence to demonstrate separability.

A remarkable anomaly, and one apparently not elsewhere recorded, is the presence of another "adventitious bone," or of an anterior process of the same one, in the postglenoid process, labeled Xa in the figures. The separability of this from the tympanic is clear, a distinct suture being present throughout (e.g., sections 15, 20). It is equally distinct from the pars epitympanica and the periotic, both of which are in contact with it but without even a sutural union. In its more medial part, separation from the inferolateral part of the squamosal is not clearly shown, because of cracks in this region, and, doubtfully, partial fusion, but laterally it has a distinct suture against the pars glenoidea of the squamosal (e.g., section 10). In the sections this is unmistakably a true suture, and it is, furthermore, clearly visible on the other, unsectioned, half of the skull running transversely across the glenoid surface to the squamosotympanic suture anterior to the fissura Glaseri, exactly corresponding with its course as shown in the sections.

On present data it seems impossible to offer a reasonable explanation of these two adventitious bones, or two parts of one as the case may prove to be. The relationships are not perfectly clear in any described specimen,

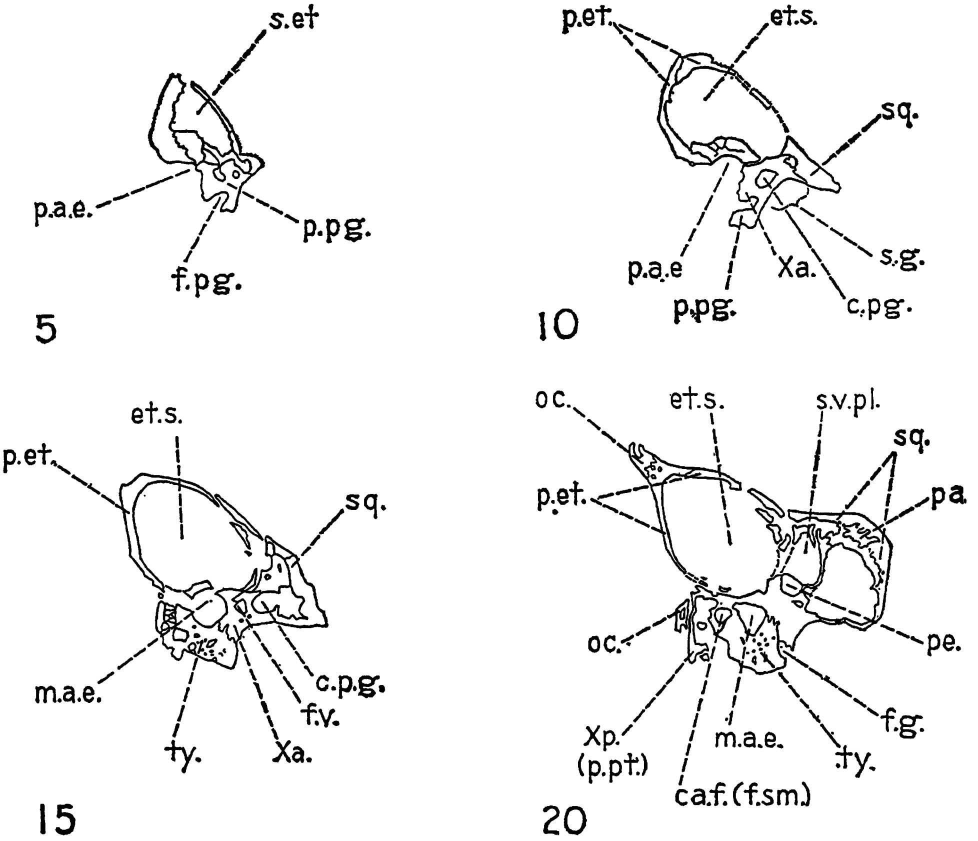

FIG. 9. *Oldfieldthomasia debilitata* Ameghino, A.M.N.H. No. 28600, serial parasagittal sections of right half of cranium. Numbers are those of complete series of sections (see text). Anterior end of specimen to right. ×1.25.

Abbreviations: ca. f. (f. sm.), canalis facialis (stylomastoid foramen); ca. f. (f. sm. p.), canalis facialis (foramen stylomastoideum primitivum); c. pg., postglenoid canal; et. s., epitympanic sinus; f. g., fissura Glaseri; f. pg., postglenoid foramen; f. v., venous foramina; m. a. e., external auditory meatus; oc., occipital bone; pa., parietal bone; p. a. e., porus acusticus externus; pe., periotic; p. et., pars epitympanica of squamosal bone; p. pg., postglenoid process; s. et., epitympanic sinus (same as et. s.); s. g., glenoid surface; sq., squamosal bone; s. v. pl. posterolateral venous sinus; ty., tympanic bone; Xa., "anterior adventitious element"; Xp. (p. pt.), part of "posterior adventitious element" forming base of posttympanic process.

and the observation of the anterior element, or part, depends solely on this one specimen. Speculation on these grounds seems unwarranted, and the observations are merely recorded to form, it is hoped, a basis for the accumulation of essential further data.[1]

In the more lateral sections (especially sections 7–12) there is a bone in the base of the epitympanic sinus, above and lateral to the porus acusticus, which is consistently

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[1] Not to prejudice more definitive work, I apply no name to either part. The posterior part is the posttympanic of Roth and some others following him, but Scott apparently used the term in a somewhat different sense. The name may become fixed in this usage if the element is a unit, since it does in many cases, or invariably, form the true posttympanic process and is descriptively posttympanic in position, but it would seem to be inappropriate and confusing if this is part of the same bone that forms the postglenoid process. Incidentally, in the latter case the whole element would seem to correspond more nearly to the "pars serrialis" of human anatomy than does the epitympanic wall to which several workers apply this name—reason for rejecting Roth's usage of the name in the latter application among notoungulates.

separate in the sections. This region is, however, badly cracked, and it seems probable that the bone in question is not really a separate element. At least it should not be accepted as such without further evidence.

Lying loose and out of position in the medial part of the tympanic cavity (sections 50–53) is an auditory ossicle, probably the malleus, but the section interval is too great for useful reconstruction of its form. In sections 34–36 is another small bone in the bottom of the bulla, which may be another auditory ossicle or may be only a fragment of the broken wall of the bulla.

No other bone elements are present in the preserved part of the cranium.

MEATUS AND SINUSES: The roughly circular porus acusticus of this form has its upper rim nearly on a level with the glenoid surface, and from it the meatus runs forward, inward, and downward, although it is less oblique than in many later notougulates. The meatus (from the point where it is completely encircled by bone) runs through 11 sections (13–23, about 4 mm.). Nearly circular at first, it becomes distinctly triangular (sections 19 and following), with one of the three approximately equal angles downward, into the tympanic. The floor of the meatus is formed throughout by a thick, somewhat spongy plate of the tympanic, which also seems to form at least half of the posterior wall, and in some sections apparently most of this wall. The rest of the posterior wall, the roof, and the anterior wall are formed by the "adventitious elements," as discussed elsewhere.

The serial sections prove beyond any question that the ventral closure of the meatus is by a thickened extension of the tympanic, which everywhere separates the postglenoid and posttemporal processes. This strongly corroborates Patterson's view (1932, p. 18) that in toxodonts this plate is also part of the tympanic, not mastoid as Scott supposed. Conditions in this respect seem to be rather uniform throughout the Notoungulata, and all the specimens known to me permit the generalization that there is in this order invariably a tympanic plate between the postglenoid and posttympanic process. The occurrence of a meatus spurius reported by Sinclair (1909) for *Protypotherium*, Scott (1912b) for *Homalodotherium*, and Van Kampen (1905) for "*Typotherium*" (i.e., *Mesotherium*) is in no case substantiated, and probably the report is due to failure to recognize the separate origin of a fused tympanic extension.[1]

The crista meatus (Patterson, 1934a) is strongly developed on the present specimen and was apparently very prominent, although somewhat broken and hence not well known in the sections. The crest is double, because of the development in it of a deep, very sharply defined, longitudinal groove.[2] The posterior crest, or posterior rim of the groove on the crista, abuts simply against the bulla posterior to the vagina processus hyoidei. The anterior crest swings forward on the external part of the bulla and ends internal to the glenoid fossa. Between the end of this and the postglenoid process, immediately posterior to the fissura Glaseri, there is an isolated papilla of bone on the tympanic.

Upon arriving at the tympanic cavity, the internal lower rim of the meatus flairs out, becoming a semicircle of greater diameter than the meatus proper, and projects into the cavity as a pronounced crista tympanica,[3] which is open above (see section 25).

As in all notoungulates, the bulla is completely ossified, inflated, and (except, of course, for part of its dorsal wall) entirely formed by the tympanic,[4] which is without any distinct trace of sutures. The recessus epitympanicus and, still more, the sinus epitympanicus are very distinct, although opening into the tympanic cavity, but the primary tympanic cavity and hypotympanic sinus are completely hollow and poorly or not

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[1] The reported instances have all been denied by other workers. Scott seemed to contradict Sinclair's statement, and Patterson's studies negated those of Scott and of Van Kampen.

[2] Possibly a canal, as a possible junction below may be broken away, but such a break seems improbable. Another skull of *Oldfieldthomasia* has an even larger groove, also open as preserved. Both crests are certainly tympanic.

[3] Note that the "tympanic crest" of Patterson's first paper (1932) is not the "crista tympanica" of other anatomists, and that he later (1934a) renamed it the "crista meati" (a *lapsus calami* for the grammatically correct crista meatus).

[4] I use "tympanic" for the entire element, without regard to a possible combination of ectotympanic and entotympanic elements.

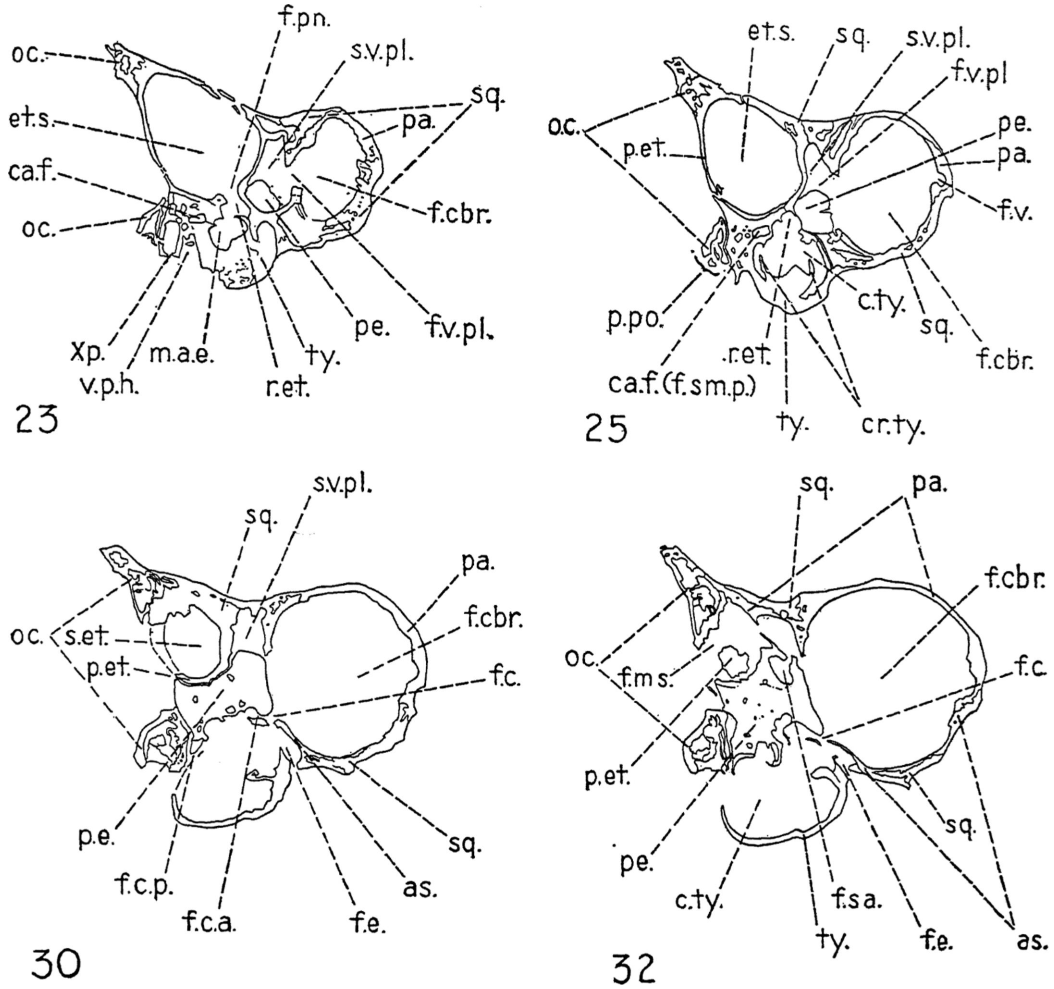

FIG. 10. *Oldfieldthomasia debilitata* Ameghino. A.M.N.H. No. 28600, serial parasagittal sections of right half of cranium, continuing mediad from those shown in figure 9. Numbers are those of complete series of sections (see text). Anterior end of specimen to right. ×1.25.

Abbreviations: as., alisphenoid bone; ca. f. (f. sm. p.), canalis facialis (stylomastoid foramen); c. ty., tympanic cavity; cr. ty., crista tympanica; et. s., epitympanic sinus; f. c., carotid foramen; f. c. a., foramen caroticum anterius; f. cbr., cerebral fossa; f. c. p., foramen caroticum posterius; f. e., Eustachian foramen and canal; f. ms., mastoid foramen; f. pn., foramen pneumaticum of sinus epitympanicus; f. sa., fossa subarcuata; f. v., venous foramina; f. v. pl., posterolateral cerebral venous foramen; m. a. e., external auditory meatus; oc., occipital bone; pa., parietal bone; pe., periotic; p. et., pars epitympanica of squamosal bone; p. po., (broken base of) paroccipital process; r. et., epitympanic recess; s. et., epitympanic sinus (same as et. s.); sq., squamosal bone; s. v. pl., posterolateral venous sinus; ty., tympanic bone; v. p. h., vagina processus hyoidei; Xp., "posterior adventitious element."

differentiated from each other. The complications in the walls of this large cavity are very few, the internal wall being for the most part a simple curved surface parallel to the visible outer surface.

There is a semicircular lateral extension of the cavity around the crista tympanica (sections 24–26). Immediately medial to this point there is a large but shallow pocket in the lateral wall at the posteroinferolateral

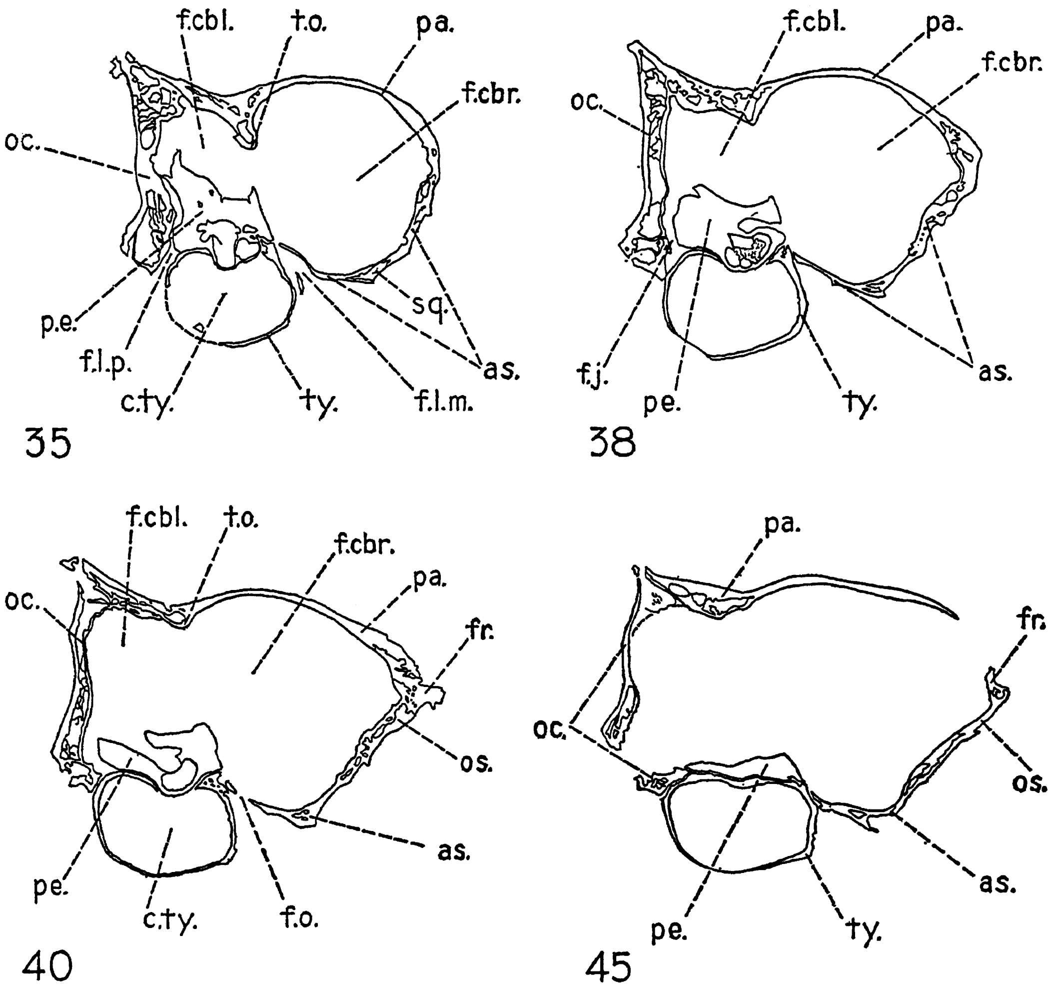

FIG. 11. *Oldfieldthomasia debilitata* Ameghino, A.M.N.H. No. 28600, serial parasagittal sections of right half of cranium, continuing mediad from those shown in figure 10. Numbers are those of complete series of sections (see text). Anterior end of specimen to right. ×1.25.

Abbreviations: as., alisphenoid bone; c. ty., tympanic cavity; f. cbl., cerebellar fossa; f. cbr., cerebral fossa; f. j., jugular foramen and canal; f. l. m., foramen lacerum medium; f. l. p., foramen lacerum posterius; f. o., foramen ovale; fr., frontal bone; oc., occipital bone; os., orbitosphenoid bone; pa., parietal bone; pe., periotic; sq., squamosal bone; t. o., tentorium osseum; ty., tympanic bone.

point of the bulla (section 28) and immediately dorsal to this is a small projection, which disappears between two sections (present in section 28, completely absent from section 29). In section 29 a small pocket in the anterior wall of the bulla appears, and posterior to this, projecting into the tympanic cavity, are two low but definite projections. In the next section, 30, the small pocket merges into the general lumen of the bulla, and the ridge is single but with a hooked end and is considerably more prominent. Hence, in sections 31 to 33, the ridge becomes lower but stouter and more dorsal, until it reaches and passes into the dorsoanterior edge of the bulla wall. After this point the wall of the cavity is smooth and evenly curved.

Patterson (1936) has noted the presence of a septum bullae in hegetotheres and toxodonts, and it is well known that the hypotympanic sinus may be cancellous in various notoungulates. In the present skull it is not cancellous, and it seems unlikely that any real homologue of a septum bullae is present, although it is perhaps conceivable that the ridge just described is a vestige of that structure. The condition is, in this respect, much as in the typothere studied by Patterson.

The tympanic gap ("Tympanicumdefekt") extends to the extreme lateral edge of the cavity and, indeed, of the meatus, the tympanic itself not forming a closed ring until section 43. In the meatus and in small part at the beginning of the tympanic cavity the gap is apparently filled by the "adventitious elements," discussed elsewhere. In section 25 the periotic also appears in the roof of the gap which by section 28 it entirely occupies. The gap is here at its maximum. In section 33 it begins to be noticeably smaller and in section 43 the edges of the tympanic meet beneath the periotic and the gap is closed, although the periotic continues to overlie the thin superior wall of the cavity nearly as far as the latter extends. The structure of the exposure of the periotic in the tympanic cavity is discussed below.

The course of the entocarotid artery is not shown with complete clarity, and the following observations, although highly probable, are not certain. This vessel apparently enters the tympanic cavity through a very small foramen, entirely in the tympanic, opening into the fissure between the posterior edge of the bulla and the paroccipital process, immediately medial to the more produced part of the latter, and lateral to the foramen lacerum posterius, which is included in the medial extension of the same fissure. The course of the entocarotid from this point within the bulla cannot be followed, not being clearly impressed on any osseous part, but presumably it traversed the bulla around (medial to) the promontorium. In section 31, immediately lateral to the promontorium, a groove appears below and anterior to the last trace of the latter, immediately anterior to what is rather surely the sulcus facialis, which is in all probability a sulcus caroticus, and this is seen in the same section (also in sections 30–32) to run anteriorly into a foramen. The roof, lateral wall, and floor of this foramen are formed by the periotic, the latter by a small reflected process from near the base of the processus perioticus superior. The medial wall is formed by the edge of the tympanic, which here rises to abut against the anteroinferior angle of the body of the periotic (section 33 and all medial to that). It seems sufficiently probable, although not certain, that this foramen is the foramen caroticum anterius. Although the course of the carotid within the bulla cannot have been straight, this anterior foramen is almost exactly anterior to the probable foramen caroticum posterius, both appearing in the same section (31). It opens into the large fissure anterolateral to the bulla, above the canalis tubarius, and lateral to the foramen ovale. The artery did not course for any distance along this fissure, however, for immediately anterior to the probable foramen caroticum anterius and scarcely separated from it is a foramen between the periotic and the alisphenoid, into the posterobasal part of the cerebral fossa which must (if other identifications here made are correct) be the (true or primary) foramen caroticum.

In any case it is certain that the entocarotid does not in this genus, as it does in *Hegetotherium* and some other notoungulates, pass between the tympanic and periotic on one side and the basioccipital and basisphenoid on the other, wholly outside the tympanic cavity.

The Eustachian tube apparently left the bulla through the gap (prominent in section 30) immediately below the reflected periotic process flooring the foramen caroticum anterius, between this and the tympanic, and entered a short, oblique canalis tubarius running downward, forward, and medially, between the tympanic and the alisphenoid. This opens inferiorly along the fissure on the anterolateral edge of the bulla, posterolateral to the foramen ovale, and well removed from the anterior point of the bulla. There is no styliform process. This arrangement may be primitive for notoungulates, but in many later forms the tube, after emerging, channels the outer surface of the bulla nearly or quite to its anterior end and a styliform process is often developed. Its orifice is surrounded by the tympanic in all the forms investigated by Patterson (1936).

The epitympanic recess has the form of a

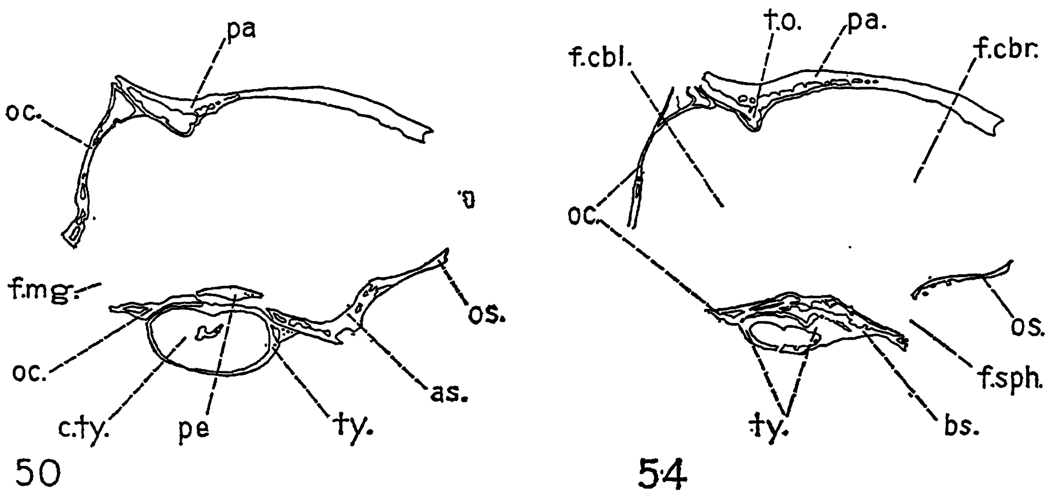

FIG. 12. *Oldfieldthomasia debilitata* Ameghino, A.M.N.H. No. 28600, serial parasagittal sections of right half of cranium, continuing mediad from those shown in figure 11. Numbers are those of complete series of sections (see text). Anterior end of specimen to right. ×1.25.

Abbreviations: as., alisphenoid bone; bs, basisphenoid bone; c. ty., tympanic cavity; f. cbl., cerebellar fossa; f. cbr., cerebral fossa; f. mg., foramen magnum; f. sph., sphenorbital foramen; oc., occipital bone; os., orbitosphenoid bone; pa., parietal bone; pe., periotic; to., tentorium osseum; ty., tympanic bone.

nearly cylindrical meatus from the tympanic cavity into the epitympanic sinus. Its mouth is visible in section 25, opening in the extreme superolateral part of the cavity, above the inner end of the external auditory meatus. Thence it runs externally (in reverse order of numbering sections) and upward. Section 24 is near the outer edge of the opening into the tympanic cavity, and the inner part of the opening into the epitympanic sinus is just appearing. In section 22 the canal is above the inner end of the auditory meatus, from which it is here completely separated by a bony wall, and widely open into the epitympanic sinus, appearing as a groove on the floor of the latter. This groove disappears at about section 19, which is at the midpoint of the sinus (midpoint from side to side).

The epitympanic sinus is well developed, as it is in all notoungulates. It has approximately the size, and somewhat the shape, of the bulla, being egg-shaped, with its larger end directed downward and forward. Above the external auditory meatus the floor of the sinus, formed by the thick roof of the meatus, is bowed upward. As one follows the sections toward the midline, this irregularity disappears, and the opening into the epitympanic recess, already described, appears. Aside from these features, the wall of the cavity is very simple and smoothly concave. The wall is somewhat cracked and broken, especially the more lateral parts, so that the absence of other openings cannot be positively affirmed, but none can be surely identified, and any present must have been small and insignificant.

PERIOTIC: The outer form of the periotic is very complex, but without marked differentiation into distinct elements. The central mass comprises the pars vestibularis sive canalium, which is more posteroexternal and is the principal part cut by sections 27–33, and the pars cochlearis, which is more anterointernal and forms the greater part of sections 38–42, the sections between these showing both about equally.

The posterior part of the bone is exposed over a small area on the occiput (limited by dotted lines in sections 29–33). It is clear that the exposed part is virtually undifferentiated from the pars canalium and represents no marked projection of the bone. Descriptively this is a pars mastoidea, very poorly developed. It is, of course, impossible to determine in a fossil whether a separate center of ossification is really represented, nor is it of any great consequence. The important

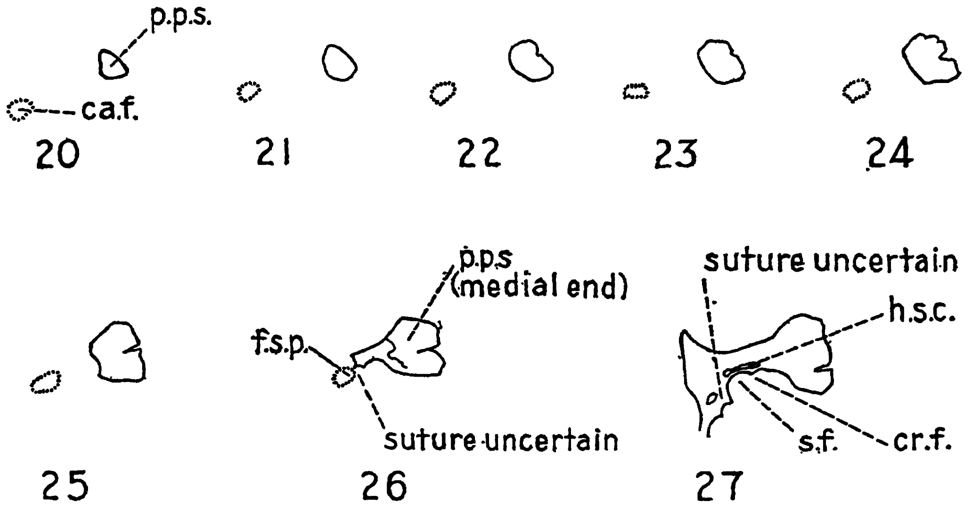

FIG. 13. *Oldfieldthomasia debilitata* Ameghino, A.M.N.H. No. 28600, parasagittal sections of right periotic bone. Numbers are those of complete series of sections (see text). Anterior end of specimen to right. ×1.25.

Abbreviations: ca. f., canalis facialis; cr. f., crista facialis; f. s. p., foramen stylomastoideum primitivum; h. s. c., horizontal semicircular canal; p. p. s., processus perioticus superior; s. f., sulcus facialis.

points are that the mastoid region is poorly developed, uninflated, surely has nothing to do with the epitympanic sinus (not even being exposed in the floor of the latter), and develops no true processus mastoideus. These characters seem to be common to all notoungulates, as far as I can surely determine. In *Oldfieldthomasia*, at least, this small occipital exposure is the only point at which the periotic is visible externally in an undamaged skull. In other cases even this small exposure may occur in so deep and narrow a cleft as to be virtually invisible from the outside.

The periotic is produced medially into a thin, sharp crest loosely overlying the inner edge of the tympanic (the bulla), from which it departs far enough to leave a noticeable gap. The basioccipital and basisphenoid here separate and leave a gap beneath the periotic, so that, although the latter tends to overlap them, it is no more than barely in contact with them at any point, and they do not really separate the periotic from the tympanic. The medial periotic surface above this crest is a sloping, simple surface with few features beyond the internal auditory meatus and the fossa subarcuata. The latter is broad and shallow, much less pronounced than in *Protypotherium*, for instance. The anterior surface, which abutted against the pyriform lobe of the cerebrum, is approximately triangular in plan, nearly plane, and slopes upward and backward.

The inferior, or inferolateral, surface has on its medial and posteromedial parts a large, nearly smooth surface which is more or less closely applied to the corresponding part of the tympanic here roofing the bulla. Lateral to this, nearly in the middle of the inferior periotic face but nearer its anterior border, the strong, swollen promontorium appears. It is inserted in one side of the tympanic gap, so is exposed in the tympanic cavity. On the lateral side of this appear the several openings into the middle ear, discussed below, and above these the shelflike projection of the prominentia canalis lateralis, which reaches to the edge of the epitympanic recess, and the lower surface of which forms the tegmen tympani.[1] From the anterolateral point of the main body of the periotic arises a strong, conical or styliform process,

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[1] Commonly so-called, but not entirely analogous to the part so designated in human anatomy, which is the roof of the epitympanic recess. In *Oldfieldthomasia* the periotic reaches the recess but forms no significant part of its walls, so that a tegmen tympani in the human sense is lacking.

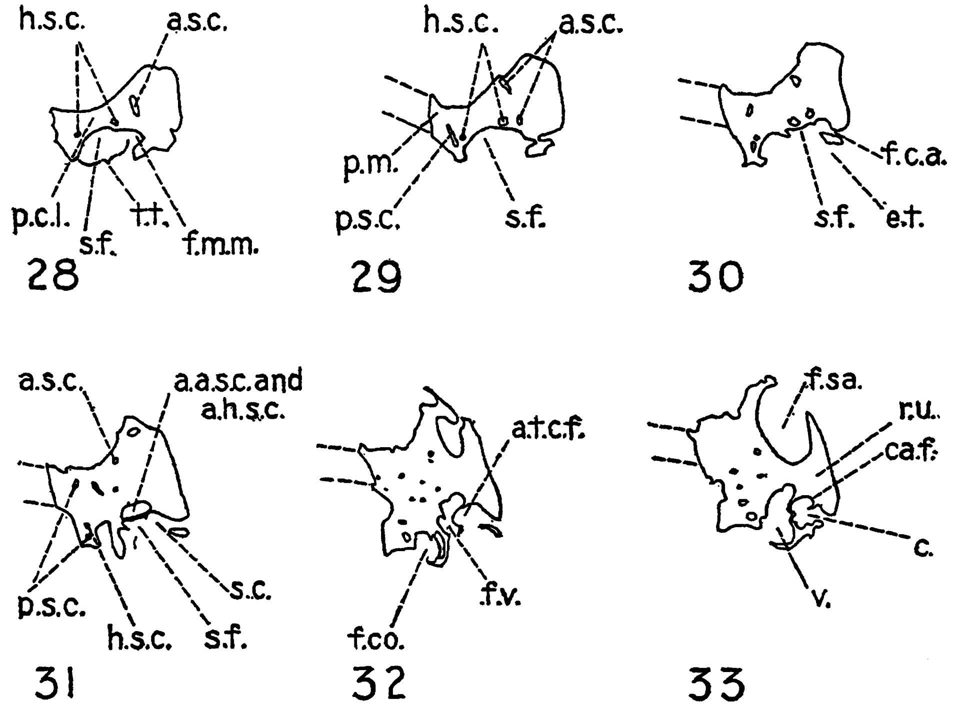

FIG. 14. *Oldfieldthomasia debilitata* Ameghino, A.M.N.H. No. 28600, parasagittal sections of right periotic bone, continuing mediad from those shown in figure 13. Numbers are those of complete series of sections (see text). Anterior end of specimen to right. ×1.25.

Abbreviations: a. a. s. c., ampulla of anterior semicircular canal; a. h. s. c., ampulla of horizontal semicircular canal; a. s. c., anterior semicircular canal; a. t. c. f., apertura tympanica canalis facialis; c., cochlea; ca. f., canalis facialis; e. t., Eustachian tube; f. c. a., foramen caroticum anterius; f. co., fenestra cochlearis; f. m. m., fossa muscularis major; f. sa., fossa subarcuata; f. v., fenestra vestibuli; h. s. c., horizontal semicircular canal; p. c. l., prominentia canalis lateralis; p. m., pars mastoidea of periotic bone; p. s. c., posterior semicircular canal; r. u., recessus utriculi; s. c., sulcus caroticus; s. f., sulcus facialis; t. t., tegmen tympani; v., vestibule.

more than 2 mm. in length, which extends almost straight laterally along the floor of the posterolateral cerebral venous sinus. This is at least analogous to a processus perioticus superior, and I have so designated it. Its relations are well shown in section 20, the most lateral section showing it, and in section 25, which is immediately lateral to its merging with the main body of the periotic. In the latter, the anterior face of the process shows a deep fissure, also visible in sections 24 and 26–28, which is not shown by the sections to be the mouth of a canal, and the function of which I do not know.

In the internal structure of the periotic, the course of the facialis nerve is shown clearly. It enters, as usual, by the internal auditory meatus, where an upper groove for it is first (in proceeding from the midline) seen clearly in section 40. In section 39, where the meatus is enclosed, this is a marked superoanterior pocket, and in section 38 it becomes a separate canal above the cochlear cavity, into which the duct of the auditory nerve has now entered. In the same section the canalis facialis shows a branch that runs straight forward and opens into the cerebral cavity. This is clearly the hiatus canalis facialis for the nervus petrosus superficialis major. The canalis facialis proper continues internally above the anterior part of the cochlea and anterior to the vestibule, from which it is at times separated only by a very thin film of bone, and finally in section 32 emerges into the tympanic cavity through the apertura tympanica canalis facialis, immediately anterior to the fenestra vestibuli. It crosses the roof of the tympanic cavity in a shallow open groove, running at first a little laterally, then almost straight posteriorly. Section 29 is cut almost along this part of the sulcus facialis, and most of the lower margin of the periotic in this section was probably underlain by the facialis. At the edge of the periotic, in section 27, the facialis is in a more pronounced groove, and here turns and runs more externally, leaving the periotic and (section 26) entering another canal through the foramen stylomastoideum primitivum. Although here beyond the periotic, its further course may be followed. It continues in this canal, which is in the unidentified postero-inferior (?)squamosal element near its suture with the tympanic, and passes laterally through the bone above and very slightly anterior to the vagina processus hyoidei. It there bends very slightly backward, and emerges at the stylomastoid foramen, immediately below and behind the porus acusticus and lateral to the vagina processus hyoidei.

The angle between the planes of anterior and posterior semicircular canals is approximately 85 degrees; between those of anterior and horizontal canals, about 90 degrees. The other characters of the semicircular canals are well shown in the sections and present no notable peculiarities.

In section 36 a canal is seen to leave the superoposterior part of the vestibule, and a canal is seen (as also in section 37) entering the cerebellar cavity posterior to the fossa subarcuata. The canal being of smaller diameter than the section distance, 0.4 mm., its intermediate portion is lost and was not

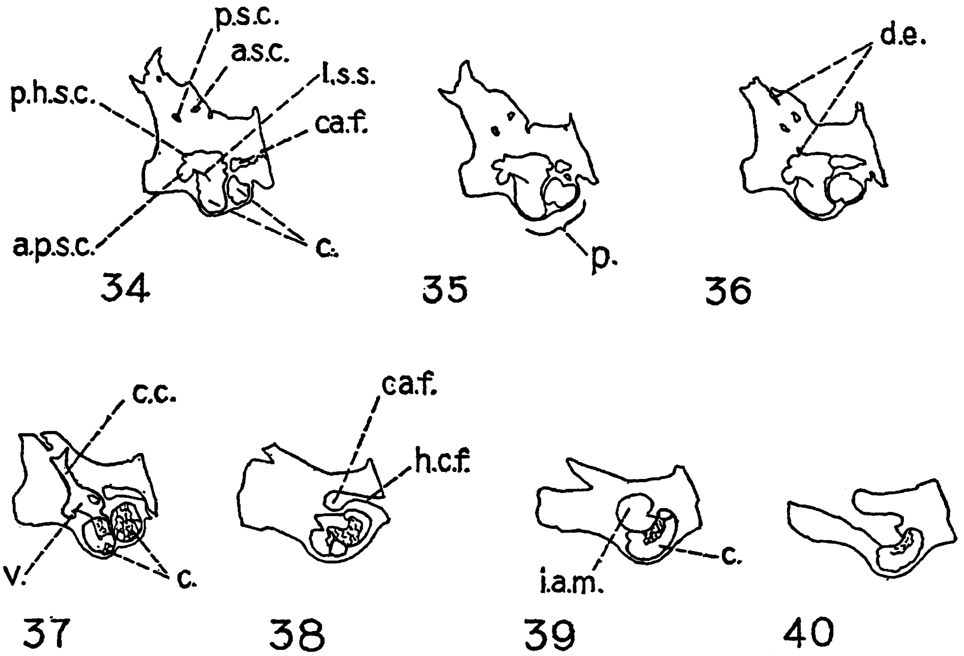

FIG. 15. *Oldfieldthomasia debilitata* Ameghino, A.M.N.H. No. 28600, parasagittal sections of right periotic bone, continuing mediad from those shown in figure 14. Numbers are those of complete series of sections (see text). Anterior end of specimen to right. ×1.25.

Abbreviations: a. p. s. c., ampulla of posterior semicircular canal; a. s. c., anterior semicircular canal; c., cochlea; ca. f., canalis facialis; c. c., crus commune; d. e., ?ductus endolymphaticus; h. c. f., hiatus canalis facialis; i. a. m., internal auditory meatus; l. s. s., lamina spiralis ossea; p., promentorium; p. h. s. c., posterior opening of horizontal semicircular canal; p. s. c., posterior semicircular canal; v., vestibule.

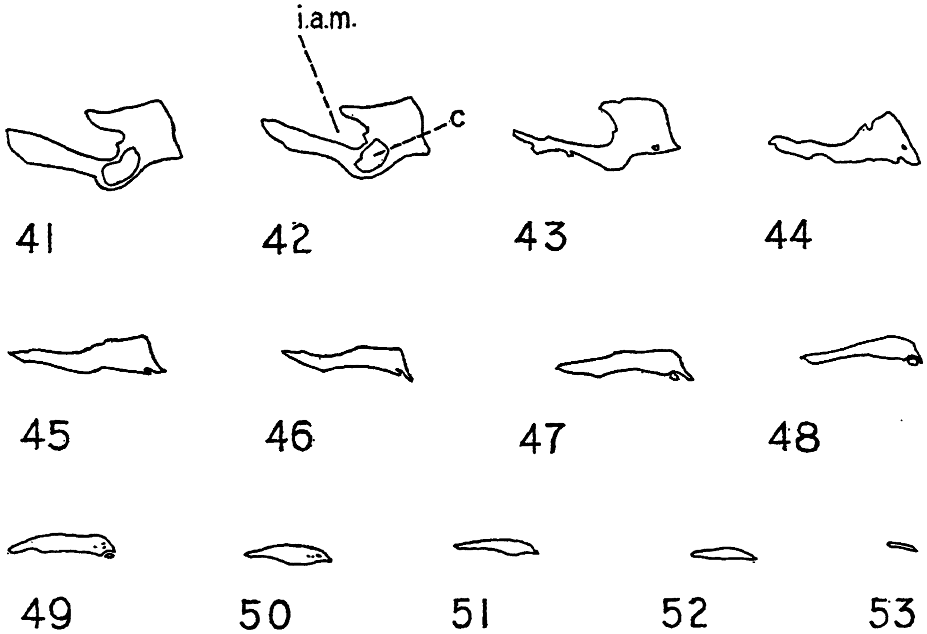

FIG. 16. *Oldfieldthomasia debilitata* Ameghino, A.M.N.H. No. 28600, parasagittal sections of right periotic bone, continuing mediad from those shown in figure 15. Numbers are those of complete series of sections (see text). Anterior end of specimen to right. ×1.25.

Abbreviations: c. cochlea; i.a.m., internal auditory meatus.

noticed when the section was ground, but it is probable that these are the two ends of the same canal and that it is for the ductus endolymphaticus. In section 31 another extremely small canal is seen in the area between the various sections of the semicircular canals. Between sections 30 and 31 this was seen to continue in the direction of its long diameter in section 31 and to open into the small gap between the petrosal and the wall of the epitympanic sinus, but its lower end could not be followed. Aside from a few extremely minute holes, barely visible under a binocular (e.g., in section 32), which seem merely to be slight defects in ossification or traces of cancellous structure, no other small canals were observed.

The cochlea and vestibule are well shown in the sections and seem to present no marked peculiarities. The sections do not suffice for one to determine the number of turns of the cochlea, but apparently there were few, perhaps less than two, although a skull of *Hegetotherium*, broken so that the cochlea lies partly open, apparently has two and one-half turns, as in most ungulates. The fenestra vestibuli and fenestra cochleae are not very clear, since their rims are nearly in the plane of the section and the bone is very thin, but, when the sections are superposed as transparencies, their character can be made out. The fenestra vestibuli is smaller than the fenestra cochleae and is elongate in an anteroinferior-posterosuperior direction, whereas the fenestra cochleae is more nearly circular, although slightly elongate in the same direction. They are separated by a thin bridge of bone. In one section (32) the fenestra cochleae, fenestra vestibuli, and apertura tympanica canalis facialis may be seen arranged in a row from posteroinferior to anterosuperior, in the order named, separated by thin bony plates, appearing here as grooves since their lips are more medial.

The fossa muscularis major, for the tensor tympani, is well defined and easily recognizable, particularly in section 28, as a pocket, extending forward and upward, lateral to the apertura tympanica canalis facialis and internal to the epitympanic recess. It lies immediately above the posterior end of the canalis tubarius, from which it is, however, quite separate, and immediately lateral to and slightly above the (probable) foramen caroticum anterius.

The last-named foramen, described above with the bulla, is the only other important structure involving the periotic.

EXTERNAL FORAMINA: The optic foramen is not preserved in this specimen.

The sphenorbital foramen is more on the inferior than on the lateral side of the cranium and is unusually close to the anterior margin of the bulla, although such a position may be accentuated to a small degree by breakage of the foramen wall.

A rather large, elongate fissure at about the middle of the anterolateral border of the bulla, and hence distinctly external in position, represents the foramen lacerum medium. As shown by the internal structure, its more anteromedian end is the foramen ovale, its more posterolateral the Eustachian foramen, and above the latter is the true carotid foramen which, however, does not appear at all externally.

There are no foramina at the anterior or posteromedian ends of the bulla or along its median border.

A distinct but small and irregular fissura Glaseri is visible medial to the glenoid surface, anterior to the crista meatus, at the external angle of the bulla.

The sections show that there are several postglenoid canals, but their external relationships are obscured by breakage. All are analogous in structure and function. The opening of the largest, which is the (or the principal) postglenoid foramen is between the glenoid surface and the porus acusticus externus, appearing as a vertical channel between postglenoid process and crista meatus before it turns and runs into the bone in an anteromedian direction.

The porus acusticus externus is described in connection with the auditory chambers.

The stylomastoid foramen, which is directed laterally rather than inferiorly, is immediately posteroinferior to the porus, from which it is separated by a bony wall, and directly above and lateral to the vagina processus hyoidei.

The vagina processus hyoidei (which, of course, is not properly a foramen, having an unperforated roof) is a relatively large and deep pit in the usual notoungulate position, that is, at the posterolateral angle of the bulla. Its anteromedian wall is formed by the bulla, anterolateral by the inner end of the posterior crest of the crista meatus, posterolateral by a small bridge of bone joining the crista meatus and posttympanic process below the stylomastoid foramen, and posteromedian by the external part of the paroccipital process. On the unsectioned half of the skull there is a circular opening at the posterior edge of the vagina processus hyoidei which appears to be a foramen, but from the sections it appears without much doubt that this is merely a break exposing the cancelli of the adjacent bone.

A deep, narrow, vaguely double fissure on the posterior border of the bulla, between the latter and the median part of the paroccipital process, is the foramen lacerum posterius, which, as is the foramen lacerum medium, is thus displaced laterally with respect to the more usual position. The more lateral part of the fissure was apparently entered by the entocarotid and contains, on its anterior wall and scarcely visible externally, the foramen caroticum posterius, whereas the more median and more open part is the foramen jugulare.

The hypoglossal (or condylar) foramen is broken away on the sectioned half, and only partly preserved on the unsectioned portion. On the latter it may, however, be seen that it was relatively large, freely exposed, and approximately circular. Its opening forms a pit immediately posterior to the most posterior (posteromedian) point of the bulla, whence the canal runs upward, backward, and medially. There is a small circular opening on the anterior wall of the pit which may, however, be an artifact.

The margins of the foramen magnum are broken. In another specimen of *Oldfieldthomasia* it is preserved, but presents no marked peculiarities, being a simple transverse ellipse with a large, rounded, basal notch.

A small opening, which may be at least descriptively accepted as a mastoid foramen, is left by the incomplete filling of the gap on the occiput of the pars mastoidea. This opens into a channel posteromedian to the epitympanic sinus and above the pars mastoidea, opening into the posterolateral part of the cerebellar fossa.

There are several small and variable venous foramina on the roof of the skull in the squamosal and parietal near their suture with each other, and at least one in the anterolateral cerebral wall.

POSTGLENOID, POSTTYMPANIC, AND PAROCCIPITAL PROCESSES: These processes are very incomplete on both sides of the sectioned skull, but are fairly well shown by another skull of the same species.

The postglenoid process is large and prominent, compressed anteroposteriorly. Its lateral end passes into a ridge which runs upward and then curves backward, forming a semicircular eminence anterior and superior to the porus acusticus. The median end abuts against the middle of the anterolateral side of the meatus, being separated from the crista meatus by a notch, which continues posteriorly and then superiorly as the groove running into the postglenoid foramen.

A posttympanic process is usually present as a morphological element in notoungulates, being a downward projection of the squamosal or of the "posterior adventitious bone," but in most cases it is applied to the side of the paroccipital process and is not topographically separate from the latter. In *Oldfieldthomasia*, however, or at least in A.M.N.H. No. 28896, it has a distinct apex, lateral to the paroccipital process, formed entirely by the exoccipital, is very prominent, directed straight downward, and apparently was simply styliform (the end is broken on all available specimens). In any case it clearly had no striking specialization such as, for instance, that of *Pachyrukhos*.

ENDOCRANIUM: The general plan of the endocranium is similar to that of *Notostylops* (Simpson, 1933f), the differences being slight and of degree only. The indicated brain cast might be summed up as intermediate between *Notostylops*, more primitive in this respect, and *Hegetotherium* (Simpson, 1933i), more advanced, but nearer the former.

MANDIBLE

The horizontal ramus is more slender than in most allied or comparable genera. In 10 adults from Colhué-Huapí the internal depth below the anterior root of M_1 varies from 11.3 to 15.3 mm., mean 12.7. The symphysis is long, shallow, spoutlike, and completely fused. There is an irregular and highly variable series of three or more small mental foramina, the most posterior usually beneath P_4. The dental foramen is large and well below the dental level. The angle is large and flattened, with evenly curved border, projecting little below the lower border of the horizontal ramus. The coronoid is not preserved but was very short anteroposteriorly. The condyle is elevated well above the teeth and is convex and somewhat transverse.

Oldfieldthomasia parvidens Ameghino, 1901

Plate 7, figures 1, 2

Oldfieldthomasia parvidens AMEGHINO, 1901, p. 368; 1904b, p. 45, figs. 35, 44.

Oldfieldthomasia pulchella AMEGHINO, 1901, p. 368.

TYPE: M.A.C.N. No. 10763, associated right P^4–M^2 (type) and three isolated, not associated, upper cheek teeth.

TYPE OF SYNONYM: M.A.C.N. No. 10756, fragment of left maxilla with dm^{3-4} and M^1.

HYPODIGM: Types and M.H.N. Tournouër Collection No. 21, broken facial part of skull with right P^3–M^3 and left P^1–M^3.

HORIZON AND LOCALITY: Known specimens from the Casamayoran, south of Colhué-Huapí.

DIAGNOSIS: Closely similar to *O. debilitata* but slightly smaller, with upper cheek teeth slightly less transverse.

This species was defined on its small size, more or less equal inner lobes united to summits, median anteroposterior fossettes, and the belief that M^1 was notably larger than M^2. The second and third of these characters are equally developed in all specimens of *Oldfieldthomasia* and most allied genera, and the last is not correct. The tooth lengths of the type are in the range of those of *O. debilitata* nominally, but actually are shorter than in specimens referred to that species in a comparable stage of wear. The widths are slightly less than in specimens surely referred to that species.

The validity of the species, rather dubious on the basis of the Ameghino specimens alone, is supported by the relatively good specimen in the museum in Paris (listed in the hypodigm, above). Structurally this specimen has no evident differences from *O. debilitata*, but the lengths of the upper cheek teeth are all near (for LM^1 below) the minima observed in the latter species and the widths are consistently and decisively lower. If allowance be made for differences in wear, the dimensions are in close agreement with the type of *O. parvidens*.

Oldfieldthomasia pulchella was defined in the belief that its type has P^4–M^2. These teeth are almost certainly dm$^{3-4}$ and M^1. Although M^1, poorly preserved, provides scant basis for comparison, it is indistinguishable from that of *O. parvidens*, and it is impossible to separate the species.

Measurements are given in table 8.

Oldfieldthomasia anfractuosa Ameghino, 1901

Plate 7, figure 3

Oldfieldthomasia anfractuosa AMEGHINO, 1901, p. 369.

Oldfieldthomasia amphractuosa (*lapsus* or misprint): AMEGHINO, 1904b, p. 191, fig. 252 (probably not this species).

TYPE: M.A.C.N. No. 10746, fragment of right maxilla with dm^3–M^2 (type or lectotype), also right maxilla with P$^{2-3}$, and right lower jaw with M$_{1-3}$, not associated.

TABLE 8

TOOTH DIMENSIONS OF *Oldfieldthomasia parvidens* COMPARED WITH THOSE OF *O. debilitata*

		O. parvidens			*O. debilitata*	
		M.A.C.N. No. 10763	M.A.C.N. No. 10756	M.H.N. Tournouër No. 21	A.M.N.H. No. 28691	Means
P^1						
	L	—	—	5.0	—	—
	W	—	—	3.5	—	—
P^2						
	L	—	—	6.1	—	6.7
	W	—	—	5.2	—	6.2
P^3						
	L	—	—	6.0	—	6.5
	W	—	—	6.5	—	7.7
P^4						
	L	6.0	—	6.3	—	6.6
	W	7.5	—	7.8	—	9.1
M^1						
	L	6.6	*ca.* 6½	5.8	—	6.9
	W	9.0	*ca.* 9	9.0	—	9.7
M^2						
	L	7.0	—	6.9	—	7.6
	W	9.5	—	9.3	—	10.6
M^3						
	L	—	—	6.7	—	7.4
	W	—	—	8.4	—	10.0
dm^3						
	L	—	6.4	—	6.7	—
	W	—	6.0	—	7.0	—
dm^4						
	L	—	6.2	—	6.9	—
	W	—	7.4	—	7.9	—

Hypodigm: Types only.

Horizon and Locality: Casamayoran. Type from "Colhué-Huapí Norte."

Diagnosis: Relatively large. Dm^4 slightly more transverse than in known specimens of other species.

Aside from the size, the original definition was distinctive only in stating the internal side of P^4 to be bilobed as on M^1—a misapprehension as the supposed P^4 is almost surely dm^4. The specimen is very poorly preserved, but it falls outside the known size range of specimens of *O. debilitata* from south of Colhué-Huapí. A lower jaw apparently from the same locality and believed by Ameghino to be *O. anfractuosa* is indistinguishable from that of *O. debilitata*. The status of the species is uncertain.

The measurements (all approximate) of the teeth of the type are: dm^4, length, 7, width, 9$\frac{1}{2}$; M^1, length, 8$\frac{1}{2}$, width, 11$\frac{1}{2}$; M^2, length 9, width, 13$\frac{1}{2}$.

The original of Ameghino (1904b, fig. 252), labeled as this species, is not the type but M.A.C.N. No. 10759, from south of Colhué-Huapí, and probably belongs to *O. debilitata*.

Oldfieldthomasia transversa Ameghino, 1901

Plate 7, figure 4

Oldfieldthomasia transversa Ameghino, 1901, p. 368; 1904b, p. 47, figs. 40, 90, 175; 1906, p. 311, fig. 122.

Type: M.A.C.N. No. 10754, two associated left upper teeth, probably dm^4 and M^1.

Hypodigm: Type only.

Horizon and Locality: Casamayoran, south of Colhué-Huapí.

Diagnosis: ?Dm^4 measuring about 7.0 by 7.2 mm.; ?M^1, 7.0 by 8.2.

It is highly probable that the type teeth are dm^4 and M^1. If so, this could be a variant of *O. debilitata*, and it is probably a synonym of that species. If, however, these teeth are M$^{1-2}$, as Ameghino believed, the species is valid. The single fragmentary specimen is inadequate, and the species is highly dubious.

ULTRAPITHECUS Ameghino, 1901

Ultrapithecus Ameghino, 1901, p. 359; 1906, p. 466.

Type: *Ultrapithecus rutilans.*

Distribution: Casamayor, Patagonia.

Diagnosis: P^1 one-rooted, wider than long. P$^{2-4}$ strongly transverse, parastyle fold strong and sharp, paracone fold large but indefinite, metacone region vaguely convex. P^4, and to less extent P^3, tending to be subquadrate, usually with an internal groove. No mesostyles on premolars or molars. M^1 with small, definite, subequal paracone and metacone folds, metacone fold vestigial on M$^{2-3}$. Main fossa strongly oblique, without spur, anteroexternal fossette very small and evanescent, posteroexternal fossette well developed. Lower dentition about like that of *Oldfieldthomasia.*

Ultrapithecus rutilans Ameghino, 1901

Plate 7, figures 5–7; plate 8

Ultrapithecus rutilans Ameghino, 1901, p. 359; 1904b, p. 168, fig. 214.

Type: M.A.C.N. No. 10818, right maxilla with P^1–M^2.

Hypodigm: Type and six specimens in the American Museum of Natural History, especially: A.M.N.H. No. 28706, palate with P^1–M^3 of both sides; A.M.N.H. No. 28583, palate with left di^2–dm^4 and M^1, right dm$^{1-4}$, M^1, and inner half of M^2; also M.H.N. Tournouër Collection No. 23, part of left maxilla with P^2–M^3, deeply worn, and M.H.N. Tournouër Collection No. 24, associated maxilla with P^2–M^3 of both sides and alveoli of P^1.

Horizon and Locality: Casamayoran, Patagonia. Known specimens from south of Colhué-Huapí, except M.H.N. Tournouër Collection No. 24, from north of Lago Musters.

Diagnosis: Sole species surely referable to genus; measurements are given in table 9.

This genus and species are rare, the Ameghino Collection including only one specimen, the American Museum of Natural History six, and the Tournouër Collection two referable to it, yet the type is unusually adequate, and the genus and species can be considered well established.

As shown by the measurements given in

TABLE 9

MEASUREMENTS OF TEETH OF *Ultrapithecus rutilans*

		M.A.C.N. No. 10818, Type	A.M.N.H. No. 28706	A.M.N.H. No. 28583	A.M.N.H. No. 28853	M.H.N. Tournouër No. 23	M.H.N. Tournouër No. 24
P^1	L	3.8	3.7	—	—	—	—
	W	5.0	4.7	—	—	—	—
P^2	L	4.5	4.5	—	4.7	4½[a]	4.3
	W	6.4	6.2	—	7.1	6[a]	6.2
P^3	L	5.0	5.1	—	5.1	5.2	4.9
	W	7.1	7.2	—	7.8	7.1	7.0
P^4	L	5.1	5.7	—	5½[a]	6.1	5.6
	W	8.0	8.3	—	8.7	8.2	8.2
M^1	L	*ca.* 7	6.2	7.2	—	6.7	6.8
	W	9.0	8.6	8.2	—	8.5	8.6
M^2	L	8.4	8.2	—	—	8.7	8.7
	W	10.2	9.4	—	—	10.5	9.0
M^3	L	—	7.5	—	—	6.5	7.7
	W	—	8.6	—	—	8.9	8.9
dm^1	L	—	—	3.7	—	—	—
	W	—	—	4.6	—	—	—
dm^2	L	—	—	4.7	—	—	—
	W	—	—	5.4	—	—	—
dm^3	L	—	—	5.1	—	—	—
	W	—	—	6.0	—	—	—
dm^4	L	—	—	6.4	—	—	—
	W	—	—	6.6	—	—	—

[a] Approximate.

table 9, the specimens placed here differ considerably in size and proportions, but the structure is almost exactly the same in all, and the differences in dimensions are inadequate to establish any probable taxonomic distinctions. The marked variation in the length of M^1 is at least partly due to wear, for the youngest individual is longest, 7.2 mm., and the oldest is shortest, 6.2 mm. At a level corresponding to that reached by wear in the latter, this measurement in the former would be about 6.5 mm. There is considerable size difference not greatly affected by wear in, for instance, the width of P^2, which is 6.4 in the type, 6.2 in our most complete specimen and in one of the Paris specimens, and 7.1 in a more fragmentary specimen of our collection. The latter may be incorrectly referred but is not shown to be on these data. The maximum difference is 15 per cent, which does not necessarily imply a coefficient of variation greater than four and is an entirely normal difference for such dimensions in individuals of one species. A still greater absolute difference is seen in the width of M^2 in the two Paris specimens, but this, again, is only about

15 per cent of the smaller measurement.

The incisors and canines are unknown except in A.M.N.H. No. 28583, in which they are presumably the deciduous teeth, since none of the premolars appears yet to have been replaced in this individual. Di^2–dc are compressed teeth, the crown expanded beyond the roots, with a sinuous apex with one asymmetrical cuspule. Di^2 is slightly the smallest, and dc slightly the largest, of these three teeth.

P^1 is wider than long. Any apical pattern it may have is early entirely obliterated and is not seen in the available material. P^{2-4} are much alike save in size and proportions. They are all strongly transverse and relatively symmetrical. The outer wall has a strong and sharp parastyle fold, projecting more anteriorly than externally, followed by a sharp and definite vertical groove. Posterior to this the whole wall is bulbous, with a vague but large paracone fold and a relatively smaller and very ill-defined metacone swelling. There is a low and inconspicuous anterior cingulum. On the known specimens it is almost completely obliterated, but a high posterior cingulum was doubtless present. On worn teeth there is a single deep fossa, somewhat elongate anteroexternal-posterointernally, or progressively more so from P^2 to P^4. On the least worn specimens available, there is also a small anteroexternal fossette. The inner side of P^4 is flattened and vaguely grooved.

On the ectoloph wall of M^1 there are restricted, well-defined, nearly equal paracone and metacone folds separated by a nearly plane or somewhat depressed area, and the paracone is preceded, the metacone followed, by narrow, flattened areas. On M^{2-3} the area posterior to the paracone fold is relatively larger, but the metacone fold is very weak. There is no mesostyle. Protocone, hypocone, and cingula are almost exactly like those in *Oldfieldthomasia*. The internal groove is sharp but does not end basally in a definite pocket. The typical worn apical pattern is distinctive, the central fossa reaching nearly to the anterior corner, and there is a single external fossette, posteroexternal. There is no median projection from the main fossa. On almost completely unworn teeth there are traces of a very small fossette separate from the main fossa in the extreme anteroexternal corner, but even at this stage this fossette is shallow, and it disappears almost immediately. In early wear stages, the high posterior cingulum may also enclose a small transverse fossette. The difference from *Oldfieldthomasia* is real, but it might easily be exaggerated in verbal description, and the elements really appear to be homologous and the differences rather slight and variable, in no way fundamental. In terms of crests, emphasis is on a single long crochet, not unlike that of *Notostylops* but much stronger (involved in a much deeper apical pattern) and connected to the ectoloph at its anterior end, or to a very short crista.

Dp^{2-3} differ from P^{2-3} chiefly in having more definite metacone folds. Dp^4 is fully molariform but, as usual, less transverse and with lower crown than the true molars.

Lower teeth have not surely been associated with these upper dentitions. A specimen with P_4–M_1 that I think probably belongs here is like *Oldfieldthomasia* as far as can be determined except in size and proportions.

Little is known of the osteology of the genus, but one specimen shows the jugal splint on the anteroinferior orbital rim, so that this region and the whole zygomatic root were apparently like those of *Oldfieldthomasia*.

Measurements of the principal specimens are given in table 9.

MAXSCHLOSSERIA AMEGHINO, 1901

Maxschlosseria AMEGHINO, 1901, p. 413; 1906, p. 468.

Paracoelodus AMEGHINO, 1904a, vol. 56, p. 199; 1904b, p. 46; 1906, p. 467.

TYPE: *Maxschlosseria praeterita*.

TYPE OF *Paracoelodus*: *Oldfieldthomasia marginalis* Ameghino, 1901.

DISTRIBUTION: Casamayoran, Patagonia.

DIAGNOSIS: Primitive, small, brachydont notoungulates with dentitions closely resembling those of *Ultrapithecus* and, less closely, those of *Oldfieldthomasia*. P^1 longer than wide and P^{2-3} also relatively less transverse than in *Ultrapithecus*. P^{3-4} in some cases with slight metacone fold. P^4 rounded-triangular, without internal groove. No mesostyle folds. Metacone fold present but usually weak on M^1, vestigial on or absent from M^{2-3}. Upper molar coronal pattern about like that in *Ultrapithecus*, with distinct, small, posteroexternal fossette and large, main, internal fossette, anteroexternal fossette poorly distinguished from latter, and median external fossette lacking. Occasionally slightly more complex, but less so than in *Oldfieldthomasia.* Lower dentition virtually indistinguishable from that of *Oldfieldthomasia.*

Under this genus I propose to group 11 of Ameghino's species, placed by him in nine genera and five families, as follows:

Archaeopithecidae
  Ultrapithecus rusticulus
Notopithecidae
  Antepithecus plexostephanos
Acoelodidae
  Oldfieldthomasia septa
  Paracoelodus marginalis[1]
Isotemnidae
  Isotemnus emundatus
  Isotemnus consumatus
  Maxschlosseria praeterita[1]
  Maxschlosseria anatona
  Pleurostylodon minimus
  Eochalicotherium minutum
Notostylopidae
  Eostylops obliquatus

With the exception of the two genotypes and of *Ultrapithecus rusticulus,* these species were all decidedly aberrant in the genera to which they were referred, as Ameghino recognized. All are of approximately the same size, and all share the rather generalized molar structure suggested in the diagnosis. The differences from *Notopithecus* or *Antepithecus* and from true notostylopids are great, when adequate material is compared, but the resemblances to *Ultrapithecus, Isotemnus* (including *Eostylops* and *Eochalicotherium*), *Pleurostylodon,* and *Oldfieldthomasia* are real and pronounced, as suggested by Ameghino's referring part of his material to each of these genera, according to what supposedly distinctive character happened to be most apparent in each of the fragments at hand.

With the exception of one specimen found by us and described below, the material is fragmentary, and much of it is of doubtful affinities. The present conception of the genus is necessarily based largely on the one good specimen that does not belong to the type species but has the same probable generic characters as far as the specimens are comparable. It is entirely possible that more than one genus is included among the various remains now assembled here, but, even if such proves to be true, the present arrangement is unlikely to lead to any serious confusion. It seems certain that these various species are very closely related, if not all congeneric. With the exception of the species referred to *Ultrapithecus, Paracoelodus,* and *Maxschlosseria,* it is almost certain that none belonged in the genera to which they were formerly assigned. Their union in this genus, even if it should turn out not absolutely correct in all cases, clarifies the limits of the genera from which they are removed. Since only two genotypes are involved, it is unlikely that any false generic synonymy is created.

Among contemporaneous forms, closest resemblance is to *Ultrapithecus,* and this is so close that there is serious question whether the two genera are really separable. *Maxschlosseria praeterita,* the genotype, is clearly distinct from *Ultrapithecus* only on the probably smaller and simpler P^4, a character of doubtful value. It may have had lower crowns, but is so worn that this is very uncertain, and it is not true of some other species referred to *Maxschlosseria.* Our specimen of *M. consumata* shows other differences that have been used to support the tentative separation from *Ultrapithecus.* Even if these genera are separable, it is quite possible that some species now placed in *Maxschlosseria* really belong in *Ultrapithecus,* since some of the fragmentary type specimens show none of the characters used to separate the genera. It has, however, seemed more practical to leave *Ultrapithecus* as a well-delimited genus resting on its type species alone and to use *Maxschlosseria* as a collective genus for doubtful forms.

The upper teeth are easily distinguishable from those of *Oldfieldthomasia,* despite a resemblance consistent with fairly close affinity. *Maxschlosseria* and *Oldfieldthomasia* cannot be clearly or absolutely distinguished on the basis of the lower jaw and dentition, yet these virtually identical lower dentitions are known from positive individual associations to belong with obviously different upper teeth. This fact emphasizes, again, the impossibility of achieving any definitive arrange-

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[1] Genotypes.

ment of the present fauna until such associations have been established in all cases. The resemblance to *Isotemnus* is almost equally close, in this case rather more in the upper than in the lower teeth, but separation is facilitated in practice by the much larger size of the species surely referable to *Isotemnus*.

The dentition is so like that of *Oldfieldthomasia* and *Ultrapithecus* that it need not be described in detail. P^1, known only in our specimen of *M. consumata*, is like that of *Oldfieldthomasia*, but somewhat more rounded in outline and more bulbous on the outer face. P^{2-4} are also almost exactly like those teeth in *Oldfieldthomasia*, as far as can be judged from somewhat worn specimens, except for the very feeble metacone fold. The upper molar pattern is that described for *Ultrapithecus*, except that the central enamel lake is in some cases, but not invariably, branched at the anterior end. This effect arises in three different ways, or combinations of them, apparently very distinct but in part illusory, as affected by wear, and in part merely individual variants: by the projection of the crochet beyond its usual junction with the crista, by the presence of another crista anterior to that invariably present, and by the presence of an antecrochet.

The lower canine and all the lower cheek teeth are known in *M. consumata*, and they agree word for word with my description of the homologous teeth in *Oldfieldthomasia*.

Maxschlosseria praeterita Ameghino, 1901

Plate 9, figures 1, 2

Maxschlosseria praeterita AMEGHINO, 1901, p. 413.

TYPE: M.A.C.N. No. 10624, part of left maxilla with deeply worn P^4–M^3.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayoran, "Oeste de Río Chico," Chubut.

DIAGNOSIS: M^3 triangular, rounded internally. Molar paracone folds sharp and strong. No distinct metacone fold on M^2. Size small; see measurements below.

The type is the only known specimen. Unfortunately it is sharply distinct, specifically, from the forms on which conceptions of the genus are now necessarily based in large part. Ameghino stated that the internal side of the molars is not bilobed, but the statement is true only of their bases. Protocone and hypocone are united by deep wear, but were certainly well separated and subequal on M^{1-2}. He further stated that the enamel folds and similar features of related genera are absent but are simulated by superficial lines. These "lignes superficielles" are in fact enamel rings, following the pattern of related forms in a similar advanced stage of wear.

The measurements of the teeth of the type are: P^4, length, 3.5, width, 5.9; M^1, length, 5.8, width, 7.1; M^2, length, 6.2, width, 8.1; M^3, length, 5.7, width, 7.3.

Maxschlosseria minima (Ameghino, 1897), new combination

Plate 9, figures 3–5

Pleurostylodon minimus AMEGHINO, 1897a, p. 486; 1898, p. 171.

Antepithecus plexostephanos AMEGHINO, 1902a, p. 9.

Maxschlosseria anatona AMEGHINO, 1902a, p. 28.

TYPE: M.A.C.N. No. 10572, isolated left M^2 (lectotype) and right M^3.

TYPE OF *Antepithecus plexostephanos*: M.A.C.N. No. 10840, a right upper molar, probably M^2, lacking the anteroexternal angle; this is the type or lectotype and the original diagnosis was based largely or wholly on it. Under the same number are a complete upper tooth, perhaps dm^4, and two inner sides of upper molars, not associated and perhaps not this species.

TYPE OF *Maxschlosseria anatona*: M.A.-C.N. No. 10617, part of right maxilla with P^4–M^1 and parts of M^{2-3}.

HYPODIGM: Types only.

HORIZON AND LOCALITY: Casamayoran, Patagonia. No other data for type. Other Ameghino specimens from "Oeste de Río Chico," Chubut.

DIAGNOSIS: Parastyle somewhat weaker than in *M. praeterita*. Size larger (see below).

Referring them to three different genera, Ameghino did not make any explicit comparison of these three species. *Maxschlosseria anatona* was defined as being larger than *M. praeterita*, with the lines simulating enamel folds more marked but shallow and with a vestige of division on the inner side. Except for size, these are due to less extreme wear, and as far as these types are preserved I see no good difference except size. The slightly weaker paracone fold (more evident in "*Pleurostylodon*" *minimus*) is perhaps only individual. *Maxschlosseria anatona* has the only adequate type of the three here involved, but it is not distinguishable from the very poor type of "*P.*" *minimus*, which has clear priority.

Measurements are given in table 10.

Maxschlosseria rusticula (Ameghino, 1901), new combination

Plate 9, figures 8, 9

Ultrapithecus rusticulus Ameghino, 1901, p. 360.

Oldfieldthomasia marginalis Ameghino, 1901, p. 367.

Paracoelodus marginalis: Ameghino, 1904a, vol. 56, p. 199 (made type of new genus); 1904b, p. 46, figs. 38, 408, 409, 448.

Isotemnus emundatus Ameghino, 1901, p. 412.

Type: M.A.C.N. No. 10819, part of right maxilla with P^4–M^3, much worn, with outer wall of M^1 absent (type or lectotype), also left P^4–M^3, all badly preserved, and a left lower jaw with M_{1-3}, somewhat broken.

Type of *Paracoelodus* or *Oldfieldthomasia marginalis:* M.A.C.N. No. 10751, left upper jaw with P^4–M^2, type. Under same number a left upper jaw with poorly preserved M^{1-2}, part of a left lower jaw with P_2–M_1, not associated but probably this species, and two other lower jaw fragments probably not of this species.

Type of *Isotemnus emundatus:* M.A.C.N. No. 10578, right upper jaw with P^4 complete but worn, and broken M^{1-3}.

Hypodigm: Types and associated specimens, as above.

Horizon and Locality: Casamayoran, all known material from "Oeste de Río Chico," Chubut.

Diagnosis: About the size of *M. minima*, but with P^4 relatively larger and M^2 relatively smaller. Protocone with some tendency to be bifid on M^{1-2}.

Here again the three evidently synonymous species were not compared because they were referred to different genera. *Paracoelodus* was based principally on the bifid protocone. This peculiarity, somewhat overemphasized by Ameghino, is seen also in other members of this genus and some allied forms and is, in some cases at least, individually variable. It is also most prominent in one special wear stage, which happens to be that of this type. Its origin appears to be the presence of an internal groove on the basal part of the protocone not exactly corresponding with the protocone-hypocone notch, a peculiarity already emphasized in *Notostylops* and of rather frequent but sporadic occurrence in various other groups of notoungulates.

The lower jaws referred by Ameghino to *Ultrapithecus rusticulus* and to *Paracoelodus marginalis* (with the exception of the last two fragments listed with the type of the latter) were apparently not associated with upper teeth but occlude well and probably do belong to this species. Except for size and proportions they have no distinctive characters.

The dimensions of the types and of these referred lower teeth are given in table 11.

Maxschlosseria septa (Ameghino, 1901), new combination

Plate 9, figure 6

Oldfieldthomasia septa Ameghino, 1901, p. 369.

Type: M.A.C.N. No. 10758, fragment of a

TABLE 10

Measurements of Teeth of Types of *Maxschlosseria minima* and its Synonyms

M.A.C.N. No.	P^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W
10572[a]	—	—	—	—	8.1	10.1	7.6	9.7
10840	—	—	—	—	*ca.* 8½	*ca.* 11	—	—
10617	*ca.* 4	6.8	*ca.* 6	8.1	*ca.* 8	*ca.* 10	—	—

[a] Note that these two teeth are not associated. They do seem to be of the same species.

TABLE 11

MEASUREMENTS OF TEETH OF *Maxschlosseria rusticula*

	M.A.C.N. No. 10819	M.A.C.N. No. 10751	M.A.C.N. No. 10578
P^4			
L	5.7	5.8	4.9
W	8.3	8.5	8.2
M^1			
L	*ca.* 6	6.5	*ca.* 5½
W	*ca.* 9	9.1	—
M^2			
L	7.5	7.4	*ca.* 7
W	10.0	9.7	*ca.* 9½
M^3			
L	*ca.* 7½	—	*ca.* 7½
W	10.0	—	*ca.* 9
P_2			
L	—	*ca.* 4½	—
W	—	*ca.* 3	—
P_3			
L	—	*ca.* 5½	—
W	—	*ca.* 3¼	—
P_4			
L	—	*ca.* 5½	—
W	—	*ca.* 4	—
M_1			
L	*ca.* 6	*ca.* 6	—
W	*ca.* 4	*ca.* 4	—
M_2			
L	6.9	—	—
W	4.6	—	—
M_3			
L	9.5	—	—
W	4.5	—	—

left maxilla with three teeth, the first and third broken. Also four isolated lower teeth, not associated and not properly part of the type.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayoran, "Oeste de Río Chico," Chubut.

DIAGNOSIS: Based on upper teeth of doubtful homologies. M^1 is either considerably less transverse than in other species or is like that of *M. consumata*, with which this species may thus be synonymous.

As a species of *Oldfieldthomasia*, this was distinguished principally by the absence of a mesostyle fold, which is, with respect to *Oldfieldthomasia*, the most diagnostic character of *Maxschlosseria* and *Ultrapithecus*. The teeth partially preserved in the type resemble P^4–M^2, and the species was defined on that basis. If these homologies were correct, the species would be very distinctive in the proportions of M^1 and the relative sizes of P^4–M^2. It is, however, very likely that these teeth are really dm^{3-4} and M^1, as suggested by the proportions of dm^4 (by this homology) and also its rather low crown and divergent roots. In this case M^1, the last tooth in the specimen, is indistinguishable from that of the following species, *M. consumata*, and the two would have to be considered synonymous. The two names were proposed at the same time, *septa* on a prior page, neither on a good type.

The measurements (very approximate for the broken first and third teeth) are: dm^3 or P^4, length, *ca.* 7, width, —; dm^4 or M^1, length, 7.7, width, 8.0; M^1 or M^2, length, *ca.* 8, width, *ca.* 10.

Maxschlosseria consumata (Ameghino, 1901), new combination

Plate 9, figures 7, 10, 11; plate 10, figures 1–4

Isotemnus consumatus AMEGHINO, 1901, p. 412.
Eostylops obliquatus AMEGHINO, 1901, p. 424; 1904b, p. 410, fig. 537.

TYPE: M.A.C.N. No. 10580, fragment of left maxilla with parts of deeply worn and broken P^4–M^3.

TYPE OF *Eostylops obliquatus:* M.A.C.N. No. 10482, fragment of right maxilla with deeply worn M^2.

HYPODIGM: Types, as above; and A.M.-N.H. No. 28753, associated upper and lower jaws with right P^1–M^3, left P^3–M^2, right C–M_3, and left P_4–M_2 and trigonid of M_3, also skeletal fragments; also numerous isolated teeth in the American Museum of Natural History collection.

HORIZON AND LOCALITY: Casamayoran, Chubut. Type from "Oeste de Río Chico." American Museum specimens from Cañadón Vaca. M.A.C.N. No. 10482 from south of Lago Colhué-Huapí.

DIAGNOSIS: Much larger than *M. praeterita*. M^{2-3} about the size of those of *M. minima* but P^4–M^1 relatively larger. M^2 with small, distinct metacone fold. M^3 with internal groove.

TABLE 12

STATISTICAL DATA ON M_3 OF *Maxschlosseria consumata*

	N	R	$\bar{X}$	s	V
LM_3	12	9.2–10.9	10.11±.14	0.50±0.10	5.0±1.0
WM_3	12	4.9– 6.1	5.45±.10	0.34±0.07	6.4±1.3

The type, very poorly preserved, is not generically separable from *Isotemnus*, *Ultrapithecus*, or *Maxschlosseria*, although in any of these genera it would be a distinctive species (except for possible identity with *M. septa*, as already noted). A.M.N.H. No. 28753 is from the same general area as the type, is not specifically distinguishable from it, and may therefore be used to place the species on a firm basis. It is distinguishable from *Isotemnus* and (less decisively) from *Ultrapithecus*, belongs to the same group, at least, as *Maxschlosseria praeterita*, and has therefore been used, as stated above in the generic discussion, to permit the retention of *Maxschlosseria* for various species of this general sort.

Eostylops obliquatus is almost or quite indeterminate and might have been simply designated as a *nomen vanum*. It is markedly distinct from the genotypic *Eostylops diversidens*, which belongs in *Notostylops*. It cannot be distinguished from *Maxschlosseria*, in the present usage, and if placed in this genus is indistinguishable from *M. consumata*, in the synonymy of which it may thus reasonably be buried. It is, however, almost devoid of generic characters and might conceivably have belonged elsewhere. There is further doubt concerning it because it is said to be from south of Colhué-Huapí, whereas all the other specimens now referred to *Maxschlosseria* are, as far as known, from "Oeste de Río Chico" (and Cañadón Vaca, which is also west of the Río Chico).

The essential dental characters have been adequately mentioned and illustrated. In addition to A.M.N.H. No. 28753, we have many isolated teeth. The most adequate sample is that of M_3, which gives the numerical data of table 12.

Morphological variation is most obvious around the anteroexternal part of the upper molar central fossa, as already mentioned. There is one tooth in our collection that may be dm^4 of this species, as it resembles a permanent molar except in being smaller, lower-crowned, and less transverse, measuring 7.7 by 8.5 mm. It is a little more transverse than the possible dm^4 of *M. septa*, but close enough to be the same species.

M^2 of the type measures approximately 8.5 by 11 mm. A.M.N.H. No. 28753 approaches this well within probable specific limits, and a referred M^2 in our collection, surely conspecific with our better specimen, measures 8.6 by 10.7 mm., which amounts to identity, given the approximate nature of the type measurements. The type M^2 of "*Eostylops obliquatus*" measures 8.4 by 10.9, which is also appreciably identical.

The following measurements are of associated upper and lower teeth of the right side of A.M.N.H. No. 28753: P^1, length, 5.0, width, 3.7; P^2, length, 6.1, width, —; P^3, length, 6.1, width, 7.4; P^4, length, 6.3, width, 9.1; M^1, length 8.0, width, 10.6; M^2, length, 8.9, width, 11.6; M^3, length, 7.6, width, —; C, length, 5.1, width, 2.3; P_1, length, 5.4, width, 2.3; P_2, length, 6.4, width, 3.3; P_3, length, 6.6, width, 3.8; P_4, length, 6.5, width, 4.6; M_1, length, 7.1, width, 5.5; M_2, length, 8.5, width, 5.6; M_3, length, 9.6, width, 4.9.

Maxschlosseria minuta (Ameghino, 1901), new combination

Plate 9, figure 12; plate 10, figures 5, 6

Eochalicotherium minutum AMEGHINO, 1901, p. 418.

TYPE: M.A.C.N. No. 10595, fragment of right lower jaw with roots of P_4 and crowns of M_{1-2}.

HYPODIGM: Type, and A.M.N.H. No. 28660, left lower jaw with M_{1-3}.

HORIZON AND LOCALITY: Casamayoran, "Oeste de Río Chico," Chubut. Referred specimen from Cañadón Vaca.

DIAGNOSIS: Lower teeth of general *Old-*

TABLE 13

MEASUREMENTS OF TEETH OF *Maxschlosseria minuta*

	M_1		M_2		M^3	
	L	W	L	W	L	W
M.A.C.N. No. 10595	5.2	3.9	6.1	4.3	—	—
A.M.N.H. No. 28660	6.2	4.5	6.3	4.8	7.8	4.7

fieldthomasia-Ultrapithecus-Maxschlosseria type, with external cingula; dimensions as given in table 13.

Lower teeth in this group do not show any clear generic characters, so that the position of this species must be uncertain. It is, however, of a size appropriate for a species of *Maxschlosseria* and has the same locality data, so that reference to this genus is definitely the most probable. The size is smaller than the lower teeth referred to *M. rusticula*, but the difference is not great enough to exclude the possibility of specific identity. Agreement in size with *M. praeterita*, of which only the upper teeth are known, is probably still closer. The present species is probably synonymous with that or with some other species based on upper teeth.

A.M.N.H. No. 28660, from Cañadón Vaca, is a left lower jaw with M_{1-3}, tentatively referred to *M. minuta*. It is larger than the type, but not enough to be surely distinct. It is surely too small to belong with *M. consumata* from the same approximate horizon and locality, d/s for the length of M_3 being −4.4. It also has the external cingula seen in *M. minuta* and not in *M. consumata*. A further peculiarity, probably also present in the type of *M. minuta* but there somewhat uncertain because of wear, is that the bifurcation of the metaconid is slightly more distinct and the anterior cuspule or spur slightly less internal than in average specimens of *M. consumata* and definitely more than in *Oldfieldthomasia debilitata*. The measurements of this specimen and of the type are given in table 13.

?Maxschlosseria expansa (Ameghino, 1902), new combination

Plate 9, figure 13

Infrapithecus expansus AMEGHINO, 1902a, p. 9.

TYPE: M.A.C.N. No. 10856, three partial lower jaws, not associated, of which one with P_{2-4} is type or lectotype.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayoran, Patagonia. No other data.

DIAGNOSIS: Lower teeth generally similar to those of *Maxschlosseria*, *Ultrapithecus*, or *Oldfieldthomasia*, not more exactly definable.

This form surely does not belong to *Infrapithecus* (=*Notopithecus*). The teeth do not seem to be generically distinctive, but resemble those of *Maxschlosseria* as much as anything and may be tentatively placed in this genus. If this assignment is correct, the species is probably a synonym of one based on upper teeth, such as *M. rusticula*.

TSAMNICHORIA SIMPSON, 1936

Tsamnichoria SIMPSON, 1936d, p. 84.

TYPE: *Tsamnichoria cabrerai*.

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: Known parts similar to *Maxschlosseria* and allied genera, but P^{2-4} with distinct internal groove and P^4, particularly, subquadrate. Metacone fold well developed on all molars and well removed from posteroexternal angle. Fossette pattern, at least after slight wear, relatively simple, no median external fossette, and anteroexternal fossette confluent with main fossa. Lower molar entoconids sharply crested, not expanded, almost fully confluent with external crescents. Symphysis short but procumbent. Horizontal ramus elongate but not quite so slender as in *Oldfieldthomasia*, for instance.

This variation of the rather monotonous early notoungulate dentition is quite characteristic, and the associated dentitions cannot be confused with any other genus known to me. There are, one might say "of course," resemblances to several families, including the Archaeopithecidae, Isotemnidae, and even the Interatheriidae (Notopithecinae), but on the whole the greatest resemblance is to *Ultrapithecus* and allied Casamayoran genera here united in the Oldfieldthomasiidae. The bifid internal faces of the upper premolars and the slender, strongly crested molar entoconids, firmly united with the external crescents, are particularly distinctive, but the beginnings of the former character are suggested in the older genus *Ultrapithecus* and the entoconids are not very different from some variants of *Oldfieldthomasia*. Resemblance to typical Archaeopithecidae and Isotemnidae is not so close.

There is nothing else like this in the known Mustersan faunas, and *Tsamnichoria* apparently represents the last survivor of this primitive, early group, as such. The genus has so far been found at only one locality, but it is well represented in the Roth Collection.[1]

Tsamnichoria cabrerai Simpson, 1936

Text figures 17, 18

Tsamnichoria cabrerai SIMPSON, 1936d, p. 85, figs. 2–3.

TYPE: L.P.M. No. 12-1739, right maxilla with P^2–M^2.

HYPODIGM: Type, and the following: L.P.M. No. 12-1742, left lower jaw with P_4–M_3; L.P.M. No. 12-1735, left lower jaw with P_2–M_3; L.P.M. No. 12-1738, left lower jaw with M_2 and parts of other teeth, right lower jaw with P_4–M_3, and right lower jaw with M_{1-3}, from three different individuals.

HORIZON AND LOCALITY: Mustersan, north of Colhué-Huapí (probably Cerro del Humo).

DIAGNOSIS: Only known species of genus. Measurements are given in table 14.

TABLE 14

MEASUREMENTS OF TEETH OF *Tsamnichoria cabrerai*

		M.L.P. No. 12-1739	M.L.P. No. 12-1742	M.L.P. No. 12-1735
LP^2–M^2		28	—	38
P^2	L	3.9	—	—
	W	5.6	—	—
P^3	L	5.4	—	—
	W	6.3	—	—
P^4	L	6.0	—	—
	W	7.8	—	—
M^1	L	7.5	—	—
	W	8.7	—	—
M^2	L	8.9	—	—
	W	9.6	—	—
P_2	L	—	—	5.3
	W	—	—	3.4
P_3	L	—	—	6.2
	W	—	—	3.9
P_4	L	—	6.3	6.7
	W	—	3.9	4.2
M_1	L	—	6.4	6.8
	W	—	4.6	4.3
M_2	L	—	7.4	7.0
	W	—	5.0	4.8
M_3	L	—	9.1	8.9
	W	—	4.7	4.5

Upper and lower jaws were apparently not found in association, but I think there can be no doubt that they belong to a single species. All are from the same deposit, they occlude well, and no other upper teeth are known with which these lower teeth could correspond.

On P^{2-4} there is a strong paracone fold, little anterior to the middle of the outer face, and a weaker but definite parastyle fold. As preserved in middle-wear stages, each of these teeth has a single, small, deep, central fossette. On all three the inner face is distinctly bifid, and it appears, as far as one can judge from worn teeth, that the posterior cingulum ended on the lingual side in a small, definite,

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[1] In view of this fact, of the distinctive nature of the genus, and of the plethora of generic names proposed by Roth and Ameghino, it is rather surprising that no name had been applied by either of them. Roth had tentatively identified two specimens as *Transpithecus* and *Henricosbornia*, genera to which they could not possibly belong, but he did not know these genera at first hand, and it was exceedingly difficult to get a clear idea of them from the published information then available.

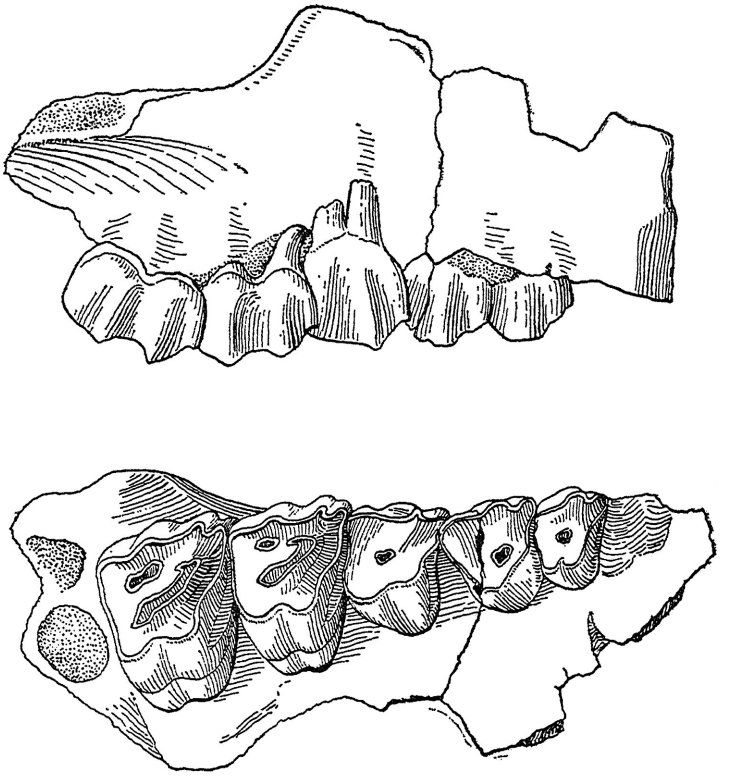

FIG. 17. *Tsamnichoria cabrerai* Simpson, M.L.P. No. 12-1739, type, right maxilla with P^2–M^2, buccal and crown views. ×2.5.

cingular hypocone, considerably lower than the protocone. There are no internal or external cingula on any of the known cheek teeth, upper or lower.

On M^{1-2} the protocone and hypocone are subequal and are connected nearly to the tips (which are worn off on the known material), but distinguished by a sharp vertical sulcus on the inner face. On these teeth the parastyle and paracone folds are strong, subequal, and closely approximated. Distinct but less sharp metacone folds occur only slightly posterior to the middles of the outer faces. The mesostyle and metastyle regions are nearly flat, without distinct folds. In the known stage of wear, there is a large, deep, oblique, central fossa with a hooklike, posteriorly directed branch at the anteroexternal end, and a small, separate, somewhat elongate, posteroexternal fossette.

Their alveoli suggest that the lower incisors were subequal and not enlarged and the canine was also unenlarged. P_{2-4} are not much compressed laterally. Both protoconid and metaconid have rapidly falling ridges extending posteriorly along the edge of the tooth. The anterior end of the heel crescent abuts against the metaconid on P_2 and against the middle of the transverse trigonid crest on P_3–M_3. The heel is very short on P_{2-4}, with the entoconid and hypoconulid apparently not distinct from the lophid.

M_{1-3} have short trigonids, without closed basins, each with a slight anterior transverse crest dropping sharply from the anteroexternal corner and a very short anteroposterior external crest at the same level as the slightly oblique, transverse, main crest. The metaconids are simple. On M_{1-2} the entoconids are near the posterior end and merge into the crescent with moderate wear. The hypoconulids are not distinct on these teeth. On M_3 the hypoconulid is set off by a vertical external groove, but is otherwise merged with the crescent. The entoconids on all three molars are simple, not expanded, but strongly

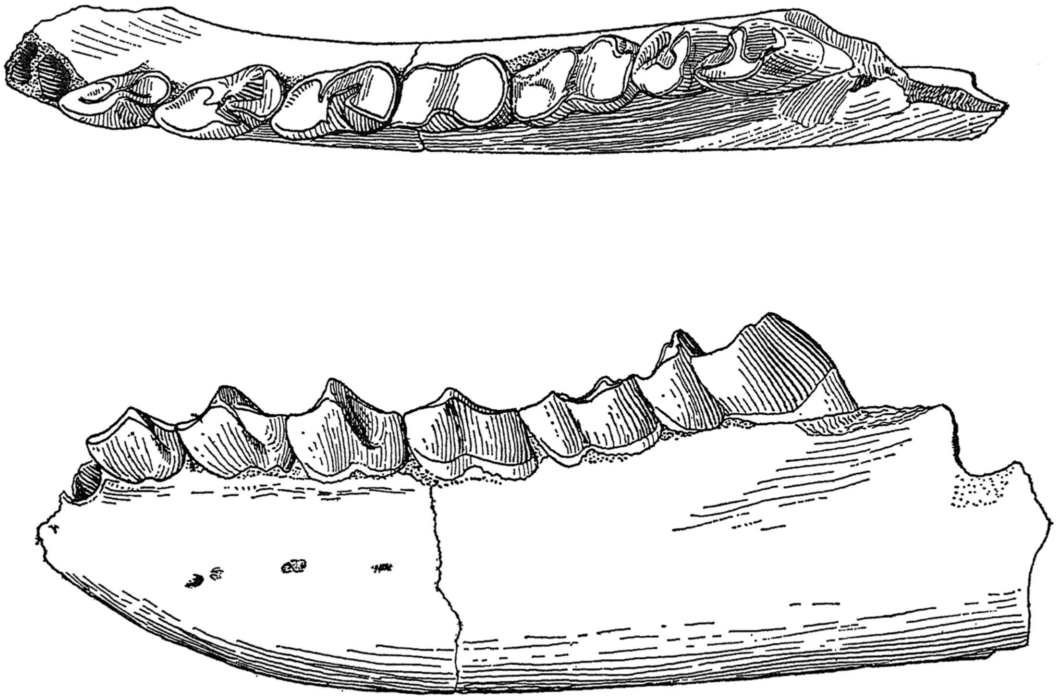

FIG. 18. *Tsamnichoria cabrerai* Simpson, M.L.P. No. 12-1735, left mandible with P_2–M_3, crown and buccal views. ×2.5.

crested transversely and fully fused at the outer end with the crescent.

The horizontal ramus is long and rather shallow, but relatively rather less so than in *Oldfieldthomasia*. The symphysis is short, ending at the level of P_2, but is procumbent. The angular region is expanded ventrally. The dental foramen is well below the molar level.

Measurements are given in table 14.

ACOELODUS Ameghino, 1897

Acoelodus Ameghino, 1897a, p. 454; 1901, p. 467. Schlosser, 1923, p. 609. Scott, 1937a, p. 516.

Type: *Acoelodus oppositus*.

Distribution: Casamayoran, Patagonia.

Diagnosis: A primitive notoungulate with a closed, complete, evenly graded dental series broadly comparable with that of *Oldfieldthomasia*, but I^2 no larger than I^3, metacone fold very weak, and mesostyle absent throughout, and length and breadth of M^3 nearly equal.

The status of this genus is extremely confused, even for a member of this fauna in which taxonomic confusion is more nearly the rule than the exception. The genus was originally based on a lower jaw fragment with P_{2-3} and part of P_4, all much worn. This specimen, on which technically the genus wholly depends, is virtually indeterminate. Later Ameghino (1901) referred to the type species the poorly preserved anterior part of a skull (M.A.C.N. No. 10753), with most of the dentition but with the cheek teeth too worn to show the coronal pattern. Thereafter Ameghino's conception of the genus was based in part on this skull and in part on other referred specimens and species which do not now appear to be congeneric either with the original type or with this skull.

It is dubious whether the skull, M.A.C.N. No. 10753, essentially a neotype for Ameghino, is really conspecific or congeneric with the true type, M.A.C.N. No. 10770. Since they have no parts in common, direct comparison is impossible. No other specimen just like either one has been found, and the association cannot be established indirectly. There are so many forms of several different families with teeth somewhat, but not precisely, like these that it is entirely possible that such isolated materials are of different families, and certainly there is no presumption that they are of the same species. In fact there is some contrary evidence. Among generally similar oldfieldthomasiids in which association of upper and lower teeth is established, P^3 and P_3 are invariably of about the same length, but P_3 of the type of *A. oppositus* is 6.8 mm. in length and P^3 of the referred skull or neotype is 7.8 mm. long, or 15 per cent longer. Given the fact that these are different individuals, the discrepancy does not exclude their being conspecific but it casts doubt on it.

Nevertheless, I propose to accept *Acoelodus* and to redefine it in terms of the neotype skull. To do so permits retention of Ameghino's widely known (but invariably misunderstood) name, and it provides a name for the skull, which apparently does represent a distinct genus, whatever may be true of the original type. It is an extraordinary fact that, as far as I have been able to find, no other known specimen is probably conspecific or congeneric with this skull. If my proposal to accept it as a neotype is accepted, it becomes in effect all that is known of the genus *Acoelodus.* It is just well-enough preserved to show that it is distinctive, but not well enough to show many of the important characters or for one to determine its affinities with any great probablility. The general character and seriation of the dentition are rather like those in *Oldfieldthomasia,* as Ameghino noted, and still more like those in *Maxschlosseria* or *Ultrapithecus,* so that tentative reference to the Oldfieldthomasiidae is warranted. The species is much larger than any other referred to this family. The teeth are so worn that all that remains of the cheek-tooth coronal pattern is the bottom of the main fossette, and in this stage of wear this feature is much the same in almost all Casamayoran notoungulates. Generic definition depends on the outlines of the various teeth and the outer molar walls, as noted in the diagnosis.

Ameghino referred the following species to *Acoelodus: A. oppositus* Ameghino, 1897; *A. connectus* Ameghino, 1901; *A. debilitatus* Ameghino, 1901; *A. microdon* Ameghino, 1901; *A. proclivus* Ameghino, 1902; *A. terminalis* Ameghino, 1902.

Acoelodus debilitatus certainly belongs in *Oldfieldthomasia* and has been described under that genus. *Acoelodus connectus* and *A. microdon,* which might be synonymous, are almost indeterminate, but it is very unlikely that they belong to *Acoelodus,* and they seem to be close to *Paginula,* in connection with which they are discussed in this revision. *Acoelodus proclivus* and *A. terminalis* clearly do not belong to *Acoelodus,* but I am unable to place them in any other genus at present, so discuss them briefly below as "*Acoelodus*" *proclivus* and "*A.*" *terminalis.*

As noted under *A. oppositus,* previous figures published as of *Acoelodus* do not really represent this genus, under any currently possible concept of it.

Acoelodus oppositus Ameghino, 1897

Plate 11, figures 1–3

Acoelodus oppositus AMEGHINO, 1897a, p. 454; 1898, p. 161; 1901, p. 365; 1904b, p. 44, figs. 33, 87, 168, 227, 239, 284, 285, 406, 407; 1906, p. 311, fig. 124. (These figures are not really of this species; see below.)

TYPE: M.A.C.N. No. 10770, fragment of left lower jaw with P_{2-3} and anterior end of P_4, all much worn.

NEOTYPE: M.A.C.N. No. 10753, poorly preserved skull, lacking posterior end, with right C and P^2–M^3 and left I^{1-3}, C, and P^2–M^3, all deeply worn.

HYPODIGM: Neotype only. (The indeterminate type is only nominally a member of the actual hypodigm.)

HORIZON AND LOCALITY: Casamayoran. No locality record for type; neotype from south of Colhué-Huapí.

DIAGNOSIS: Sole species now referred definitely to genus. Measurements in table 15.

As far as can be seen, the teeth of the (original) type are of the primitive pattern nearly universal in Casamayoran notoungulates regardless of suborder or family. They are closely similar to those of *Oldfieldthomasia* but are relatively broader. Their lengths are in the range of those of *O. debilitata,* but the widths are significantly greater.

TABLE 15

MEASUREMENTS OF TEETH OF *Acoelodus oppositus*

		M.A.C.N. No. 10770, Type	M.A.C.N. No. 10753, Neotype
P_2			
	L	5.4	—
	W	3.7	—
P_3			
	L	6.8	—
	W	4.6	—
I^1		—	7.0[a]
I^2		—	5.5[a]
I^3		—	5.6[a]
C		—	6.0[a]
P^2			
	L	—	7.5
	W	—	7.8
P^3			
	L	—	7.8
	W	—	8.5
P^4			
	L	—	7.5
	W	—	9.9
M^1			
	L	—	8.0
	W	—	11.5
M^2			
	L	—	8.5
	W	—	11.8
M^3			
	L	—	10.0
	W	—	10.7

[a] Maximum diameters.

As noted above, the present conception of the species is based on the neotype, which may or may not be really conspecific with the type. In comparison with that of *Oldfieldthomasia debilitata*, the neotype skull is larger, the facial part apparently longer and more slender, and the lacrimal tubercle probably larger, but the details of structure are not visible in the poorly preserved specimen.

The figures given by Ameghino as of this species are based neither on the type nor on the neotype and do not really represent this genus or species. Figures 33, 87, 168, 239, 284 of Ameghino (1904b) and figure 124 of Ameghino (1906), all repetitions of the same drawing, are based on M.A.C.N. No. 10745, an isolated right M^1 or M^2. This tooth is much smaller than either M^1 or M^2 of the neotype and has a conspicuous metacone fold, the outer wall being quite unlike that of *Acoelodus*. This tooth may belong to *Maxschlosseria*. Figures 227 and 285 of Ameghino (1904b), repetitions of the same drawing, do not agree exactly with the drawing just discussed, but seem to have been based on the same specimen. Figures 406 and 407 of Ameghino (1904b), different views of the same specimen, as stated by Ameghino, are based on M.A.C.N. No. 10740,[1] an isolated right P^4. The outline seems to be quite different from any premolar of the neotype of *A. oppositus*, and the whole structure is like that of *Oldfieldthomasia*.

Measurements are given in table 15.

"Acoelodus" proclivus Ameghino, 1902

Acoelodus proclivus AMEGHINO, 1902a, p. 12.

TYPE: M.A.C.N. No. 10752, isolated upper molar, probably M^1. Under the same number is a jaw fragment with left P_{3-4}, not associated with the upper tooth and not to be considered part of the type.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayoran, south of Colhué-Huapí.

DIAGNOSIS: Based on a brachydont, primitive notoungulate upper molar measuring 13.2 mm. in length and 15.0 mm. in width. Strong parastyle and paracone folds, slightly weaker metacone fold, and an extremely faint mesostyle fold. An internal cingulum on the protocone, but not on the hypocone.

This is probably a distinct species, but it can hardly belong to *Acoelodus*, the sculpture of the external face of the molar being stronger and more complex. The coronal surface is too worn to show anything but the main fossa, the outer side of which is thrown into small folds. The generic and even the family position is uncertain.

"Acoelodus" terminalis Ameghino, 1902

Plate 11, figure 4

Acoelodus terminalis AMEGHINO, 1902a, p. 12, *nomen dubium.*

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[1] Although this specimen is surely the original of the figures of "*Acoelodus oppositus*," as cited, it was labeled as "*Oldfieldthomasia septa*" in Ameghino's hand in the collection. The label may have been misplaced, or Ameghino may later have referred the specimen to *Oldfieldthomasia*, which appears to be correct.

TYPE: M.A.C.N. No. 10755, an isolated right upper molar, perhaps M^1.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayoran. Locality unknown.

DIAGNOSIS: Upper molar similar to that of type of "*A.*" *proclivus*, measuring 11.3 mm. long by 12.7 wide, external folds, especially metacone, stronger, no mesostyle, internal cingulum complete.

In general this tooth is like that of "*A.*" *proclivus* and also has the outer part of the main fossa thrown into many small, deep folds. It is even less like *Acoelodus* than is "*A.*" *proclivus*. It could be an individual or position variant of the latter species, but might be quite distinct. True generic and family position is unknown.

PAGINULA AMEGHINO, 1901

Paginula AMEGHINO, 1901, p. 415; 1906, p. 468.

TYPE: *Paginula parca*.

DISTRIBUTION: Casamayoran, Patagonia.

DIAGNOSIS: Small notoungulate lower teeth of generalized, primitive type. Affinities and diagnostic characters essentially unestablished.

As already emphasized, it is virtually impossible to distinguish oldfieldthomasiid genera on the basis of lower teeth alone, and indeed it is sometimes impossible to distinguish families on this basis in the Casamayoran. In *Paginula* are united several lower jaw fragments which probably belong to the same species but which are of uncertain generic or family position. The tooth structure is particularly similar to that of the oldfieldthomasiids, so that tentative reference to this family is warranted, but possible pertinence to the Archaeopithecidae, Isotemnidae, or Interatheriidae is not wholly excluded. It is probable that these lower jaws pertain to a species known from upper teeth and placed in some other genus, but the association is unknown. The name *Paginula* is therefore retained, even though it is not really defined, for these lower teeth which do seem to represent a recognizable species.

Ameghino's characterization of genus and species referred to the small size, short trigonids, swollen talonids, large and relatively posterior entoconid, shallow ramus, and deep masseteric fossa. The size is (specifically) distinct from that of most comparable materials, but the other characters cited are virtually universal in the more primitive notoungulates of several families and many genera.

Ameghino referred to *Acoelodus*, as types of *A. connectus* and *A. microdon*, two lower jaw fragments from animals of almost exactly the same size as *Paginula parca* and with only insignificant structure differences from the latter. If genus or species is to be recognized at all, it seems that all these specimens must be combined in it.

Paginula parca Ameghino, 1901

Plate 11, figures 5–11

Paginula parca AMEGHINO, 1901, p. 415.
Acoelodus connectus AMEGHINO, 1901, p. 365.[1]
Acoelodus microdon AMEGHINO, 1901, p. 365.[1]

TYPE: M.A.C.N. No. 10596, fragment of right lower jaw with M_3 and heel of M_2.

TYPES OF SYNONYMS: Of *A. connectus*, M.A.C.N. No. 10747, fragment of left lower jaw with M_{1-3}. (Three other jaw fragments preserved with this are not types and are of doubtful specific identifications.) Of *A. microdon*, M.A.C.N. No. 10698, fragment of left lower jaw with P_{2-4}.

HYPODIGM: Types, as above; and M.H.N. Tournouër Collection No. 22, right lower jaw with P_3–M_3; and M.H.N. Tournouër Collection No. 29, right lower jaw with P_{3-4}.

HORIZON AND LOCALITY: Casamayoran, Chubut. M.A.C.N. Nos. 10596 and 10747 are from "Oeste de Río Chico." M.A.C.N. No. 10698 has no recorded locality. M.H.N. Tournouër Collection Nos. 22 and 29 are from Cerro Negro, south of Colhué-Huapí.

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[1] Both these species have page priority over *P. parca*. Recognition of page priority often tends to defeat the purpose of nomenclature and of the Code. This purpose is not (as might superficially appear from some nomenclatural activities) to provide reasons for changing names but to minimize the changing of names. In the present instance it seems obviously desirable and more likely to promote stability to keep *Paginula* linked through its type species to the one specimen on which the genus was actually based. This can be done only by ignoring page priority. The current form of the Code (Stoll *et al.*, 1964, Article 24) excludes page priority and gives selection to the first reviser on grounds of stability.

DIAGNOSIS: Sole recognized species of the genus. Measurements are given in table 16.

Acoelodus conncetus was not compared by Ameghino with *Paginula parca*. M_3 in the former seems to have the trigonid somewhat less compressed and the entoconid more expanded, but the difference is slight and seems well within possible individual variation. The type of *Acoelodus microdon* includes only premolars and hence could not be compared with the other two types. M.H.N. Tournouër Collection No. 22, noted above, has the premolars essentially like those in *Acoelodus microdon* and the molars essentially like those in *Paginula parca* and *Acoelodus connectus* and thus links the three together in a fairly conclusive way. All these specimens agree closely in size as well as structure, as shown in table 16.

FAMILY **ARCHAEOPITHECIDAE**
AMEGHINO, 1897

DEFINITION: Small, primitive notoungulates closely resembling the Notopithecinae (early Interatheriidae) in most respects, but lacking the characteristic zygomatic specialization of that group. Dental series complete and closed. Molars rooted, sub-brachydont, but distinctly higher-crowned than in any contemporaneous notoungulates except Archaeohyracidae. Incisors and canines simple, subconical, nearly equal in size. P^{1-2} with distinct protocones. P^4 transversely subquadrate, with strong median internal sulcus, almost fully molariform. P^4–M^3 with strong parastyle and paracone folds, weaker metacone fold, and no mesostyle. Upper molars in typical wear stages with small anteroexternal and posteroexternal fossettes and a large internal fossa with a small, median, external projection, the whole forming a pattern like a caricature of a face. Lower molar talonids forming closed fossettes with wear. Zygomatic base and orbital rim unspecialized, jugal forming whole outer face of anterior part of zygoma and continuing to lacrimal as a narrow splint.

DISTRIBUTION: Casamayoran, Patagonia.

Although Ameghino's original definitions (1897a) of the Notopithecidae and Archaeopithecidae were verbally different, they did not in fact give any structural distinction between the two families. In restudying the Ameghino Collection, I thought that it was clear that *Notopithecus* and *Archaeopithecus* are different genera, but I could find no good reason for placing them in different families. The cheek-tooth structure is almost precisely the same in the two, presenting only such minor distinctions as commonly occur between closely related genera. It was therefore quite surprising when we obtained skull material of *Acropithecus*, a genus that seems to be really close to *Archaeopithecus*, to find that the zygoma and jugal are primitive and *Oldfieldthomasia*-like. In *Notopithecus*, otherwise so similar, the zygoma has already achieved the peculiar specialization of the Interatheriidae, to which family that genus is now referred. *Notopithecus* also has a primitive interatheriid type of anterior teeth, and *Acropithecus* does not. It is thus clear that *Acropithecus*, and with it *Archaeopithecus*, must be placed in a separate family from *Notopithecus* if, as I think proper, the Interatheriidae are extended vertically downward to include the earlier forms surely allied to those of the Deseadan and later.

Nevertheless, the close and detailed resemblance of the Archaeopithecidae and the

TABLE 16

MEASUREMENTS OF TEETH OF *Paginula parca*

	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.A.C.N. No. 10596	—	—	—	—	—	—	—	—	—	—	7.5	3.5
M.A.C.N. No. 10747	—	—	—	—	—	—	4.4	3.2	5.0	4.0	7.5	3.8
M.A.C.N. No. 10698	3.2	2.5	3.8	2.9	4.1	3.2	—	—	—	—	—	—
M.N.H. Tournouër No. 22	—	—	4.2	2.5	4.2	3.2	4.3	3.2	4.8	3.3	7.6	3.3

early Interatheriidae (i.e., the Notopithecinae) does exist, and it is evidence for rather close relationship. It is again clear that in the Casamayoran we are very near the base of notoungulate differentiation. Forms that must be placed in different families, when account is taken of the later lines, and that could even be placed in different suborders from this point of view, are here really quite closely related from the point of view of their horizontal and immediately ancestral relationships.

On the other hand, the Archaeopithecidae also resemble the Oldfieldthomasiidae and the Archaeohyracidae rather closely, and are not separated from those families by zygomatic structure. The zygomata in all three are, however, merely primitive, and it is probable that the three groups do represent distinct and perhaps even fairly fundamental lines of differentiation, given the fact that all notoungulates were so much alike at this time. It would be plausible on morphological grounds to unite the Archaeopithecidae with one or both of the Oldfieldthomasiidae and Archaeohyracidae, but, since the family has long been distinguished and in view of the whole pattern of incipient divergence at this time, it may be more conservative to retain the family for the time being.

The definition given above does distinguish this group from any other known, but it is not very satisfactory. It is based mainly on *Acropithecus*, and some of the characters given may prove to differentiate that genus rather than a true family. Other characters are of a sort that often represent merely progressive steps within a single lineage, for instance, the relatively high crowns. Nevertheless, when contemporary rather than successive groups are compared, a character like accelerated hypsodonty may be an indication that one is dealing with a more or less sharply distinct line of development. For instance, in the Interatheriidae are included genera completely brachydont and others completely hypsodont, with rootless teeth, yet at a given time the degree of hypsodonty is characteristic with respect to various contemporaneous lines.

Ameghino's reference of the Archaeopithecidae to the "Prosimiae" is among the more peculiar of his phylogenetic speculations. This was apparently done in the first place (1897a) because of resemblances to the "Notopithecidae," which at least are fully brachydont and do have a distantly primate-like aspect of the mandible. But the most distinctive general character of the archaeopithecid cheek teeth (all he then knew) is their accelerated hypsodonty, which is a strongly non-primate characteristic. Later (1904b) he spoke of the Archaeopithecidae as being related and perhaps ancestral to the Acoelodidae (i.e., Oldfieldthomasiidae) and in turn derived the toxodonts from the latter (as well as the plainly extraneous hyracoids and horses)—true relationships in a broader sense, although the lineation suggested is highly improbable. Despite this statement of toxodont affinities, in formal classification he continued to call the archaeopithecids "Prosimiae."

As noted above, the present conception of the Archaeopithecidae is based mainly on *Acropithecus*, a genus that closely resembles *Archaeopithecus* but is now much better known than the latter. *Acropithecus* was originally placed in the Notopithecidae by Ameghino, which illustrates the difficulty, or near impossibility, of distinguishing these groups by cheek teeth alone. The problem of defining this group of families is further illustrated by the genera that Ameghino did place in the Archaeopithecidae: *Archaeopithecus*, *Ultrapithecus*, and *Pachypithecus* of the Casamayor and *Guilielmoscottia* of the Mustersan. *Ultrapithecus* seems surely close to *Maxschlosseria*, placed by Ameghino in the Isotemnidae and here referred tentatively to the Oldfieldthomasiidae. *Pachypithecus* is a *nomen vanum*, based on a symphyseal fragment without teeth, probably not of this family but completely indeterminate at present. *Guilielmoscottia* was removed to the Notopithecidae by Schlosser, and I agree that this position is probably correct. Thus for the present only *Archaeopithecus* and *Acropithecus* are placed in the Archaeopithecidae. From the foregoing, it is clear that some Notopithecinae or Oldfieldthomasiidae now known by cheek teeth alone may eventually prove to belong here, if, indeed, the family Archaeopithecidae is permanently retained.

There may perhaps be a question as to

whether *Archaeopithecus* and *Acropithecus* belong together, since the anterior teeth and skull are unknown in the former, and so many forms of probably different family position have similar cheek teeth. The resemblance in this case does, however, seem so particularly close as to warrant at least tentative collocation. Thus it will be noted that I consider a species formerly referred to *Acropithecus* synonymous with the genotype of *Archaeopithecus* and one formerly referred to *Archaeopithecus* synonymous with the genotype of *Acropithecus*.

The dentition of *Acropithecus* is so well represented in our collection and is so characteristic of this oldfieldthomasiid-archaeopithecid-notopithecine complex that it is described in detail as a type of primitive but, for its time, fully characteristic notoungulate dentition.

ARCHAEOPITHECUS AMEGHINO, 1897

Archaeopithecus AMEGHINO, 1897a, p. 422; 1906, p. 466. SCHLOSSER, 1923, p. 609. SCOTT, 1937a, p. 516.

TYPE: *Archaeopithecus rogeri*.

DISTRIBUTION: Casamayoran, Patagonia.

DIAGNOSIS: Apparently closely similar to *Acropithecus*, but premolars, and most notably P^{1-2}, more transverse, more symmetrical, ectoloph columns less pronounced. P^1 markedly wider than long.

The genotype was founded on a right maxilla with six teeth, a relatively good type for this fauna, yet the specimen is deeply worn and poorly preserved, and the status and nature of the genus are therefore somewhat obscure. Unfortunately no additional material probably of this form has come to light except a mere fragment on which Ameghino based another species.

In Ameghino's original figure (1897a, fig. 8) he labeled the known teeth as P^1–M^2 (M^{1-6} of his notation), but he later (1904b, fig. 402) considered the first three of these teeth as P^{2-4}, and hence implied that the series at hand is P^2–M^3. It is probable that the first of these opinions was correct, as it is decidedly more consistent with relative wear, the character of the last tooth preserved (unlike any M^3 known in a related animal but normal for M^2), and the shape of the maxilla as preserved. If these teeth were P^2–M^3, the generic characters would be different but not less distinctive. P^2 would still be more transverse than in *Acropithecus*, and also relatively much smaller, but M^3 would be unlike that of any other known genus of this general group in being quadrate and larger than M^2 in both dimensions.

More material is necessary before the characters of the genus can be considered adequately known, but in the meantime it seems probable that it is closely allied to but distinct from *Acropithecus*, and knowledge of this group depends on the latter, much better known genus.

Ameghino placed three species in this genus: *A. rogeri*, *A. rigidus*, and *A. alternans*. The last two seem to me to be synonymous and to belong to *Acropithecus*. I very tentatively place in *Archaeopithecus* Ameghino's "*Notopithecus*" *fossulatus*, which quite surely is not *Notopithecus*.

Archaeopithecus rogeri Ameghino, 1897

Plate 12, figures 1, 2

Archaeopithecus rogeri AMEGHINO, 1897a, p. 422, fig. 8; 1898, p. 150; 1904b, p. 303, fig. 402.

Adpithecus plenus AMEGHINO, 1902a, p. 8.

Acropithecus plenus: AMEGHINO, 1904a, vol. 56, p. 195.

TYPE: M.A.C.N. No. 10816, right maxilla with P^1–M^2.

TYPE OF SYNONYM: M.A.C.N. No. 10851, inner half of left M^1 and all of M^2, deeply worn (type or lectotype); also a right lower jaw fragment with deeply worn M_{2-3}, not associated and probably not this species.

HORIZON AND LOCALITY: Casamayoran, Patagonia. Type without locality data, but probably from south of Colhué-Huapí; type of synonym labeled as from that locality.

DIAGNOSIS: Sole species surely referable to genus. Measurements are given below.

Adpithecus plenus, later transferred to *Acropithecus*, was not directly compared with *Archaeopithecus rogeri*. Its type is very poor and almost indeterminate. No generic distinction has yet been established for M^2 between *Archaeopithecus* and *Acropithecus*, and to this extent Ameghino was quite justified in placing the species in the latter genus. The type of this species does, however, agree just as closely with *Archaeopithecus*, the only possible morphological distinction in M^2 from *A. rogeri* being the doubtfully stronger internal sulcus, a difference not probably of more than individual value, if it is real at all. The size, 5.0 by 7.9 mm., is almost exactly that of M^2 of *A. rogeri*, and it is highly probable that both are from the same locality. *Acropithecus* is at least extremely rare at that locality, and its presence there has not been definitely established. On these grounds it is maintained that *A. plenus* is almost surely synonymous with *A. rogeri* and certainly is indistinguishable from it.

We have no material referable to this species.

The measurements of the teeth of the type are: P^1, length, *ca.* 3, width, 4.2; P^2, length, 3.7, width, 5.6; P^3, length, *ca.* 4, width, 6.1; P^4, length, 4.5, width, *ca.* 7; M^1, length, 4.2, width, 6.8; M^2, length, 4.9, width, 7.7.

?Archaeopithecus fossulatus (Ameghino, 1897)

Plate 12, figures 3, 4

Notopithecus fossulatus Ameghino, 1897a, p. 421, fig. 6; 1898, p. 150.

Type: M.A.C.N. No. 10824, fragment of left lower jaw with P_{3-4} (lectotype); also part of right lower jaw with P_4–M_1 and a left $P^{2?}$, not associated.

Horizon and Locality: Casamayoran, Patagonia. No other data, but described at same time as *Archaeopithecus rogeri* and almost surely from same locality, which was probably south of Colhué-Huapí.

Diagnosis: Practically indeterminate and probably synonymous with *A. rogeri*. Based essentially on lower premolars closely similar to those of *Acropithecus rigidus* but below average size for the latter.

Ameghino's description stated that the last four molars (i.e., P_4–M_3) each measured 4.0 by 3.0 mm. Nevertheless it is probable that he did not have any specimen that showed all these teeth and that he inferred the character of some or all of the (true) molars, as he (in common with Marsh and others) sometimes did describe or mention parts that he had not actually seen. The rest of his description could be based entirely on the lectotype, and this and the isolated $P^{2?}$, which was not mentioned in any way in the description, were the only specimens figured. That he did not actually have M_{2-3} (and possibly not M_1) is the more likely because his statement that P_4–M_3 were all of the same dimensions is incredible.

This species is probably the same as either *Archaeopithecus rogeri* or *Acropithecus rigidus*, but, since the synonymy cannot be surely established at present, it is listed separately. The P_{3-4} on which it is based are nearly indistinguishable from individual variants of *Acropithecus rigidus*. The morphology is virtually identical, but the lengths of the teeth are well below the means of our Cañadón Vaca series of *A. rigidus* (see table 17). Finally, the types of *A. rogeri* and *A. fossulatus* were described at the same time and are almost surely from the same locality, whereas *A. rigidus* was collected and described later and all the known specimens are from localities probably distant from those of the other two types.

The dimensions of the lectotype teeth are included in table 18. The difference is only doubtfully significant.

Direct comparison with *A. rogeri* is impossible, as lower teeth certainly of that species are unknown. Nevertheless this seems to be the probable synonymy. The structural similarity of P^3–M^1 of *A. rogeri* to *A. rigidus* is so close that it may be assumed that P_{3-4} were also close and hence that *A. fossulatus* is morphologically appropriate for the lower dentition of *A. rogeri*. The shorter P_{3-4} of *A.*

TABLE 17

Measurements and Comparisons of the Teeth of the Lectotype of *?Archaeopithecus fossulatus*

	P_3		P_4	
	L	W	L	W
Measurements of lectotype	4.3	3.0	4.3	*ca.* 3½
Comparison by d/s with series of *Acropithecus rigidus* from Cañadón Vaca	−2.2	−0.8	−2.6	0.0

fossulatus with respect to the mean for *A. rigidus* also is appropriate for occlusion with *A. rogeri*, in which P^{2-3}, and to less extent P^4, are likewise shorter than in *A. rigidus*.

ACROPITHECUS AMEGHINO, 1904

Acropithecus AMEGHINO, 1904a, vol. 56, p. 194; 1906, p. 466.

TYPE: *Acropithecus tersus* Ameghino, 1904 [=*Acropithecus rigidus* (Ameghino, 1901)].

DISTRIBUTION: Casamayoran, Patagonia.

DIAGNOSIS: With the characters given for the family. P^1 longer than wide and P^2 less transverse than in *Archaeopithecus*. P^{1-3} asymmetrically triangular. Ectoloph columns strong.

Ameghino's definition of this genus was valid and distinctive, except that the material available to him did not permit good differentiation from *Archaeopithecus*, which, indeed, is not yet accomplished to complete satisfaction. Thus it is that two species that he had previously placed in *Archaeopithecus* (*A. rigidus* and *A. alternans*) were not transferred to *Acropithecus* when the latter genus was named. On the other hand, the second species placed in *Acropithecus* by Ameghino, *A. plenus* (first referred to *Adpithecus*, a synonym of *Notopithecus*) probably does belong to *Archaeopithecus*, as discussed above.

The morphology of the genus and the taxonomy of the supposed species are described below in the discussion of the genotype.

Acropithecus rigidus (Ameghino, 1901)

Plate 12, figures 5–7; plate 13

Archaeopithecus rigidus AMEGHINO, 1901, p. 359; 1904b, p. 303, figs. 403–405.

Archaeopithecus alternans AMEGHINO, 1901, p. 359.

Acropithecus tersus AMEGHINO, 1904a, vol. 56, p. 194; 1904b, p. 177, figs. 231, 280.

TYPE: M.A.C.N. No. 10813, nine different specimens, each consisting of one to five upper teeth, representing at least six and probably nine different individuals; most of these, but perhaps not all, are conspecific. I select the fragment of left maxilla with P^4–M^2 as lectotype. The other specimens were probably all syntypes.

TYPES OF SYNONYMS: Of *Archaeopithecus alternans*, M.A.C.N. No. 10815, part of right maxilla with M^{1-3}. Of *Acropithecus tersus*, M.A.C.N. No. 10850, three upper teeth, two stuck together as if associated, but not correctly. The lectotype is the tooth, almost certainly M^3, figured as M^2 by Ameghino (1904b, fig. 231).

HYPODIGM: The types, as above, and the following specimens in the American Museum of Natural History: A.M.N.H. No. 28782, much of skull and mandible, with most of the teeth, deeply worn, except upper canines and some anterior lower teeth; A.M.N.H. No. 28884, associated left P^2–M^3, right M^{1-3}, right M_{1-3}, and left M_{2-3} (some of these teeth very fragmentary); A.M.N.H. No. 28895, poorly preserved skull, mandible, and limb fragments; three partial maxillae with teeth; seven partial mandibles with teeth; about 150 isolated identified upper cheek teeth; and about 150 isolated identified lower cheek teeth. (These specimens are all from Cañadón Vaca, and at nearly the same level, so that they form an excellent homogeneous sample for the determination of variation in the dentition.)

HORIZON AND LOCALITY: Casamayoran, Patagonia. Types, and also type of "*A. alternans*," from "Oeste de Río Chico." Type of "*A. tersus*" of unrecorded locality, perhaps also "Oeste de Río Chico." New referred specimens all from Cañadón Vaca.

DIAGNOSIS: Sole species certainly referred to genus. Measurements and other data follow.

This species is very abundant in Cañadón Vaca but elsewhere rare or absent. Of Ameghino's specimens, most are surely from "Oeste de Río Chico," in the vicinity of Cañadón Vaca, and all may be. Our abundant material gives unusually good information, especially as regards the cheek teeth, which are set forth in detail because these teeth typify an interesting evolutionary stage in the development of notoungulate dentitions.

Some of the fragmentary specimens included among Ameghino's types diverge enough from our suite so that they might possibly belong to a different species, although they do not surely do so, and they are closely related in any case. As lectotype I have taken one of the specimens surely within the range

TABLE 18

COMPARISON OF TYPES OF *Acropithecus rigidus* AND ITS PROBABLE SYNONYMS WITH MEANS FOR SERIES OF *A. rigidus* FROM CAÑADÓN VACA

	d/s							
	P^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W
A. rigidus	−0.1	−1.7	In range	In range	—	—	—	—
A. alternans	—	—	In range	In range	In range	In range	1.9	2.9
A. tersus	—	—	—	—	—	—	0.7	2.0

of our sample, as only in this way can the name be positively established.

In defining *A. alternans*, Ameghino gave no real distinction from *A. rigidus*. The type is very poorly preserved but shows no characters not exactly paralleled in *A. rigidus*.

Although *Acropithecus* was correctly defined, the definition did not exclude species referred to *Archaeopithecus* with which no comparison was explicitly made. Implicitly, the distinction was based on an error. Ameghino placed together two isolated teeth and had them drawn and labeled as if they were M^{2-3} of one individual (1904b, fig. 231). They are not in contact with each other, and the association is certainly incorrect, if for no other reason than that the supposed M^3 is relatively more worn than the supposed M^2. In fact, our series shows certainly that the supposed M^2 is an M^3. The other tooth may also be M^3 but is more dubious. The sure M^3, lectotype, is exactly similar to homologous teeth in our series of *A. rigidus*.

The dimensions of the various types are compared with our Cañadón Vaca series in table 18.

The difference in width of M^3 has possible statistical significance, but we have one specimen that matches it exactly, and the other differences of the same specimen are not significant.

DENTITION

Alveoli indicate that the upper dental formula was surely and the lower probably complete. The dentition was continuous or nearly so.

UPPER TEETH: The incisors are known only in A.M.N.H. No. 28782. They are markedly different in size, shape, and proportions from those known in any other genus in this fauna. They differ relatively little in size, but I^1 is the largest and I^3 is very slightly larger than I^2. All have nearly circular roots, and the crowns, when unworn, probably differed little from curved cones, not being compressed. The crowns are of limited height and have heavy enamel on the external faces and apparently very thin enamel on the unworn parts of the internal faces. On I^1 the internal face is completely removed by a large posterior (lingual) wear facet. On I^{2-3} the main wear facet is posterointernal, and there is on each a smaller anterointernal facet, the internal surface between these being simply convex in horizontal section. The external surfaces are similarly convex and simple. There is a suggestion of a posterior ridge at least on I^3, but wear has made this obscure and uncertain.

The crown of the upper canine is not known, but the root was nearly circular in section and about the size of that of I^3. It is immediately adjacent to P^1. Crushing makes it impossible to say that there was surely no space between the canine and I^3, but there probably was not.

The cheek teeth are basically similar to those of *Notopithecus*, which is to say that they have the fundamental primitive typothere-toxodont pattern, but they are distinctive in certain details. They are, for this fauna, relatively high-crowned. The available indices of hypsodonty for teeth unworn, or nearly so, are given in table 19. All these indices are distinctly higher than those in *Notopithecus* which nevertheless is (at least structurally) ancestral to a group in which all but the most anterior teeth were already completely hypsodont (rootless) in the Deseado.

P^1 is a small triangular tooth, longer than wide but with a well-developed, low protocone. The pattern is wholly obliterated by wear in A.M.N.H. No. 28782. An isolated tooth identified with probability as P^1 of this species has the coronal pattern very shallow, without distinct fossettes, and the paracone and metacone distinct in the ectoloph.

P^2 is the first cheek tooth well represented in the collection, with nine individuals in various stages of wear. It is slightly wider than long, but is less transverse than the following teeth. The parastyle is sharply cut off by grooves from the rest of the tooth. The paracone fold, on the external face of the ectoloph, is prominent and sharply defined. The metacone, when unworn, is slightly larger than the paracone, but its fold is less sharp, the posterior slope is longer, and the groove following it, as well as the metastyle fold, is inconspicuous and variable. Five of the nine specimens show no other complications on the external face. One has a small distinct cuspule at the base of the groove between paracone and metacone folds. The other three have a cuspule or cuspidate cingulum across the base of the metacone fold or between the higher part of this and the feeble metastyle fold, and in each of these three it is unlike the others in prominence and in distance from the junction of crown and root. This certainly is an individual character, as there can be no real question that all these teeth are of one species. The protocone is sharp and strong, but lower than the ectoloph. A strong loph[1] runs to the posteroexternal corner. An unworn specimen shows the apex of this to be separate from the ectoloph, but even the slightest wear unites them completely. Below this is a cingulum which is early united to it by wear. Immediately anteroexternal to the protocone is a vertical groove, external to which the loph expands anteriorly, making it sinuous. At the base of the groove the cingulum forms a pit, variable in size and depth but present on all our specimens not too worn to show it, and this forms a small, closed fossette when worn. The first wear union of cingulum and loph is immediatley external to this, and still farther externally in an appropriate stage of wear another fossette, longer but shallower, may temporarily appear, although this is variable in size and probably would not occur at all in three out of the six individuals on which it can be checked. The anterior loph[2] is directly transverse and abuts against the ectoloph internal to the groove between paracone and metacone folds. It is more slender than the posterior loph and is deeply notched, so that it becomes a continuous crest on the grinding surface only when the crown is about half worn away. Immediately internal to the parastyle, toward the base of the crown, is a variable pit. It may be very ill defined and open, or may be a deep and large pocket forming a definite fossette in advanced wear stages. Where it is relatively strong, its wall is usually prolonged into a nearly vertical, sharp, cingulum-like crest rising to the region of the apical notch in the anterior loph. Aside from this structure, there is no anterior cingulum. On an unworn tooth the coronal surface is irregular and papillate, and there are variable pits. The only constant feature is a single deep fossette, which opens through

TABLE 19

INDICES OF HYPSODONTY (100 TIMES ECTOLOPH HEIGHT OVER ECTOLOPH LENGTH) IN *Acropithecus rigidus*

P^1	76	
P^2	116	
P^3	147	(somewhat worn)
P^4	135	
	152	
	143	(somewhat worn)
M^{1-2}	118	(slightly worn)
	120	(somewhat more worn)
	116	(somewhat more worn)
	111	(somewhat more worn)
M^3	133	(somewhat worn)
	130	(somewhat worn)
	119	(somewhat worn)
	116	(somewhat worn)

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[1] This may be homologous with the metaloph of more progressive genera of this group, or serially analogous to the molar metaloph, but topographically the term seems inapplicable, and the homology is by no means certain.

[2] Here again, it is not clear that this is a protoloph either in topography or in homology.

the notch in the anterior loph until closed by wear. In a few cases, there is another much smaller and shallower fossette external to this.

On P^3 the metacone fold and the groove following it tend to be slightly more definite than on P^2. No external cingulum or basal cuspule is present on any of the 25 individuals examined. The small cingular pit or fossette posterior to the protocone is variable in size, but is apparently invariably present. The posteroexternal cingular fossette is apparently more frequent than on P^3, but is not invariably present. The anteroexternal fossette is constantly present and large, and its wall is high and forms a loph, continuous with the homologue of the anterior loph of P^2. It is notched, but soon is continuous on the wear surface.[1] The notch in the homologue of the anterior loph of P^2 is more shallow, or perhaps absent (all the specimens are somewhat worn). The principal fossette as seen on P^2 is strong and is generally crescentic, convex internally. A smaller fossa external to this, and connected with it by an isthmus (or strait) until an advanced stage of wear, is present on all the moderately worn teeth. On those least worn there is also a smaller posteroexternal fossette, but this was soon worn away and may not have been present in every individual. Three specimens (of 23 determinable) have a very slight anterior basal cingulum.

P^4 is almost exactly similar to P^3 in structure, the only apparently constant difference (aside from average size and proportions) being that the internal face of the protocone is marked by a sharp, vertical groove. The available unworn specimens (only two) have small and very shallow posteroexternal coronal fossettes, but moderate wear removes these almost at once. The walls of the other fossettes, especially the external wall of the main (internal) fossette, are occasionally folded but usually single. In one case there are two distinct median external fossettes, that is, two main external folds of the internal fossette.

The other more variable structures are the posteroexternal cingulum fossa, which is more or less definitely present in 15 specimens and absent from 12 (indeterminate in all the others), but even when absent there is here a cingulum which may, however, be extremely feeble. An anterior basal cingulum is present in 12 specimens and absent from 26. When present it is generally very weak and may be papillated. In one case it is represented by a fairly definite small cuspule.

The external wall varies indefinitely in details but hardly at all in essential structure. There is, however, one specimen, which seems to be definitely teratological, with a sharply distinct column and cusp that appears to be stuck onto the posterior part of an otherwise normal ectoloph face.

In terms of crests, the unworn coronal pattern could be described as having protoloph, metaloph, two cristae, and a crochet structurally like that of P^4 of *Rhynchippus*, and other more specialized toxodonts and typotheres. With wear the second crista unites with the metaloph, and the fossa between them disappears almost at once; the first crista early unites with the protoloph, but the fossa between them remains until a very advanced stage of wear. The two cristae do not unite with each other until the base of the crown is nearly reached.

M^1 and M^2 are so much alike that they cannot always be distinguished as isolated teeth. They differ from P^4 principally in being relatively longer, with the whole ectoloph face flatter but especially that part of it posterior to the paracone fold, the outline of the tooth more quadrate, the internal side divided into two distinct cusps with a vertical internal groove, and the posteroexternal fossette constant and deep. The fossette pattern is thus of the "face tooth" type of *Notopithecus*, the pattern lasting longer than in that genus. The protocone and hypocone tips are separate, but wear soon unites them into an "entoloph." The groove on the internal face between them is not directly related to the notch between protocone and hypocone (unworn) apices as would be supposed and generally does not originate at that notch but anterior and basal to it. The protocone tip is larger than the hypocone, but the basal lobes formed by the groove are nearly equal, or the posterior is a little the larger. This groove is generally single, but in one case

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[1] Topographically this, and not the stronger main anterior loph or anterior loph of P^2, is more like a protoloph.

TABLE 20

ASSOCIATION OF FEATURES DUE TO WEAR ON CROWN PATTERN OF M^3 IN *Acropithecus rigidus*

	Specimens with Hypocone and Protocone Still Separate on Wear Surface	Specimens with Hypocone and Protocone United on Wear Surface
Posterior cingulum unworn	6	0
Posterior cingulum beginning to wear	7	0
Posterior cingulum worn to enclose a fossette	11	1
Posterior cingulum gone, outer fossettes intact	3	6
Anteroexternal fossette obliterated	1	1

there are two distinct parallel grooves, and in several there is a small pocket at the base which in one specimen is remarkably large and fossette-like. An anterior cingulum is present on 39 specimens and known to be absent from 10, hence being more common than on P^4, but it varies greatly, from a faint papilla or line to a definite cuspule or strong ridge enclosing a small fossette. The metaloph is straight, or nearly so, not sinuous as on the premolars, and the posterior cingulum is likewise straight and parallel to it so that it does not tend to enclose a definite posterointernal fossette as on the premolars, although the narrow transverse valley between cingulum and loph is irregular and may break up into several tiny fossettes for a very brief period of wear before the early merging of these two crests.

M^3 has the outer wall more inclined, or at a smaller angle to the protoloph, and the posterointernal lobe reduced, both correlated with a shorter metaloph, giving the tooth a more triangular or trapezoidal outline, but in all these respects it is highly variable. The internal sulcus is on an average much less prominent than on M^{1-2}, and it may be almost indistinguishable. In every case it is wholly separate from the notch between protocone and hypocone and decidedly anterior to this, on the inner face of the protocone. The protocone-hypocone notch is deeper than on M^{1-2}, but its depth varies greatly, or conversely the point of junction of these two cusps varies greatly, as suggested by table 20, showing association with the effects of wear on other structures.

On worn teeth the hypocone seems to be relatively external or virtually absent, and the notch seems to be between the protocone and posterior cingulum loph, but on less worn specimens the hypocone seems, in every instance, to be internal and intercalated between protocone and cingulum. The posterior cingulum tends to form a more distinct and lasting fossette than on M^{1-2}. The posteroexternal fossette generally closes later than in M^{1-2}, opening through a notch in the metaloph which is also suggested on M^{1-2} but there is generally less distinct or deep. On this tooth the posteroexternal fossa is generally obliterated after the anteroexternal (i.e., the latter is less deep) but before the internal and median external, whereas on P^3–M^1 the anterointernal fossa usually lasts a little longer than the posterointernal, and on M^2 they disappear at about the same time.

No lower jaw in the collections has the incisors, canine, or P_1 in place, although A.M.-N.H. No. 28782 has the alveoli of these teeth imperfectly preserved. With this specimen in undoubted association but not in place in the crushed sockets were found three loose anterior teeth, a pair and one odd tooth. The odd tooth might be, but probably is not, an upper canine. The pair cannot be upper teeth and must be lower incisors or canines. Their importance is that they are simple, nearly conical teeth, quite unlike any incisors or canines of *Notopithecus* or most related forms. They are modified only by being slightly recurved, with barely suggested anterior and posterior keels. The roots are almost perfectly circular in section. The anterior alveoli on this specimen are deeply broken, and only two roots definitely occur anterior to P_1, but there is a strong possibility that two others, smaller and less deep, also occurred. Uncertain but suggestive indications are that the median incisors were reduced and that the larger teeth are I_{2-3} or I_3 and the canine.

The crown of P_1 is not known. In A.M.-N.H. No. 28782 it probably had a single, cylindrical root. P_2 has a sinuous, essentially continuous main crest and various minor features. The protoconid is nearly on the longitudinal midline, but anterior to the center of the tooth. The crest anterior to this, which tends to form a vague paraconid, is excavated on the internal side and may be distinctly crescentic but is nearly straight in one or two specimens. The outer face may likewise have a much less pronounced concavity. The crest posterior to the protoconid is modified first by a sharp, deep, oblique external valley and then by a smaller valley at the posterointernal end of the tooth. The crest as such may be said to end near the middle of the posterior border, but a lesser, sharp, often nodulated crest falls away from it here internally along the posterior border, bounding the last-mentioned valley, and ending at the posterointernal corner. A rounded, nearly vertical, secondary ridge descends the posteroexternal protocone slope into the mouth of the main external valley, and when little worn this appears to bear an incipient cuspule. One specimen (out of seven well preserved) has an anomalous posteroexternal accessory cuspule on the base of the outer slope of the heel crescent.

P_3 differs primarily from P_2 in being relatively wider, less triangular, with all the folds more pronounced. From the protocone the crest runs almost straight anteriorly to the anteroexternal corner, then turns sharply and falls to the anterointernal corner—the strength and differentiation of this last part of the crest, along the anterior border, vary greatly, some specimens differing little from P_2 and others having a strong and high transverse crest here. The protoconid is more or less transverse, and at its internal end there is an angulation, and the crest is prolonged posterointernally to where it ends abruptly on the internal border anterior to the posterior end. This part of the crest, when unworn, has the apex differentiated from the protoconid and forming an imperfectly separated metaconid. The talonid crest, when little worn is quite distinct from the trigonid crest on P_3 and abuts against the latter on the external face of the metaconid. It is sharply crescentic and has three poorly distinguishable cusps: the hypoconid, external, the hypoconulid, nearly posterointernal, and the entoconid, anterointernal to and very poorly separated from the hypoconulid. The central talonid valley is nearly closed (or in some cases, at the base, quite closed) by the approximation of entoconid and metaconid, and furthermore, except in the simplest variants, is invaded by highly irregular swellings and small crests from the inner side of the main talonid crest. When quite unworn this central mass has a papillate apex, and when worn it forms a fairly complex re-entrant or even one or more closed fossettes, not the same in any two specimens. The posteroexternal angulation on the protocone slope is less constant than on P_2 and, when present, has more distinctly the nature of an accessory cuspule. It is apparently absent from 15 specimens and present in nine, varying from a faint suggestion to a definite cusp. There is a small, sharp, basined, basal cingulum on the internal part of the posterior border of all these teeth.

P_4 is essentially similar to P_3 but is still more quadrate, the transverse anterior crest constant and stronger, the whole trigonid more compressed anteroposteriorly and its valley narrower, the talonid crest still more distinct from that of the trigonid, and the entoconid better differentiated from the hypoconulid. Two completely unworn teeth show that the transverse anterior crest consists of an external part continuous with the protoconid crest and an internal part, the apex of which is lower than and disconnected from the external portion, both parts being vaguely bifid on the summit. Slightly worn specimens show an imperfectly differentiated hypostylid, and one of them has a papilla in the trigonid valley not present on any other of the specimens determinable in this respect. The basal cuspule posterior to the protoconid is definitely present, but small, on two specimens and absent from 19.

M_{1-2} differ from P_4 in having the trigonid still more compressed anteroposteriorly, so that on them it is shorter than the talonid. Specimens in an appropriate stage of wear all show the internal part of the anterior transverse crest as lower than and distinct from the external part, but no two are alike in details of length, height, and apical structure of this part of the crest. The entoconid is now strongly differentiated, and there is a prominent vertical groove between this and the hypoconulid. The bottom of the groove is occasionally open, but usually partly or quite closed by a low, cingulum-like wall, probably analogous to the posterior premolar cingulum which is otherwise absent. This often forms a short-lived fossette in the last stages of wear and in one specimen is deep and circular. The main valley of the talonid apparently invariably forms a fossette. Its exact structure is extremely variable, and it may be very simple and nearly circular, or may be filled by an irregular papillate mass, but there is a fairly constant usual basic structure: the entoconid pillar is usually attached to the hypolophid, at a high level, about midway between hypoconid and hypoconulid. From near the middle of the anterior face of the entoconid crest a short spur projects, free in its upper portion and attached to the posterior slope of the metaconid in its lower part. The valley internal to this, toward the border of the tooth, is commonly open but may be closed by a low crest or (in two cases) a distinct but tiny cuspule. In all cases this fossette is, however, very shallow. The bottoms of the external and of the trigonid valleys also, in many cases but not all, are narrow, shallow fossettes. These teeth are in an interesting stage of transition from brachydont molars with open valleys and distinct cusp structure, as in the most primitive notoungulates, to progressive hypsodont types with complex, infolded crowns, generally with several closed fossettes, and subordinate and vague apical cusp pattern. Some variants are closer to the more primitive type, and some seem already definitely to belong to an advanced group.

Of the 73 determinable specimens of M_1 or M_2, none has the basal cuspule posterior to the protocone, which is common on P_3 and rare on P_4.

M_3 has the talonid more elongate than on M_{1-2}, the hypoconulid projecting more posteriorly and set off from the hypoconid by a distinct external groove, but otherwise it is like those teeth. The projection of the hypoconulid also makes the internal basin between it and the entoconid larger and more definite and constant than on M_{1-2}.

In considering variation of the dimensions of these teeth (and also in the morphological characters now described), I found it possible to sort all the teeth with little chance of error, except that there are some isolated upper and lower molars such that it cannot be certainly said whether they are first or second molars. Even though many or most of these isolated teeth can be identified, doubt about some of them makes the distinction of no value because an unbiased sample cannot be obtained. For the lower molars, there are seven examples of M_1 and four of M_2 in jaws so that there are these inadequate but unbiased samples for these teeth, but the upper molars in jaws are badly preserved and very few, so that no useful data for M^1 or M^2 separately can be obtained.

For practical purposes of measurement, it is almost necessary to use the maximum lengths of the teeth as preserved, and generally these are sufficiently accurate. In the present case some teeth (notably P^4) are relatively hypsodont and have one dimension (length) greatest near the apex, so that the measurement made in this way is smaller on senile than on juvenile specimens. The distribution is thus not strictly single and normal, but is more exactly the sum of a series of possibly normal distributions, one for each age group. Table 21 shows the influence of this factor in the most extreme case—the length of P^4.

The differences are real but are not very noteworthy, the greatest deviation of the means of the smaller samples from that for the whole sample being very nearly within 1s of the latter. The adult subsample is near the mean for the whole sample, and the principal result of subsampling is to reduce the coefficient of variation. Even in this extreme case, very little would be gained by age grouping, which is furthermore impossible for many of the variates, and something would be lost. Moreover, few dimensions are so definitely affected by wear. For the length of M^3, for instance, the means for juvenile, adult, and senile specimens are 4.7, 4.8, and 4.6, respectively—virtually identical, and with no definite trend.

TABLE 21

Statistical Data on the Length of P^4 in *Acropithecus rigidus*, Grouped by Age as Shown by Degree of Wear

Sample	*N*	OR	$\bar{X}$	s	V
All	32	3.9–5.5	4.75±.06	.34±.04	7.1±0.9
Juvenile	8	4.6–5.5	5.05±.11	.32±.08	6.4±1.6
Adult	16	4.6–5.2	4.85±.04	.15±.03	3.2±0.6
Senile	8	3.9–4.7	4.38±.08	.24±.06	5.4±1.4

The available statistical data are given in tables 22 and 23.

Skull

The skull material is all very imperfect, but it shows some valuable details.

The premaxillo-maxillary suture is straight and slopes backward slightly. There is no posterosuperior premaxillary process. Unlike the condition in *Notopithecus* and most other typotheres, the premaxillae have large horizontal palatal processes and the anterior palatal foramina are small and well separated from each other. The facial part of the maxilla is large and somewhat excavated anterior to the orbit, but this excavation does not definitely extend to the premaxillary and is weaker than in most typotheres. The infraorbital foramen is above the posterior end of P^3 and anterior end of P^4 in old adults and is relatively smaller than in *Notopithecus*. The sutures in the maxillo-frontal region are not clear, but it seems certain that nothing comparable to the structure of *Pachyrukhos* occurs here, and probable that this region is more toxodont- than interathere-like. The nasals are long and slender, apparently not notched anteriorly, slightly expanded anteriorly and more, but still very little, posteriorly. They are partly inserted into the frontals, and this suture is strongly curved.

The palatines are narrower than in *Notopithecus*, not extending to near the alveolar border, and also shorter, the anterior end approximately on a level with M^1. The posterolateral notches were apparently similar but slightly shallower.

The anterior zygomatic root is stout and is opposite M^{1-3}, slightly more posterior than in *Notopithecus*. The form of the root is more or less like that of the least specialized interatheres, but the descending process is weaker, being only faintly indicated. The posterior part of the zygoma is inadequately known, but the anterior free portion consists of a vertical plate, deeper than in *Notopithecus*, divided by a vertical median suture, the whole external face covered by the jugal and

TABLE 22

Statistical Data on Upper Teeth of *Acropithecus rigidus* from Cañadón Vaca

Variate	*N*	OR	$\bar{X}$	s	V
LP^2	7	4.5–4.9	4.66±.05	.14±.04	3.0±0.8
WP^2	7	5.2–6.0	5.56±.10	.26±.07	4.7±1.3
LP^3	23	4.0–5.2	4.67±.06	.27±.04	5.8±0.9
WP^3	23	6.1–7.6	6.70±.07	.33±.05	5.0±0.7
LP^4	32	3.9–5.5	4.75±.06	.34±.04	7.1±0.9
WP^4	32	6.1–7.7	6.94±.07	.38±.05	5.5±0.7
LM$^{1-2}$	50	4.6–5.9	—[a]	—	—
WM$^{1-2}$	50	6.1–8.1	—[a]	—	—
LM^3	36	4.2–5.3	4.70±.05	.27±.03	5.8±0.7
WM^3	36	5.4–6.7	6.04±.04	.23±.03	3.9±0.5

[a] Since these samples are heterogeneous, the usual constants have no comparative value.

TABLE 23

Statistical Data on Lower Teeth of *Acropithecus rigidus* from Cañadón Vaca

Variate	*N*	OR	$\bar{X}$	s	V
LP$_2$	7	3.9–4.9	4.44±.11	.29 ±.08	6.6±1.8
WP$_2$	7	2.4–2.8	2.63±.05	.23 ±.04	4.9±1.3
LP$_3$	25	4.3–5.2	4.83±.05	.24 ±.03	5.1±0.7
WP$_3$	25	2.7–3.7	3.20±.05	.24 ±.03	7.7±1.1
LP$_4$	24	4.5–5.5	4.95±.05	.25 ±.04	5.0±0.7
WP$_4$	24	3.2–4.0	3.50±.04	.204±.029	5.8±0.8
LM$_1$	7	4.3–4.9	4.57±.08	.21 ±.06	4.6±1.2
WM$_1$	7	3.2–3.9	3.40±.09	.23 ±.06	6.7±1.8
LM$_2$	4	4.7–5.5	5.00	$\sum(d^2) = .3600$	—
WM$_2$	4	3.5–3.9	3.73	$\sum(d^2) = .0876$	—
LM$_3$	39	5.5–6.9	6.24±.05	.32 ±.04	5.1±0.6
WM$_3$	39	3.1–3.8	3.53±.03	.178±.020	5.0±0.6

the internal by the maxilla. At the posterior end of the root, the internal suture turns upward abruptly, so that most of the root proper is formed by the maxilla alone. The jugal continues upward and forward as a thin splint forming the rim of the orbit to the lacrimal. Its facial expanse here is very narrow, the intraorbital part wider. There is a small, sharp, postorbital process on the zygoma, probably formed by the jugal.

The fronto-parietal suture follows the sharply divergent crests from the sagittal crest to the supraorbital processes. The latter are poorly preserved but were probably large and formed partly or mainly by the parietals. Posterior to this region nothing distinctive is known of the parietals.

Most of the median orbital wall is preserved in the best specimen, but it is so crushed that little that is distinctive can be made out with certainty. The orbit is very large and the wall is high and without any pronounced vacuities. What appears to be the optic foramen is small, elevated well above the anterior lacerate foramen, and directed more externally than anteriorly.

The glenoid fossa is nearly flat, transverse, and seems to be little elevated above the dental level, perhaps less than in *Notopithecus* and probably less than in most typotheres. The bulla has few or no septa. The epitympanic sinus has an external lateral triangular area as in *Notopithecus*, but this area and the sinus as a whole, as well as the bulla, are relatively smaller than in that genus. Aside from these details and evident general notoungulate character, distinctive features of the ear region cannot be made out. The occiput is unknown. The material suggests a shorter, deeper cranium than that of *Notopithecus*, but this might be misleading.

Mandible

The horizontal ramus is stout and of moderate depth, increasing slightly posteriorly. There is a large mental foramen in the vicinity of P$_1$ or the canine and a small posterior foramen beneath P$_3$ or, in one case, P$_4$. Between these other small and variable foramina may occur. The symphysis is fused, at least in adults, and is somewhat procumbent, the posterior end beneath P$_3$. Posterior to the dental region, the lower border curves downward and may be slightly inflected. The dental foramen is slitlike and slightly below the alveolar level. The condyle is poorly preserved, but may have been much like that in interatheres.

Skeleton

There are a few postcranial fragments with A.M.N.H. No. 28895. The only ones with much character are second and third right metacarpals and a fragment of the ulna. Except for their longer size and slightly more robust proportions, the metacarpals resemble those of *Pachyrukhos*. The distal articulation, at least on III, is transversely cylindrical, with a palmar keel. The ulna fragment is also similar to that of the later genus, and is not markedly longer—a discrepancy that may speak against its correct association.

FAMILY **INTERATHERIIDAE** AMEGHINO, 1887

In its typical development this family is Deseadan and later, and definition and discussion of the family as a whole concern the student of the later faunas rather than of the three stages covered in this memoir. The Riochican to Mustersan representatives of the family form a distinctive unit defined and discussed below as a subfamily, the Notopithecinae. Although the differentiating characters of this early group are mainly primitive, it is so strikingly unlike the later forms that it was until recently always granted family status as the Notopithecidae Ameghino, 1897. Ameghino did recognize from the start (1897a) that his Notopithecidae were closely related to the Interatheriidae ("Protypotheriidae"), but, in keeping with his phylogenetic dualism and his obsession with the Patagonian origin of all orders and of the Primates in particular, he stressed rather the belief that the Notopithecidae, near the Interatheriidae on one hand, were on the other hand ancestral to the prosimians, simians, and ultimately man. Hence the now confusing ending "-pithecus" for all the genera placed in this group by Ameghino.

This view was not shared by any later student, and it has long been recognized that the "Notopithecidae" were, in a general way, typotheres, although their exact position in the Typotheria was not fully established until recently. Schlosser (1923) did consider them ancestral to the Interatheriidae, but he also considered them ancestral to the Hegetotheriidae. In a study that was, in a sense, preliminary to the present monograph, Riggs and Patterson (1935) showed that *Notopithecus* already had the peculiar zygomatic specialization of the Interatheriidae, with the jugal excluded from the orbit and confined to the middle of the zygoma. They therefore considered Notopithecidae as a synonym of Interatheriidae. My own studies confirm the fact that *Notopithecus* has the basic interatheriid characters, not only in the zygoma but in other parts of the skull and in some features of the dentition.

It is thus proper, if not necessary, in evolutionary classification to refer *Notopithecus* and its closer allies to the Interatheriidae. It nevertheless remains a fact that these earliest interatheriids form a rather compact group in themselves, that there is a profound phylogenetic gap between them and the typical interatheres of the Deseadan, and that, in spite of having the most basically diagnostic interathere characters, they are on the whole more like some contemporaneous non-interatheres, especially the Archaeopithecidae, than like later interatheres. It therefore seems warranted and is convenient to distinguish them from later interatheres on some supergeneric level, and I have already (Simpson, 1945) done so by placing them in a distinct subfamily, which is Ameghino's Notopithecidae scaled down to allow for recognition of the undoubted fact that these are early interatheres.

SUBFAMILY **NOTOPITHECINAE** SIMPSON, 1945

Notopithecidae AMEGHINO, 1897a, p. 415.
Notopithecinae: SIMPSON, 1945, p. 128.[1]

DEFINITION: Early and primitive Interatheriidae. Dental series complete and closed. incisors scalpriform, I^1 somewhat enlarged. Canines not differentiated, incisiform. All teeth brachydont. Upper premolars triangular, internal sulcus typically absent but may be present. M^{1-2} subquadrate, not particularly transverse, protocone and hypocone distinct but invariably confluent basally and usually united nearly to their apices, coronal pattern variable but substantially as in Archaeopithecidae and Oldfieldthomasiidae. Lower premolars and molars also as in Archaeopithecidae and Oldfieldthomasiidae, molar hypoconulids poorly distinguished, entoconids little or not expanded, no closed fossettes. Skull and jaws relatively short and deep, snout compressed laterally. Orbit relatively far forward, weak postorbital process near middle of skull, lacrimal foramen on inner side of orbital rim, tubercle small or absent. Anterior zygomatic root expanded laterally, squared, with small ventral tubercle and incipient specialization for rodent-like anterior attachment of masseter. Jugal re-

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[1] The current Code (Stoll and others, 1964) makes Ameghino author of the name Notopithecinae, and the data here given suffice to indicate the usage enjoined by the Code. I cannot, however, bring myself to cite as author of a name one who did not in fact use that name.

duced, confined to middle of zygoma, not reaching lacrimal. Bullae and epitympanic sinuses relatively enormous, ear region otherwise of primitive typothere type.

DISTRIBUTION: Riochican through Mustersan, Patagonia.

The definition given above is designed to distinguish the Notopithecinae not only from their later allies or descendants, the Interatheriinae, but also from their contemporaries of other families, among which the Oldfieldthomasiidae and the Archaeopithecidae are particularly similar. The definition is based on *Notopithecus* mainly, but does not exclude the other genera here referred to the subfamily and will on the whole, if not in all details, probably be found applicable to them if, when their skull structure becomes known, they do prove to be correctly placed here.

Ameghino (e.g., 1906) referred eight genera to his Notopithecidae: *Notopithecus*, *Adpithecus*, *Transpithecus*, *Antepithecus*, *Infrapithecus*, *Epipithecus*, *Acropithecus*, and *Gonopithecus* (misspelled "*Goniopithecus*" in Ameghino, 1906). A newly discovered skull of *Acropithecus* shows that it does not belong here, and it is described above under the Archaeopithecidae. *Notopithecus* and *Transpithecus* are evidently valid genera, and *Antepithecus* is somewhat more doubtfully retained. The other genera listed above all seem with little doubt to be synonyms of one or another of those three genera. *Patriarchippus*, placed in the Notohippidae by Ameghino, and *Pseudadiantus*, placed in the Adiantidae, seem to be synonyms of *Antepithecus* and are therefore here placed in the Notopithecinae. *Guilielmoscottia*, a valid genus placed in the Archaeopithecidae by Ameghino, may be more closely related to *Transpithecus* than to *Archaeopithecus*, and it is accordingly transferred to the Notopithecinae. It is, however, possible that both *Transpithecus* and *Guilielmoscottia* should be placed in the Archaeopithecidae.

As here treated, the subfamily thus includes only four recognized genera, *Notopithecus*, *Antepithecus*, *Transpithecus*, and *Guilielmoscottia*, of which only the first certainly belongs here and the second is here placed with high probability. There are some fragmentary Riochican specimens, now tentatively referred to *Transpithecus*, that may prove to belong to a new genus when better material is available, and it is also probable that a Mustersan species here tentatively retained in *Notopithecus* should be placed in a new genus.

The known morphology of the subfamily is described under the genera and species below.

NOTOPITHECUS AMEGHINO, 1897

Notopithecus AMEGHINO, 1897a, p. 419; 1906, p. 406. SCHLOSSER, 1923, p. 607. SIMPSON, 1932e, p. 10. SCOTT, 1913, p. 462; 1937a, p. 516.

Nothopithecus [error]: ROTH, 1927, p. 236.

Adpithecus AMEGHINO: 1901, p. 356; 1906, p. 466.

Epipithecus AMEGHINO: 1904a, vol. 56, p. 193; 1906, p. 466.

Gonopithecus AMEGHINO: 1904a, vol. 56, p. 196.

Goniopithecus [*lapsus* or invalid emendation]: AMEGHINO, 1906, p. 167.

TYPE: *Notopithecus adapinus*.

TYPES OF SYNONYMS: *Adpithecus secans*, *Epipithecus confluens*, *Gonopithecus trigodontoides*.

DISTRIBUTION: Casamayoran and doubtfully Mustersan, Patagonia.

DIAGNOSIS: Typical of the subfamily as defined above. P^4 with slight or no internal sulcus. Internal lobes of upper molars about equal, poorly separated, protocone and hypocone strongly united, anterior cingula well developed. Slightly more hypsodont than *Antepithecus*, protocone and hypocone more connected, cheek teeth less elongate, horizontal mandibular ramus deeper.

Notopithecus adapinus, with its numerous probable synonyms, and *Antepithecus brachystephanus*, with its, are clearly distinct species in typical form, but closely similar to each other to the point of intergrading in some variates and some variant specimens. I have long vacillated between referring them to one genus and recognizing *Antepithecus* as distinct. I have here finally but quite tentatively adopted the latter course, which seems in this instance more conservative from a nomenclatural point of view. For purposes of description and comparison, however, they are considered together in this section.

The supposed genera here involved fall naturally into two groups. One, based on specimens belonging or very closely allied to *Notopithecus adapinus*, includes the following:

Notopithecus
Adpithecus
Epipithecus
Gonopithecus

The other is based on specimens belonging or very closely allied to *Antepithecus brachystephanus* and includes the following genera:

Antepithecus
Infrapithecus
Pseudadiantus
Patriarchippus

It is these two groups that are now provisionally accepted as two (not more) genera.

Notopithecus was originally described as having only two incisors, a statement based on a single specimen in which the incisors were lacking and the alveoli deeply broken. In fact it could well have had three incisors and, from comparison with other specimens, surely did. *Adpithecus* was distinguished as having three incisors and the horizontal ramus as being longer and shallower. The latter distinction, also, is invalid, for measurements of the types and of specimens referred by Ameghino show no significant difference in jaw length or depth. The type species of the two supposed genera show no constant or probably significant differences and are synonymous.

Epipithecus was based on a description which contains little that is distinctive from *Notopithecus* in a comparable stage of wear. The apparently more distinctive characters, such as the supposed triangular upper molars with narrow, undivided, strongly convex inner side, apply only to one of the three teeth of the type specimen and are normal characters of P^4 in *Notopithecus*, this tooth in this instance being mistaken for M^1. The type species is inseparable from *N. adapinus*.

Gonopithecus was also proposed and described without explicit comparison with previously named genera. It was based on three isolated teeth apparently assumed to be M^{1-3}, but not really of one individual and probably all M^3. The characters ascribed to the genus are for the most part those of M^3 of *Notopithecus*. The type may show some slight variation from *N. adapinus*, as mentioned below, but cannot be distinguished generically and probably not specifically.

Antepithecus does show certain differences from *Notopithecus adapinus* considered by Ameghino to be of generic rank. It is demonstrated on a page below that these differences are all highly variable and that the species, although valid, nearly intergrade. The rather slender basis for generic separation is reflected in the respective generic diagnoses below.

Infrapithecus was essentially an artificial genus for lower jaws of this general group. It included one species clearly synonymous with *Notopithecus adapinus*, another probably belonging to *Ultrapithecus* (now considered an oldfieldthomasiid), and a third, the type, now shown by associated specimens to be the lower dentition of *Antepithecus brachystephanus*.

Pseudadiantus was referred to the Adiantidae and not compared with notopithecines. Both its supposed species are virtually identical in size and structure with the type of *Infrapithecus* and, like the latter, are the lower dentition of *Antepithecus brachystephanus*.

Patriarchippus was likewise proposed without comparison with the Notopithecinae, which it resembles to the point of identity. Although slightly variant, the one known specimen is very close to *Antepithecus brachystephanus* and may well belong to that species.

VARIATION AND SPECIFIC TAXONOMY

Notopithecus and *Antepithecus* are among the more abundant genera in the collections and have afforded an opportunity to determine the amount of variation and, it is hoped, to put the taxonomy on at least a somewhat firmer basis. I have studied about 40 specimens in the Ameghino Collection and more than 75 in the collections of the American Museum of Natural History, the Field Museum of Natural History, and the Muséum National d'Histoire Naturelle in Paris. These include good skulls and jaws and a few skeletal parts. An independent taxonomic study of them was made, and this was then related to

TABLE 24

MEASUREMENTS OF LOWER JAWS OF *Notopithecus* AND *Antepithecus* FROM COLHUÉ-HUAPÍ

Depth of Mandible on Internal Side Beneath Anterior Root of M$_1$	Number of Specimens
8.5– 9.4	4
9.5–10.4	6
10.5–11.4	1
11.5–12.4	1
12.5–13.4	0
13.5–14.4	0
14.5–15.4	1
15.5–16.4	2

Ameghino's types and nomenclature as far as possible.

In the first instance grouping is based on a large series (Scarritt Collection in the American Museum of Natural History), all from south of Lago Colhué-Huapí and of exactly known horizon. The majority of them are from a single bed, evidently deposited rapidly and representing a sample of essentially contemporaneous animals. The lower jaws in this lot presented a marked discontinuity in the distribution of their depths, there being a sharp separation into shallow-jawed and deep-jawed forms, as recorded in table 24.

The shallow-jawed forms are referable to *Antepithecus brachystephanus;* the deep-jawed, to *Notopithecus adapinus.* Although each group is variable, there is no evidence in the morphology or in the distributions of variates that either one is heterogeneous, and all the evidence suggests that each is an indivisible unit. These pure samples of known jaw depth were then compared by Student's t-test as regards their tooth dimensions, with the results given in table 25.

Thus P$_3$, P$_4$, M$_1$, and M$_2$ are significantly longer in *Antepithecus brachystephanus* than in *Notopithecus adapinus.* The observed ranges of these dimensions do not overlap, but in several cases they come so near to doing so that they probably would intergrade to some extent were large samples at hand. Nevertheless the groups are surely distinct. The widths of these teeth are not significantly different in the two groups, with the possible but improbable exception of M$_1$, and both dimensions of M$_3$ are indistinguishable in the two species.

These lower teeth show no noteworthy morphological differences correlated with either species. I am unable to distinguish isolated last lower molars of the two species, and other isolated lower teeth are difficult or at times impossible to distinguish if they happen to be small variants of *Antepithecus brachystephanus* or large variants of *Notopithecus adapinus.* Most of the jaws of which the depth cannot be measured can nevertheless be referred with probability to one spe-

TABLE 25

OBSERVED RANGES, MEANS, AND COMPARISON OF LOWER TOOTH DIMENSIONS IN *Antepithecus brachystephanus* AND *Notopithecus adapinus*

Variate	Pure Sample *Antepithecus brachystephanus*			Pure Sample *Notopithecus adapinus*			N$_1$+N$_2$	t	P
	N$_1$	OR	$\bar{X}$	*N*$_2$	OR	$\bar{X}$			
LP$_3$	6	4.1–4.6	4.3	3	3.3–3.7	3.5	9	5.68	<.01
WP$_3$	6	2.0–2.4	2.1	3	2.2–2.4	2.3	9	−1.74	>.10
LP$_4$	8	4.1–4.8	4.5	4	3.6–4.0	3.8	12	4.95	<.01
WP$_4$	8	2.5–3.0	2.7	4	2.4–2.7	2.6	12	1.08	>.30
LM$_1$	9	4.1–5.2	4.7	3	3.7–4.0	3.9	12	3.85	<.01
WM$_1$	9	2.7–3.4	3.0	3	2.5–2.7	2.6	12	2.67	>.02
LM$_2$	9	4.6–5.4	5.0	2	4.1–4.3	4.2	11	3.58	<.01
WM$_2$	9	3.0–3.7	3.2	2	2.8–3.0	2.9	11	1.65	>.10
LM$_3$	9	5.3–6.7	5.9	2	5.6–5.7	5.7	11	0.77	>.40
WM$_3$	9	2.7–3.4	3.0	2	2.7–3.3	3.0	11	0.00	>.90

cies or the other by the lengths of P_3–M_2. The jaw depth is more variable than our range would suggest, for the addition of the Ameghino specimens makes the two ranges closely approach each other, but the depth in *N. adapinus* is invariably greater than in *A. brachystephanus.*

This jaw depth is in part a function of age. We do not have any juvenile specimens certainly referable to *N. adapinus,* but the following figures show that the depth increases with age even in the shallow-jawed *A. brachystephanus:* A.M.N.H. No. 28695, M_1 in place, M_2 not erupted: depth 8.3 mm.; A.M.N.H. No. 28701, M_2 in place, M_3 not erupted: depth 8.7; adult jaws, with M_3 in place: range 9.1–11.5, mean 9.9.

The difference between the two groups in jaw depth and tooth length is not, however, due to age, although possibly accentuated by this factor. The *A. brachystephanus* sample does average slightly younger individually, but it includes senile individuals, and these have more shallow jaws and longer teeth than the youngest individuals of *N. adapinus.*

That the difference between these two groups is sexual is conceivable, cannot be ruled out altogether, but seems improbable. In our samples from one horizon, remains referable to *A. brachystephanus* (32 individuals) are more than three times as numerous as those referable to *N. adapinus* (10 individuals), but in the Ameghino Collection, undoubtedly from different exact levels and localities, these proportions are about reversed. Although not conclusive, these figures would be more readily explicable as due to facies differences of two species than as due to varying proportions of the two sexes of one species. Furthermore the upper teeth, at least, show some apparent morphological differences between the two such as would be most unusual as a sexual distinction.

The Ameghino Collection has several individuals of *N. adapinus* with associated upper and lower jaws, and the Scarritt Collection includes one example of that association and one of associated upper and lower jaws of *A. brachystephanus.* The latter is a juvenile individual, but has M_{1-2}^{1-2} in place and serves to fix the association. We have, in all, four partial upper dentitions referable with considerable certainty to *A. brachystephanus* and six apparently typical of *N. adapinus,* from which the comparison of observed ranges and means is given in table 26.

As in the lower dentitions, *A. brachystephanus* averages longer than *N. adapinus,* although the ranges nearly overlap for lengths and do overlap for widths. The samples are too small to guarantee the constancy of the distinction, but in the specimens available *A. brachystephanus* has P^4–M^2 (the only permanent upper teeth surely identified) with the crowns slightly lower, the central fossa more shallow and less closed, and the protocone and hypocone better separated than does *N. adapinus.* The structure is otherwise almost identical in the two.

In addition to the samples of unified origin on which the preceding remarks are principally based, we have a sample of six identifiable and evidently conspecific specimens from a zone 45 to 65 feet lower than that of

TABLE 26

OBSERVED RANGES AND MEANS OF UPPER TOOTH DIMENSIONS OF *Antepithecus brachystephanus* AND *Notopithecus adapinus*

Variate	*N. brachystephanus*			*N. adapinus*		
	N	OR	$\bar{X}$	*N*	OR	$\bar{X}$
LP^4	1	—	4.4	6	3.3–4.4	3.9
WP^4	1	—	4.9	6	4.0–5.0	4.6
LM^1	3	5.0–5.1	5.1	4	3.9–4.5	4.2
WM^1	4	4.8–5.8	5.2	4	4.0–5.0	4.5
LM^2	3	5.0–5.6	5.4	5	4.2–4.6	4.5
WM^2	3	5.2–6.1	5.6	5	4.1–5.1	4.7
LM^3	0	—	—	5	4.4–4.7	4.6
WM^3	0	—	—	5	4.2–4.8	4.5

the samples just discussed, as well as several other specimens also from low levels (but not so exactly measurable) and probably of the same species. (Unless otherwise stated, the latter, less certain, specimens are not included in the following discussion.) The jaw depth is measurable on two of these and is 10.8 and 12.3, nearer that of our pure sample of *A. brachystephanus* than that of *N. adapinus*. As far as available data go, these could belong to either group as regards jaw depth alone, but probably belong to neither. By the t-test, P with respect to the pure sample of *brachystephanus* is between 0.02 and 0.01 and with respect to *adapinus* is the same—in both cases the difference is probably significant. The tooth dimensions of this sample compare very closely with those of *N. adapinus*, as shown by the comparison of ranges and means in the homogeneous samples given in table 27.

These two samples are indistinguishable morphologically except for the shallower jaws of the sample called *N. adapinus reduncus*, and most of the tooth dimensions are also almost the same. In the lower jaws the only apparent distinction of possible value is the shorter M_3 in *N. a. reduncus*, but with the small sample in hand this is not significant (by the t-test, P is greater than 0.05). In the upper jaws most of the dimensions are also the same in the two, as nearly as these samples can demonstrate, but M^3 is shorter in *N. a. reduncus* and in this case the difference is shown to be significant (P is less than 0.01).

In short, these two forms, which do not occur together in our samples of exactly known origin, are certainly very closely allied and cannot be distinguished at all on the basis of the usual fragmentary specimens or if considered purely as isolated individuals, but by group comparisons they are shown surely to differ significantly in the mean length of M^3, probably in mean depth of jaw, and possibly in mean length of M_3. A reasonable probability of genetic difference is established, but this is of less than specific value by conservative taxonomic principles and may be recognized tentatively as subspecific. Ameghino's specimens of *N. adapinus* apparently include both these forms and possibly others of less than specific value, but in most cases it is hopeless to attempt their subspecific classification in view of the inadequacy or total absence of exact data as to provenience. One of his types, however, that

TABLE 27

OBSERVED RANGES AND MEANS OF TOOTH DIMENSIONS OF TWO SUBSPECIES OF *Notopithecus adapinus*

Variate	*N*	*N. a. adapinus* OR	$\bar{X}$	*N*	*N. a. reduncus* OR	$\bar{X}$
LP_3	3	3.3–3.7	3.5	4	3.2–3.6	3.4
WP_3	3	2.2–2.4	2.3	4	1.9–2.1	2.0
LP_4	4	3.6–4.0	3.8	4	3.6–3.9	3.7
WP_4	4	2.4–2.7	2.6	4	2.3–2.6	2.4
LM_1	3	3.7–4.0	3.9	4	3.8–4.5	4.1
WM_1	3	2.5–2.7	2.6	4	2.5–2.8	2.6
LM_2	2	4.1–4.3	4.2	3	4.0–4.5	4.2
WM_2	2	2.8–3.0	2.9	3	All 2.7	2.7
LM_3	2	5.6–5.7	5.7	2	4.9–5.2	5.1
WM_3	2	2.7–3.3	3.0	2	2.6–2.7	2.7
LP^4	6	3.3–4.4	3.9	4	3.6–3.9	3.8
WP^4	6	4.0–5.0	4.6	3	4.3–4.8	4.5
LM^1	4	3.9–4.3	4.1	3	3.8–4.4	4.2
WM^1	4	4.0–5.0	4.5	3	4.2–4.9	4.5
LM^2	5	4.2–4.6	4.4	3	4.2–4.8	4.6
WM^2	5	4.1–5.1	4.7	3	4.4–4.7	4.5
LM^3	5	4.4–4.7	4.6	3	4.0–4.3	4.1
WM^3	5	4.2–4.8	4.5	3	3.9–4.4	4.1

TABLE 28

Notopithecus adapinus, COMPARISON OF THE DIMENSIONS OF THE UPPER TEETH OF AMEGHINO'S TYPES WITH THOSE OF LARGER SAMPLES OF EACH SUBSPECIES

	P^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W
OR, unified Scarritt sample, *N. a. adapinus*	3.4–4.4	4.0–5.0	3.9–4.5	4.0–5.0	4.2–4.6	4.1–5.1	4.4–4.7	4.2–4.8
Notopithecus adapinus	4.0	5.0	—	—	4.5	4.8	—	—
Adpithecus secans	3.9	4.7	4.7	4.8	4.7	4.7	4.5	4.4
Adpithecus subtenuis	3.4	4.3	4.3	4.2	4.2	4.4	—	—
Epipithecus confluens	*ca.* 3½	*ca.* 4	*ca.* 3½	*ca.* 4½	*ca.* 4	*ca.* 5	—	—
Antepithecus gradatus	—	—	4.3	4.2	4.3	4.4	—	—
Gonopithecus trigodontoides	—	—	—	—	—	—	4.3	4.3
OR, Scarritt sample, *N. a. reduncus*	3.6–3.9	4.3–4.8	3.8–4.4	4.2–4.9	4.2–4.8	4.4–4.7	4.0–4.3	3.9–4.4

of *Adpithecus reduncus*, seems rather surely to belong to the variety with smaller M_3^3 and shallower jaw, as shown by these figures of the length of M_3: pure sample of *N. adapinus*, 5.6–5.7; our sample of *N. a. reduncus*, 4.9–5.2; type of "*Adpithecus*" *reduncus*, 5.1.

Ameghino also defined this supposed species as having a shallower jaw than "*A. secans*" (=*N. adapinus*), which is probably true of the type although uncertain, as the lower margin of the jaw is broken. The comparison in any event is sufficiently close to warrant accepting *reduncus* as the name of the subspecies of *N. adapinus* here recognized. Whether some of Ameghino's other types, not including M_3^3 or showing exact jaw depth, belong to this subspecies rather than to *N. adapinus adapinus*, is entirely and, it seems, permanently indeterminable, so that they can be compared only with *N. adapinus* in general.

The collections now available do not permit the certain recognition of any species of *Notopithecus* other than *N. adapinus* (with two known subspecies: *N. a. adapinus* and *N. a. reduncus*) or of any of *Antepithecus* other than *A. brachystephanus*. Tables 28 and 29 show how completely various of Ameghino's types enter into the known ranges of variation for the two subspecies of *N. adapinus*. Measurements of Ameghino's supposed species are of the type in each case.

Only three of the 32 measurements of Ameghino's type upper jaws fall outside the observed range of our samples, and the latter are so small and the deviations so slight that all are well within the probable real range. Furthermore, two of these three deviations are approximate measurements only, for "*Epipithecus confluens*," and as such are not significant. The other, LM^1 of "*Adpithecus secans*," is well within a reasonable range of

TABLE 29

Notopithecus adapinus, COMPARISON OF THE DIMENSIONS OF THE LOWER TEETH OF AMEGHINO'S TYPES WITH THOSE OF LARGER SAMPLES OF EACH SUBSPECIES

	P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W
OR, Scarritt sample, *N. a. adapinus*	3.6–4.0	2.4–2.7	3.7–4.0	2.5–2.7	4.1–4.3	2.8–3.0	5.6–5.7	2.7–3.3
Adpithecus secans	4.0	—	4.3	—	4.3	—	—	—
Infrapithecus diversus	4.0	2.6	—	—	—	—	—	—
Adpithecus reduncus	—	—	—	—	4.0	2.8	5.1	2.8
OR, Scarritt sample, *N. a. reduncus*	3.6–3.9	2.3–2.6	3.8–4.5	2.5–2.8	4.0–4.5	2.7	4.9–5.2	2.6–2.7

TABLE 30

Antepithecus brachystephanus, COMPARISONS OF THE DIMENSIONS OF THE UPPER TEETH OF AMEGHINO'S TYPES WITH THOSE OF THE SCARRITT SERIES

	P^4		M^1		M^2	
	L	W	L	W	L	W
OR, Scarritt sample	4.4	4.9	5.0–5.1	4.8–5.8	5.0–5.6	5.2–6.1
Antepithecus brachystephanus	—	—	—		5.7	5.7
Antepithecus interrasus	4.7	5.1	5.0	5.5	5.1	—
Patriarchippus annectens	—	—	4.8	5.5	5.3	6.0

variation, as the following figures for the whole sample referred to *N. adapinus* (with the approximations of the *confluens* type omitted) show: $N = 10$; $\mathrm{OR} = 3.8–4.7$; $\bar{X} = 4.27 \pm 0.08$; $s = 0.26 \pm 0.06$; $V = 6.0 \pm 1.3$.

None of the figures for the lower teeth is outside the observed ranges (and the same is also true of such measurements of more anterior teeth as can be made on the specimens).

Similar comparisons are given in tables 30 and 31 for our series referred to *Antepithecus brachystephanus* and the types of Ameghino's species considered synonymous with this. We have only one specimen of P^4, so that the deviations shown, 0.3 and 0.2, are quite insignificant. The other measurements also agree exceptionally well throughout, when the inadequate size of our comparative sample is taken into consideration. A specimen with M^{1-2} referred to *N. brachystephanus* by Ameghino falls virtually at the mean for our sample in all dimensions.

For P_3–M_3 we have fairly adequate samples, not fewer than six values of each variate, and in these the Ameghino specimens are within the observed ranges in every case. For P_3 we have three values of each variate, and the one Ameghino dimension that falls 0.1 mm. outside the observed range surely has no significance. For P_1 we have only one value, and the deviations of 0.3 mm. and 0.2 mm. surely are not significant.

Statistical constants for the samples adequate for this purpose are given in connection with the specific descriptions.

MORPHOLOGY

Unless otherwise stated the following descriptions apply to both *Notopithecus* and *Antepithecus* as far as known.

DENTITION

The dental formula is complete, $\frac{3143}{3143}$, and apparently is invariable. The teeth are closely crowded together, with no diastemata. Opposite I_1's are in contact at the midline. I_2–P_1 overlap slightly, the anterior end of each tooth being internal to the posterior end of that anterior or medial to it. At P_2 there is a sudden change, for the anterior end of this tooth is external (labial) to the posterior end of P_1, and P_3–M_3 likewise overlap to some extent in this way. Overlap in the upper dentition has the same character, I^2–P^1 having their anterior ends internal to the posterior ends of the preceding teeth and P^2–M^3 external. P^1_1 are thus overlapped externally by both the preceding and following teeth. In both upper and lower jaws the inner borders of P^1_1–M^3_3 lie along nearly straight lines, those of opposite sides parallel, whereas I^1_1–C form a parabolic curve.

UPPER DENTITION: I^1 is not present in any of our specimens, but is well represented in the Ameghino Collection. It is considerably larger than any of the other anterior teeth, and the compressed, expanded, spatulate crown is placed almost directly transversely. It points almost straight ventrally or even a little posteriorly. The alveoli of opposite I^1's are a short distance apart, but the roots diverge so that the crowns are tightly in contact. The root is compressed labiolingually, as is the crown but to a less degree, and may be faintly grooved, but is not bifid.

I^2–P^1 are all closely similar and are of nearly the same size, smaller than I^1, save that the canine is generally slightly longer, but not higher, than the adjacent teeth. The crowns are markedly compressed transversely (labiolingually) and are elongate,

TABLE 31

Antepithecus brachystephanus, Comparisons of the Dimensions of the Lower Teeth of Ameghino's Types with Those of the Scarritt Series

	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
OR, Scarritt sample	2.9	1.7	3.5–4.1	1.8–2.3	4.1–4.6	2.0–2.4	4.1–4.8	2.5–3.0	4.1–5.2	2.7–3.4	4.6–5.4	3.0–3.7	5.3–6.7	2.7–3.4
Infrapithecus cinctus	—	—	4.0	1.8	4.3	2.1	4.4	2.8	4.7	3.2	4.9	3.2	5.5	3.2
Pseudadiantus secans	—	—	4.0	1.8	4.1	2.2	—	—	—	—	—	—	—	—
Pseudadiantus imperfectus	3.2	1.5	3.9	1.7	—	—	—	—	—	—	—	—	—	—

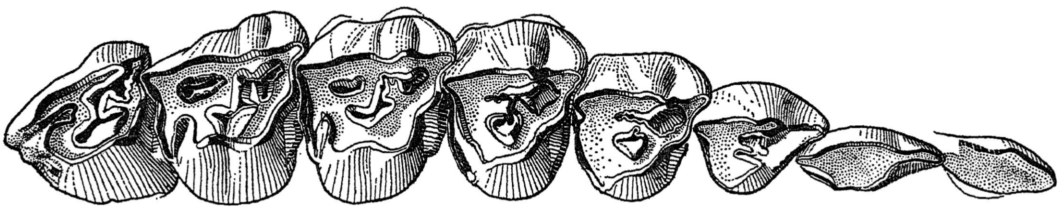

FIG. 19. *Notopithecus adapinus* Ameghino, A.M.N.H. No. 28949, C–M^3, drawn as right (reversed from left) side, crown view. ×5.

low, with a trenchant edge tending to rise to an ill-defined apex which is anterior on I^2, nearly central on P^1, and transitional between these on the intervening teeth. There is a slight internal cingulum that becomes more pronounced from I^2 to P^1, forming a slight heel on the latter. The external face is almost evenly convex save for a vague vertical crest from the apex, followed by a slight concavity. The enamel on the outer faces of these teeth is thick and strong. The lingual faces are also enameled, but the enamel is here so thin that it is partly or wholly removed by wear, even in fairly young individuals.

P^2 differs rather abruptly from P^1, forming the most obvious break in this remarkably even-graded series, and shows the beginning of the apical pattern typical of the posterior premolars and the molars. I have seen no unworn example of the premolars, but the pattern is fairly clear. P^2 is longer than wide, but is notably wider than P^1 and has a well-developed posterointernal protocone, lower than the ectoloph. The latter has a main central cusp, paracone, probably followed by a smaller and poorly differentiated metacone, further obscured by wear in the available specimens, and preceded by a parastylar spur. The latter is reflected on the outer surface by a vertical convexity or column, and there is another, longer but less distinct, corresponding to the paracone. The coronal face has a shallow pocket internal to and between the paracone and parastyle and another, deeper but smaller, in some cases branched or double, more posterointernal, between paracone and protocone. These fossae and the whole crown are surrounded by heavy enamel, but the enamel on the coronal surface was apparently very thin. The outline is asymmetrically triangular, often with a slight anterointernal emargination.

P^{3-4} are closely similar to each other save that P^4 is more transverse, and they represent a slight further elaboration of the pattern of P^2. The parastyle and paracone folds or columns of the external face are stronger and are separated by a deep and sharp vertical valley. There is a very vague corresponding metacone fold. The protocone is much longer than on P^2, but there is no suggestion of the differentiation of a hypocone. There is usually a variable, not cusplike, anterointernal cingulum and a pocket between this and the anterior slope of the protocone, and also a posterior cingulum, narrower but longer transversely, early merging into the metaloph by wear. When relatively little worn, the crown has a single tripartite fossa, but this is quickly separated by wear into an oval internal fossa and elongate or dumbbell-shaped outer or anteroexternal fossa. Advanced wear generally divides this outer fossa into two: a smaller posterior (or with respect to the whole tooth external-median) and larger anterior fossa. Expressed in terms of crests rather than of fossae, the basic (but somewhat variable) pattern is lophiodont, with a strong ectoloph and two transverse lophs from the protocone: a long, oblique, undulant protoloph to the parastyle and a short, straight, transverse metaloph to the metacone or metastyle region (neither of these cusps being well distinguished). There is a deep central fossa into which project a crochet and an antecrochet, which unite near or above the middle of the crown (vertically), and a poorly developed crista which unites with the crochet-antecrochet, or with a spur from the latter, on the more basal part of the crown.

In the one well-preserved P^4 of *Antepithecus brachystephanus* available, the central fossa seems to be divided only by one oblique partition, so that the small and variable median external fossa usually but not invariably present in *Notostylops adapinus* is here absent. Exactly this same condition is, however, seen in a few good specimens surely of *N. adapinus*, and the arrangement of these crests and fossae is so variable that such details are generally not really of taxonomic value.

M^{1-2} are closely similar to each other and are quadrate and generally longer than P^4, without being much wider, so that in effect they are less transverse. On the ectoloph, the parastyle and paracone folds are similar to those of P^4 but often less marked. There is a more distinct groove posterior to the paracone fold, and there is a well-developed metacone, about equal to the paracone and with an external fold or column in some cases about as strong as that of the latter but usually weaker. There is generally also a vaguely distinguished metastyle region, weaker than the parastyle and not projecting as does the latter. Protocone and hypocone are distinct and are nearly equal, the hypocone a little smaller. Their apices are separate, but they are united nearly to this point, so that slight wear transforms them into a single inner crest, but with their separation still distinguished by a groove on the internal slope. The molars apparently in every case have an anterior cingulum, and, as it is disconnected and low on the crown, it remains distinct until an advanced stage of wear. The posterior cingulum is higher on the crown and is connected to the metaloph near its middle or external part and merges with the metaloph with advancing wear, the internal end being the last to lose its individuality.

The molar fossae and secondary crests show much variation, but there is a basic pattern that is generally recognizable. The crown is completely surrounded by crests, the ectoloph, protoloph, metaloph, and what might be called the entoloph (protocone-hypocone crest). The deep central fossa is divided at varying levels by two cristae, the anterior uniting with the protoloph (or with a slight projection from it—antecrochet) and the posterior with the metaloph (or a projection from it—crochet), so that small, isolated, anteroexternal and posteroexternal fossettes are formed.[1] With wear, the posteroexternal fossette is usually isolated first and also disappears first, but the main or internal fossa is the last to go and may itself be divided before it disappears. A very characteristic intermediate wear stage has small anteroexternal and posteroexternal fossettes and a larger, anteroposteriorly elongate internal fossa from which a narrow spur extends externally between the two outer fossettes—a pattern ludicrously suggestive of a face. The projection from the internal fossa in some cases, but apparently not all, becomes separated by wear from the fossa itself, so that at one wear stage there may be three outer fossettes (or two, the posteroexternal fossette often disappearing before this stage is reached) and one longer internal fossa.

These molars are brachydont and rooted, but the crowns are somewhat elevated. In a slightly worn specimen of *N. adapinus* the hypsodonty index[2] on M^2 is 81 and the figure would be over 90 on unworn teeth. *Antepithecus brachystephanus* has slightly lower crowns, the index on an unworn M^2 being 72 and on one slightly worn 65. Unlike the condition in the Notostylopidae, the coronal pattern is deeply infolded, and enamel lakes do not disappear until an advanced age; indeed, they are almost as deep as the outside enamel.

M^{1-2} also differ in *A. brachystephanus* in that the protocone and hypocone are better separated, and wear does not unite them into a crest and enclose the main fossa until the external fossettes are deeply worn and well separated.

M^3 is still more variable than M^{1-2}, particularly in the development of the posterior cingulum and metaloph, in ways analogous to *Henricosbornia*. In general it agrees with M^{1-2} in structure but is narrower posteriorly than anteriorly and looks as if the hypocone

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[1] Here and throughout, I use the terms "metaloph," "crochet," and many others to facilitate description and not to imply or demand homology with these features in any other group of mammals. It is, for instance, certain that the crochet of a horse and the crochet of a notoungulate are not homologous under any acceptable definition of homology.

[2] 100 times ectoloph maximum height divided by ectoloph length.

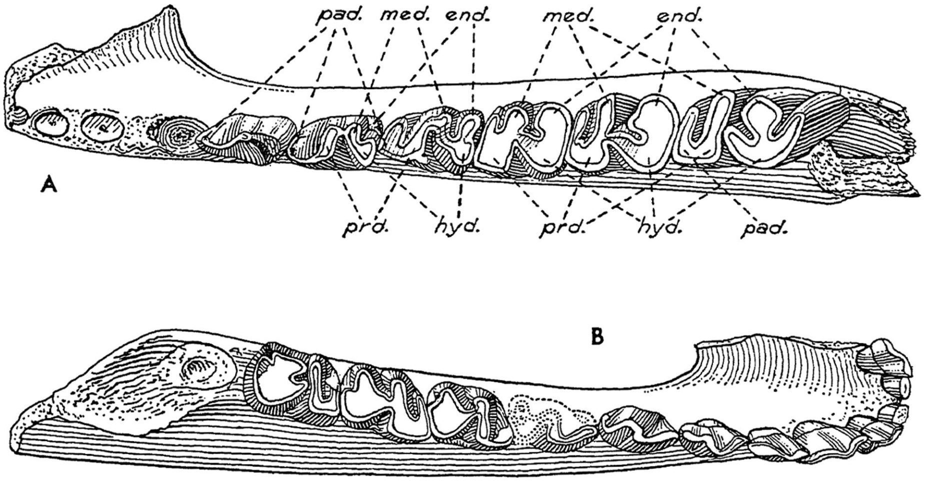

FIG. 20. *Notopithecus adapinus* Ameghino. A. C.N.H.M. No. P13439, left ramus with P_2–M_3, crown view. B. C.N.H.M. No. P14718, symphysis and right ramus with right I_1–M_2, left I_{1-2}, crown view. After Riggs and Patterson (1935). Both ×3.

Abbreviations: end., entoconid; hyd., hypoconid; med., metaconid; pad., paraconid; prd., protoconid.

had been very much reduced and almost completely fused with the protocone.[1]

LOWER DENTITION: In the lower jaw the median incisors are the smallest teeth and I_2–C are progressively larger. This difference in proportions from the upper teeth results in peculiar occlusion: I_{1-2} occlude with I^1, I_3 with I^2, the lower canine with I^3, P_1 with the upper canine, P_2 with P^1. Only with P_3, which occludes between P^2 and P^3, are more usual relationships established. The lower incisors are procumbent and wear truncates them almost at right angles to the long axis, whereas the upper incisors wear mainly on their lingual surfaces.

I_{1-3} have simple outer faces, but the internal face of each has a pronounced longitudinal excavation, so that the unworn tips are bifid. I_3 also has a small posterior projection or heel tending to form a third cusp, and this is more pronounced on the canine, although still vague.

The first premolar is about as long as the canine but is lower and less procumbent. Its internal face has two nearly equal excavations, the anterior somewhat larger, and there is a very vague external excavation between the position of these two and posterior to the middle. The apex is an undulant, obscurely tricuspid crest. P_2 has these same features but in more accentuated form, transitional to P_3. P_{3-4} are well divided into a longer trigonid and shorter talonid by the external groove, here sharp and deep. The apical crest is anteroposterior along the external border of the trigonid, turns at a right angle at the anteroexternal corner, and sinks rapidly to the base of the crown at the anterointernal corner. The (topographically) protoconid-metaconid crest is almost directly transverse and in fact is not clearly differentiated into two cusps, even when wholly unworn. From the topographic position of the metaconid it turns and runs posteroexternally to the position of the hypoconid (which is vaguely differentiated), falling as it goes. Usually on P_4 and often on P_3 there is a spur or projection from the metaconid angle falling straight posteriorly, so that this could also be described as the end of the metalophid, and the talonid crest could be said to abut against its angle, but in other cases the two are perfectly continuous. This striking distinction

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[1] Such is probably not a description of what has occurred phylogenetically, but it gives the appearance of the tooth. Phylogenetically, it is reasonably certain that M^3 has always been terminalized and never had a well-distinguished hypocone.

is highly variable and has no apparent taxonomic value, for we have specimens from exactly the same horizon and locality, of the same size and same structure in all other respects, belonging to a single species beyond any reasonable doubt, in some of which this more specialized structure occurs on both P_3 and P_4, in some on P_4 only, and in some on neither. It may be more common on P_3 in *N. adapinus* than in *A. brachystephanus*, but it can surely be distinguished only on little-worn teeth. Our material does not establish the difference as statistically significant, and the character is variable in both genera.

On P_3 the crest doubles back from the hypoconid and tends to end in a poorly distinguished hypoconulid near the midline, the entoconid, slightly transverse, being internal to this and basically continuous with it, so that even moderate wear obliterates the distinction. On P_4 the entoconid is usually slightly more distinct.

The molars represent a logical further development of the pattern of P_4, although in fact there is a visible discontinuity at this point and isolated P_4's can immediately and certainly be distinguished from isolated M_1's. One obvious distinction is that the external groove is posterior to the middle of the tooth on all the premolars and anterior on all the molars. The transverse trigonid crest of the molars neither passes without interruption into the talonid crest, as on the anterior premolars, nor turns backward into a definite column as, in some cases, on P_{3-4}, although it may approach this condition, but ends abruptly in the metaconid, which is a distinct but poorly differentiated cusp, the highest on the tooth. The talonid crescent abuts against the posteroexternal part of the metaconid, at a point progressively slightly more external from M_1 to M_3. The entoconid is somewhat swollen and is prolonged externally into a transverse crest, but does not seem quite to establish other definite connections in this genus. It is more distinct on the molars than on the premolars, but the exact degree of distinction and distance from the end of the talonid crescent are highly variable.

MILK DENTITION: Upper milk teeth are known only in A.M.N.H. No. 28701, *Antepithecus brachystephanus*. Dc–dm^3 do not differ much from C–P^3 of *N. adapinus* (these teeth not being surely known in *A. brachystephanus*) except that they have lower crowns, with the coronal pattern extremely shallow and the apical enamel very thin or perhaps absent from places. Dm^4 is broken on both sides and also deeply worn but clearly was much more molariform than P^4 of either species. It had the paracone and metacone well separated and each with a distinct external fold. Protocone and hypocone are likewise differentiated as in the molars, and there is a posteroexternal fossette. The crown is lower than in the permanent molars.

This same specimen shows dm_{1-4} and another jaw of the same species, A.M.N.H. No. 28695, has dm_{2-4}, and another of doubtful species, A.M.N.H. No. 28821, perhaps *N. adapinus reduncus*, also has dm_{2-4}. Description is based on the first two specimens, with A.M.N.H. No. 28821 mentioned only as far as it differs. Dm_{1-4} are all relatively much longer than P_{1-4}, the crowns are lower, and the structure is more complex. Aside from the general characters mentioned, dm_1 is not very unlike some specimens of P_1 in *A. brachystephanus*. Dm_2 has a long anteroposterior, anteroexternal shearing blade, not unlike that of P_2, separated by a small notch (much as in many carnivore carnassials) from the protoconid apex. From the latter a slight crest falls away directly posteriorly, and another, strong and continuous, runs posterointernally, then doubles back to the posteroexternal corner, then turns sharply again, and ends near the posterointernal corner. In A.M.N.H. No. 28821 the first crest from the protoconid is sharper and stronger, and the second is similar but less angulate and more median. On dm_3 the trigonid is similar to that of P_3, and the first-mentioned crest from the protoconid is feeble. The metaconid is developed as a high cusp partly differentiated from the protoconid, compressed transversely and crested longitudinally. This does not pass directly into the talonid crest as on dm_2, but the latter is distinctly separate and lower and abuts against the external face of the metaconid. This structure is approached in P_4 and occasionally in P_3 but has not been observed ever to be so highly differentiated on those teeth as on dm_3. The talonid crest runs to the posteroexternal corner, turns sharply there, and thence runs to the posterointernal corner. There is a small but separate entoconid. Dm$_4$ is similar save for the shorter, more quadrate trigonid and more expanded heel. It resembles the most complex examples of P$_4$ except for the relatively much more elongate heel, with more open basin, which makes it definitely more molariform. On A.M.N.H. No. 28821 dm$_4$ is nearly like that just described but has the entoconid larger and more distinct. Dm$_3$ is very peculiar, the postero-external crest from the protoconid strong, the protoconid apex nearly central, the partly differentiated metaconid apex posterior to the internal part of its curving, crestlike top, the talonid crest departing directly from this metaconid apex and forming a single, small crescent, concave internally, without distinct entoconid.

Although dm$_4$ is distinctly more molariform in both these types of milk dentitions than is P$_4$ in this genus, the structure of dm$_{2-3}$, particularly in A.M.N.H. No. 28821, seems rather to be specialized in a somewhat different direction and not to represent

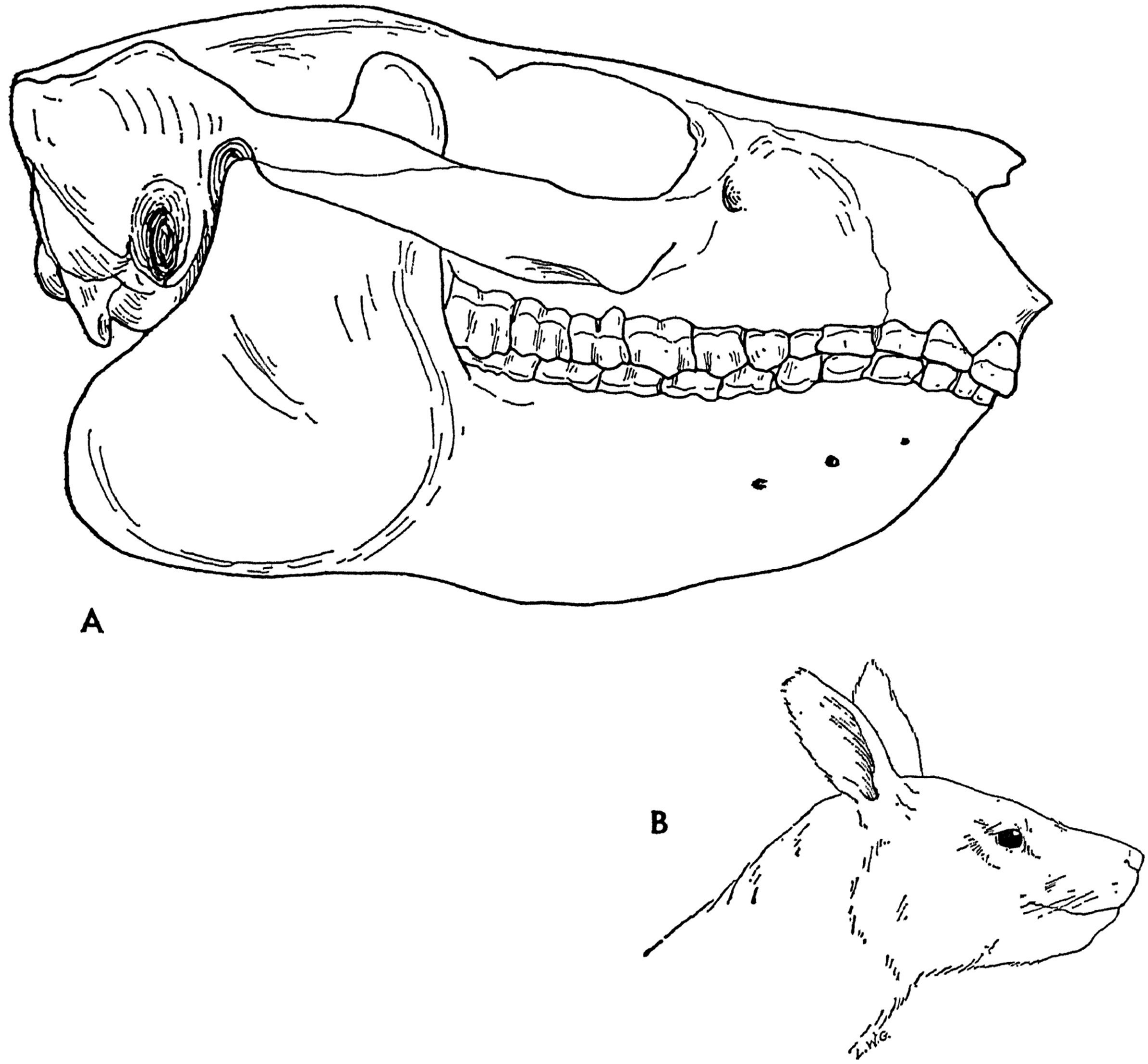

FIG. 21. *Notopithecus adapinus* Ameghino. A. M.A.C.N. No. 10787, articulated skull and jaws, slightly reconstructed. ×2. B. Life restoration based on A.

either a direct structural approach toward the molars or any probable stage in the evolution of the latter.

SKULL

The Ameghino Collection contains several excellent skulls, notably the following, all referred (by me) to *N. adapinus* (by Ameghino to *Adpithecus secans*): M.A.C.N. No. 10790, skull lacking right half of cranium, with partial mandible (type of *A. secans*); M.A.C.N. No. 10787, nearly complete, interlocked skull and mandible; and M.A.C.N. No. 10788, interlocked skull and mandible, lacking all of cranium except right otic region.

Aside from fragments showing details of various regions, the following are the chief Scarritt specimens, all *N. adapinus:* A.M.N.H. No. 28949, nearly perfect skull, lacking tip of muzzle and part of right zygoma (found by C. S. Williams, 1934); A.M.N.H. No. 28627, facial part of skull, lacking anterior ends of nasals (found by Justino Hernández, 1930); A.M.N.H. No. 28882, most of maxilla and zygoma, lower jaw, and other fragments (found by Justino Hernández, 1930); A.M.N.H. No. 28894, right zygoma, most of occiput and auditory region, partial lower jaw, and other fragments (found by Justino Hernández, 1930); A.M.-N.H. No. 28673, parts of both maxillae, occiput, and left auditory region (found by C. S. Williams in 1930).

The Chicago collection has the following fragment: C.N.H.M. No. P13298, palatines and most of right maxilla (described by Riggs and Patterson, 1935).

The Paris collection includes M.H.N. Tournouër Collection No. 34, crushed cranium with associated upper and lower jaws with complete dentition.

All these specimens, and many others, have been studied, but the following description is based mainly on the Scarritt Collection, which includes representatives of all the characters known.

In general aspect, the skull considerably resembles that of *Notostylops*, but it is more elongate and less expanded transversely, the brain case is relatively larger, and the whole cranial region is much longer and narrower, the muzzle is deeper, the zygoma more slender and less sigmoid, and the hypotympanic and, particularly, epitympanic cavities are relatively larger, the whole auditory region more inflated. Comparison with later, related typotheres such as *Cochilius* also shows the skull of *Notopithecus*, and especially the cranium, to be more elongate and slender and the auditory region to be relatively more inflated. The postorbital constriction is markedly stronger.

The nasals are long slender bones, slightly expanded and distinctly arched transversely at the anterior ends. The posterior portion is wider than the anterior, is flat, and ends in a nearly straight transverse suture anterior to the orbits, much as in *Protypotherium.*

The premaxilla is a short, high, triangular bone. The suture against the maxilla is nearly straight and vertical, but there is a very small posterosuperior insertion between maxilla and nasal. On the palate, the premaxilla forms the lateral anterior borders of the large anterior foramina, opposite I^{1-3}, and forms at least part, perhaps nearly all, of the median bar separating these foramina.

The maxilla is remarkably similar to that of *Protypotherium*, but the facial part is somewhat shorter and deeper. It is broadly excavated anterior to the orbit. Posterosuperior to this a triangular process is inserted over and into the frontal on the anterosuperior orbital rim. It appears that a frontal process did not exclude this from the actual orbital rim, as it does in *Protypotherium* and several other genera. The anterior root of the zygoma is opposite P^4–M^2, is very stout, and has a small descending process, slightly more distinct than in *Protypotherium* but much less than in *Interatherium.* The maxilla forms the whole lower border of the zygoma to the glenoid fossa. The infraorbital foramen is above the anterior end of P^3, and is single and of moderate size. The infraorbital canal is very short, its length less than the greater diameter of the foramen. The palatine process of the maxilla is somewhat arched and nearly featureless.

The palatine is large and widely expanded on the palate, forming virtually the whole width of the latter to the anterior end of M^1 and being opposite the middle of P^4 at the midline, the most anterior point on the curved maxilla-palatine suture. It bears several small foramina in its anterior portion. The choanae are very narrow and just touch a line tangential to the posterior ends of the last molars, a position more anterior than in the Santa Cruz genera. Relatively large and deep lateral notches are developed, as in *Protypotherium* but also more anterior than in that genus. Posterior to this the palatine expands laterally into an alate process which is not free but is supported by a similar and opposite (anteriorly expanded) process of the alisphenoid into which the pterygoid, which is not certainly distinguishable, may also enter.

The sutures of the orbital wall are not perfectly clear, but evidently the frontal forms almost all of this wall, followed posteroinferiorly by the oval orbitosphenoid, below which is the quite limited orbital process of the palatine. The optic foramen is developed in the posterior part of the relatively small orbitosphenoid, and the large anterior lacerate foramen is at the anterior margin of the alisphenoid in the deep pocket above its flange to the alate process of the palatine. Above this point the alisphenoid extends upward to contact with the parietal and posterior end of the frontal in the usual way.

The lacrimal is small and is entirely intraorbital, the foramen well within the raised anterior orbital rim. This character is one of the many interatheriid characters already well established in the Casamayor form.

The frontal is quadrate and flattened anteriorly. It is inserted into the parietals posteriorly at the midline, as in so many notoungulates. The parietal extends forward only for a short distance lateral to this, and below this process of the parietal the frontal is widely expanded ventrally and posteriorly in the cranial and interorbital wall. It has a prominent vascular foramen in its posterior part directly above the optic foramen. The superior orbital rim is sharp, and there are small postorbital processes, much less pronounced than in *Protypotherium*. Divergent crests from the anterior end of the sagittal crest run first along the frontoparietal suture and then on each frontal to the tip of, not directly into, the postorbital process.

The parietals are remarkably long and narrow, in our best skull (A.M.N.H. No. 28949) measuring 36.5 mm. in length and only 15 mm. in greatest width (of both together), across the anterior part of the cerebrum. They do not narrow so much posteriorly as in *Protypotherium* and other brachycephalic types, the least posterior width (of both together) being more than 10.0 mm., immediately anterior to the lambdoid crest. In adults at least, the parietals are completely fused along the sagittal crest, which is sharp and high and extends without division to the frontal suture.

In its general features the squamosal is like that of *Protypotherium*. The epitympanic sinus is relatively still larger, as is the triangular lateral area developed on the pars epitympanica between the lambdoid crest and the crest continuous with the upper edge of the zygoma. The glenoid surface is more nearly flat, wide transversely, and less dorsal than in the later genus. As in the latter, the squamosal forms the whole upper rim of the zygoma posterior to the orbit, and the jugal is a small lenticular slip of bone confined to the zygoma, in a nearly horizontal position above the maxilla and below the squamosal.

The occiput is likewise closely similar to that of later interatheriids, with the occipital bones fused and with large semicircular lateral emarginations. The pars epitympanica of the squamosal occupies the dorsal and lateral parts of each emargination. At the most medial point are a pit and vacuity in which there is a small exposure of the mastoid. Below this and ventromedial to the pars epitympanica, clearly suturally separate from the latter, is the so-called adventitious bone, common in notoungulates but otherwise of unknown homology. It forms a small posttympanic process closely applied to the most posterior point of the bulla. On the specimens studied this is not separable from the paroccipital process, and the two together are small, not strongly produced, and unspecialized. The vagina processus hyoidei is between these joined processes and the bulla.

The bulla is shaped much as in the later interatheriids but is more elongate and larger relative to the skull as a whole. In this very early form both epitympanic and hypotympanic inflations reach nearly their greatest relative development among notoungulates.

The condylar foramen is simple and is immediately anterior to the lateral part of the

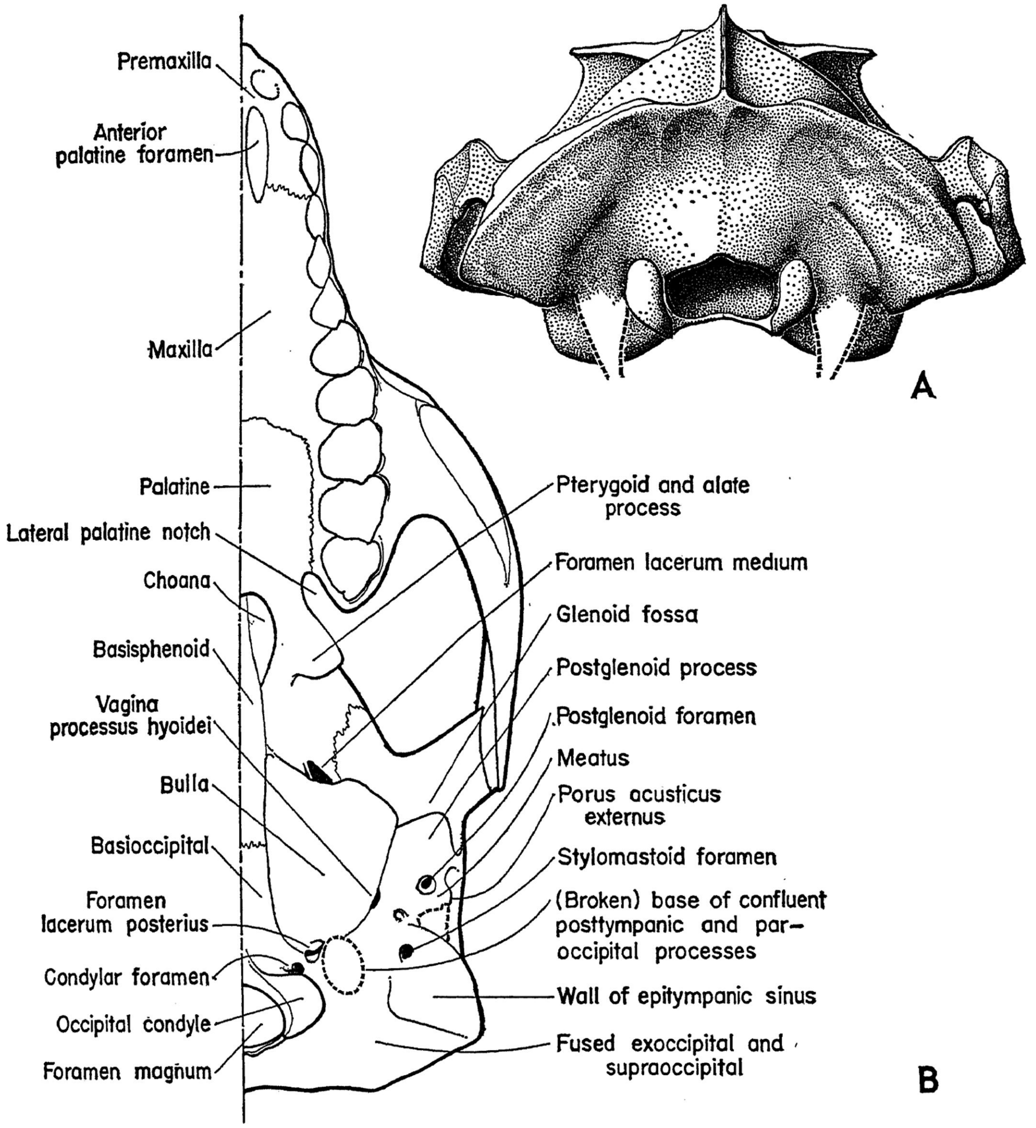

FIG. 22. *Notopithecus adapinus* Ameghino, A.M.N.H. No. 28949, with added details from A.M.N.H. Nos. 28627 and 28894, reconstruction of skull. A. Posterior view. ×2. B. Diagram of ventral view.

condyle. Immediately anterolateral to this, at the posterior margin of the bulla, is the posterior lacerate foramen. There are no foramina along the medial side of the bulla, and only a single large foramen on its anterior side, lateral to its anteromedial point, which must represent the eustachian, oval, and anterior lacerate foramina. There appears to have been an internal septum dividing the latter two, but this is not perfectly visible in any case. There is a tiny but distinct fissura Glaseri at the posteromedial angle of the glenoid fossa.

A postglenoid process is well developed but not very distinct, since its apex does not project ventrally beyond the level of the meatus, with which it is fused. In one specimen the external surface of the process bears a flat, vertical, triangular surface immediately anteroventral to the porus, but in other speci-

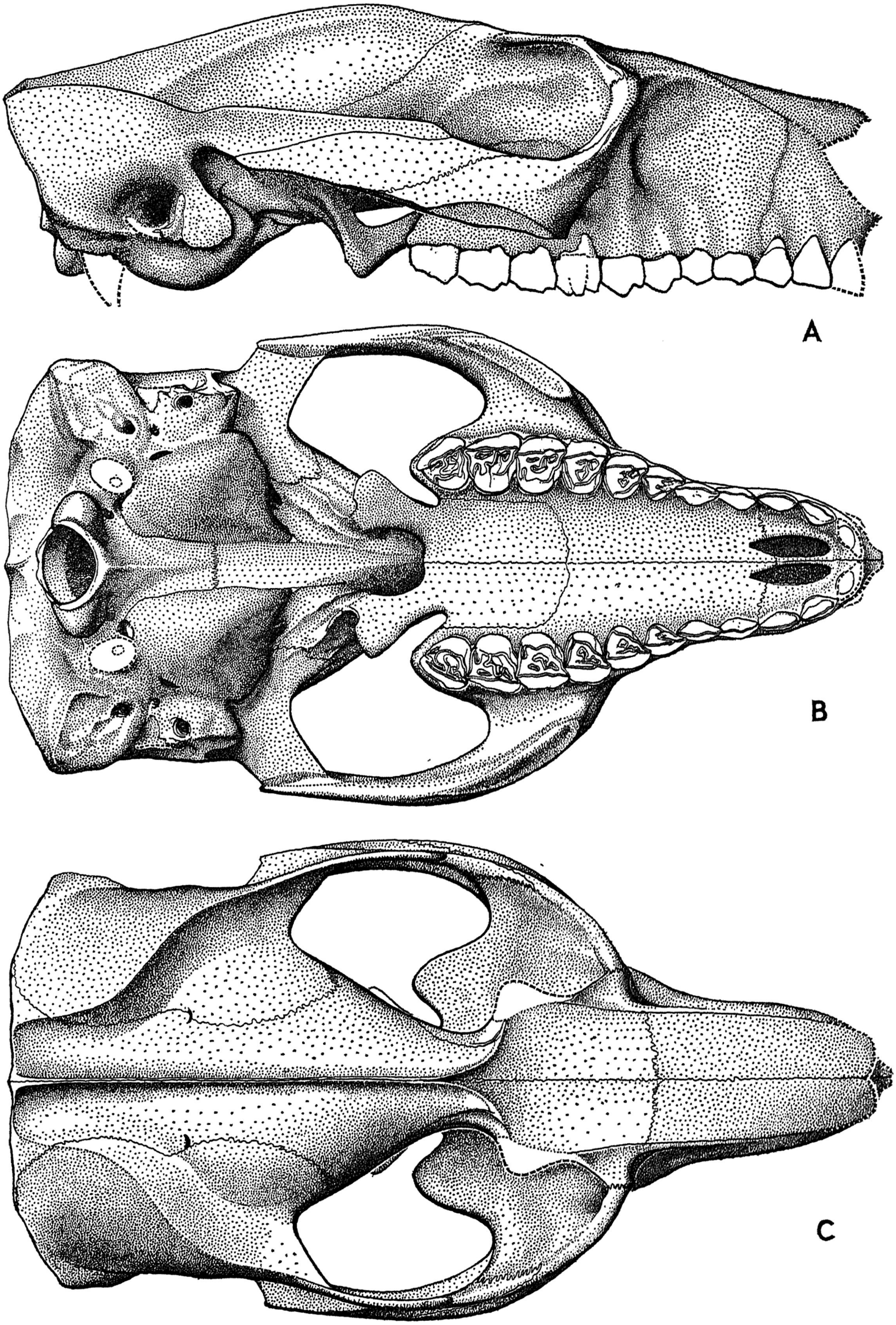

FIG. 23. *Notopithecus adapinus* Ameghino, A.M.N.H. No. 28949, with added details from A.M.N.H. Nos. 28627 and 28894, reconstruction of skull. A. Right lateral view. B. Ventral view. C. Dorsal view. ×2.

mens this is smaller or virtually absent. The postglenoid foramen is large and single and lies on the common postglenoid-meatus ventral surface on what appears to be the suture between these two elements. The tympanic circles the meatus ventrally and anteriorly and is exposed on the ventral surface between postglenoid and posttympanic processes, but its exposure here is evidently less than in most later forms, and I do not distinguish a distinct crest on it. The meatus is shorter than in the later forms and slopes in the same direction but somewhat less steeply, the meatus being relatively low. This whole region is decidedly more like that in later interatheres than like that of other typotheres, but is somewhat distinctive even from that of *Protypotherium*.

The bulla does not seem to have been cancellous or septate, but the material does not permit the establishment of this point with certainty.

MANDIBLE

The marked variation in depth of the mandible between and within *Notopithecus* and *Antepithecus* is mentioned above. Especially in the deep-jawed, but also to less extent in the more shallow-jawed, forms there is a gentle concavity in the outline of the lower border beneath M_3. This may foreshadow the curious "double angle" of later interatheriids, but if so is very much less developed, is more anterior, and no part of this region is distinctly inflected. The mandible is otherwise generally similar to mandibles of the later forms.

Notopithecus adapinus Ameghino, 1897

Plate 12, figures 8–12; plate 14, figures 1–7; plate 15; text figures 19–23

Notopithecus adapinus AMEGHINO, 1897a, p. 420, figs. 1–5; 1898, p. 150; 1904d, p. 74, fig. 66; 1906, p. 290, fig. 71. SIMPSON, 1932e, p. 10, fig. 6. SCOTT, 1937a, p. 517, fig. 326.

Adpithecus secans AMEGHINO, 1901, p. 355; 1904b, p. 178, figs. 233, 281. SCHLOSSER, 1923, p. 667, fig. 750.

Notopithecus secans: CABRERA, 1935, p. 14. RIGGS AND PATTERSON, 1935, p. 212, fig. 3, pl. 5, figs. 4, 5.

Adpithecus subtenuis AMEGHINO, 1902a, p. 7.

Adpithecus reduncus AMEGHINO, 1902a, p. 8.

Notopithecus reduncus: RIGGS AND PATTERSON, 1935, p. 212, pl. 5, figs. 2, 3.

Infrapsthecus diversus AMEGHINO, 1902a, p. 9.

Epipsthecus confluens AMEGHINO, 1904a, vol. 56, p. 193; 1904b, p. 167, figs. 213, 282.

Antepsthecus gradatus AMEGHINO, 1904a, vol. 56, p. 196.

Gonopithecus trigodontoides AMEGHINO, 1904a, vol. 56, p. 196; 1904b, p. 177, fig. 232.

TYPES: M.A.C.N. No. 10822, right maxilla with C–M^2, lower jaw fragments with right P_3 and left M_1, left humerus, partial tibia, partial astragalus, one phalanx, and five broken vertebrae, labeled "todo de uno" and probably correctly associated. Lectotype. No locality data, but probably from south of Colhué-Huapí.

M.A.C.N. No. 10843, left maxilla with P^{2-3}, fragment of right lower jaw with M_3 and part of M_2, and two isolated lower molars, probably not all associated. This was used in the original description and is essentially a syntype, but differs as much from the lectotype as do certain of Ameghino's supposed species. No locality data, but probably from south of Colhué-Huapí.

TYPES OF SYNONYMS: Of *Adpithecus secans:* M.A.C.N. No. 10790, somewhat broken skull and jaws with most of the dentition, labeled "tipo" by Ameghino. There are eight other specimens referred to the species by Ameghino, and these may have been included in his hypodigm. No locality data for type, referred specimens mostly from south of Colhué-Huapí, one from "Colhué-Huapí Norte." Of *Adpithecus subtenuis:* M.A.C.N. No. 10834, right maxilla with P^3–M^2 (lectotype) and another right maxilla with P^4–M^2. From south of Colhué-Huapí. Of *Adpithecus reduncus:* M.A.C.N. No. 10858, part of right lower jaw with M_{2-3} (lectotype), and another with M_{1-2}. No locality data. Of *Infrapithecus diversus:* M.A.C.N. No. 10838, part of left lower jaw with P_{2-4}. From "Colhué-Huapí Norte." Of *Epipithecus confluens:* M.A.C.N. No. 10862, part of right maxilla with broken P^4–M^2. From Pico Salamanca. Of *Antepithecus gradatus:* M.A.C.N. No. 10828, two left upper molars, probably M^{1-2}, and a maxillary fragment. No locality data. Of *Gonopithecus trigodontoides:* M.A.C.N. No. 10827, three right upper molars and a right upper premolar, not associated. Two of these teeth, the types or lectotypes, are placed together as preserved and were figured (1904b, fig.

232) as M$^{2-3}$ of one individual, but they are actually isolated teeth, not in the maxilla as the figure suggests, and are almost surely not associated but both M^3. From "Oeste de Río Chico."

Hypodigm: The types, as above, and a large series of other specimens in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," the American Museum of Natural History, the Field Museum of Natural History, and the Muséum National d'Histoire Naturelle in Paris, the more important of which are listed above.

Horizon and Locality: Casamayoran, Patagonia. A widespread species occurring at almost all Casamayor localities.

Diagnosis: The only species certainly referable to the genus as now defined. See numerical data in tables 24–29, 32–34.

The invalidity of supposed distinctions in size between the various species here united is demonstrated on previous pages. In most cases no comparison was made directly with *N. adapinus* or with others of these synonymous species because of the assumption, now found to be erroneous, that they belonged to different genera. Once the generic references are seen to be incorrect, the specific distinctions also disappear.

Adpithecus secans was defined as having three, and *N. adapinus* two, incisors, an error in the latter case. *Adpithecus subtenuis* was defined chiefly on its being smaller than *A. secans*, a difference so slight as surely not to be of specific value, and was described morphologically in a way equally applicable to *A. secans* and *N. adapinus*. *Adpithecus reduncus* was defined as being of the same size as *A. secans* but with a shallower jaw and as having the inner cusps of the lower molars very high and pointed, the anterior higher than the posterior and both inclined forward. The latter details simply describe little-worn teeth of all members of this genus. The jaw depth is not actually determinable from the type, but probably was slightly less than in typical *N. adapinus*, a difference possibly significant and here recognized as one of the features of a subspecies, *N. a. reduncus*.

Infrapithecus diversus and *Antepithecus gradatus* are distinct from other species referred to those genera, and to this extent their definitions were valid, but they are apparently synonymous with *Notopithecus adapinus* and *Adpithecus secans*, with which they were not compared. *Epipithecus confluens* and *Gonopithecus trigodontoides* were likewise defined as generically distinct, and the invalidity of the genera leaves no specific distinctions from *N. adapinus*, with which they were not compared. The differentiation of the second of these supposed species was apparently based largely on a false association of isolated teeth.

Aside from the two fairly well-distinguished subspecies found at different levels south of Colhué-Huapí, other scattered lots suggest some local or temporal racial or subspecific differentiation within this species, but in no case is this sufficiently well established for formal recognition. Ameghino's types of *Epipithecus confluens* and *Gonopithecus trigodontoides* are from localities some distance from Colhué-Huapí, but the scanty material enters into *N. adapinus* with no distinction that can certainly be recognized as of taxonomic value.

We have several fragmentary specimens from the still more distant locality, Rinconada de los Lopez. Among the lower teeth, only three last lower molars can be measured. These are smaller than any others known to me, length 4.4–4.7, and width 2.1–2.7 mm., and may well represent a new subspecies (Ameghino had no material from near this locality), but are inadequate for one to establish this. Upper teeth from the same locality do not include M^3, and P^4–M^2 are not distinctive. Measurements of them are given in table 32.

We also have several specimens from near

TABLE 32

Measurements of Upper Teeth of *Notopithecus adapinus* from Rinconada de Los Lopez

P^4		M^1		M^2	
L	W	L	W	L	W
3.6	4.1	4.1	4.3	4.1	—
—	—	4.4	4.7	4.6	4.9
—	—	—	—	4.4	4.5
—	—	3.9	4.7	4.3	4.7

TABLE 33

MEASUREMENTS OF UPPER TEETH OF *Notopithecus adapinus*

	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
M.A.C.N. No. 10790[a]	3.5	2.0	3.7	2.8	3.7	4.0	3.9	4.7	4.7	4.8	4.7	4.7	4.5	4.4
A.M.N.H. No. 28949[b]	3.8	1.8	3.7	2.8	2.8	3.8	3.9	4.5	4.3	4.6	4.5	4.7	4.6	4.1
A.M.N.H. No. 28627[c]	3.4	1.6	3.5	2.7	3.7	3.9	3.8	4.5	4.1	4.9	4.2	5.1	4.0	4.1
A.M.N.H. No. 28950[d]	—	—	3.0	3.1	3.6	4.2	3.7	—	3.8	4.9	4.2	4.7	3.9	4.4

[a] Type of "*Adpithecus secans.*"

[b] From Colhué-Huapí, referred to *N. adapinus adapinus.*

[c] From near Parada Valle Hermoso; subspecies uncertain, perhaps *N. a. reduncus.*

[d] From a low horizon at Colhué-Huapí, referred to *N. a. reduncus;* teeth deeply worn.

Parada Valle Hermoso, a locality near Colhué-Huapí. They are evidently *N. adapinus* and probably, but not certainly, the typical subspecies.

C.N.H.M. No. P13442, from Casamayor, is a lower jaw belonging to this species, and very close to *N. adapinus adapinus* but with M_{1-2} below the usual size.

Measurements of cheek teeth of a few of the more extensive specimens are given in tables 33 and 34.

Notopithecus adapinus adapinus (Ameghino, 1897), new form

Text figure 25A

TYPE: As for *N. adapinus*, see above.

HYPODIGM: Series of specimens in the American Museum of Natural History discussed above.

HORIZON AND LOCALITY: South of Lago Colhué-Huapí, and probably elsewhere in the Casamayoran, Patagonia.

DIAGNOSIS: The typical and most abundant form of *N. adapinus*, with mandible deep, commonly 13.0 mm. or more beneath M_1, and with M^3 relatively large. See measurements cited above.

Notopithecus adapinus reduncus (Ameghino, 1902), new form

Text figures 24, 25B

TYPE AND HYPODIGM: See above.

HORIZON AND LOCALITY: South of Lago Colhué-Huapí and probably elsewhere in the Casamayoran, Patagonia.

DIAGNOSIS: Closely similar to *N. a. adapinus*, but jaw shallower, commonly 12.0 mm. or less beneath M_1, and M^3_3 relatively small. See measurements cited above.

Notopithecus spp. indet.

Fragments from the Riochican and the Mustersan indicate that typical *Notopithecus* or very close allies may occur in the earlier and later stages. Cabrera (1935, p. 14) reported "*Notopithecus secans*" from the uppermost Riochican of the Bajo de la Palangana near Pico Salamanca on the basis of a jaw fragment with left P_4 and an isolated M_3. I do not believe that this species (=*N. adapi-*

TABLE 34

MEASUREMENTS OF LOWER TEETH OF *Notopithecus adapinus*

	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
M.A.C.N. No. 10860[a]	—	1.5	3.3	1.6	3.7	2.1	4.1	2.5	3.8	2.3	4.4	2.7	—	—
A.M.N.H. No. 28882[b]	3.0	1.6	3.3	2.0	3.4	2.4	3.6	2.7	3.7	2.7	4.3	3.0	5.7	3.3
A.M.N.H. No. 28792[c]	2.9	1.5	2.9	1.9	3.3	2.1	3.6	2.4	3.9	2.6	4.1	2.7	4.9	2.7

[a] Specimen referred by Ameghino to "*Adpithecus secans*" = *N. a. adapinus.*

[b] Specimen from Colhué-Huapí, referred to *N. a. adapinus.*

[c] From Colhué-Huapí, referred to *N. a. reduncus.*

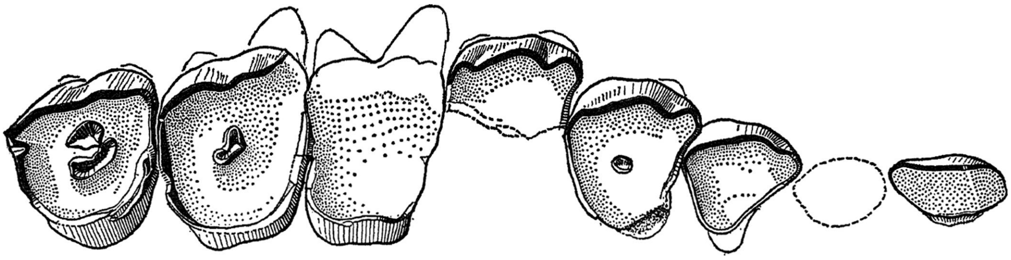

FIG. 24. *Notopithecus adapinus reduncus* (Ameghino), A.M.N.H. No. 28950, incomplete right C–M^3, crown view. ×5.

nus) can be positively identified from such fragments, but the record does probably indicate a notopithecine at this level, where there is a fauna nearly like that of the Casamayoran.

M.L.P. No. 12–2184, figured by Roth (1927, pl. 13, fig. 8), includes associated P^{2-3} and separate P^4, M^1 or M^2, and M^3, which may or may not be associated. This specimen is, or these specimens are, referable with probability to *Notopithecus* and are near *N. adapinus* but not surely of that species. The lot is labeled as from the "upper Cretaceous of Lago Musters," and most of the specimens so labeled are Mustersan. There are, however, some Casamayoran exposures in that vicinity (Cerro del Humo) and this may be from an earlier horizon than the bulk of the material so labeled by Roth.

?Notopithecus amplidens (Ameghino, 1901)

Adpithecus amplidens AMEGHINO, 1901, p. 356.
?Notopithecus amplidens: SIMPSON, 1936d, p. 83.

TYPE: M.A.C.N. No. 10895, a right maxilla with P^3–M^3, lectotype, and another with dm^{2-4}, M^{1-2}. The original description also mentioned lower molars, which would presumably be syntypes, but they are not surely identified as such in the collection.

HYPODIGM: Syntypes, and M.A.C.N. No. 10901, four isolated specimens: left C–P^3, left P^4–M^2, right M_3, and an upper premolar; M.L.P. No. 12-2183, isolated M^1 (referred to *Guilielmoscottia plicifera* by Roth); and M.L.P. No. 12-2281, four right upper teeth, probably P^2–M^1, possibly associated.

HORIZON AND LOCALITY: Mustersan. Localities of Ameghino specimens unknown. Museo de La Plata specimens from Roth's "Upper Cretaceous of Lago Musters," probably Cerro del Humo.

DIAGNOSIS: Larger than other recognized species of *Notopithecus*. Upper cheek teeth relatively low-crowned. Molars more transverse but pattern that of *Notopithecus*.

This species seems to be valid and is, indeed, so distinctive that it will probably prove to be generically distinct when better known. It is, however, close to *Notopithecus* and generic definition would not be clear or fully objective on these materials. It does not seem to be more advanced than the Casamayoran species in spite of its later age.

The measurements of the lectotype, M.A.C.N. No. 10895, are: P^3, length, 4.5, width, 5.6; P^4, length, 5.5, width, 6.3; M^1, length, 5.5, width, 6.5; M^2, length, 5.8, width, 6.7; M^3, length, 5.4, width, 6.0.

Ameghino referred a lower jaw to this species and included this or another specimen with lower molars among his syntypes or in his original hypodigm. There are also specimens in the Museo de La Plata and the American Museum of Natural History that could be lower jaws of this species, but I have not been able surely to distinguish between *?N. amplidens* and *Guilielmoscottia plicifera* on the basis of such fragments. These specimens are briefly discussed below, following the treatment of the latter species.

ANTEPITHECUS AMEGHINO, 1901

Antepithecus AMEGHINO, 1901, p. 356; 1906, p. 466.
Infrapithecus AMEGHINO, 1901, p. 357; 1906, p. 466. ROTH, 1927, p. 236. SCHLOSSER, 1923, p. 607.
Pseudadiantus AMEGHINO, 1901, p. 372; 1906, p. 967.
Patriarchippus AMEGHINO, 1904b, p. 135; 1906,

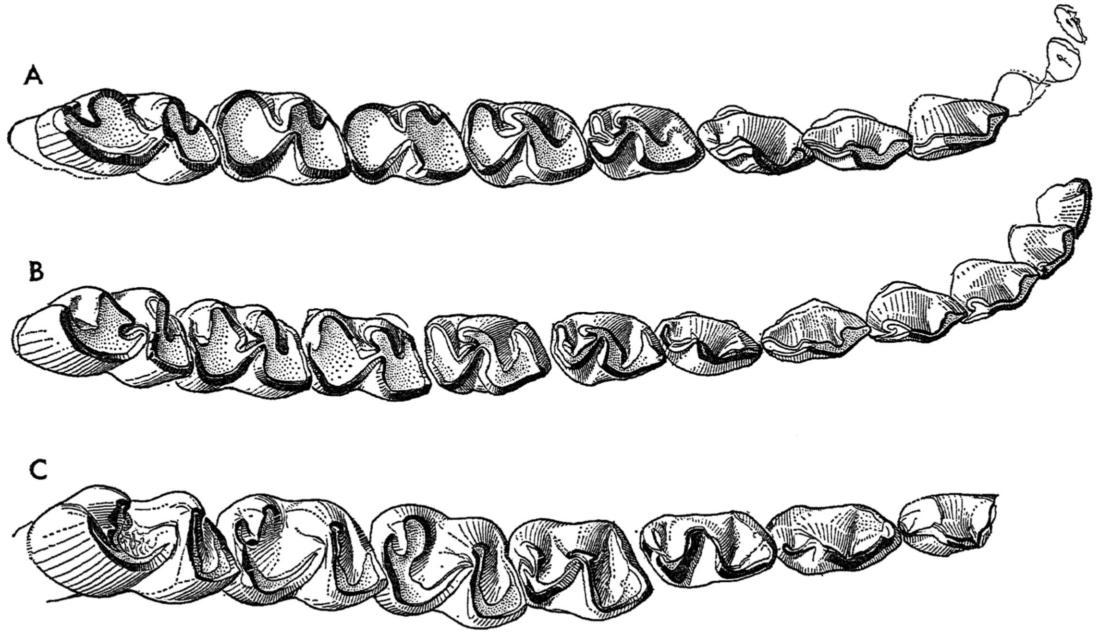

FIG. 25. *Notopithecus* and *Antepithecus*. A. *Notopithecus adapinus adapinus* (Ameghino), A.M.N.H. No. 28718, C–M$_3$, drawn as right, reversed from left, side, with some restoration from right canine. B. *Notopithecus adapinus reduncus* (Ameghino), A.M.N.H. No. 28792, I$_1$–M$_3$ drawn as right, P$_2$–M$_3$ reversed from left, side. C. *Antepithecus brachystephanus* Ameghino, A.M.N.H. No. 28707, right P$_2$–M$_3$, crown views. All ×4.5.

p. 467. (Not stated to be new in Ameghino, 1904b, but no older publication found.)

Patriarchus [error]: Ameghino, 1904b, p. 143.

Type: *Antepithecus brachystephanus*.

Types of Synonyms: *Infrapithecus cinctus*, *Pseudadiantus secans* (*nec Adpithecus secans*), *Patriarchippus annectens*.

Distribution: Casamayoran, Patagonia.

Diagnosis: Closely resembling *Notopithecus* but slightly more brachydont, protocone and hypocone less united, cheek teeth more elongate, horizontal mandibular ramus shallower.

The reasons for the synonymy here adopted are given in the discussion of *Notopithecus*, and the morphology of *Antepithecus* is also considered with that of the preceding genus.

Antepithecus brachystephanus Ameghino, 1901

Plate 14, figure 8; plate 16, figures 1–7; text figures 25C, 26

Antepithecus brachystephanus Ameghino, 1901, p. 356.

Antepithecus brachystephanos [*lapsus* or invalid emendation]: Ameghino, 1902a, p. 9; 1904b, p. 178, fig. 234.

Infrapithecus cinctus Ameghino, 1901, p. 357.

Pseudadiantus secans Ameghino, 1901, p. 372.

Pseudadiantus imperfectus Ameghino, 1901, p. 373.

Antepithecus interrasus Ameghino, 1904a, vol. 56, p. 195.

Patriarchippus annectens Ameghino, 1904b, p. 135, figs. 161, 360[1]; 1906, p. 312, fig. 126.

Type: M.A.C.N. No. 10841, seven isolated upper teeth, a fragmentary upper jaw, and two fragmentary lower jaws, not all associated. The lectotype is an isolated M^2 measuring 5.7 by 5.7 mm. From south of Colhué-Huapí.

Types of Synonyms: Of *Infrapithecus cinctus:* M.A.C.N. No. 10826, left lower jaw with P$_2$–M$_3$; from south of Colhué-Huapí. Of *Pseudadiantus secans:* M.A.C.N. No. 10669-

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[1] This was not given as new in 1904b, but I have not noticed any earlier citation, and the data in that publication are sufficient to establish the name in nomenclature.

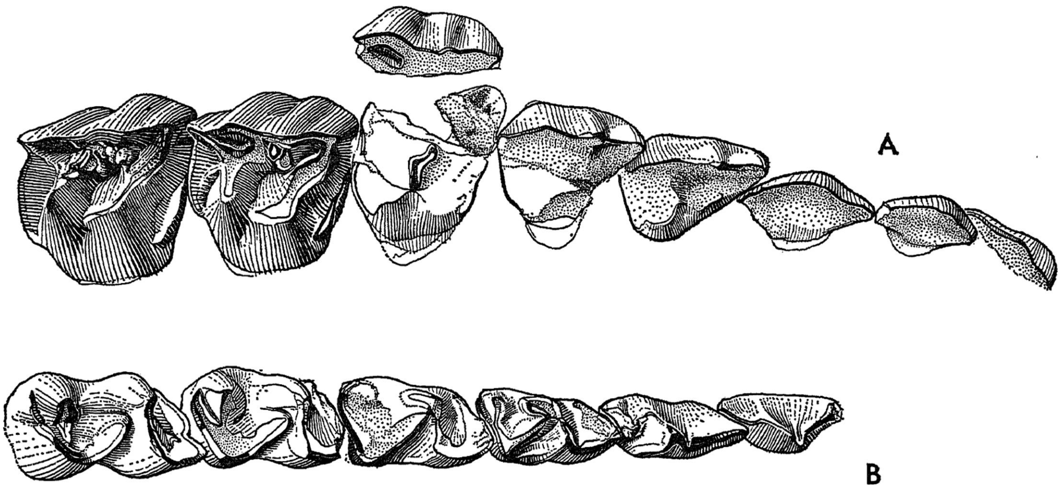

FIG. 26. *Antepithecus brachystephanus* Ameghino, A.M.N.H. No. 28701, crown views. A. di^3–dm^4 and M^{1-2}, composed from both sides and drawn as if right side (di^3, dc, dm^1, dm^3, most of dm^4, M^2 from right side; dm^2, ectoloph of dm^4, and M^1 from left side). B. Right dm_{1-4}–M_{1-2}. Both ×4.5.

(a), right lower jaw fragment with P_{2-3}; no locality data; of *Pseudadiantus imperfectus:* M.A.C.N. No. 10669(b), left lower jaw fragment with P_{1-2}; no locality data. Of *Antepithecus interrasus:* M.A.C.N. No. 10859, part of right maxilla with P^2–M^2, P^3 and M^2 broken; from south of Colhué-Huapí. Of *Patriarchippus annectens:* M.A.C.N. No. 10691, part of left maxilla with M^{1-2} (lectotype) and an isolated, not associated, right M^2; no locality data.

HYPODIGM: Types, a series of specimens in the American Museum of Natural History, discussed above, and a few specimens in the Muséum National d'Histoire Naturelle in Paris.

HORIZON AND LOCALITY: Casamayoran, Patagonia. All certainly identified specimens from south of Lago Colhué-Huapí.

DIAGNOSIS: The only species surely referable to the genus as now defined. See numerical data in tables 35 and 36.

As with *Notopithecus adapinus*, the multiplicity of names for this species is largely the result of the placing of fragmentary remains in diverse genera so that they were not directly compared.

Antepithecus interrasus was based essentially on the stronger relief of the external upper molar walls than in *A. brachystephanus*. There is a difference in the types in this respect, but it is very slight, and variant specimens show that this degree of difference is not constant or characteristic.

Pseudadiantus imperfectus was separated from *P. secans* by characters that all depend on the identification of the two teeth of the type of the former as P_{2-3}, whereas they are P_{1-2}. P_2, the only tooth these types have in common, is virtually identical in the two.

This species occurs at some of the same horizons and localities as *Notopithecus adapinus*, and, although their extreme variants are very distinct, they so nearly intergrade in some parts that there are specimens that could belong to either. In our collection *A. brachystephanus* is the more abundant species of the two, owing merely to chances of collecting, because Carlos Ameghino found many more specimens of *N. adapinus*. It is also noteworthy that the good partial skulls and upper jaws are all of *N. adapinus* and that upper jaw material of *N. brachystephanus* is rare and poor in both collections. Measurements of all our upper jaw fragments and of the most complete of our many lower jaws are given in table 35.

Our collection suffices to provide statistical constants for most of the lower tooth dimensions. The data in table 36 are all

TABLE 35

MEASUREMENTS OF TEETH OF *Antepithecus brachystephanus*

		A.M.N.H. No. 28701	A.M.N.H. No. 28722	A.M.N.H. No. 28748	A.M.N.H. No. 29402	A.M.N.H. No. 28707
P^4	L	—	—	4.4	—	—
	W	—	—	4.9	—	—
M^1	L	5.0	5.1	5.1	—	—
	W	5.0	5.2	5.8	4.8	—
M^2	L	5.0	—	5.6	5.6	—
	W	5.2	—	6.1	5.6	—
P_1	L	—	—	—	—	2.9
	W	—	—	—	—	1.7
P_2	L	—	—	—	—	3.5
	W	—	—	—	—	2.0
P_3	L	—	—	—	—	4.1
	W	—	—	—	—	2.2
P_4	L	—	—	—	—	4.1
	W	—	—	—	—	3.0
M_1	L	—	—	—	—	4.5
	W	—	—	—	—	3.4
M_2	L	—	—	—	—	4.8
	W	—	—	—	—	3.5
M_3	L	—	—	—	—	6.1
	W	—	—	—	—	3.3

TABLE 36

STATISTICAL DATA ON A UNIFIED SAMPLE OF LOWER TEETH OF *Antepithecus brachystephanus*

Variate	*N*	OR	$\overline{X}$	s	V
LP_3	6	4.1–4.6	4.31±.09	.21±.06	5.1±1.5
WP_3	6	2.0–2.4	2.13±.06	.14±.04	6.5±1.9
LP_4	8	4.1–4.8	4.45±.07	.21±.05	4.8±1.2
WP_4	8	2.5–3.0	2.69±.06	.17±.04	6.3±1.6
LM_1	9	4.1–5.2	4.66±.11	.32±.07	6.8±1.6
WM_1	9	2.7–3.4	2.99±.08	.24±.06	8.1±1.9
LM_2	9	4.6–5.4	4.97±.09	.27±.06	5.5±1.3
WM_2	9	3.0–3.7	3.21±.08	.24±.06	7.4±1.7
LM_3	9	5.3–6.7	5.90±.14	.42±.10	7.1±1.7
WM_3	9	2.7–3.4	3.00±.08	.23±.05	7.7±1.8
Depth of jaw on inner side below anterior root of M_1	12	9.1–11.5	9.88±.20	.70±.14	7.1±1.5

TABLE 37

Statistical Data on LP_4 for Various Samples of the Notopithecinae

	N	OR	$\bar{X}$	s	V
All notopithecines in Scarritt Collection from Colhué-Huapí	27	3.4–5.1	4.21 ± .08	.44 ± .06	10.4 ± 1.5
All notopithecines from the richest single stratum	19	3.4–5.1	4.30 ± .10	.44 ± .07	10.3 ± 1.7
Shallow-jawed specimens from single stratum (=*A. brachystephanus*)	8	4.1–4.8	4.45 ± .07	.21 ± .05	4.8 ± 1.2

based on a sample from a single stratum and all from south of Lago Colhué-Huapí.

The data of table 37 on a representative and typical dimension, the length of P_4, for various samples selected on a basis not directly related to that dimension show the improvement in agreement with the hypothesis of pertinence to a single species achieved by the method of selection here utilized.

The sample selected only by locality shows a wider range and greater variation than are generally consistent with a single species. The subsample selected by horizon shows no improvement in these respects. The second subsample further selected by jaw depth, however, is entirely consistent with pertinence to one species.

?**Antepithecus innexus** (Ameghino, 1904)

Plate 16, figure 8

Antepithecus innexus Ameghino, 1904a, vol. 56, p. 195.

Type: M.A.C.N. No. 10839, isolated upper molar.

Hypodigm: Type only.

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

Diagnosis: Upper molar structurally similar to that of *Antepithecus brachystephanus* but slightly longer and markedly more transverse, measuring 6.1 by 7.6 mm.

This may, after all, be an extreme variant of *N. brachystephanus*, but it is outside the probable range of variation for the latter as now known. It will probably prove to be a distinctive form, but the single tooth on which it is based is inadequate for one to determine either its generic or family position, and for the present it is a dubious form.

TRANSPITHECUS Ameghino, 1901

Transpithecus Ameghino, 1901, p. 356; 1906, p. 466. Schlosser, 1923, p. 607. Roth, 1927, pp. 195, 236. Scott, 1937a, p. 516.

Type: *Transpithecus obtentus*.

Distribution: Casamayoran, Patagonia.

Diagnosis: Upper teeth similar to those of *Notopithecus* but without anterior cingula, division of molars into two internal lobes more pronounced, posterior lobe markedly larger than anterior on M^{1-2} and about equal on M^3.

This genus is rather sharply set off from *Notopithecus* and *Antepithecus*, the only genera with which it might easily be con-

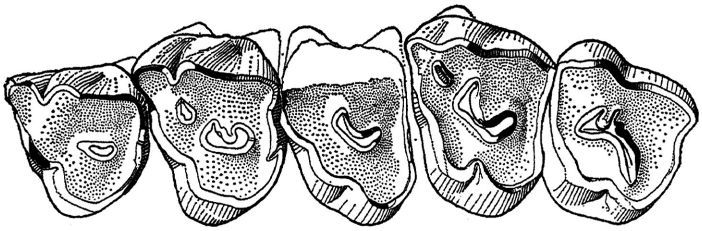

Fig. 27. *Transpithecus obtentus* Ameghino, A.M.N.H. No. 28953, left P^3–M^3, crown view. ×4.5.

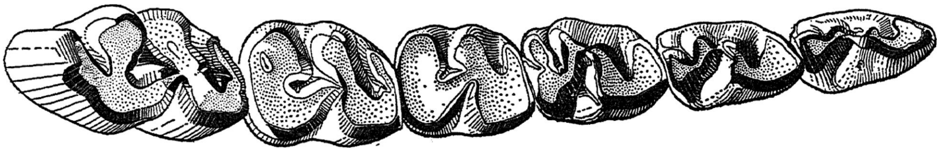

FIG. 28. *Transpithecus obtentus* Ameghino, C.N.H.M. No. P13439, P_2–M_3, drawn as if right, reversed from left, side. ×4.5.

fused in the Casamayoran, by the peculiar structure of the inner sides of the upper teeth.

P^{2-4} are much like those of *Notopithecus*, but there is a pronounced curving vertical groove on each, internal to the middle of the anterior (or anterointernal) face. A similar groove sometimes occurs above the anterior cingulum in *Notopithecus*, but apparently it is weak or nearly absent when that cingulum is poorly developed and in no case is it so strong as in *Transpithecus*. In the known specimens of the latter there is no anterior cingulum. In the molars of *Transpithecus* the groove between (nominal) protocone and hypocone is not median-internal as in *Notopithecus*, but decidedly anterointernal. The posterointernal lobe is thus markedly larger than the anterointernal and also projects farther internally on M^{1-2}. On M^3 the two are of about equal size, instead of the posterior lobe's being greatly reduced or virtually absent as in *Notopithecus*. In the type specimen the division between protocone and hypocone is also relatively deeper than in *N. adapinus*, as is, apparently, the connection between the main fossa and anteroexternal fossette, and there seems to be no tendency to form a median external fossette. The other known specimens are more worn, but suggest that these connections are variable, and without more material they cannot certainly be assigned taxonomic value. The external walls of premolars and molars and most other characters are nearly as in *Notopithecus*.

Two specimens show the root of the zygoma, and the jugal is not visible, so that it was probably reduced more or less as in *Notopithecus*, but such reduction cannot be considered certain.

The lower dentition of this genus may be represented by C.N.H.M. No. P13439, from near Punta Casamayor, a left lower jaw with P_2–M_3. This jaw is generically distinct from any others known to me, is notopithecine in general character, and occludes well (for a different individual) with A.M.N.H. No. 28953, an upper jaw referred to *Transpithecus obtentus*. In size and in structure there is a marked resemblance to *Antepithecus brachystephanus*. The dimensions of P_3–M_2 are all nearly within the demonstrated upper limit for *A. brachystephanus*, but M_3 is significantly longer, d/s for its length being +3.1. The crowns are somewhat higher. On P_{2-4} there is a cuspule posterior to the metaconid, nearly confluent with the latter but with a distinct apex, much smaller than the metaconid on P_2, about equal on P_3, and larger on P_4. The hypoconids and entoconids of P_{3-4} are also more distinct and higher than in *A. brachystephanus* and the (anterior) talonid valley is deeper and narrower. On the molars this valley is also deep and narrow, nearly or quite ending in a small closed fossa, and the entoconids are more swollen.

These characters, including size, are all specializations suggestive of *Acropithecus rigidus*,[1] but *Acropithecus* has still higher crowns, the posterior premolars are more advanced, more, and more normally, molariform, and the expansion and complication of the entoconid and cutting off of enamel lakes on the molars are also more advanced. Whether *Transpithecus* is truly notopithecine or whether it should be transferred to the Archaeopithecidae will depend on knowledge of the anterior teeth and the skull, especially the zygoma.

In the other directions, *Transpithecus* is

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[1] In Ameghino's arrangement of his collection there is evidently some confusion between *Acropithecus*, *Archaeopithecus*, *Transpithecus*, and perhaps also *Notopithecus*, a confusion made almost inevitable by such a transitional form as this. Doubtless such errors are still made in the sorting of poorly preserved specimens, but the better material shows that these genera are really quite distinct.

still closer to the Mustersan *Guilielmoscottia*, to which it is probably ancestral.

Transpithecus obtentus Ameghino, 1901

Plate 16, figure 11; text figures 27, 28

Transpithecus obtentus AMEGHINO, 1901, p. 356.

TYPE: M.A.C.N. No. 10833, fragment of left maxilla with M^{1-3} (lectotype); also four isolated teeth not associated and not all of this species.

HYPODIGM: Lectotype only, but some other specimens are doubtfully referred; see below.

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

DIAGNOSIS: Sole defined species of genus; measurements as given in table 38.

That some of the material referred by Ameghino to *Archaeopithecus rigidus* belongs to

TABLE 38

MEASUREMENTS OF TEETH OF *Transpithecus obtentus*

		M.A.C.N. No. 10833[a]	A.M.N.H. No. 28953	A.M.N.H. No. 28791	C.M.N.H. No. P13439[b]
P^2	L	—	—	4.5	—
	W	—	—	—	—
P^3	L	—	4.1	4.8	—
	W	—	4.5	4.4	—
P^4	L	—	4.4	4.8	
	W	—	5.5	5.6	—
M^1	L	*ca.* 4.8	—	—	—
	W	*ca.* 6	—	—	—
M^2	L	5	4.6	—	—
	W	6.2	5.6	—	—
M^3	L	4.8	4.7	—	—
	W	5.6	4.9	—	—
P_2	L	—	—	—	4.4
	W	—	—	—	2.3
P_3	L	—	—	—	4.4
	W	—	—	—	2.5
P_4	L	—	—	—	4.5
	W	—	—	—	3.2
M_1	L	—	—	—	4.3
	W	—	—	—	3.2
M_2	L	—	—	—	5.1
	W	—	—	—	3.7
M_3	L	—	—	—	7.2
	W	—	—	—	3.8

[a] Lectotype.
[b] Doubtfully referred.

this species is probable but too uncertain to help in an interpretation of the species. Otherwise, the only additional materials are A.M.N.H. No. 28953, a left upper jaw with P^3–M^3, and A.M.N.H. No. 28791, associated right and left P^{2-4}, both from Colhué-Huapí. These almost surely belong to this genus. As shown by the figures in table 38 the size is close enough to that of *T. obtentus* to make specific identity possible, but not to prove it.

M^{1-3} are so much more worn in A.M.N.H. No. 28953 than in the type that no useful comparison of apical pattern is possible. Pending discovery of more material, I consider all three specimens to represent the same species.

Measurements of C.N.H.M. No. P13439, the doubtfully referred lower jaw, are also given in table 38.

?Transpithecus sp.

As previously reported (Simpson, 1935a, p. 16), A.M.N.H. No. 28578, from the Riochican *Kibenikhoria* faunule of Canadon Hondo, a maxillary fragment with M^1 and part of M^2, resembles *Transpithecus* but is inadequate for secure generic or specific determination. Its only importance is that it does demonstrate the presence of a notopithecine-like form at this early horizon.

GUILIELMOSCOTTIA AMEGHINO, 1901

Guilielmoscottia AMEGHINO, 1901, p. 360; 1904b, p. 65; 1906, p. 469. SCHLOSSER, 1923, p. 607. ROTH, 1927, p. 235, pl. 13, fig. 9. SCOTT, 1937a, p. 516.

TYPE: *Guilielmoscottia plicifera.*

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: P^{1-3} longer than wide, P^4 and M^3 nearly equidimensional and M^{1-2} slightly wider than long. P^{2-4} with progressively larger inner lobe, divided by an anterointernal sulcus into two lobes, of which the more anterior is progressively larger but is constantly smaller and less internal than the posterior lobe. On M^{1-2} protocone and hypocone closely appressed but separated by a sharp sulcus, subequal but the hypocone projecting farther internally than the protocone and lapping forward around it a little. M^3 more triangular, with hypocone much smaller and less internal than the protocone. Parastyle and paracone folds definite on all cheek teeth, metacone region of outer wall convex but without definite fold.

This is a very distinctive genus. Among other known forms it most closely resembles the Casamayoran *Transpithecus* and could be derived from the latter by accentuating the peculiar character of the inner lobes of the molars, carrying this forward in attenuated form to the premolars, and having M^3 more triangular or "terminalized."

Ameghino put *Transpithecus* in the Notopithecidae and *Guilielmoscottia* in the Archaeopithecidae. The two genera seem to be closely related and should be placed in the same family in the absence of evidence to the contrary. This family could be either the Interatheriidae (Notopithecinae) or the Archaeopithecidae. A definite conclusion will depend on parts not now known in *Transpithecus* or *Guilielmoscottia*, but on the whole both of those genera seem to resemble *Notopithecus* more than they do *Archaeopithecus*, so they are tentatively placed in the Notopithecinae.

Guilielmoscottia plicifera Ameghino, 1901

Plate 16, figures 9, 10

Guilielmoscottia plicifera AMEGHINO, 1901, p. 360; 1904b, p. 65, figs. 60, 451. SIMPSON, 1936d, p. 83.

TYPE: M.A.C.N. No. 10898, part of left maxilla with P^1–M^3.

HYPODIGM: Type, and M.L.P. No. 12-2183, isolated upper molar.

HORIZON AND LOCALITY: Mustersan. Locality of type unknown. Museo de La Plata specimen from Roth's "Upper Cretaceous of Lago Musters," probably Cerro del Humo.

DIAGNOSIS: Only known species of the genus. Measurements given below.

The upper molar, M.L.P. No. 12-2280, figured by Roth (1927, pl. 13, fig. 9) as *Guilielmoscottia* resembles that of this genus more than any other known to me but is larger than any tooth of the type of *G. plicifera*, measuring 5.8 by 7.0 mm. It may be a large variant of *G. plicifera* or may be another species of this or an allied genus. M.L.P. No.

TABLE 39

MEASUREMENTS OF LOWER TEETH OF *Guilielmoscottia plicifera* OR *?Notopithecus amplidens*

	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
M.A.C.N. No. 10786	4.4	1.8	4.8	2.4	5.3	—	5.5	—	5.1	—	5.3	—	6.5	—
A.M.N.H. No. 29479	—	—	—	—	4.4	3.1	4.6	3.6	5.2	4.2	5.7	4.3	6.7	3.9

12-2183, measuring 5.4 by 6.0 mm., is more confidently placed in *G. plicifera.*

The lower teeth are probably present in collections but have not been surely distinguished from those of *?Notopithecus amplidens* (see below).

The measurements of the teeth of the type are: P^1, length, 5.3, width, 3.2; P^2, length, 5.6, width, 4.3; P^3, length, 5.8, width, 4.6; P^4, length, 5.5, width, 5.3; M^1, length, 5.0, width, 6.6; M^2, length, 5.3, width, 6.2; M^3, length, 5.4, width, 5.5.

Guilielmoscottia plicifera or ?Notopithecus amplidens

Plate 16, figure 12

Although, on the basis of the upper cheek teeth, these two species clearly belong to different genera, they are of about the same size. There are several known partial lower jaws of about the right size to occlude with either of these species, and in this general group it is difficult, at times to the point of impossibility, to distinguish lower cheek dentitions generically except by associations with upper teeth. These lower jaws surely belong to one or the other of these two species based on upper jaws or, since they vary considerably, may well include representatives of both species. I have not, however, been able to decide which is which, and a decision will be difficult until associated uppers and lowers are found or some pocket is discovered where one species is abundant and the other rare or lacking.

In view of their doubtful identifications, detailed descriptions of these lower dentitions would serve little purpose. They are of the rather stereotyped notopithecine type, but are in general larger and more robust than the characteristic Casamayoran notopithecines. The metaconids seem to be somewhat more expanded than in the Casamayoran forms, but the teeth are no more hypsodont and are little if any more progressive than in the earlier species. The principal specimens are: M.A.C.N. No. 10786, right lower jaw with P_1–M_3, no locality data; M.L.P. No. 12-2279, right lower jaw with P_3–M_3, "Upper Cretaceous of Lago Musters"; M.L.P. No. 12-2288, right lower jaw with P_4–M_3, "Upper Cretaceous of Lago Musters"; A.M.N.H. No. 29479, left lower jaw with P_3–M_3, Cerro del Humo.

Some measurements are given in table 39.

SUBORDER HEGETOTHERIA SIMPSON, 1945

The nominate and central family of this suborder, Hegetotheriidae, was placed by Ameghino (e.g., 1906) and almost everyone else until 1945 in the Typotheria, near the Mesotheriidae ("Typotheriidae"). However, more detailed studies showed that the skull, and especially the ear region (Patterson, 1936), and to less extent but still definitely the endocranium (Simpson, 1933i; Patterson, 1937), are distinct in the two groups. It is probable that the functional resemblance of the rodent-like habitus common to the two is in large part if not wholly convergent. In 1945 I therefore proposed a then new suborder Hegetotheria for the hegetotheres, strictly speaking, the pachyrukhines, and the peculiar genus *Munizia* Kraglievich. This arrangement was accepted by Lavocat (1958) and some others, but without special discussion. It rests largely on additional unpublished observations and interpretations by Patterson (MS, and personal communication) and on post-Mustersan materials. Redefinition and further descussion are therefore not appropriate in the present memoir.

The most important change here made is reference of the Archaeohyracidae to this suborder.

FAMILY **ARCHAEOHYRACIDAE** AMEGHINO, 1897

DEFINITION: Early notoungulates with accelerated hypsodonty (not reaching continuous growth). Dental series usually complete and closed, but P_1 absent and a corresponding diastema developing in the latest forms. Incisors becoming hypsodont and moderately scalpriform, but not markedly specialized. Canines present, incisiform. Upper cheek tooth series rather evenly graded, but P^4 not fully molariform, all premolars more triangular than the molars, which are trapezoidal. All upper cheek teeth strongly oblique in section, their inner sides deflected posteriorly. Crowns strongly bowed, convex externally and concave internally. Outer walls rather flat, but with distinguishable parastyle and paracone folds at least. Protocone and hypocone united nearly, but not quite, to apex. Upper molars as a whole suggestive of those of Rhynchippinae, but pattern in detail more like that in Oldfieldthomasiidae (e.g., *Ultrapithecus*): first crista constant, reaching and fusing with the very oblique protoloph; second crista present but variable; crochet strong, running to junction of crista and protoloph; metaloph short and straight, followed by cingulum, with a fossette between cingulum and metaloph. Lower premolars and molars of generalized notoungulate type but with expanded entoconids and at least one closed talonid fossette. Skull (known in *Archaeohyrax* only) of primitive, rather toxodont-like type, nasals not retracted, postorbital process on frontals but not on zygoma, zygoma relatively slender and straight, no zygomatic plate, bulla and epitympanic process small, crista meatus prominent, massive.

DISTRIBUTION: Latest Riochican to Deseadan, Patagonia.

These are rather rare animals in the three stages here under consideration, and they are at the same time perhaps the most interesting and surely among the most puzzling animals of their time. They are the most hypsodont and in some other respects also among the most specialized members of these faunas, although in the Deseadan they have been passed by so many other lines that they seem primitive. They thus present the evolutionary picture of being among the most rapidly evolving forms in the early faunas and yet among the more slowly evolving between Mustersan and Deseadan.

Ameghino consistently referred the archaeohyracids to the Hyracoidea, although he wavered as to further relationships with other ungulates. By almost all other students (e.g., Sinclair, 1909) the family has been included in the Notoungulata and usually in the Typotheria. I (Simpson, 1945) previously placed it in the Toxodonta on the basis of the numerous mainly primitive notoungulate characters that it shares with the Oldfieldthomasiidae and the Archaeopithecidae. That arrangement has been accepted (e.g., by Lavocat, 1958; Romer, 1945) but without further study. It is, nevertheless, probable that the resemblances on which I relied, mostly in the dentition, are indeed primitive and that the progressively specialized characters mark rapid and significant divergence from the basal toxodont (or toxodont-like) complex. The only well-known species is *Archaeohyrax patagonicus*, Deseadan in age, in which the whole skull and mandible are known. That species and its allies have now been studied in full detail by Patterson, who finds that the skull structure and some other features are unmistakably hegetothere-like. He therefore places the Archaeohyracidae as a whole in the Hegetotheria. The pre-Deseadan forms referred to this family offer no evidence for it at present. I therefore now follow Patterson (MS revision of the Deseadan Archaeohyracidae), but publication of the evidence must await completion of his work in progress. (Throughout the treatment of the Hegetotheria here I am much indebted to Patterson not only for the use of the manuscript mentioned but also for other notes and discussions.)

In addition to *Archaeohyrax*, Ameghino placed *Acoelohyrax*, *Eohyrax*, and *Pseudhyrax* in this family. *Acoelohyrax* is probably identical with *Plexotemnus* and certainly a close relative. Pertinence to the Archaeohyracidae is not quite impossible, but on the whole resemblance to the Isotemnidae seems somewhat closer. *Acoelohyrax* is therefore now referred to the latter family, where Ameghino did put *Plexotemnus*. *Acoelohyrax* has priority over *Plexotemnus* and is a valid generic name. *Eohyrax* and *Pseudhyrax* are also valid and are retained in the Archaeohyracidae. Roth's *Pseudopithecus*, *Degonia*, and *Rankelia* seem to be synonymous with one another and with Ameghino's *Pseudhyrax*, although the pertinent comparisons were not made by Roth or Ameghino. Both Ameghino and Roth referred some Mustersan specimens to the otherwise Deseadan genus *Archaeohyrax*, recognizing a real relationship but probably exaggerating its closeness. It now seems that the species so placed are generically distinct in spite of close affinity with *Archaeohyrax*, and a new generic name is here applied to them.

The scrappy materials available from pre-Deseadan deposits are here especially difficult to sort out in a biologically meaningful way. These isolated teeth or jaw fragments with a few teeth involve special problems because the aspect of the teeth even in a single individual changes radically with stages of wear—more so than in any other pre-Deseadan group. The materials in hand do not suffice for more than what is hoped to be a single step toward eventual clarification of the systematics of the group.

EOHYRAX Ameghino, 1901

Eohyrax Ameghino, 1901, p. 363; 1904b, p. 49; 1906, pp. 467, 469. Schlosser, 1923, p. 609. Scott, 1937a, p. 516.

Type: *Eohyrax rusticus.*

Distribution: Casamayoran, Patagonia. (And very doubtfully latest Riochican, Mustersan.)

Diagnosis: Generally less hypsodont than *Pseudhyrax*. Metacone fold weak on M^1 and nearly absent from M^{2-3}. P_1 present, one-rooted, P_1 and P_2 elongate, simple, without fossettes. P_3 also elongate, with transitory talonid fossette. Talonid fossettes of molars single, simple, and trigonid fossettes with little or no closure. Upper molars with little anteroexternal projection, three rather persistent external fossettes, labial groove slight.

Ameghino described the Casamayoran *E. rusticus* and the Mustersan *E. strangulatus* at the same time, but the earlier species was placed first, and its selection as a genotype simplifies the nomenclatural problem. Ameghino continued to place both Casamayoran and Mustersan species in the same genus, although he certainly was not given to the broad use of genera. He also did distinguish some Mustersan specimens as *Pseudhyrax.* Roth distinguished the Mustersan forms as *Degonia* (and two other, synonymous genera). The somewhat more advanced and typically Mustersan forms near *Eohyrax* are here recognized as generically distinct and referred to *Pseudhyrax.*

Ameghino named three Casamayoran and three Mustersan species. The three Casamayoran species are here retained, although at least two of them may be synonymous. One Mustersan species is now a *nomen vanum*, one is of doubtful age and generic reference, and one is referred to *Pseudhyrax.* The genus doubtfully occurs in the Riochican, but is Casamayoran as far as definitely established.

The morphology is described under the species.

Eohyrax rusticus Ameghino, 1901

Plate 17, figures 1, 4

Eohyrax rusticus Ameghino, 1901, p. 363; 1904b, p. 182, figs. 240, 289.

Type: M.A.C.N. No. 10775, five jaw fragments, apparently syntypes. Lectotype, left P_4–M_2. Other syntypes: right M_{1-2}, left M^{1-3}, left P^1–M^2, and left M^{1-3}, all worn and poorly preserved.

Hypodigm: The syntypes. M.A.C.N. No. 10777, eight dissociated fragments, mostly isolated teeth, was referred by Ameghino but may represent a small variant of *E. isotemnoides* (if that species is distinct). M.A.-C.N. No. 10778 was figured as this species (Ameghino, 1904b, figs. 240, 289) but is now referred to *E. isotemnoides.*

Horizon and Locality: Casamayoran, syntypes from west of the Río Chico. Doubtfully referred specimens from south of Colhué-Huapí.

Diagnosis: Smaller than *E. isotemnoides* and larger than *E. praerusticus.* Measurements as given in table 40.

The only parts known in this species and not in the generally better known *E. isotemnoides* are the upper premolars, but un-

TABLE 40

MEASUREMENTS OF LOWER TEETH OF *Eohyrax*

	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
E. rusticus														
M.A.C.N. No. 10775[a]	—	—	—	—	—	—	6.7	4.8	7.7	5.8	8.0	5.8	—	—
E. isotemnoides														
M.A.C.N. No. 10776[b]	—	—	—	—	—	—	8.3	5.8	8.0	5.9	8.6	6.3	—	5.4
A.M.N.H. No. 28665	6.0	3.0	7.6	3.7	7.3	4.5	8.2	5.6	8.3	*ca.* 6	9.0	6.4	13.5	6.2
A.M.N.H. No. 28629	5.8	2.5	7.2	3.2	7.2	4.2	7.8	5.2	7.4	5.6	9.0	6.0	12.4	5.5
E. praerusticus														
M.A.C.N. No. 10780[a]	—	—	—	—	—	—	—	—	7.0	4.4	—	—	—	—
?*E. platyodus*														
M.A.C.N. No. 10908[a]	—	—	—	—	—	—	—	—	5.5	4.1	—	—	—	—
?*E.* sp.														
A.M.N.H. No. 29388	—	—	—	—	6.7	*ca.* 6	7.3	*ca.* 6½	7.6	*ca.* 6½	9.5	7.0	15.7	6.8
A.M.N.H. No. 29387	—	—	—	—	—	—	—	—	*ca.* 9.1	*ca.* 6	—	—	—	—

[a] Lectotype.
[b] Type.

fortunately the one specimen that has these is deeply worn and heavily coated with a manganiferous concretion. It shows little except that these teeth have the obliquely triangular contour characteristic of the family. P^1 is distinctly wider than long.

Three doubtfully referred M_3's are 10.0–11.4 mm. in length and 4.7–4.9 mm. in width. Measurements of the lectotype are given in table 40.

Eohyrax isotemnoides Ameghino, 1904

Plate 17, figures 2, 3, 5, 7–11; plate 18

Eohyrax isotemnoides AMEGHINO, 1904a, vol. 56, p. 200.

TYPE: M.A.C.N. No. 10776, part of left lower jaw with P_4–M_3. Under the same number, and probably of the same species, but not part of the type, are an isolated right upper molar and an isolated right M_3.

HYPODIGM: Type and the two other specimens under the same number. Also M.A.C.N. No. 10778, an isolated upper M^1 or M^2 (figured by Ameghino, 1904b, figs. 240 and 289, as *E. rusticus*), an isolated right M_3, and a right lower jaw fragment with M_3 and the heel of M_2; A.M.N.H. No. 28665, right lower jaw with P_1–M_3; A.M.N.H. No. 28628, associated right lower jaw with P_1–M_3 (except heel of P_4) and left lower jaw fragment with P_4–M_2 and part of P_3; A.M.N.H. No. 28844, associated left M^{1-2}; M.H.N. No. 31, three upper molars, apparently not associated.

HORIZON AND LOCALITY: Casamayoran, known specimens from south of Colhué-Huapí except M.H.N. Tournouër Collection No. 31, from Casamayor.

DIAGNOSIS: Slightly larger than *E. rusticus*, perhaps a synonym of that species. Measurements are given below and in table 40.

Ameghino gave several supposed distinctions from *E. rusticus*, but, except for the size, these seem to me to be due to differences in wear or minor individual fluctuations. He gave the size as half again that of *rusticus*, but in fact the type molars are less than 10 per cent larger in any dimension and P_4 is 24 per cent longer and 21 per cent wider, as preserved—also influenced by differences in wear. The species may be synonymous, but there is a good chance that more abundant material will prove them to be distinct, especially as *E. rusticus* is from west of the Río Chico and *E. isotemnoides* mainly from south of Colhué-Huapí: localities that often prove to have closely related but different species when the material is sufficient to check this.

The three Tournouër specimens from Casamayor (M.H.N. No. 31) may represent animals somewhat larger than those from Colhué-Huapí, but the difference is not great and the available comparative materials are scanty so that specific separation is not clearly warranted. One of these teeth, M^1 or M^2, is almost completely unworn. Its hypsodonty index, 100 times ectoloph height divided by ectoloph length, is 120—a value rather subhypsodont than fully hypsodont. There is a small notch on the rim between protocone and hypocone, but these are united nearly to their apices so that the whole crown is surrounded by a nearly continuous wall, including protoloph, ectoloph, metaloph, and "entoloph." The internal space is nearly filled by the two cristae and the strong crochet, but there are deep, narrow fossae delimited by these elements and the surrounding lophs.

The first crista, strongly anterior, is joined to the protoloph at a high level. Earliest wear unites these and leaves a tiny antero-external fossette between first crista, protoloph, and ectoloph. This fossette is shallow and is soon obliterated by wear. The second crista projects straight inward from the middle of the ectoloph and is united with the plump crochet at a level deeper than the first crista-protoloph union. At a level apparently quite variable in different specimens, the united second crista and crochet also unite with the protoloph. There is a small external fossette on each side of the second crista, the anterior of the two fossettes apparently normally disappearing first with advanced wear. Between the crochet plus second crista and the "entoloph" is a very deep fossette, persisting after all other coronal detail is lost, obliquely elongate anteroposteriorly.

There is a strong posterior cingulum, from ectoloph to hypocone, and this has a narrow, transverse basin which, for a brief period when the crown is about half worn down, forms a small fossette.

The lower incisors and canine are unknown, but all lower premolars and molars are well represented although not in completely unworn condition. The whole lower cheek dentition is of the now familiar basic notoungulate type as in oldfieldthomasiids. The only striking differences from that of *Ultrapithecus*, for instance, are that the crowns are considerably higher and that the molar entoconids, firmly attached to the external crescent, are plump and expanded anteriorly. They here fuse basally with the metaconid, so that in an advanced wear stage a closed fossette is briefly present on the talonid immediately posterior to the trigonid. The internal fold of the trigonid and the posterior talonid between entoconid and hypoconulid are deep and narrow but do not form closed fossettes. On P_{3-4} there is also a tendency to form a transitory, nearly or quite closed anterior talonid fossette, but here the closure is not caused so much by the anterior expansion of the entoconid as by the stronger development of the posterior crest from the metaconid, a feature lacking on the molars. P_1 is one-rooted, and both P_1 and P_2 are simple, compressed, elongate teeth almost exactly like those in oldfieldthomasiids. The measurements of the principal specimens are given in table 40. Those of the upper teeth of A.M.-N.H. No. 28844 are: M^1, length, 8.2, width, 10.3; M^2, length, 9.0, width, 11.9. The lengths of M_1 and M_2 particularly are considerably affected by wear, and much variation must be expected for this reason.

Eohyrax praerusticus Ameghino, 1902

Plate 17, figure 6

Eohyrax praerusticus AMEGHINO, 1902a, p. 11; 1904b, p. 49, figs. 46, 410. CABRERA, 1935, p. 14.

TYPE: M.A.C.N. No. 10780, five isolated upper and lower molars. These were apparently all used by Ameghino as a basis for the species and are thus syntypes, and the upper premolar figured in 1904 was perhaps also a syntype (it was not found in the collection). As lectotype I take the most *Eohyrax*-like lower molar, perhaps a right M_1.

HYPODIGM: Lectotype only (none of the other syntypes).

HORIZON AND LOCALITY: Casamayoran, south of Colhué-Huapí.

DIAGNOSIS: Smaller than other species referred to *Eohyrax* except *?E. platyodus*. Lectotype ?M_1 measuring 7.0 by 4.4 mm.

The isolated specimens on which this species was based seem to me to represent at least two genera and three species. It is very doubtful whether any other specimen is conspecific with the lectotype, and the species as redefined rests on the very slender basis of this one tooth. This tooth resembles in appearance a miniature M_1 of *Eohyrax rusticus.* It is enough smaller to make specific separation possible, but the species remains very dubious as to validity and as to generic position.

?**Eohyrax platyodus** Ameghino, 1904

Eohyrax platyodus AMEGHINO, 1904a, vol. 56, p. 200.

TYPE: M.A.C.N. No. 10980, six isolated lower teeth. These were apparently syntypes, but it is improbable that all belong to one species. A left M_1 is taken as lectotype. A left M_3 is probably conspecific.

HYPODIGM: Lectotype and the left M_3 syntype (not other syntypes).

HORIZON AND LOCALITY: Mustersan, *fide* Ameghino. No locality data.

DIAGNOSIS: Agreeing with Casamayoran and differing from other Mustersan representatives of this phylum in being probably relatively low-crowned and having the trigonid groove or incipient fossette well open to the bottom. Comparable with *E. praerusticus* but still smaller, lectotype M_1 measuring 5.5 by 4.1 mm. and syntype M_3 7.8 by 4.0 mm.

This seems to be an archaeohyracid more primitive than *Eohyrax rusticus.* Its presence in the Mustersan would be anomalous. There may be some confusion as to stage. The species is too poorly known to warrant any definite conclusion as to its status or affinities.

?**Eohyrax** sp.

A.M.N.H. Nos. 29387 and 29388 are partial lower jaws probably referable to *Eohyrax* and possibly from the Casamayoran of Cerro Talquino. They are from an odd lot of materials, not collected by the Scarritt Expeditions, that accidentally became pied, in the typographic sense, scattered out of context and separated from their field data. For further comments, see the heading *?Acoelohyrax* spp. in the Isotemnidae on a page below, where other specimens of this lot are discussed.

A.M.N.H. No. 29388, a right lower jaw with P_3–M_3, is nearly senile, all teeth deeply worn, and the tooth lengths, especially the length of M_1, are consequently significantly shorter than they would be on a younger animal of the same size. A.M.N.H. No. 29387 is a right lower jaw with dm_{3-4} and M_{1-2}. M_1 is unworn, and M_2 is still deep in its crypt. The difference in age could account for the apparent differences from A.M.N.H. No. 29388, and both could be of the same species, larger than known *E. isotemnoides.* This could be an unnamed species, but especially in view of the uncertainty as to age and locality it seems best not to apply a new name at this time.

Eohyrax brachyodus Ameghino, 1902,
nomen vanum

Eohyrax brachyodus AMEGHINO, 1902a, p. 11.

TYPE: Probably an isolated M_1. Not found in the Ameghino Collection.

HYPODIGM: Published description only.

HORIZON AND LOCALITY: Mustersan, *fide* Ameghino. Locality unknown.

DIAGNOSIS: Indeterminate as to genus or species. M_1 said to measure 6 by 4 mm. and to be 5 mm. in height.

The type is lost and was not figured. Ameghino's description is distinctive only as regards size and the statements that the molars are low crowned and without a posterointernal sulcus or notch ("coche" in the original French). If these features were not due solely to wear, the specimen could hardly belong to this genus or, indeed, family. The status of the supposed species is altogether indeterminate, and the name has no present meaning.

There are two referred specimens in the Ameghino Collection, but one clearly is not *Eohyrax* and the other is of altogether doubtful reference.

?**Eohyrax** sp. indet.

Cabrera (1935, p. 14) recorded *Eohyrax praerusticus* from the uppermost Río Chico of the Bajo de la Palangana, on the basis of a maxilla with M^{1-3}, not described or figured. I have not seen the specimen, but, in spite of Cabrera's great authority, I question the specific identification. It was presumably made by comparison with Ameghino's syntype upper teeth, and these do not, in my opinion, belong to *E. praerusticus* and in part not to *Eohyrax*. Presumably the record indicates the presence of an archaeohyracid, but it should perhaps be considered undetermined.

PSEUDHYRAX AMEGHINO, 1901

Pseudhyrax AMEGHINO, 1901, p. 362; 1904b, p. 51; 1906, p. 469.

Pseudopithecus ROTH, 1902, p. 251; 1927, p. 194. SIMPSON, 1936d, p. 87 (as a synonym of *Degonia*).

Degonia ROTH, 1902, p. 251; 1927, p. 235. SIMPSON, 1936d, p. 86 (as a possible synonym of *Eohyrax*); 1964, p. 16 (as *Degonia* or *Eohyrax*).

Rankelia ROTH, 1902, p. 252. SIMPSON, 1936d, p. 87 (as a synonym of *Degonia*).

TYPE: *Pseudhyrax eutrachytheroides*.

TYPES OF SYNONYMS: *Pseudopithecus modestus*, *Degonia kollmanni*, *Rankelia elegans*.

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: Closely similar to *Eohyrax* and probably directly derived from and intergrading with that genus, but more progressive, more hypsodont, lower molars tending to develop a second closed talonid fossette and a closed trigonid fossette.

Roth (1902) named and described *Pseudopithecus modestus*, *Degonia kollmanni*, and *Rankelia elegans* (in that order) successively in the same publication. He recognized the fact that they are related but he distinguished them on characters now seen to depend on age (i.e., state of wear) and misidentification of teeth (e.g., taking deciduous for permanent molars). I (Simpson, 1936d) pointed out that the three species, and therefore of course the three genera, are probably synonymous. I then took *Degonia* as the valid name, but considered that genus doubtfully separable from *Eohyrax*. That doubt was based principally on belief, which still seems to me to be likely, that "*Eohyrax strangulatus*" is congeneric with the type species of *Degonia*. I expressed doubt as to whether "*E. strangulatus*" belongs in *Eohyrax* (a genus otherwise mainly or entirely Casamayoran). I now believe that the Mustersan species here designated, including "*E. strangulatus*," are generically distinct from Casamayoran *Eohyrax*.

When I studied the Ameghino Collection, no specimens referred to *Pseudhyrax eutrachytheroides* were found, and I tentatively considered the genus distinct from *Degonia* on the basis of Ameghino's somewhat unsatisfactory description (1901, p. 362) and figures (1904b, figs. 48, 176, 344). Bryan Patterson later found the type of *P. eutrachytheroides* in the relocated and resorted collections in the Museo Argentino de Ciencias Naturales and kindly provided me with comparative descriptions and measurements. From these it appears that *P. eutrachytheroides* is not distinguishable from *Degonia kollmanni*, over which it has priority. *Pseudhyrax* is thus synonymous with *Degonia* and has priority.[1]

It now seems reasonably certain that the type species of the four genera here placed in synonymy are also synonymous. "*Eohyrax*" *strangulatus* also belongs to *Pseudhyrax* but, with great doubt, may be a valid species. "*Trimerostephanos cuneolus*" Ameghino belongs to this genus and not to *Trimerostephanos*. It is synonymous with *Pseudhyrax strangulatus*, if that species is valid, and otherwise with *P. eutrachytheroides*. *Pseudhyrax* thus has one certain and one doubtful recognized species. As far as definitely known, it is confined to the Mustersan.

Pseudhyrax eutrachytheroides Ameghino, 1901

Plate 19; plate 20, figures 1, 2, 5–7

Pseudhyrax eutrachytheroides AMEGHINO, 1901, p. 362; 1904b, p. 51, figs. 48, 176, 344.

Pseudopithecus modestus ROTH, 1902, p. 251.

Degonia modesta: SIMPSON, 1936d, p. 66.

Degonia Kollmanni ROTH, 1902, p. 251. SIMPSON, 1936d, p. 66.

Rankelia elegans ROTH, 1902, p. 252. SIMPSON, 1936d, p. 66 (as synonym of *Degonia kollmanni*).

TYPE: Maxillary fragment with dm^{2-4}, M^1, in the Museo Argentino de Ciencias Naturales (information from Bryan Patterson; specimen not catalogued).

TYPES OF SYNONYMS: Of *Pseudopithecus modestus*, M.L.P. No. 12-2200, fragment of right maxilla with three teeth, probably dm^{2-4}. Of *Degonia kollmanni*, M.L.P. No. 12-2199, three upper molars, probably M^1, M^2, M^3, possibly of one individual. If these

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[1] This has the incidental and happy result of expunging *Degonia* from valid usage. The name is highly objectionable on non-zoological grounds (see Simpson, 1962).

should prove to be incorrectly associated, the probable M^3 may be taken as lectotype. Of *Rankelia elegans*, M.L.P. No. 12-2286, isolated right upper molar, deeply worn, perhaps M^2.

Hypodigm: Types, as above, and numerous other specimens, including M.L.P. No. 12-1740, right lower jaw with P_2–M_3; M.L.P. No. 12-1741, right lower jaw with M_{1-3}; M.L.P. No. 12-1590, left lower jaw with P_4–M_3, poorly preserved; M.L.P. No. 12-1594, left lower jaw with P_2–M_1; M.L.P. No. 12-1591, left lower jaw with P_2–M_1; M.L.P. No. 12-1592, right lower jaw with M_{1-3}; M.L.P. No. 12-1582, right lower jaw with P_4–M_3; A.M.N.H. No. 29406, right lower jaw with M_{1-3}; A.M.N.H. No. 29469, right lower jaw with M_{1-2}; A.M.N.H. No. 29410, right lower jaw with M_{1-3}; A.M.N.H. No. 28883, fragment of right maxilla with M^{1-3}.

Horizon and Locality: Mustersan. Museo de La Plata specimens from "upper Cretaceous of Lago Musters," probably equal to Mustersan of the Cerro del Humo. A.M.N.H. No. 29469 from Cerro del Humo, A.M.N.H. Nos. 29406, 29410, and 28883 from Cerro Blanco.

Diagnosis: Typical of the genus. Larger than *E. strangulatus*.

Roth's supposed species had not been compared with *P. eutrachytheroides* until such a comparison was made by Patterson, who found no reliable specific distinctions (personal communication).

Although the types of "*Degonia kollmanni*" are upper teeth, in practice Roth referred other upper teeth to "*Pseudopithecus modestus*" and lower teeth to "*D. kollmanni.*" The "*Pseudopithecus*" referred specimens are mainly premolars, so not directly comparable with the "*D. kollmanni*" type molars, but they are compatible with molars of that size and sort. The single tooth on which "*Rankelia elegans*" was based is rather clearly a more deeply worn "*D. kollmanni*" molar and hence also referable to *Pseudhyrax eutrachytheroides*.

The molar structure is best shown by A.M.N.H. No. 28883, which is from a different locality from the type but is so similar in size and character that reference to this species is justified. The unworn pattern is not known. The general aspect of the teeth is suggestive of *Eohyrax*, but the crowns are much higher. The internal groove is indicated in upper M^{1-3}, but is shallow and poorly defined. There are three small external fossettes, nearly in a straight line, and all three, including the one in the middle, are widely separated from the main, internal fossa, the anterior end of which often projects farther externally in comparable wear stages of *Eohyrax* (and usually does so in other forms of similar coronal pattern) and communicates with the median external fossette. This feature is, however, variable in *Eohyrax*.

The lower molar structure is also *Eohyrax*-like, but the crowns are higher, and the expansion of the entoconid, to less extent also that of the metaconid, is still more pronounced. In some cases, perhaps not all, there is an evanescent closed fossette in the middle of the trigonid, distinct from the internal groove, and another, even more rapidly obliterated by wear, on the talonid between the entoconid and hypoconulid (in addition to the anterior talonid fossette, already present in *Eohyrax*). On M_3 of A.M.N.H. No. 29410 and also M.A.C.N. No. 10774 there is a small papilla or pillar between the entoconid and hypoconulid and this may be a constant feature. Other available teeth are too worn to show it, if it was present.

Measurements are given in tables 41 and 42. It should be noted that measurements accessible on the wear surfaces of the teeth change radically with wear on these very high-crowned teeth, the different sides of which are not vertical or at right angles to the same plane. Rather large differences in recorded measurements thus do not necessarily indicate real differences in individual size.

Pseudhyrax strangulatus (Ameghino, 1901), new combination

Plate 21, figures 1–3

Eohyrax strangulatus Ameghino, 1901, p. 363.
Trimerostephanos cuneolus Ameghino, 1901, p. 416.

Type: M.A.C.N. No. 10774, part of right lower jaw with P_4–M_2. Three isolated teeth and some other fragments are included under the same number but are doubtfully conspecific and not part of the type.

TABLE 41

Upper Teeth of *Pseudhyrax eutrachytheroides* and Synonyms

	dm^2		dm^3		dm^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W	L	W	L	W
Pseudhyrax eutrachytheroides, type	9.3	6.9	9.2	8.5	9.8	9.1	10.2	—	—	—	—	—
Pseudopithecus modestus, type	—	—	8.6	7.8	9.9	9.4	—	—	—	—	—	—
Degonia kollmanni, type	—	—	—	—	—	—	*ca.* 9½	*ca.* 11	10.8	*ca.* 13½	9.7	—

Type of *Trimerostephanos cuneolus*: M.A.C.N. No. 10968, six associated lower cheek teeth and jaw fragments. Part of a right lower jaw with M_{1-3} is included under the same number but is not of this genus or species.

Hypodigm: The types (but not the other specimens in the same lots), also M.A.C.N. No. 10913, part of left lower jaw with M_{1-2} and part of P_4 (but not two other fragmentary specimens in the same lot); M.L.P. No. 12-2198, part of left lower jaw with P_4–M_3.

Horizon and Locality: Mustersan. No localities for the Museo Argentino de Ciencias Naturales specimens. Museo de La Plata specimen from Roth's "Lago Musters" locality, probably Cerro del Humo.

Diagnosis: Closely similar to *P. eutrachytheroides* and perhaps synonymous, but diagnosed as smaller and somewhat different in proportions; see measurements in table 43.

The synonymy of *Trimerostephanos cuneolus* depends on which of the specimens now preserved under M.A.C.N. No. 10968 is taken as the type. Ameghino did not figure this species, and his descriptions and measurements do not seem to apply precisely to either specimen. The lower jaw fragment with M_{1-3} does belong to *Trimerostephanos*, and on this account it might be assumed to be the type of this species, referred to that genus. Such reference, however, can hardly be correct. Ameghino mentioned premolars, not present in this specimen, and he gave the length of a series of six teeth, whereas this specimen has only three. He also said that the species is a little smaller than *T. sigma*, and this specimen is larger than the type of *T. sigma*. All these statements could apply to the other specimen, six associated teeth, under the same number, and I therefore take this to be the type, but it is certainly not *Trimerostephanos*. It seems to belong to *Pseudhyrax*, and I cannot distinguish it from *P. strangulatus*.

Although most lower jaws referred to *P. eutrachytheroides* are fairly distinctive from the type of *P. strangulatus*, the latter could be within the range of variation or could be the female of *P. eutrachytheroides*. A specimen inseparable from *P. strangulatus* is labeled as from the type locality of *P. eutrachytheroides*, which reduces the chances that the two are really distinct species.

TABLE 42

Lower Teeth of *Pseudhyrax eutrachytheroides*

	P_1		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. 12-1740	9½	4	9	6	9	6½	8½	7	10	7	15	6½
M.L.P. No. 12-1594	8½	4½	8½	5½	9	6	9½	6	—	—	—	—
A.M.N.H. No. 29410	—	—	—	—	—	—	—	6.9	9.3	7.0	13.9	6.8
A.M.N.H. No. 29406	—	—	—	—	—	—	8.2	6.3	9.7	6.4	—	—
A.M.N.H. No. 29458	—	—	6.9	5.6	7.2	5.8	7.6	6.5	9.2	6.5	15.0	6.7

TABLE 43

MEASUREMENTS OF TEETH OF *Pseudhyrax strangulatus*

	P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W
M.A.C.N. No. 10774	7.7	4.8	7.9	5.3	8.6	5.5	—	—
M.L.P. No. 12-2198	7.5	5.0	7.8	5.8	8.8	—	13.1	—

?**Pseudhyrax** sp., Mustersan

Plate 20, figures 3, 4

A.M.N.H. No. 29458, a fragment of right maxilla with P^{3-4} and part of M^1, is somewhat *Pseudhyrax*-like but probably does not belong to *P. eutrachtheroides* and cannot be placed in the genus with any strong probability. The poorly preserved and dubious possible upper premolars of *Pseudhyrax* offer insufficient basis for comparisons, and M^1 of this specimen lacks the outer half. It seems to be smaller and lower-crowned than M^1 of *Pseudhyrax*, with a more pronounced internal sulcus. These differences make it rather closely resemble M^1 referred to Casamayoran *Eohyrax*, but its age is definitely Mustersan. All three teeth also resemble those of *Tsamnichoria cabrerai* (tentatively placed in the Oldfieldthomasiidae), but the species is considerably larger, and the crowns are higher. P^{3-4} are triangular but have the inner angle flattened or truncated, with a slight sulcus, more distinct on P^4. There is a metacone fold, although it is weaker than paracone or parastyle folds. In this worn stage there seem to be a small first crista attached to the protoloph, a second crista barely indicated as a slight fold, a short crochet, and a still shorter antecrochet.

?**Eohyrax** or ?**Pseudhyrax** sp.

M.H.N. Tournouër Collection No. 25 consists of two associated lower teeth, probably M_{1-2}, collected by Tournouër at his Cerro Negro locality and recorded as Casamayoran in age. This locality is south of Colhué-Huapí, and Mustersan beds do occur there, so there is a possibility of mistake as to age, yet all the other specimens with this record in the Tournouër Collection are unmistakably Casamayoran. In spite of this supposed age, the specimen is a relatively robust and progressive archaeohyracid. It is quite as advanced as *Pseudhyrax eutrachytheroides* and would probably be referred to that species with little question were it known to be of Mustersan age. I see no good way of deciding, at present, whether the specimen is really Mustersan or whether there were among the variable archaeohyracids of Casamayoran time a few already as advanced as the usual Mustersan forms.

The presumed M_1 is 8.8 mm. in length and 5.7 in width. The following tooth measures 9.5 by 5.6.

BRYANPATTERSONIA, NEW GENUS[1]

TYPE: *Bryanpattersonia nesodontoides* (*Archaeohyrax nesodontoides* Ameghino, 1901).

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: An archaeohyracid approaching and probably ancestral to *Archaeohyrax* of the Deseadan, but less hypsodont, and dental characters generally more primitive. More hypsodont than contemporaneous *Pseudhyrax* but teeth rooted. Upper premolars and molars early losing labial fossettes by wear, internal fossette more persistent. Ectolophs nearly smooth, projecting anteroexternally to a parastylar point, paracone fold, slight metacone fold virtually absent. P^4 submolariform, more so than in *Pseudhyrax* but more triangular than the molars; molars trapezoidal, with variable but distinct lingual sulcus. On lower molars deep labial sulcus between protoconid and hypoconid, its lingual extremity forming a separate fossettid with advanced wear.

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[1] For Prof. Bryan Patterson, who has contributed so significantly to knowledge of South American mammals and birds. I have followed Ameghino in using both given name and surname for a genus of these faunas to memorialize a colleague.

So many genera of these faunas have already received not only one but frequently numerous names that basing a new generic name on specimens known to Ameghino and Roth may seem anomalous. Nevertheless, there is no serious doubt that Mustersan specimens referred by them to the Deseadan genus *Archaeohyrax* warrant generic distinction. They are, indeed, closely related to *Archaeohyrax* and in part, at least, probably ancestral to the latter, but they are quite as distinct as most groups granted generic status in conservative classification. For confirmation of this point I am indebted to Patterson, for whom I have named this genus, and to his as yet unpublished monograph on Deseadan archaeohyracids.

The two Mustersan species referred to *Archaeohyrax* by Ameghino are both now referred to this new genus. They are undoubtedly valid species and indeed may be so distinct as to warrant erection of two genera, but present evidence in my hands does not make such separation clearly necessary. "*Archaeohyrax*" *gracilis*, described by Roth as from what would now ordinarily be considered Deseadan, is almost certainly Mustersan and a probable synonym of Ameghino's "*Archaeohyrax*" *sulcidens*. "*Eomorphippus rutilatus*" is not an *Eomorphippus* but is congeneric, and with high probability also conspecific, with the type of *Bryanpattersonia*. Thus the genus as here understood includes two species, both Mustersan, sharply distinct and possibly meriting generic separation.

Bryanpattersonia nesodontoides
(Ameghino, 1901)

Plate 21, figures 4, 5

Archaeohyrax nesodontoides Ameghino, 1901, p. 361.

Eomorphippus rutilatus Ameghino, 1901, p. 373; 1904b, p. 310, fig. 413.

Type: M.A.C.N. No. 10905, 10 lower and seven upper teeth, all isolated, including representatives of P_4–M_2 and P^4–M^3. The lectotype is a right M_1, with the top of the crown measuring 12.2 by 6.3 mm.

Type of *Eomorphippus rutilatus:* M.A.C.N. No. 10915, a right upper premolar, two left and one right upper molars. These are probably not associated, and the premolar, although figured by Ameghino, is doubtfully referable to this species as represented by Ameghino's diagnosis and other referred specimens. The right upper molar is essentially the type, or is taken as lectotype.

Hypodigm: The types listed above and also, but doubtfully, M.A.C.N. No. 10911, 18 isolated upper and lower teeth, some but perhaps not all of this species; M.A.C.N. No. 10912, two isolated lower molars, referred by Ameghino to *Eohyrax brachyodus* but surely not that species; M.A.C.N. No. 10921, six upper teeth, mostly broken, probably of this species, five incisors of doubtful affinities, two lower molars also of doubtful affinities, all referred to *Eomorphippus rutilatus* by Ameghino.

Horizon and Locality: Mustersan, Patagonia (more exact localities unknown).

Diagnosis: The larger species now referred to the genus.

Except for size, the specific description given by Ameghino involves characters in common with Deseadan species of *Archaeohyrax* or simply due to wear. In fact it is difficult to distinguish isolated and worn teeth from some Deseadan specimens of *Archaeohyrax*, and Ameghino's conservative reference of them to that genus was proper in the state of knowledge at that time.

Five syntype teeth identified as M_1 range from 10.6 to 12.2 mm. in length and 6.3 to 7.0 mm. in width. Four syntype teeth identified as M_2 range from 11.7 to 13.0 mm. in length and 5.7 to 6.0 mm. in width. An isolated M_3 under M.A.C.N. No. 10911, perhaps rather small for this species, is 16.0 mm. long and 6.3 mm. wide at the base—both dimensions are considerably less than at points higher on the crown.

Bryanpattersonia sulcidens (Ameghino, 1902)

Text figures 29, 30

Archaeohyrax sulcidens Ameghino, 1902a, p. 10.

Archaeohyrax gracilis Roth, 1904, p. 154.

Type: M.A.C.N. No. 1096, many isolated teeth; essentially syntypes, but Ameghino's definition was based primarily on a left M_1 measuring 6.5 by 3.6 mm., and this is taken as lectotype.

Type of *A. gracilis:* Said by Roth to be

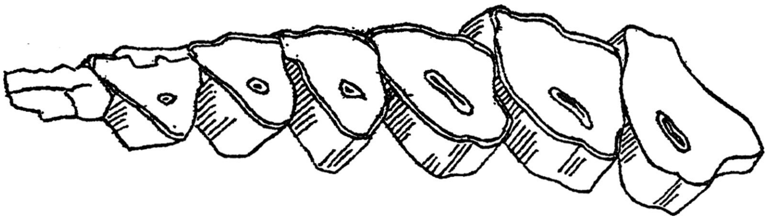

FIG. 29. *Bryanpattersonia sulcidens* (Ameghino), M.L.P. No. 12-1522, left P^{1-2} (broken) and P^3–M^3, crown view; type or lectotype of "*Archaeohyrax gracilis*." Drawn by M. T. Cabrera for B. Patterson. ×3.

upper and lower jaws of the same individual. These are probably M.L.P. No. 12-1522, left upper jaw with P^1–M^3, and M.L.P. No. 12-1518, left lower jaw with P_1–M_3. If the association is not correct, M.L.P. No. 12-1522 is to be taken as lectotype.

HYPODIGM: The types specified above.

HORIZON AND LOCALITY: Mustersan, Patagonia (more limited localities not known).

DIAGNOSIS: Significantly smaller than *A. nesodontoides*.

Ameghino's definition mentions other supposed distinctions of doubtful value.[1] Among Ameghino's specimens are four probable first lower molars 6.5 to 7.0 in length and 3.6 to 3.8 mm. in width; three probable second lower molars 7.2 to 7.5 mm. by 3.6 to 3.7 mm.; and one M_3 10.2 by 4.0 mm. at the base.

Roth's "*Archaeohyrax gracilis*" was published as from "Formación terciaria inferior," which by Roth's conceptions of Patagonian stratigraphy should be equivalent to our Deseadan. Patterson (personal communication) has shown, however, that specimens so labeled include some from Casamayoran and Mustersan as well as Deseadan. (See remarks elsewhere under *Anisolambda* and *Eomorphippus*.) I have not seen Roth's specimens, but Patterson studied them and concluded that they belong to Ameghino's species *sulcidens*. Largely on the basis of those specimens, Patterson also concluded that the species belong to an unnamed genus allied to but distinct from the one I now call *Bryanpattersonia*. I do not doubt his judgment, but I cannot, from my own knowledge, provide an adequate diagnosis, and I therefore keep the species in *Bryanpattersonia* pending completion of Patterson's studies of this whole group.

?**Bryanpattersonia** sp.

Plate 21, figures 6–9

In 1934 in the Rinconada de Lopez, on the west flank of the Meseta Canquel, Justino Hernández, working with the Scarritt Expedition, found a small, isolated exposure on the surface of which he collected remains now referred to *Bryanpattersonia* and to *Eudolops*, a typically Casamayoran polydolopid marsupial. Hernández was working alone at the time and was not a trained stratigrapher, but he had considerable collecting experience and was aware of the importance of not mixing fossils of different levels or localities. I later examined the exposure, but found no more material. It seemed improbable but not absolutely impossible that specimens from

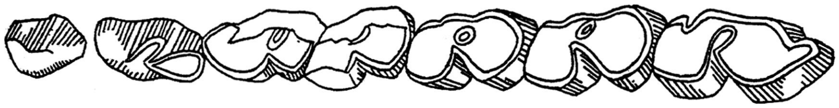

FIG. 30. *Bryanpattersonia sulcidens* (Ameghino), M.L.P. No. 12-1518, left P_1–M_3, crown view; probably same individual as M.L.P. No. 12-1522 (fig. 29), and in that case part of type of "*Archaeohyrax gracilis*." Drawn by M. T. Cabrera for B. Patterson. ×3.

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[1] There are two important misprints in Ameghino's definition. In line 5, for "externe" read "interne," and in line 7 for "transverse" read "antero-postérieur."

different levels had become mixed on the surface there. It is highly unlikely that an archaeohyracid as advanced as *Bryanpattersonia* and probably belonging to that genus, otherwise definitely Mustersan, should occur in the Casamayoran. It is also highly unlikely that *Eudolops*, typically Casamayoran and not otherwise known in any other stage, should occur in the Mustersan.

In spite of the apparent anomaly, I think that these specimens of *?Bryanpattersonia* are Mustersan. They are of morphological interest and warrant some further mention and figuring.

A.M.N.H. No. 28944 includes a right lower M_3, right lower M_2 (or just possibly M_1), and right P_4 (or just possibly P_3) in a fragment of jaw. These teeth may be but probably are not from one individual. They closely resemble those of *B. nesodontoides* in morphology but may be significantly smaller, the probable P_4 measuring 10.6 by 6.2 mm. and the probable M_2, 10.0 by 6.3. Such a size is probably significantly larger than that of *B. sulcidens*.

A.M.N.H. No. 28955 is associated P^2–M^3. These, too, closely resemble teeth in the Ameghino Collection now referred to *B. nesodontoides*, but comparison is inadequate and specific identity is not established. The morphology, strikingly unlike that of any other known pre-Deseadan genus, is clearly shown in plate 21, figures 8 and 9. The measurements of these teeth are: P^2, length, 10.5, width, *ca.* 9; P^3, length, 10.0, width, —; P^4, length, 10.4, width, *ca.* 10½; M^1, length 10.9, width, *ca.* 11; M^2, length, 13.0, width, *ca.* 10; M^3, length, 12.8 width, *ca.* 8. These measurements were taken on the wear surfaces; both dimensions would increase considerably with further wear.

A.M.N.H. No. 28943 includes an isolated upper molar, probably M^3, which is almost completely unworn and reveals the full coronal pattern, not hitherto known in the family. The first crista is very short but distinct and already fully united to the protoloph in spite of the slight wear. A second crista is barely indicated. The crochet is long and large, slightly papillate, on its outer side, and touches the protoloph but does not merge with it at this level. No antecrochet is visible. There is a large notch in the "entoloph," between protocone and hypocone, but this would be obliterated and the "entoloph" would become continuous with moderate wear. Roots had not yet formed, and the coronal fossettes can be seen as papillae or tubes inside the pulp cavity: two round external papillae, the anteroexternal and posteroexternal fossettes, ending at about the same level near the middle of the height of the tooth, and the main internal fossette, elongate, flattened, and simple except for an anteroexternal fold, extending to the base of the crown as far as yet formed and there still open.

?HEGETOTHERIA INCERTAE SEDIS

EOHEGETOTHERIUM AMEGHINO, 1901

Eohegetotherium AMEGHINO, 1901, p. 370; 1906, p. 469. SCHLOSSER, 1923, p. 608.

TYPE: *Eohegetotherium priscum.*

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: Based on a hypsodont upper molar with wear surface longer than wide; labial and lingual surfaces almost parallel; strong paracone and weak metacone folds; hypocone and protocone confluent high on the crown; oblique lingual fossa present; labial fossettes early obliterated by wear; lingual face slightly wavy but without groove; enamel thin on or absent from posterior face.

The isolated tooth on which, essentially, this genus was based is not exactly like any other known to me. It perhaps most nearly resembles *Pseudhyrax*, but still is so distinctive that it is not likely to be a variant, wear stage, or even a distinctive species of that genus. Reference to the Archaeohyracidae is more probable than to the Hegetotheriidae, and recording the presence of the latter family in the Mustersan is not warranted on this basis.

Eohegetotherium priscum Ameghino, 1901

Text figure 31

Eohegetotherium priscum AMEGHINO, 1901, p. 370.

TYPE: Not found at the time of my original study of the Ameghino Collection, but in 1955 in the new quarters I came across a lot of three jaw fragments and 21 isolated cheek

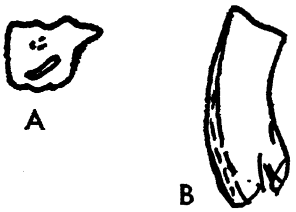

Fig. 31. *Eohegetotherium priscum* Ameghino, lectotype, in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," isolated right upper molar. A. Crown view. B. Posterior (proximal) view (crown up). Rough sketches by the author. ×2.

teeth with a loose label in Ameghino's hand indicating the type of this species. Although most of these seem to be archaeohyracids, and several perhaps are of this species, the identification is doubtful, and no two are probably from the same individual. Ameghino's description mentioned only a supposed M^1, which has not previously been figured. I take as lectotype an upper molar, freer of manganese stains than most of the specimens, and most nearly agreeing with Ameghino's description and measurements.

Hypodigm: The lectotype only. Some of the other ostensible syntypes may belong here but are not now included in the hypodigm.

Horizon and Locality: Mustersan, Patagonia; more exact locality not known.

Diagnosis: Only species referred to the genus. Wear surface of lectotype measuring 6.5 by 5.6 mm.

EOPACHYRUCOS Ameghino, 1901

Eopachyrucos Ameghino, 1901, p. 370. Schlosser, 1923, p. 608.

Eupachyrucos [*lapsus*]: Ameghino, 1906, p. 469.

Type: *Eopachyrucos pliciformis.*

Distribution: Mustersan, Patagonia.

Diagnosis: Upper molar hypsodont; tapering rapidly from roots to apex; wear surface near apex longer than wide; labial surface of ectoloph with strong, subequal paracone and metacone ridges; two circular, equal labial fossettes retained to late wear stage; deep bifid groove between protocone and hypocone retained (open and not as fossa) to late wear stage.

The one isolated tooth on which this genus is based somewhat resembles a tooth of *Pseudhyrax* and also that of *Eohegetotherium*, but in addition to details it differs sharply from teeth of both of those genera and from those of all definitely classified archaeohyracids in the persistent separation of protocone and hypocone and consequent presence and persistence of a deep, slightly bifid, labial sulcus. A persistent sulcus does occur in some hegetotheriids, e.g., *Prosotherium*, but the resemblance is not otherwise close. There is also some, but again not close, resemblance to some typotheres, such as *Argyrohyrax*, and probably still more distantly to some notohippids. The tooth may belong to the Hegetotheria, but definite reference to the suborder, *a fortiori* to the family Hegetotheriidae, is not warranted.

Eopachyrucos pliciformis Ameghino, 1901

Eopachyrucos pliciformis Ameghino, 1901, p. 370.

Type: M.A.C.N. No. A55-12, an isolated left upper molar. (Not found during my revision of the Ameghino Collection, but later located by Cattoi and made available to me; the specimen was not figured and Ameghino's description is not absolutely definitive, but one of two labels with the specimen has this name in Ameghino's hand, and it almost certainly is the type.)

Hypodigm: The type only.

Horizon and Locality: Mustersan, Patagonia; more precise locality not known.

Diagnosis: Sole species referred to the genus. Dimensions of wear surface of an upper molar 3.9 by 2.6 mm.

Ameghino referred this very dubious form to the Hegetotheriidae in his two published mentions of it (1901 and 1906, as cited under the genus), but it is interesting that he also found in it some equivocal resemblances to the group we now call Interatheriinae, true typotheres and not hegetotheres. A second label with the type, also in Ameghino's hand, is, "Eoprotypotherium souche protypotheri astraponoth." That indicates that he at some time considered it ancestral to *Protypotherium.*[1]

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[1] The indication "astraponoth." was a usual way for Ameghino to label specimens from his *Astraponotus* beds, Mustersan in present terminology.

PSEUDOPACHYRUCOS AMEGHINO, 1901

Pseudopachyrucos AMEGHINO, 1901, p. 371; 1906, p. 469. SCHLOSSER, 1923, p. 608.

TYPE: *Pseudopachyrucos foliiformis.*

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: Based on wholly dubious teeth, near a flattened and pointed ellipse in section and highly elongate (hypsodont), untapering and without known roots.

The tiny teeth on which Ameghino based this genus are not like anything else known to me, and I do not have any idea as to their affinities. The reason for considering them at this point is to indicate that there is no adequate reason for placing them in the Hegetotheriidae and that, again, the supposed presence of that family in pre-Deseadan faunas is unconfirmed. The generic and specific names are *nomina vana* at present, although it is probable that they can be defined and classified if homologous teeth are found in jaws with tooth series.

Pseudopachyrucos foliiformis AMEGHINO, 1901

Pseudopachyrucos foliiformis AMEGHINO, 1901, p. 371.

TYPE: M.A.C.N. No. A55-11, three isolated, broken teeth. Not found during my first study of the Ameghino Collection, but located in 1955 by Cattoi. Ameghino's label does not specify "tipo," but has the generic and specific names, and no other specimens in his collection could possibly be the basis for those names. Although none of the specimens agrees closely with Ameghino's published measurements (2.5 by 1 mm. in cross section and 9 in height), I believe that these must be his syntypes. As lectotype I select the specimen nearest to Ameghino's measurements, which, when I studied it, measured 2.7 by 1.4 mm. in section and 6.0 in height. (It is likely that approximately 3 mm. of the height had broken off and been lost.)

HYPODIGM: The three syntypes.

HORIZON AND LOCALITY: Mustersan, Patagonia; more precise locality not known.

DIAGNOSIS: Sole species now referred to the genus. Measurements of lectotype as given above.

Besides the name, Ameghino's label says, "souche Hegetot Astraponot," i.e., an ancestor of *Hegetotherium* from the Mustersan.

SUBORDER **TOXODONTA** SCOTT, 1904

DEFINITION: Notoungulates of moderate to elephantine size and generally of herbivorous ungulate habitus. Dentition mostly complete and in continuous series, but lateral incisors and canines lost and diastemata developed in some late forms. Canines caniniform only in most primitive members, later reduced and often incisiform. One or another pair of incisors tending to become enlarged. Cheek teeth brachydont in most members, becoming hypsodont in toxodontids and notohippids. Basic molar pattern as in Isotemnidae (below), not much modified in later groups except as affected by increasing lophodonty in the hypsodont forms and by some secondary simplification in persistently brachydont forms. Skull and jaws generally conservative, without development of markedly rodent-like habitus as in Typotheria and Hegetotheria. "Hypotympanic sinus as large as or larger than the tympanic cavity and ventral to it, these cavities forming with the epitympanic sinus a dorso-ventral row of three interconnecting chambers; a small horizontal septum between the tympanic cavity and the hypotympanic sinus; a projecting laterally compressed styliform process usually present; internal carotid traversed the bulla" (Patterson, 1936, for the Toxodonta of some previous authors plus *Homalodotherium*; generally valid for the suborder Toxodonta as here understood). Well-developed crista meatus. Feet generally hoofed, polydactyl, almost symmetrically mesaxonic, except in Homalodotheriidae, which developed aberrant asymmetry and pseudo-claws.

DISTRIBUTION: Paleocene to Pleistocene, South America; Pleistocene, Central America.

As explained above, I now tentatively exclude the Oldfieldthomasiidae and Archeopithecidae from this suborder, even though the most primitive toxodonts (in the present sense) are difficult to distinguish from those families. As in my previous classification (Simpson, 1945) the suborder Entelonychia of most earlier students is merged with the

Toxodonta, for reasons given in part in the discussion of the Isotemnidae. The families now referred to the suborder are Isotemnidae, Homalodotheriidae, Leontiniidae, Notohippidae (including Rhynchippinae), and Toxodontidae. In the Riochican and Casamayoran the known Toxodonta are all isotemnids. Isotemnids are still common in the Mustersan, where rarer notohippids first appear. The other three families are unknown in the ages here under consideration.

Family **ISOTEMNIDAE** Ameghino, 1897

Definition: Primitive notoungulates, prototypal to the toxodonts (in the sense of this classification). Dentition complete and closed except, in some instances, moderate spacing around canines. Incisors spatulate or lobed, never gliriform, increasing in size from first to third, I^3 and P_1 in some cases tending to be caniniform but smaller than canine. Canines usually enlarged. Cheek teeth brachydont, usually lower than in Homalodotheriidae. Upper premolars triangular, with no division of inner lobe. M^{1-2} bilobed internally, but protocone and hypocone more or less connate at bases, at least. Basic molar pattern with ectoloph fully united with oblique protoloph and shorter, more transverse metaloph, these two early united internally by wear, a small first crista with free internal end, and a second crista fully united with a crochet so as to form a single oblique crest from metaloph to ectoloph, cutting off a posteroexternal fossette. This basic pattern, always visible, is commonly complicated by additional crests and folds within the coronal area bounded by the major lophs. P_{2-4} progressively more molariform, but talonids short and entoconids rudimentary or atypical in comparison with molars. Lower molars with short trigonids, vestigial basin, strong transverse lophid with two poorly distinguished terminal cusps and an additional cuspule on the anterior side of the internal end of the lophid, varying from a barely distinguishable accessory cuspule or duplication on the metaconid to a relatively strong and fully distinct cusp. Talonids simple, with external crescent and a lower, single, transverse entoconid crest.

Skull of almost completely generalized notoungulate-toxodont type. Nasals not retracted, and nares terminal. Zygoma slender, moderately sigmoid. Basicranium without marked shortening, deepening, or flexure. Epitympanic sinus about equal to tympanic cavity and both small in comparison with those of most later notoungulates. Porus acusticus circular and low on skull. Meatus strongly but simply crested.

Limb segments retaining primitive, condylarth-like proportions and structure. Feet pentadactyl, no digital reduction, terminating in simple hoofs.

(Skulls and feet are known in only a few genera, as noted below, and some exceptions to the characters given for them may conceivably, but improbably, be found.)

Distribution: Riochican to Deseadan, Patagonia.

This family is defined mostly by primitive characters, a procedure which is not wholly satisfactory but to which there seems to be no good alternative in this case. All the Riochican and Casamayoran notoungulates are very primitive, and all are basically quite similar. In many respects the isotemnids may be considered the most primitive or, at least, the most generalized of all. The henricosborniids seem to be on a still lower level within the Notoungulata, but the skull and skeleton are unknown in them, and even the dentition is not fully known. The notostylopids seem also to represent a lower level of differentiation (for instance, they lack the cristae and other coronal complications present in isotemnids and universal in later notoungulates), but on this level they have acquired some divergent characters, notably gliriform incisors. (Gliriform incisors repeatedly and independently arose in different lines of notoungulates.) The Oldfieldthomasiidae and other groups here tentatively placed in the Typotheria are on about the same level as the isotemnids and almost if not quite as generalized on that level. Indeed, it is difficult to distinguish some isotemnids and some oldfieldthomasiids, and it is quite possible that some of the less well-known genera are wrongly distributed in these two families. Yet among the apparently still closer allies of the oldfieldthomasiids, as appears on other pages of this memoir, are some that show incipient and more or less typothere-like specializations. Almost the only isotemnid character that might be considered a specialization (one that assists greatly in the identification of isolated specimens as to family) is the accessory cuspule on the molar trigonids.

The combination in the isotemnids of the basic characters common to all higher notoungulates (that is, all above the notioprogonian level), the fact that these characters are here in almost completely generalized, diagrammatic form, and the absence of any of the definite further specializations that characterize each of the diverse lines in later formations—these features do make the Isotemnidae a distinctive and usually readily recognizable group. They also suggest that, with the usual possible exception of some genera based on very fragmentary materials, the family is a natural phylogenetic unit. It is probably unified by a closely antecedent monophyletic ancestry, although it is potentially highly polyphyletic as to its further evolution.

It was already recognized by Ameghino and has been stressed by most of his successors that forms here called isotemnids particularly resemble *Homalodotherium* and its allies among mid-Tertiary groups. Ameghino placed *Thomashuxleya* and *Anisotemnus* in the Homalodotheriidae ("Homalotheriidae"), and until recently most other students have placed the Isotemnidae and Homalodotheriidae together in a suborder Entelonychia. The sequence *Thomashuxleya–Periphragnis–Asmodeus–Homalodotherium* is a fairly good structural line and could conceivably represent a direct ancestral and descendant phylum, although it has lately been found that the gap between *Periphragnis* and *Asmodeus* is much more profound than had been guessed from the dentitions alone. In any case, the relationship is probably real, and there is no difficulty in considering the Homalodotheriidae as descendants of the Isotemnidae.

I now believe, however, that it would be a mistake to merge the families Isotemnidae and Homalodotheriidae on this basis or even to consider this relationship as exclusive, in the sense that the two families together might be considered a taxonomic unit of some sort as they were under the name Entelonychia. The homalodotheres have the most primitive skulls and dentitions of any Santacruzian or later notoungulates. It is in these primitive characters and in these only that the homalodotheres resemble the isotemnids. Even in these parts the isotemnids lack any homalodothere characters that would not also occur in the ancestry of toxodontids, leontiniids, or notohippids. On the other hand, the homalodotheres had the most aberrant and specialized limbs and feet among notoungulates, and the isotemnids, as is now known for *Thomashuxleya* particularly, completely lack these homalodothere characters. In the limbs and feet, the isotemnids are much more like toxodontids than like homalodotheres, which, again, does not make them toxodontids because the resemblances to toxodontids in the skeleton, like those to homalodotheres in the skull and dentition, are all plainly primitive.

The isotemnids are of appropriate structure to be ancestral to any or all of the families Homalodotheriidae, Leontiniidae, Notohippidae, or Toxodontidae, i.e., of the Toxodonta as a whole, as amended particularly following Patterson's demonstration of the essential unity of basic skull structure in these four families (e.g., Patterson, 1936). Clearly transitional forms between the Isotemnidae and any of these families are unknown. The four more specialized families all appear suddenly (Notohippidae in the Mustersan and the others in the Deseadan), and an actual ancestral relationship of the Isotemnidae to any one or more of them cannot be demonstrated. In terms of over-all structure and probable genetic change involved, the gap between the Isotemnidae and Leontiniidae, Notohippidae, and Toxodontidae is probably no greater than between the Isotemnidae and Homalodotheriidae, or, if the latter transition is less radical, it is so only in the degree that homalodotheres (except for their strange limbs) were less progressive than other Toxodonta.

In all three of the stages here studied, isotemnids are among the most abundant and characteristic animals. They seldom form the majority of individuals found at any one place, but they are virtually always present in any Riochican, Casamayoran, or Mustersan faunule and usually in some variety. They are also conspicuous and most likely to turn up in casual or hurried collecting, because during these times they averaged much larger than any other notoungulates and included the largest animals of these stages except for the much rarer pyrotheres and astrapotheres.

Ameghino's final classification of 1906 placed most of the genera now considered Isotemnidae in the Ancylopoda. With the dualism now familiar in his work, he thus united an essentially natural South American group but incorrectly related it to a holarctic group, the chalicotheres, on the basis of a merely convergent adaptive resemblance (on the part of *Homalodotherium*). The families of "Ancylopoda" recognized in the Casamayoran and Musters were the Isotemnidae, here retained essentially as he used it, "Homalotheriidae," here united with Isotemnidae as far as these faunas are concerned because the genera here have no special homalodothere characters, and the Leontiniidae, now believed not to appear before the Deseadan. Seventeen Casamayoran genera were placed in the Isotemnidae and another, *Parastylops*, would probably have been placed here but was accidentally omitted. Of these, I have more or less tentatively referred *Maxschlosseria* and *Paginula* to the Oldfieldthomasiidae, and *Edvardotrouessartia*, more assuredly, to the Notostylopidae. Another, *Anisorhizus* (misspelled "*Anissorhizus*" in Ameghino, 1906) is *incertae sedis* and apparently not isotemnid. The other 13 Casamayoran isotemnid genera are retained in the Isotemnidae, mostly as synonyms. In the Mustersan, Ameghino recorded only *Trimerostephanos* as isotemnid, which is apparently correct as to family identification of the specimens, although I do not think they belong to this Deseadan genus.

Thomashuxleya and *Anisotemnus* in the Casamayoran and *Asmodeus* and *Proasmodeus* in the Mustersan were referred to the "Homalotheriidae" by Ameghino. The first two are evidently valid and are here considered isotemnids. The specimens on which the Mustersan references were based are also isotemnids, but reference to the Deseadan genus *Asmodeus* was probably incorrect, and *Proasmodeus*, although a distinctive genus in Ameghino's system, is the same as Roth's *Periphragnis*, which was named earlier.

In addition to those genera, *Anchistrum*, referred by Ameghino to the "Acoelodidae," and *Coelostylops*, referred to the Notostylopidae, are now considered isotemnids, both as synonyms of *Pleurostylodon*. *Acoelohyrax*, considered an archaeohyracid by Ameghino, is here put in the Isotemnidae. *Carolodarwinia*, referred to the Leontiniidae by Ameghino, may be an isotemnid, but reference to the Isotemnidae is dubious, and *Carolodarwinia* is here relegated to Notoungulata *incertae sedis*.

Roth named 12 genera from the Mustersan and (*Lelfunia* only) Riochican that are now considered probable isotemnids. Roth gave no formal classification of these, but from various comparisons it is clear that he recognized the mutual resemblance among most of them and also the resemblance of some of them to *Homalodotherium*.

In all, there are 29 Riochican, Casamayoran, and Mustersan genera of Roth and Ameghino now considered probably isotemnid. Definite isotemnids occur in the Riochican, but the scanty materials in hand do not distinguish them generically from Casamayoran isotemnids. In the Casamayoran, only five genera now seem to be sufficiently established: *Pleurostylodon*, *Anisotemnus*, *Plexotemnus*, *Isotemnus*, and *Thomashuxleya*. Twelve of Ameghino's and one of Roth's generic names are tentatively considered as synonyms of one or another of these five. Only two Mustersan genera are well established: *Periphragnis* and *Rhyphodon*. One of Ameghino's and eight of Roth's generic names are probable synonyms of one or the other of these two. Two of Ameghino's genera, *Carolodarwinia* and *Anagonia*, and one of Roth's, *Colhuapia*, although conceivably related to forms now placed in the Isotemnidae, are of such highly dubious affinities that they are placed under Notoungulata *incertae sedis*.

Although it is the type of the family and is not extremely rare, *Isotemnus* itself is a poorly known genus. *Pleurostylodon* is the most common genus of this family in collections and is relatively well known. The basic description of skull and dentition are devoted to this genus. Fair skulls are also known in *Thomashuxleya*, *Periphragnis*, and *Rhyphodon*, most of the skeleton is known in *Thom-*

ashuxleya, and the forefoot is known in *Periphragnis*.

Although highly variable in detail, the dentitions in this family are quite stereotyped in general pattern. It is consequently difficult to give really clear-cut diagnoses based on the dentitions, and still more so on the fragments and single teeth that are the usual types. More names have been based on such scraps of isotemnids than in any other family of these three ages, and it is certain that the great majority (three-fourths or more) of those names are synonyms. It cannot be hoped that the present attempt at revision is fully successful, but perhaps it is a step toward eventual clarification.

The following is an alphabetical list of the Casamayoran and Mustersan Ameghino and Roth genera now referred to the Isotemnidae, and the status given them here. (No new genera clearly referable to this family have been described since 1904, and none is here added.)

Amphitemnus Ameghino, 1904 = *Isotemnus*
Anchistrum Ameghino, 1901 = *Pleurostylodon*
Anisotemnus Ameghino, 1902, valid
Calodontotherium Roth, 1904 = *Periphragnis*
Coelostylops Ameghino, 1901 = *Pleurostylodon*
Colhuelia Roth, 1902 = *Periphragnis*
Dialophus Ameghino, 1901 = *Pleurostylodon*
Dimerostephanos Ameghino, 1902 = *Isotemnus*
Eochalicotherium Ameghino, 1901 = *Isotemnus*
Eurystephanodon Roth, 1904 = *Periphragnis*
Isotemnus Ameghino, 1897, valid
Lafkenia Roth, 1902 = *Rhyphodon*
Lelfunia Roth, 1902 = *Isotemnus*
Lemudeus Roth, 1903 = *Periphragnis*
Parastylops Ameghino, 1897 = *Pleurostylodon*
Paratemnus Ameghino, 1904 = *Pleurostylodon*
Pehuenia Roth, 1902 = *Rhyphodon*
Periphragnis Roth, 1899, valid
Pleurostylodon Ameghino, 1897, valid
Plexotemnus Ameghino, 1904 = (with some doubt) *Acoelohyrax*
Porotemnus Ameghino, 1902 = *Pleurostylodon*
Proasmodeus Ameghino, 1902 = *Periphragnis*
Prostylops Ameghino, 1879 = *Isotemnus*
Rhyphodon Roth, 1899, valid
Setebos Roth, 1902 = *Rhyphodon*
Tehuelia Roth, 1902 = *Periphragnis*
Thomashuxleya Ameghino, 1901, valid
Toxotemnus Ameghino, 1904 = *Anisotemnus*
Tychostylops Ameghino, 1901 = *Pleurostylodon*
(Some specimens from these stages were also referred to *Asmodeus* and *Trimerostephanos*, now believed to be Deseadan genera absent from the Riochican to Mustersan.)

PLEUROSTYLODON AMEGHINO, 1897

Pleurostylodon AMEGHINO, 1897a, p. 485; 1906, p. 468. GAUDRY, 1904, pp. 14, 16, 25, figs. 16, 26; 1906, p. 34, fig. 17. MATTHEW, 1915b, pp. 430–432, figs. 1–3: SCHLOSSER, 1923, pp. 604, 615. SIMPSON, 1936a, p. 28, figs. 10–11; 1936b, p. 2. SCOTT, 1937a, p. 518.

Parastylops AMEGHINO, 1897a, p. 491; 1904b, p. 352.

Anchistrum AMEGHINO, 1901, p. 369; 1906, p. 467.

Tychostylops AMEGHINO, 1901, p. 369; 1904a, vol. 57, p. 243; 1906, p. 468. SCHLOSSER, 1923, p. 615.

Tichostylops [*lapsus*]: AMEGHINO, 1904b, p. 525.

Dialophus AMEGHINO, 1901, p. 415; 1906, p. 468. SCHLOSSER, 1923, p. 615.

Coelostylops AMEGHINO, 1901, p. 422; 1906, p. 468.

Porotemnus AMEGHINO, 1902a, p. 28; 1906, p. 468.

Paratemnus AMEGHINO, 1904a, vol. 57, p. 242; 1906, p. 468.

TYPE: *Pleurostylodon modicus.*

TYPES OF SYNONYMS: Of *Parastylops*, *Parastylops coelodus;* of *Anchistrum*, *Anchistrum sulcosum;* of *Tychostylops*, *Tychostylops marculus;* of *Dialophus*, *Dialophus simus;* of *Coelostylops*, *Coelostylops crassus;* of *Porotemnus*, *Porotemnus crassiramis;* of *Paratemnus*, *Paratemnus geminatus.*

DISTRIBUTION: Casamayoran and possibly uppermost Riochican,[1] Patagonia.

DIAGNOSIS: P^{2-4} transverse, triangular in structure but ovoid to subquadrate in outline, paracone fold narrow anteroposteriorly, followed by flattened wall in metacone region, strong anterointernal and posterointernal cingula tending to form basins. M^{1-3} also with sharp, prominent, paracone folds, narrow anteroposteriorly, well differentiated

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[1] Occurrence in the uppermost Riochican depends on Cabrera (1935, p. 13) who referred a P^4 and an M_1 to *Pleurostylodon complanatus* "con alguna duda." The doubt must be considered great, because the type of *complanatus* (a dubious species itself) has no parts comparable with Cabrera's specimens. They were said to be from "la parte superior del 'Pehuenche,' " which is probably the uppermost Riochican. The specimens were not figured or designated by catalogue numbers.

Isotemnus (which see) does occur in the Riochican, and occurrence of *Pleurostylodon* would not be surprising, but it is not definitely established.

from parastyle fold, followed by flattened or slightly excavated wall, then by much less prominent, equally narrow metacone fold. M^{1-2} quadrate, moderately transverse, with well-developed hypocone lobes. Coronal pattern complicated by variable small crests and folds in addition to basic two cristae and one crochet. Strong anterior and posterior cingula, the former commonly continuing around the protocone as an internal cingulum. Lower premolars moderately elongate, not strongly transverse or compressed. P_3 about as molariform as P_4, both with accessory trigonid cusp as on molars but less distinct, metaconid reflected or crested posteriorly, tending to close talonid basin, entoconid crest running to hypoconid and appearing as part of talonid crescent rather than as a separate transverse crest. Accessory trigonid cusp on molars anteroexternal to metaconid, not well distinguished from latter except at unworn apex. Brachydont, but crowns somewhat higher than in *Isotemnus.*

SYNONYMY

Parastylops: When this genus was defined, it was referred to the Notostylopidae and not compared with *Pleurostylodon,* which was placed in a different family. Ameghino (1904b) transferred *Parastylops* to the Isotemnidae, but did not redefine it, except by implication. The essential type is a single M^3 which is very similar to M^3's typical of *Pleurostylodon* except for the more complete separation of protocone and metaloph and the fact that the internal cingulum is continuous around the protocone and runs into the metaloph. This is an individually distinctive structural type, but the fact that it is merely a combination of characters found separately in specimens referred to *Pleurostylodon* by Ameghino himself suggests that "*Parastylops*" represents simply a recombination of genetic variations in a *Pleurostylodon* population. Moreover, we have a specimen with "*Parastylops*" M^3 associated with M^{1-2} which are in every detail like those of *Pleurostylodon biconus,* type of the genus, except for being slightly below the average size of that species. Ameghino's exhaustive faunal lists of 1906 omit this genus, which may indicate that he then considered it invalid, but more likely was an oversight.

Anchistrum: Ameghino placed this genus in the Acoelodidae (Oldfieldthomasiidae) and never compared it with *Pleurostylodon.* Its definition depends on identification of the type teeth as P^3–M^2. We now have two specimens of *Pleurostylodon* with deciduous teeth, and these strongly suggest that "*Anchistrum*" was based on dm^{2-4} and M^1 of the former genus.

Tychostylops: Originally Ameghino (1901) referred this genus to the Trigonostylopidae, but he later (1904a) transferred it to the Isotemnidae and redefined it on that basis. The revised definition was, however, based on new specimens with no parts in common with the original type specimen of the type species and therefore of doubtful bearing on the matter. The true type specimen is somewhat distinctive from *Pleurostylodon modicus,* but not from *P. limpidus* or *P. obscurus,* which were considered merely variants of *Pleurostylodon* by Ameghino himself. The referred specimens of 1904 also seem to me to belong to *Pleurostylodon.* The only really distinctive characters in Ameghino's redefinition were the supposed procumbent canines, reduced or absent lower incisors, and low-crowned cheek teeth. The symphyseal fragment in question is broken and is like any similarly broken *Pleurostylodon* symphysis, and the cheek teeth also seem to be of comparable height except for effects of wear.

Dialophus: This genus was based on the remains of several individuals, probably not all conspecific. The upper tooth that was the essential type can be exactly matched in *Pleurostylodon,* and Ameghino's description of it cites no characters not also present in various species referred by him to *Pleurostylodon.* For the lower teeth, he noted the presence of an accessory cusp anterior to the metaconid, as in "*Eochalicotherium*" or *Isotemnus.* Later collections show that this cusp is normally present on little-worn teeth of *Pleurostylodon,* although less distinct and separate than in *Isotemnus.* "*Dialophus*" is now seen to resemble *Pleurostylodon* in this character also.

Coelostylops: Ameghino placed this genus in the Notostylopidae and, having no later occasion to refer to it, never redefined it as an isotemnid or made this comparison. Once comparison is made with isotemnids, it is at once seen that the only known specimen of "*Coelostylops*" is a poorly preserved M^3 of *Pleurostylodon.*

Porotemnus: The only character distinctive from *Pleurostylodon* in the definition of this supposed genus, or in the specimen on which it was based, is a peculiar thickening of the mandible, with an external lateral protuberance in the premolar region. The teeth are exactly like those in *Pleurostylodon.* It is highly probable that this protuberance is pathological, as such exostosis is not altogether uncommon in pathological specimens and is rarely normal—never in notoungulates, as far as known. In any case it is hardly, in itself, acceptable as a generic character without confirmation of its constancy and support by other diagnostic differences.

Paratemnus: The distinctive characters in the description of this genus were that M^2 is smaller than M^1, rather than larger as in *Pleurostylodon*, and that the upper premolars have very strong anterior and posterior cingula. The premolars of *Pleurostylodon modicus*, type of the genus, were unknown to Ameghino and are now found to have very strong cingula, as in "*Paratemnus.*" M^2 of "*Paratemnus*" is almost exactly as long as M^1 and is somewhat wider. This difference is unusual in *Pleurostylodon*, but with other characters so closely similar, it is reasonable to assume that such a difference in proportions is individual or at most a specific, not a generic, character. This was Ameghino's own practice in other cases: he often separated species, not genera, by differences in proportion much more pronounced.

MORPHOLOGY

Patterson (1934b), Riggs and Patterson (1935), and I (Simpson, 1936a) have described some of the dental and cranial characters of *Pleurostylodon.* It is unnecessary to repeat previous descriptions in full, but a general account is needed here to make this study complete and as a basis for consideration of other members of the family. Some additions and emendations are also necessary.

DENTITION: Most of the important specimens are listed under the specific hypodigms below. Specimens not specifically identified are in the main isolated teeth or dentitions too deeply worn to be of much morphological interest. An exception is A.M.N.H. No. 28646, the facial part of a skull with right I^1–M^3 complete and left I^2–M^3, one of the few specimens with the full series of upper incisors, which is thus important but which has the cheek teeth badly worn and does not seem clearly referable to an established species.

The dental formula is complete, $\frac{3\,1\,4\,3}{3\,1\,4\,3}$, and the tooth series are closed except for variable slight spacing around the canines.

I^1 and I^2 are similar, but the latter is slightly larger. They have a single, rounded apex and are simply convex on the labial side. The lingual side has a strong median crest, with concavities on each side, forming small pockets closed by a cingulum at the basal ends. I^3 is considerably larger than I^2 and is pointed and caniniform, although neither so large nor so elevated as the canine. It is slightly recurved and receives wear from the anterior face of the lower canine on its concave posterolingual surface. The upper canine is a large, protuberant, lanceolate tooth. It usually, but not invariably, has an anterior wear facet, as would be expected from occlusion with the lower canine. Unless quite unworn, it has a posterior wear facet, which may be extensive—a somewhat puzzling feature, because it seems hardly consistent with the rather feeble P_1. There are marked individual differences in the sizes of I^3 and C, and there may be some sexual dimorphism.

P^1 is one-rooted, longer than wide, irregularly triangular in plan. There is a single main mediolabial cusp, with a strongly convex labial face flanked fore and aft by hollows and then by stylar anterolabial and posterolabial projections. There is a simple, low, posterolingual talon or nominal protocone. P^{2-4} are three-rooted and closely similar to one another except that they become progressively more transverse from P^2 to P^4. There is a single, high, sharp labial cusp (nominal paracone) somewhat anterior in position, and the labial surface has a corresponding strong vertical swelling. Anterior to this are a well-defined groove and a parastylar fold, anterior more than labial to the paracone. Posterior to the paracone ridge the labial face is slightly excavated, and there may be a faint suggestion of a metacone

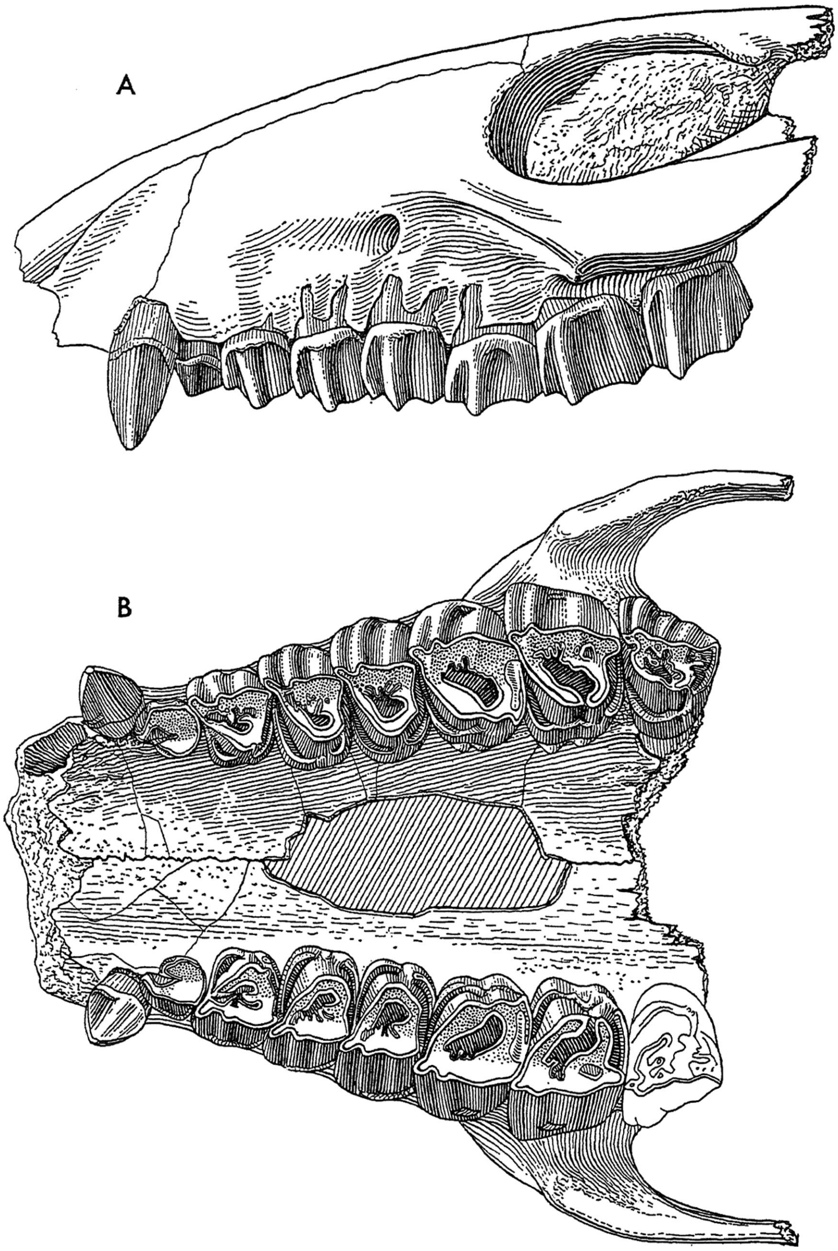

FIG. 32. *Pleurostylodon modicus* Ameghino, C.N.H.M. No. P13296, facial part of skull. A. Left side view. B. Palatal view. After Riggs and Patterson (1935). ×1.

swelling. The metastyle is slight and indistinct. The protocone is mediolingual, with sharp V-shaped crests. There are several variable cristae, the most posterior united with a strong crochet, so that together they cut off a small posterolabial fossette soon obliterated by wear. A rudimentary antecrochet may occur, but (both here and from the molars) it may be absent. Lingual to the crochet and crista is a deep fossa, elongate posterolingual-anterolabially, persisting to an advanced stage of wear. There is usually a slight, quite variable external cingulum on all the premolars. On P^{2-4} there are always strong anterior and posterior cingula, each rimming a prominent labial pocket. The extension of these cingula onto the lingual face of the protocone is highly variable; it may be nil, or the two may nearly meet here. The posterior cingulum is higher on the crown than the anterior.

M^{1-2} have definite metacones, and the ectoloph posterior to the paracone is longer than in the premolars, rather flat, but usually with a more definite metacone ridge, which is, however, much weaker than the paracone ridge. The metastyle, posterior or even posterolingual to the metacone, is also more definite than on the premolars. There is a well-defined hypocone, basally united with the protocone but apically separated by a notch, the depth of which shows much apparently individual variation. The pattern of cristae, crochet, variable rudimentary antecrochet, fossette, and fossa is as on P^{2-4}, modified only by the greater length of the crown relative to the width. There is a small external cingulum at the base of the hollow between paracone and metacone folds, in some cases strong and in others so feeble as to be barely evident. The anterior cingulum continues to some, but again a highly variable, extent around the lingual face of the tooth. It may not cross the hypocone at all, or may run right across the hypocone and abut against the more apical lingual end of the posterior cingulum. Such differences can be rather striking, and it is not surprising that Ameghino tended to give them taxonomic value in individual teeth, but in the present larger collections, even from one horizon and locality, all intermediates occur in otherwise exactly similar specimens.

M^3, as is to be expected, is more triangular than M^{1-2}, with the hypocone smaller, often hardly distinguishable. The posterior cingulum tends to run over onto the lingual face and is often, but not in every case, quite continuous around to the anterior cingulum.

The lower dentition is best known in M.A.C.N. No. 10554, referred by Ameghino to *Paratemnus geminatus*, here considered a synonym of *Pleurostylodon modicus*, to which the specimen belongs. It is a lower jaw lacking only right I_3. I_1 is small, and I_{2-3} are successively larger. All are somewhat spatulate but apparently have a single central cusp when unworn. There is a vertical medial ridge on the labial face of each, flanked by depressions or grooves, and each has a basal lingual cingulum. These sculptural features are progressively more accentuated from I_1 to I_3. The lower canine somewhat resembles I_3 but is much larger, especially higher, with a single, prominent, somewhat recurved apical cusp. It is distinctly smaller than the upper canine. It develops an anterior wear facet for I^3 and a posterior wear facet for upper C. P_1 is more or less intermediate between I_3 and C in structure and also in size although nearer I_3, much smaller and lower than C.

P_2 has a medial main apex with a posterolingual spur which if completely unworn might be double, i.e., have nearly connate nominal protoconid and metaconid tips. A curved crest descends from the protoconid apex anteriorly, then anterolingually, with a slight cuspidate swelling before it connects with the small, generally continuous internal cingulum. Posteriorly, crests descend from both the protoconid and metaconid apices, with a small hollow between them, in which at a lower point on the crown another crest appears, running straight posteriorly and rising to a low posteromedial talonid cusp. There is a minute isolated cuspule low on the crown in a posterolingual position. P_3 and P_4, closely similar, have a well-developed, sharp metalophid, the ends slightly elevated as protoconid and metaconid. From the protoconid a descending crest runs forward to the anterolabial corner, there turns sharply lingually and continues downward to the base at the anterolingual corner, where it may connect with the internal cingulum if that slight and variable feature is present. The tip of the metaconid is elongate antero-labio-posterolingually and is vaguely bifid when unworn. A talonid crest forms a crescent from the middle of the base of the metalophid to the posterolingual angle, where it abuts against a small but distinct entoconid, not set into the talonid basin or elongate transversely.

On M_{1-3} the trigonids have the structure described for P_{3-4}, but they are more com-

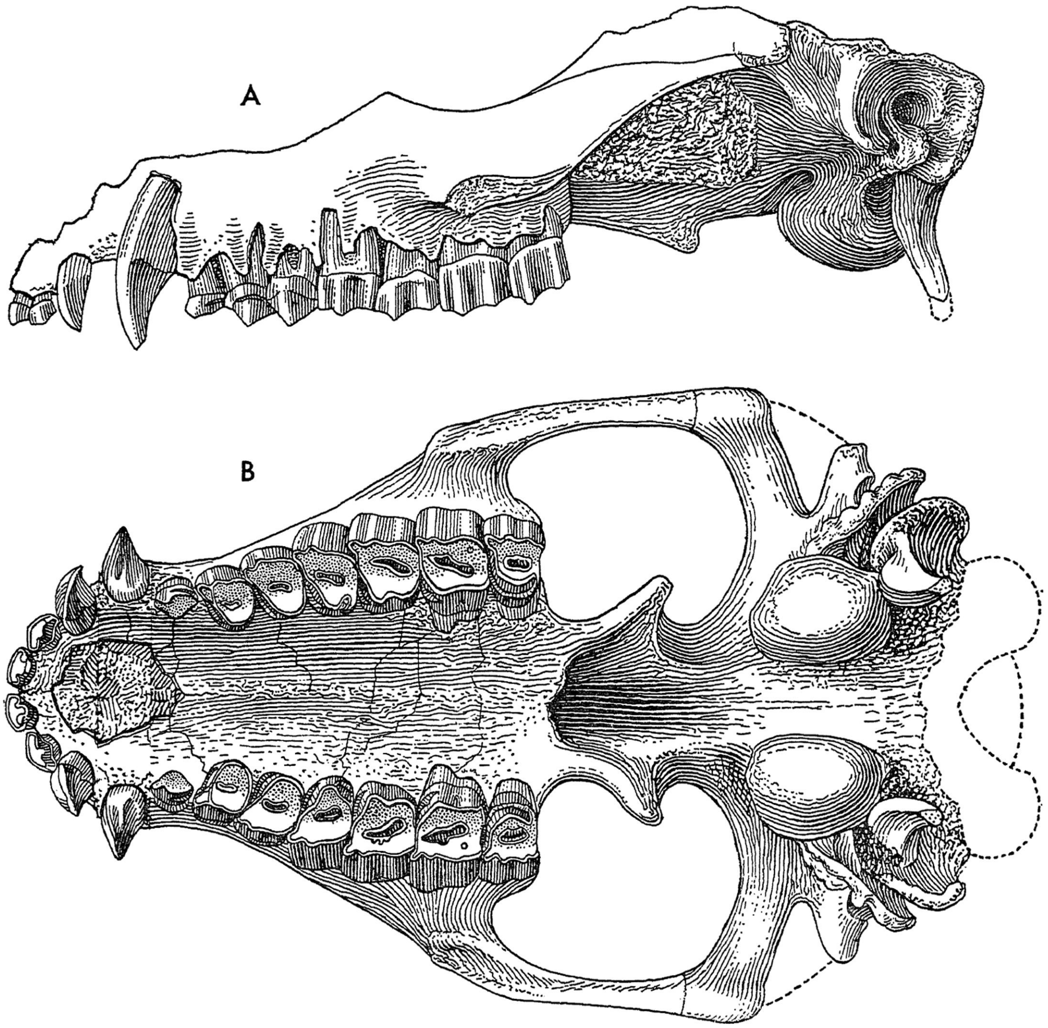

FIG. 33. *Pleurostylodon modicus* Ameghino, C.N.H.M. No. P13528, ventral parts of skull. A. Left side view. B. Palatal view. After Riggs and Patterson (1935). ×2/3.

pressed anteroposteriorly. The talonids are correspondingly relatively longer anteroposteriorly, and the entoconids are well separated from the end of the hypolophid, set into the talonid basin where they form definite transverse crests (as in notoungulates generally). As usual, M_3 differs in having a still longer talonid, with a prominent hypoconulid vaguely separated as a posteriorly projecting lobe.

SKULL AND JAWS

In general aspect and even in most details the skull resembles that of *Oldfieldthomasia*, described above, except that it is more robust throughout as befits an animal so much larger. It is, in short, a thoroughly primitive notoungulate skull with few special characteristics other than those of notoungulates generally and without such divergent characters as appear in almost all later and even some equally early (e.g., *Notostylops*) genera. There is no retraction of nasals, elongation or narrowing of snout, deepening of cranium, advancing basicranial flexure, development of zygomatic plate, partitioning of bulla, or development of cancellous tissue.

The short premaxillary ends at a point

above the canine. The nasal extends only slightly beyond the anterior orbital rim. The single, moderate, infraorbital foramen (in the adult) is above P^4 or between P^3 and P^4. The lacrimal foramen is inside the orbital rim, and there is no facial expansion of the lacrimal bone. The zygoma is long, rather slender, and gently sigmoid. The jugal is primitive, beginning posteriorly on the ventral side of the posterior root of the zygoma, just anterior to the glenoid fossa, and extending up the anteroventral orbital rim to the lacrimal. The broad glenoid fossa is concave anteroposteriorly but neither cylindrical nor deeply excavated. The blunt postglenoid process is well developed, but not so much so as in most later toxodonts, and there is none of the apparent anteroposterior contraction in the ear region as in some of the latter. The single postglenoid foramen is unusually large. The auditory region, described in some detail by Riggs and Patterson (1935) and shown here in figures 1 and 2 of plate 22, is not markedly unlike that of *Oldfieldthomasia*, fully described here on previous pages. It is suitable for ancestry of the Toxodonta, fairly conservative notoungulates in this region, but shows none of their moderate specializations. The cranium is rather slender and elongate and has a single, well-defined, sagittal crest. There are short postorbital processes, behind which is a strong postorbital or precranial constriction. An endocranial cast is not available, but it would appear that the brain must have been primitive, comparatively small, but probably markedly triangular, in outline perhaps more like that of *Hegetotherium* or *Protypotherium* (see Simpson, 1933i) than like that of the surely more nearly related *Rhyphodon* (see Simpson, 1933f, and pages, below, of this monograph).

The symphysis of the lower jaw is rather long, extending to about the level of P_2, but not strongly procumbent. The horizontal ramus is of moderate depth, with a mental foramen under P_4 and in at least one specimen another under P_3. The angular region, not completely preserved in available specimens, was broadly expanded, thin and flat, and probably, but not surely, simply rounded in posteroventral outline. The large dental foramen is only slightly below and behind the alveolar border. The transversely expanded articular condyle is far above that border, and the coronoid process, also not completely known, was apparently slender and small.

SPECIFIC TAXONOMY

Twenty-three formerly named species, all by Ameghino, are now referred to this genus, one (*?P. recticrista*) with doubt, the others with some degree of confidence. They were originally placed in 10 different genera, which means that about half of them were not compared with one another in or before definition. Even those placed in the same genus (12 were referred to *Pleurostylodon*) were commonly based on types with no parts in common and hence no possibility of direct comparison or truly differential diagnosis. Some were based on lots of scraps from different individuals and possibly different species or genera. In only a few exceptional cases did Ameghino refer two specimens to the same species. Characters considered specific include slight or moderate differences in size, proportions, development of cingula, separation of protocone and hypocone, and apparent heights of crowns. Some of the apparent characteristics were not originally variant but depended on such things as differences of age (wear). Most of them are truly variant characters of the specimens made types of species, but in terms of Ameghino's specific characters the genus is an absolute chaos of variation. That is still true, or in fact even more true, now that later collecting has more than doubled the number of available specimens, including some better than any in the Ameghino Collection.

The problem of reducing this chaos to a defensible system has seemed virtually insoluble.[1] No two specimens are exactly alike, and by Ameghino's criterion each of the scores of specimens now known would represent a different species, which is absurd. On the other hand, throughout the whole group variation from one specimen to another, directly compared or through intermediates, is so graded that all might be placed in one species, which is not absurd but is unlikely

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[1] I have attacked it repeatedly, and each time have felt defeated. That is the main reason why years have elapsed between the publication of the first and second parts of this monograph.

because the extreme differences are greater than commonly occur within a species.

The arrangement finally adopted is rather a cutting than an untying of the Gordian knot. We have fair samples of known origin from two localities, Colhué-Huapí and Cañadón Vaca. Each is from a considerable area and not precisely (but nearly) the same level, but it is a reasonable postulate that each could represent a local population over a geologically short span of time. The structure of the teeth, although greatly variable in detail, is basically similar within each locality and between the two. At least, it does not permit the dividing of these specimens into a limited number of internally consistent and externally distinctive groups. Statistics on upper cheek teeth from Colhué-Huapí are given in table 44. The specimens differ greatly in individual age and in stage of wear, which strongly influences the lengths but not the widths of the crowns as measured. Variation for length of P^{1-2} and M^{1-2} is greater than is usual in a homogeneous sample from one species of mammal, but these are exactly the dimensions that are visibly most affected by state of wear as distinct from original difference in size. The other dimensions are quite within expected ranges of variation for a single species. There is no good evidence of specific heterogeneity, and it is reasonable to conclude that this is one biological species even though heterogeneous in individual ages and, to a slight degree, in geological horizon.

The smaller Cañadón Vaca sample does not warrant statistical elaboration, but as shown in table 45 its dimensions are also consistent with pertinence to a single biological species. Its tooth patterns, with the usual variation, also show no consistent specific groupings or distinction from the Colhué-Huapí sample. Differences in dimensions of the samples from the two localities are also doubtfully or not significant, except that in the Cañadón Vaca sample the length of M^3 is decisively greater and the ratio of width to length smaller. That is not necessarily indicative of specific distinction, but it could be and it also happens to correspond very closely with the difference between two of Ameghino's most nearly distinctive types, *Pleurostylodon modicus*, with M^3 as in the Colhué-Huapí sample,[1] and *P. similis*, with M^3 as in our specimens from Cañadón Vaca. Those names are therefore applied to the two samples, which are taken as indicative of the variation within and difference between the two putative and closely related species.

As a next step, names of supposed species that seem to be close to one or another of our two samples are placed in tentative synonymy. Twelve names are thus synonymized with *P. modicus* and two with *P. similis*. Since most of Ameghino's specimens did come from Colhué-Huapí, the discrepancy in numbers of synonyms is not anomalous, although there is a possible anomaly in the fact that one type of a species ("*Tychostylops simus*") now synonymized with *P. similis* is labeled as from Colhué-Huapí. It is of course possible that some of the species here considered synonyms will eventually prove to be valid, but I think that is unlikely for any one of them. In any case, the species are not here sunk without a trace; possible distinctions of their types are given, and they can be revived easily, if occasion arises.

Another of Ameghino's species, although possibly a synonym, is distinctive enough to be given continued recognition tentatively: *P. complanatus* (with its synonyms *P. irregularis* and *P. neglectus*). "*Porotemnus*" *crassiramis* is also a possible synonym, but is tentatively retained. "*Dialophus recticrista*" is not synonymous with any (other?) species of *Pleurostylodon* and probably does not belong in this genus but is listed here *faute de mieux*. Finally, there are two *species inquaerendae*, inadequately defined and unfigured, of which I have seen no specimens and which are merely listed: *P. notabilis* and *P. bifidus*.

Pleurostylodon modicus Ameghino, 1897

Plate 22, figures 3–14; plate 23; plate 24; text figures 32, 33

Pleurostylodon modicus AMEGHINO, 1897a, p. 485, fig. 66; 1898, p. 174; 1904b, p. 175, figs. 127, 228.

Parastylops coelodus AMEGHINO, 1897a, p. 491, fig. 71; 1898, p. 175; 1904b, p. 352, fig. 464.

Anchistrum sulcosum AMEGHINO, 1901, p. 369.

Tychostylops marculus AMEGHINO, 1901, p. 396.

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[1] Although there are no locality data, it is also almost certain that this type is from the Colhué-Huapí locality, as are most or all of the Casamayoran specimens named in 1897. There are also no locality data for the type of *P. similis*, but specimens described in 1901 did include some from near or at our Cañadón Vaca locality.

TABLE 44

STATISTICS ON UPPER CHEEK TEETH OF *Pleurostylodon modicus* FROM SOUTH OF LAGO COLHUÉ-HUAPÍ

Dimension		*N*	OR	$\bar{X}$	s	V
P^1						
	L	8	6.2–10.3	8.89±.4	1.24±.31	14.0±3.5
	W	8	7.3– 8.4	7.88±.14	0.40±.10	5.1±1.3
P^2						
	L	8	8.1–11.3	10.18±.33	0.94±.24	9.2±2.3
	W	8	11.0–14.7	13.16±.38	1.07±.27	8.1±2.0
P^3						
	L	8	9.3–11.5	10.75±.22	0.63±.16	5.9±1.5
	W	8	14.7–17.6	16.35±.35	0.99±.25	6.1±1.5
P^4						
	L	8	9.7–12.8	11.61±.30	0.85±.21	7.4±1.8
	W	7	17.2–19.4	18.64±.31	0.83±.22	4.4±1.2
M^1						
	L	8	11.0–15.0	13.53±.52	1.48±.37	10.9±2.7
	W	7	18.7–21.1	19.99±.31	0.81±.22	4.1±1.1
M^2						
	L	8	13.3–17.4	15.09±.45	1.28±.32	8.5±2.1
	W	8	20.3–23.9	21.81±.39	1.09±.27	5.0±1.3
M^3						
	L	8	13.1–14.7	14.09±.20	0.58±.14	4.1±1.0
	W	8	18.5–21.2	19.46±.29	0.81±.20	4.2±1.0

TABLE 45

DIMENSIONS OF UPPER CHEEK TEETH OF *Pleurostylodon similis* FROM CAÑADÓN VACA

		A.M.N.H. No. 28636	A.M.N.H. No. 28830	A.M.N.H. No. 28685	A.M.N.H. No. 28874
P^1					
	L	10.0	7.8	—	—
	L	7.8	7.3	—	—
P^2					
	L	11.3	10.4	10.6	—
	W	14.4	14.3	—	—
P^3					
	L	11.4	10.9	11.8[a]	—
	W	17.1	16.7	—	—
P^4					
	L	12.4	11.5	11.9	—
	W	18.5	19.0	19.4	—
M^1					
	L	16.2[a]	15.0	15.0	—
	W	20.0	20.5	21.6[a]	—
M^2					
	L	17.9[a]	16.7	*ca.* 17½	15.4
	W	22.8	23.2	23.2	21.7
M^3					
	L	17.4[a]	16.5[a]	—	16.7[a]
	W	22.0[a]	22.9[a]	—	20.8

[a] Values outside observed range (OR) of Colhué-Huapí specimens. For P^3–M^2, differences from Colhué-Huapí means are probably not significant: $0.05 > P > 0.01$. For length of M^3, however, all differences are strongly significant: $P < 0.003$.

Pleurostylodon divisus AMEGHINO, 1901, p. 414; 1904b, p. 248, fig. 333.

Pleurostylodon plexus AMEGHINO, 1901, p. 414.

Dialophus simus AMEGHINO, 1901, p. 415; 1904b, p. 179, figs. 236, 310. (*Nec Tychostylops simus* Ameghino, 1904.)

Pleurostylodon sinuosus AMEGHINO, 1902a, p. 29; 1904b, p. 108, fig. 121.

Pleurostylodon limpidus AMEGHINO, 1904a, vol. 58, p. 239; 1904b, p. 347, fig. 459.

Pleurostylodon obscurus AMEGHINO, 1904a, vol. 58, p. 239; 1904b, p. 349, fig. 460.

Paratemnus geminatus AMEGHINO, 1904a, vol. 58, p. 242.

Trimerostephanos biconus AMEGHINO, 1897a, p. 484; 1898, p. 173.

Pleurostylodon biconus: AMEGHINO, 1902a, p. 29; 1904b, p. 79, figs. 235, 335, 462. SCHLOSSER, 1923, p. 615, fig. 760 (original). PATTERSON, 1934b, p. 100, fig. 17. RIGGS AND PATTERSON, 1935, p. 198, pls. 3, 4, pl. 5, fig. 1.

Dimerostephanos attritus AMEGHINO, 1902a, p. 31.

TYPE: M.A.C.N. No. 10566, fragment of right maxilla with M^{1-3}. No field data.

TYPES OF SYNONYMS: Of *Parastylops coelodus*, M.A.C.N. No. 10618, two upper and two lower molars, not of one individual; a left M^3 is taken as lectotype; no field data. Of *Anchistrum sulcosum*, M.A.C.N. No. 10767, a maxillary fragment with dm^{2-4} M^1; from south of Colhué-Huapí. Of *Tychostylops marculus*, M.A.C.N. No. 10625, deeply worn, isolated left M^3; Colhué-Huapí. Of *Pleurostylodon divisus*, M.A.C.N. No. 10567, a broken left upper molar, probably M^2 but possibly M^1, and three probably not associated upper premolars; the molar is made lectotype; Colhué-Huapí. Of *Pleurostyodon plexus*, M.A.C.N. No. 10570, isolated and not associated right M^1, left M^1, and left M^2; the left M^1 is taken as lectotype; no field data; specimens referred by Ameghino but probably not syntypes are labeled as from [south of] Colhué-Huapí and north of Colhué-Huapí. Of *Dialophus simus*, M.A.C.N. No. 10589, a lot of isolated teeth and scraps, including left M^1, right P^4, and right lower jaw fragment with M_{1-3}, another with M_2, and six other fragments of jaws or teeth. The left M^1 was figured, could be the essential basis of Ameghino's definition, and is taken as lectotype. The other fragments are not associated and may belong in part to *Pleurostylodon modicus* but probably include at least one other species and perhaps genus. Pico Salamanca. Of *Pleurostylodon sinuosus*, M.A.C.N. No. 10571, broken left M^1; no field data. Of *Pleurostylodon limpidus*, M.A.C.N. No. 10573, left M^3; no field data. Of *Pleurostylodon obscurus*, M.A.C.N. No. 10574, left M^3; Río Chico (locality, not age). Of *Paratemnus geminatus*, M.A.C.N. No. 10606, part of right maxilla with P^1–M^2; Colhué-Huapí. Of *Pleurostylodon biconus*, M.A.C.N. No. 10548, a left lower jaw fragment with M_{1-2}, another without teeth, an isolated left M_2, a broken astragalus, and a broken calcaneum, each probably from a different individual. The original description was based chiefly on the fragment with M_{1-2}, and I take that as lectotype. No field data. Of *Dimerostephanos attritus*, M.A.C.N. No. 10609, fragment of left lower jaw with roots of M_{2-3}, broken talonid of M_2, and part of trigonid of M_3; Colhué-Huapí.

HYPODIGM: The types, listed above, and more particularly other specimens from south of Lake Colhué-Huapí, including the following: M.A.C.N. No. 10554, lower jaw with all teeth of both sides except right I_3; A.M.N.H. No. 28878, partial skull (good ear region) with right P^1–M^3; A.M.N.H. No. 28644, associated left P^1–M^3 and right M^{1-3} (M^3 broken); A.M.N.H. No. 28763, part of right lower jaw with P_4–M_2; A.M.N.H. No. 28630, part of right lower jaw with P_2–M_3 (M_3 broken); A.M.N.H. No. 28689, part of right lower jaw with P_3–M_3; A.M.N.H. No. 28717, parts of associated upper and lower jaws with right P^3–M^3(M^3 broken), right P_{1-2}, and left P_{1-4}; A.M.N.H. No. 28709, associated right M_{1-3}; A.M.N.H. 28948, part of right lower jaw with P_3–M_3; A.M.N.H. No. 28880, most of skull, with deeply worn left I^3–M^3 and right I^3, C, P^2–M^3; A.M.N.H. No. 28646, facial part of skull, with deeply worn left I^2–M^2 and right I^1–M^3; C.N.H.M. No. P13528, most of skull, with worn, partly crushed and broken complete dentition; C.N.H.M. No. P13296, facial part of skull with left C–M^3 and right C–M^2; C.N.H.M. No. P13309, facial part of skull with left I^2–P^4 and right C–P^4; C.N.H.M. No. P13620, fragment of right maxilla with dm^{2-4}, M^{1-3}, and P^{2-4} in crypts above the deciduous molars.

HORIZON AND LOCALITY: Casamayoran,

TABLE 46

Measurements of Upper Teeth of Types of Some of Ameghino's Species Now Considered Synonyms of *Pleurostylodon modicus*

	P^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W
Pleurostylodon modicus	—	—	15.3	21.6	16.0	22.8	11.5	19.1
Parastylops coelodus	—	—	—	—	—	—	13.0	18.8
Anchistrum sulcosum	—	—	*ca.* 15	*ca.* 19½	—	—	—	—
Tychostylops marculus	—	—	—	—	—	—	14.7	19.8
Pleurostylodon divisus	—	—	—	—	*ca.* 18	*ca.* 22½	—	—
Dialophus simus	—	—	15.3	18.6	—	—	—	—
Pleurostylodon limpidus	—	—	—	—	—	—	*ca.* 15	*ca.* 20
Pleurostylodon obscurus	—	—	—	—	—	—	*ca.* 14	*ca.* 19½
Paratemnus geminatus	11.2	16.5	14.1	18.9	14.0	19.5	—	—

Patagonia. Especially south of Colhué-Huapí, but two Ameghino specimens now placed here are labeled as from Río Chico and Pico Salamanca.

Diagnosis: Characteristic of the genus. M^3 absolutely shorter and relatively more transverse than in *P. similis*; ratio (mean width) divided by (mean length) of M^3 about 1.4. Measurements are given in tables 44, 46, and 47.

The invalidity, or at least inadequacy, of the supposed distinctions of the genera here involved is discussed above under the genus *Pleurostylodon*. Ameghino of course did not compare species referred to different genera, and for the most part when the generic separation is removed possible specific characters are not left. Nevertheless, existing distinction not here considered specific are noted.

Parastylops coelodus type M^3 has the protocone and metaloph well separated and a strong cingulum rounding the protocone to unite with the metaloph.

Anchistrum sulcosum type M^1 has less open fossettes than the type of *P. modicus* and the internal cingulum weaker, absent from the hypocone. The other teeth are deciduous molars, not present in other types.

Tychostylops marculus type M^3 is slightly (insignificantly) larger than the type of *P. modicus* and has a somewhat weaker internal cingulum.

Pleurostylodon divisus was compared by Ameghino with *P. notabilis* (a *species inquaerenda* for me) and was said to have the upper molars more compressed anteroposteriorly, to have the inner lobes completely separated, and the anterior much larger than the posterior. The relative shortness of the type is an artifact due to breakage and incorrect repair. The separation of protocone and hypocone is unusually deep, but not outside the probable range of *P. modicus*. The proportions of those cusps are as in M^2 of *P. modicus*.

Pleurostylodon plexus was said by Ameghino to be almost as large as *P. modicus*, to have the protocone-hypocone division rather accentuated, and to have the coronal fossa with the enamel rim folded in numerous zigzags. All these characters are almost exactly as in the type of *P. modicus*.

Dialophus simus type M^1 is slightly less transverse than in the type of *P. modicus*, but I see no other differences in this poorly preserved specimen. Note that this species is distinct from *Tychostylops simus*, now also referred to *Pleurostylodon* (as a synonym of *P. similis*). The names thus become homonyms, but, as I do not consider either one valid, there is no reason to replace the junior homonym.

Pleurostylodon sinuosus was said by Ameghino to be of the size of *P. modicus* but with the posteroexternal [metastylar] crest of the upper molar strong, labial face of tooth hollowed out, and lingual side fairly well divided into two lobes. None of these characters is distinctive. The single broken tooth is essentially indeterminate, but since it cannot be distinguished from *P. modicus* it may be disposed of by placing it in synonymy.

Pleurostylodon limpidus was based on an isolated M^3, and most of the characters in Ameghino's definition are simply those normal for any last upper molar of this genus, or related genera. The internal cingulum is weak (not absent as stated), and the labial crests may be somewhat weaker than usual, but these characters, too, are well within the probable range of *P. modicus*.

Pleurostylodon obscurus type M^3 was said to differ from *limpidus* in having a shorter posterior crest and a rudimentary antero-external [parastylar] fold. Those characters do not differ significantly from those of *P. modicus*, and the other characters given by Ameghino were descriptive, not comparative.

M^{1-2} of the type of *Paratemnus geminatus* differ from the type of *Pleurostylodon modicus* in being about 10 per cent smaller, M^1 more nearly equal to M^2 in size, and the external cingulum longer anteroposteriorly. These differences seem inadequate for specific separation, although the synonymy is not certain. Ameghino also described a lower jaw supposedly of this species at the same time as the type, with which it is preserved. It does not occlude well with the type and certainly is not of the same individual, perhaps not of the same species.

Ameghino (1897a) originally based *P. biconus* on lower teeth referred to the Deseadan genus *Trimerostephanos*. In the same publication but on a later page he based the Casamayoran genus and species *Pleurostylodon modicus* on upper teeth. Thereafter Carlos Ameghino found the following lot of specimens: M.A.C.N. No. 10565, numerous isolated teeth, including left P^4, right P^4, left P^3, right P^3, right M^1 or M^2, two right P_4's, two right M_1's, left M_1, right M^3, and four other fragments of teeth; from west of the Río Chico.

Florentino Ameghino believed these probably to have come from a single individual, as indicated by a slip of paper saying "Prob. todo de uno" in his hand. However, at least four individuals and probably half a dozen or more are represented: right P_4 and M_1 are duplicated; the M_3 cannot have belonged with either M_1 because it is more worn; the upper molar is too small to occlude with any of the lower molars; one of the upper premolars is probably *Isotemnus*, not *Pleurostylodon*; the right and left P^4's are quite differ-

TABLE 47

Associated Upper and Lower Teeth of *Pleurostylodon*

		P. similis, Cañadón Vaca		*P. modicus*, Colhué-Huapí
		A.M.N.H. No. 28636	A.M.N.H. No. 28830[a]	A.M.N.H. No. 28717
P^1				
	L	10.0	7.8	—
	W	7.8	7.3	—
P^2				
	L	11.3	10.4	—
	W	14.4	14.3	—
P^3				
	L	11.4	10.9	12.1
	W	17.1	16.7	17.3
P^4				
	L	12.4	11.5	12.2
	W	18.5	19.0	19.6
M^1				
	L	16.2	15.0	13.3
	W	20.0	20.5	21.7
M^2				
	L	17.9	16.7	16.9
	W	22.8	23.2	23.0
M^3				
	L	17.4	16.5	—
	W	22.0	22.9	21.2
P_1				
	L	—	8.5	8.4
	W	—	6.2	5.9
P_2				
	L	—	10.7	10.3
	W	—	6.8	7.2
P_3				
	L	—	11.3	12.0
	W	—	8.9	8.8
P_4				
	L	13.0	13.3	—
	W	8.5	9.8	—
M_1				
	L	15.0	—	—
	W	9.9	—	—
M_2				
	L	16.6	16.2	—
	W	11.3	11.8	—
M_3				
	L	—	19.5	—
	W	—	10.8	—

[a] Deeply worn and somewhat crushed.

ent and cannot have come from the same individual or perhaps species.

On the basis of the lower teeth, Ameghino referred this pot-pourri to *biconus*, then the only similar species based on lower teeth. The upper teeth (with, as now appears, one exception) belong to *Pleurostylodon*, and in 1902 Ameghino therefore removed *biconus* to that genus. The generic reassignment was correct, even though its basis in supposed pertinence of M.A.C.N. No. 10565 to one individual was wrong. In 1902 and thereafter, Ameghino's concept of *P. biconus* was based on these materials of dubious specific pertinence and not on the type of the species. The only character then said to be definitely different from *P. modicus* (known from upper teeth only) was the absence of a buccal cingulum from the upper molars. But the upper teeth thus compared are not known to belong to *P. biconus*, and in *P. modicus* the buccal cingulum is quite variable and may be as inconspicuous as in those teeth. In fact no difference between *P. biconus* and *P. modicus* was or could be established on those materials.

We have three specimens only, with associated upper and lower teeth of *Pleurostylodon*. They are listed and measurements are given in table 47. Unfortunately the specimen referable to *P. modicus* includes no lower molars, and is not comparable with the type of *P. biconus* or the synonymous *P. attritus* (table 48). There are lower teeth almost certainly referable to *P. modicus* from Colhué-Huapí, where that is the common and perhaps the only species of *Pleurostylodon*. The type of *P. biconus* is well within their range of variation. Possible pertinence to *P. similis* is not absolutely ruled out, but the resemblance in known specimens is not so close.

There is thus a high degree of probability that *P. biconus* and *P. modicus* are synonymous, a probability further enhanced by the description of them in 1897, which indicated that they probably came from the same locality. Almost if not quite all the Casamayoran fossils then described by Florentino Ameghino had been collected by Carlos Ameghino south of Lake Colhué-Huapí.

TABLE 48

MEASUREMENTS OF TEETH OF TYPES OF *Pleurostylodon biconus* AND *P. attritus*

	M_1		M_2	
	L	W	L	W
P. biconus	12.6	9.8	14.5	9.5
P. attritus	—	—	*ca.* 15½	*ca.* 10

Pleurostylodon modicus and *P. biconus* were published simultaneously, without priority for either.[1] In such situations the Code (Stoll and others, 1964, Article 24A) states that relative priority is determined by the action of the first reviser, who "must have cited two or more such names, must have made it clear that he believes them to represent the same taxonomic unit, and must have chosen one as the name of the taxon." It is true that Schlosser (1923), Patterson (1934b), and Riggs and Patterson (1935) have used the name *P. biconus* for upper molars that could not have been identified as such by comparison with the type and that might therefore suggest that this name is considered prior, or possibly even the only one, in the genus. However, they did not fulfill any of the requirements of the Code for first reviser. Under the Code, the present publication is first revision. I have cited the two names *P. modicus* and *P. biconus*; I consider them to represent the same taxonomic unit; and I choose *P. modicus* as the name of the taxon (species).

Preference is given to *modicus* because it was the first specific name associated with the valid generic name (*Pleurostylodon*) and because its type clearly shows both generic and specific differential characters, which are at best obscure in the type of *P. biconus*.

"*Dimerostephanos*" *attritus* was not compared with *P. biconus* or other species of *Pleurostylodon*. It does not belong to "*Dimerostephanos*," which is now believed to be a synonym of *Isotemnus*. The type is extremely poor, virtually indeterminate, but it cannot be distinguished from *P.* "*biconus*"

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[1] *Pleurostylodon biconus* was on an earlier page, but it is impossible for one name to be prior (in time) to another in the same publication. The Code clearly indicates that technical nomenclatural priority is *not* established by page or line sequence within the same publication.

and may therefore be put along with the latter in the synonymy of *P. modicus.*

Pleurostylodon similis Ameghino, 1901

Plate 25, figures 1–4

Pleurostylodon similis AMEGHINO, 1901, p. 413; 1904b, p. 112, figs. 126, 458.

Coelostylops crassus AMEGHINO, 1901, p. 422.

Tychostylops simus AMEGHINO, 1904a, vol. 58, p. 244; 1904b, p. 176, figs. 229, 283. (*Nec Dialophus simus* Ameghino, 1901.)

TYPE: M.A.C.N. No. 10549, part of left maxilla with P^4–M^3. No field data.

TYPES OF SYNONYMS: Of *Coelostylops crassus*, M.A.C.N. No. 10476, isolated right M^3; west of the Río Chico. Of *Tychostylops simus*, M.A.C.N. No. 10607, right P^4 and M^{2-3}, left P^4, M^1 and M^3, of one individual; Colhué-Huapí.

HYPODIGM: Types, as above, and various specimens from Cañadón Vaca, especially A.M.N.H. No. 28830, most of skull and mandible, with worn and somewhat broken dentition; A.M.N.H. No. 28636, associated right and left P^1–M^3 and right P_4–M_2; A.M.N.H. No. 28631, right P_2–M_3; A.M.N.H. No. 28661, left P_3–M_1; A.M.N.H. No. 28797, right dm^{1-4} (or P^1 and dm^{2-4}); A.M.N.H. No. 28685, right P^2–M^2; A.M.N.H. No. 28874, left M^{2-3}.

HORIZON AND LOCALITY: Casamayoran, Patagonia. Referred American Museum specimens from Cañadón Vaca, near to or identical with Ameghino's "Oeste de Río Chico." Somewhat doubtful Ameghino specimen from Colhué-Huapí.

DIAGNOSIS: Closely similar to *P. modicus* but M^3 absolutely longer and relatively narrower, ratio (mean width) over (mean length) about 1.3. Measurements are given in table 49.

Neither of the two probable synonyms was compared with *P. similis* by Ameghino.

The type of *Coelostylops crassus* is deeply coated with manganese and is also probably broken. It is hardly identifiable but is probably *P. similis*; at least, the types show no reliable distinction.

Ameghino described the upper teeth of "*Tychostylops simus*" in great detail. Distinctions from "*Tychostylops marculus*," which I consider as a synonym of *Pleurostylodon modicus*, were said to be greater size, less depressed lingual side of upper teeth, and a stronger cingulum extending onto the inner face. These characters are not distinctive from those of either *P. modicus* or *P. similis*. M^3, however, most distinctive tooth in those species, is almost exactly like that of the type of *P. similis* and differs from that of *P. modicus* (and its synonym *Tychostylops marculus*).

Pleurostylodon complanatus Ameghino, 1902

Plate 25, figures 7, 8

Pleurostylodon complanatus AMEGHINO, 1902a, p. 30; 1904b, p. 250, fig. 336. CABRERA, 1935, p. 13.

Pleurostylodon irregularis AMEGHINO, 1904a, vol. 58, p. 238; 1904b, p. 351, fig. 463.

Pleurostylodon neglectus AMEGHINO, 1904a, vol. 58, p. 241; 1904b, p. 246, fig. 329.

TYPE: M.A.C.N. No. 10564, three unassociated upper molars, without field data. This lot has one slip in Ameghino's hand with the name *Pleurostylodon complanatus* and another saying "Tipo el diente más pequeño." The smallest tooth also agrees well with the first published description except that it is probably M^3, whereas Ameghino originally said that the type was M^1 ("M^5" in his idiosyncratic terminology), apparently in error. The tooth figured as *P. complanatus* in 1904, however, is not that smallest tooth but the more worn of the two larger teeth.

TABLE 49

UPPER TEETH OF TYPES OF *Pleurostylodon similis* AND PROBABLE SYNONYM

	P^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W
Pleurostylodon similis	11.1	18.6	15.9	19.0	16.8	21.6	16.0	19.4
Tychostylops simus	11.9	19.2	16.9	20.1	17.1	22.4	16.9	20.1

This is indeed a first molar, but otherwise it disagrees with every one of the details given as diagnostic in the original description of 1902. It must be concluded that the type is the smallest tooth of the lot and not the tooth later figured as *P. complanatus*.

TYPES OF SYNONYMS: M.A.C.N. No. 10575, an isolated right M^3, is the only specimen in the Ameghino Collection labeled as of *Pleurostylodon irregularis*, but it is not labeled as type, and it does not agree with the original description, which says that there is an indentation on the metaloph ("escotadura sobre la muralla de la cresta transversal posterior"). The figure given as *P. irregularis* in 1904 is not that specimen, but is the smallest specimen now under M.A.C.N. No. 10564, that is, is really the type of *P. complanatus*. It does have the metaloph indentation and all other characters given for *P. irregularis*. It is a right molar, whereas the original description says left, but there is no left molar that could belong to this species, and "izquierda" must be a *lapsus*. It appears that *P. complanatus* Ameghino, 1902, and *P. irregularis* Ameghino, 1904, were inadvertently based on the same tooth. They are thus objective synonyms.

The type of *Pleurostylodon neglectus* is M.A.C.N. No. 10568, isolated left M^3, without field data.

HYPODIGM: The two types, as above.

HORIZON AND LOCALITY: Casamayoran, Patagonia. More precise localities not known.

DIAGNOSIS: M^3 slightly smaller and relatively narrower than most M^3's of *P. modicus*, no vertical groove on lingual face, posterior cingulum detached lingually, nodules but no cingulum on lingual face and none on buccal face. Type M^3 measuring 12.5 by 16.8 mm.

As noted in the discussion of the types, *P. complanatus* and *P. irregularis* seem to be objective synonyms. The tooth to which Ameghino transferred the concept of *P. complanatus* in 1904 (1904a, vol. 58, fig. 336) probably belongs to *P. modicus* or, in any case, is not diagnostically distinct from that species. Ameghino, in his description of *P. neglectus*, did not compare it with *P. complanatus*, and the two types are almost identical in structure except that the type of *P. neglectus* is more worn. Its dimensions, 12.7 by 16.9 mm., are almost exactly those of the type of *P. complanatus* (and *P. irregularis*).

Although these two specimens are slightly outside the more or less established range of variation in *P. modicus*, the differences are so slight that those three names may well prove to be further synonyms of *P. modicus*.

Reference of a Riochican specimen to this species by Cabrera (1935, p. 13) cannot be confirmed, especially as it depended on characters of M_3, which is unknown in *P. complanatus*.

?Pleurostylodon crassiramis Ameghino, 1902, new combination

Plate 25, figures 5, 6

Porotemnus crassiramis AMEGHINO, 1902a, p. 28.

TYPE: M.A.C.N. No. 10610, fragment of left lower jaw with P_4. With it are loose left M_1 and right P_3, which could be but are not demonstrably associated, and another probably not associated lower premolar. The P_4 is lectotype. Colhué-Huapí, "parte superior [of the Casamayoran]."

HYPODIGM: Lectotype only.

HORIZON AND LOCALITY: Late Casamayoran south of Lake Colhué-Huapí.

DIAGNOSIS: P_4 like that of *Pleurostylodon modicus* but perhaps with crown higher than average; horizontal dimensions 11.4 by 8.9 mm. in type. A peculiar lateral (labial) protuberance on the jaw in the premolar region. In type external depth below P_4 27 mm., width on protuberance 20.7 mm.

The only correct and really distinctive character in the original description of the genus and species is the protuberance on the jaw. That is probably pathological, in which case the supposed species is not clearly distinguishable from *P. modicus*, although P_4 is so little distinctive that identity is not positively indicated. If the protuberance is normal, the species, or perhaps even the genus, is valid. That can hardly be established unless other, similar specimens are found.

?Pleurostylodon recticrista Ameghino, 1904, new combination

Plate 25, figure 9

Dialophus recticrista AMEGHINO, 1904a, vol. 58, p. 235.

TYPE: M.A.C.N. No. 10590, fragment of right lower jaw, poorly preserved, with two teeth, probably dm_4 and M_1. From west of the Río Chico.

HYPODIGM: The type only.

HORIZON AND LOCALITY: Casamayoran, west of the Río Chico.

DIAGNOSIS: Lower molars decidedly smaller than in other species referred to *Pleurostylodon*. M_1 with low crown, relatively wide and rounded in outline, with broad shallow basins and low narrow crests.

Identification of the teeth in the type as dm_4 and M_1 is uncertain, and I have no deciduous lower molars of *Pleurostylodon* for comparison. However, if these teeth were dm_{3-4} they would still almost certainly be outside the range of other species referred to *Pleurostylodon*. If they are M_{1-2}, the distinction is still greater, and reference to *Pleurostylodon* is improbable. As noted above, the type of *Dialophus* belongs to *Pleurostylodon* and probably to *P. modicus*. The present type differs from it as much as from other specimens of *P. modicus*.

Within *Pleurostylodon*, *?P. recticrista* is distinctive although inadequately known. It may belong to some other genus or species, but in any case it does not validate the supposed genus *Dialophus*.

Pleurostylodon notabilis Ameghino, 1901, *species inquaerenda*

Pleurostylodon notabilis AMEGHINO, 1901, p. 414.

No material referred to this species was found in the Ameghino Collection. The type was M^1, never figured and with no patently reliable distinctions in the descriptions.

Pleurostylodon bifidus Ameghino, 1904, *species inquaerenda*

Pleurostylodon bifidus AMEGHINO, 1904a, vol. 58, p. 240.

No material referred to this species was found in the Ameghino Collection. The type was a partial lower jaw with teeth, never figured and with no patently reliable distinctions in the description.

ANISOTEMNUS AMEGHINO, 1902

Anisotemnus AMEGHINO, 1902a, p. 25; 1906, p. 468. SIMPSON, 1964, p. 17.

Toxotemnus AMEGHINO, 1904a, vol. 58, p. 235; 1906, p. 468.

TYPE: *Isotemnus distentus*.

TYPE OF *Toxotemnus*: *Isotemnus lophiodontoides*.

DISTRIBUTION: Casamayoran, Patagonia.

DIAGNOSIS: Dentition closely similar to that of *Thomashuxleya* and that of *Pleurostylodon*. P^1 wider than long, but P^2 more triangular, less ovate-transverse than in related genera. P^{3-4} less subovate, more subquadrate. Cingula on upper cheek teeth weak. Upper molars complex, fossettes of region of cristae numerous and somewhat persistent with wear. Duplicated metaconids, or cuspules anterior to crested metaconids, subconical and distinct but connate with metalophids to high on crowns of M_{1-3}.

Ameghino originally described the type of this genus in *Isotemnus* but later removed it from that genus and from the Isotemnidae as a new genus in the Homalodontotheriidae, a possible ancestor of *Thomashuxleya*. It certainly does not belong in *Isotemnus* and is more like *Thomashuxleya*, but cannot be the ancestor of the latter as they are contemporaneous. No actual comparison was made with *Thomashuxleya* or *Pleurostylodon*, and the original description of *Anisotemnus* could apply to either of those genera except for three points: 1. The upper molars were said to have an isolated fossette in the anteroexternal corner. The specimens show that such a statement was a simple *lapsus calami*, the fossette being posteroexternal as in both *Thomashuxleya* and *Pleurostylodon*. 2. P_{2-3} were said to be compressed laterally, almost secant. This statement is an exaggeration; the teeth are somewhat crushed. 3. The lower molars were said to form a convex anteroposterior line and the upper molars a concave line in the same direction. I do not understand this last point; the lineation does not seem to differ in any way from that in any contemporaneous notoungulates.

In fact the genus does not seem to differ in any readily diagnostic way from *Thomashuxleya*, on one hand, or *Pleurostylodon*, on the other. However, the type species is sharply distinct from the types of either of those genera. Even though a clear and undoubted diagnosis is not given, the genera may provisionally be retained.

The type of *Toxotemnus* was also originally described as a species of *Isotemnus* and then removed to a new genus, but still in the Isotemnidae. The description was not differential from *Pleurostylodon* or *Anisotemnus*, doubtfully so from *Isotemnus*, although the type cannot, indeed, be kept in the latter genus. *Toxotemnus* was based essentially on a single, badly broken tooth, nearly unidentifiable but near enough to that of *Anisotemnus distentus* to be disposed of in the synonymy of that genus and species.

A second species referred by Ameghino (1901, p. 384) to *Anisotemnus*, *A. latidens*, belongs in *Isotemnus* and is treated under that genus.

Anisotemnus distentus (Ameghino, 1901)

Plate 26, figures 1, 2, 5–7

Isotemnus distentus Ameghino, 1901, p. 411.

Anisotemnus distentus: Ameghino, 1902a, p. 26. Simpson, 1964, p. 17.

Isotemnus lophiodontoides Ameghino, 1901, p. 411.

Toxotemnus lophiodontoides: Ameghino, 1904a, vol. 58, p. 235.

Type: M.A.C.N. No. 10588, crushed and broken right lower jaw with P_2–M_3, fragment of left lower jaw with P_1, loose P_{2-4}, loose right I^1 and I^2 and left I^2, fragment of upper jaw with left I^3 and C, right P^2–M^2, separated but with bone fragments adhering, and other, nondescript fragments, labeled "Todo de uno," i.e., parts of the same individual, which is probably correct. "Este de R. Chico. Golfo de S. Jorge. Pico Salamanca."

Type of *"Isotemnus" lophiodontoides*: M.A.C.N. No. 10615, broken right M^2 (type or lectotype), two not associated broken right P^4's, and three other tooth fragments; west of the Río Chico.

Hypodigm: Types, as above, and the following specimens: M.N.H. Tournouër Collection No. 30, part of right maxilla with P^1–M^3, "Cerro Negro" (the same locality as Carlos Ameghino's and our Colhué-Huapí, or south of Lake Colhué-Huapí); this is probably the original of Gaudry, (1904, fig. 16, *"Pleurostylodon"*), although the teeth are there shown reversed and M^{2-3}, although here present, seem to be based on M.N.H. No. 35. M.N.H. Tournouër Collection No. 35, left M^2 in maxillary fragment and loose, doubtfully associated left M^3, "Cerro Negro" (apparently the originals of M^{2-3} in Gaudry's curiously composite figure, 1904, fig. 16). M.N.H. Tournouër Collection No. 26, much of left lower jaw with P_2, P_4–M_3, and alveoli for all other teeth, "Cerro Negro" (the original of Gaudry, 1904, fig. 26, although P_3, absent before burial, is shown as present in that figure). A.M.N.H. No. 28696, associated parts of lower jaw with right I_2–M_3 (M_3 unerupted) and left P_3–M_2, Colhué-Huapí. A.M.N.H. No. 29389, part of right lower jaw with deeply worn P_3–M_3 (M_3 broken), Colhué-Huapí.

Horizon and Locality: Casamayoran, Patagonia, east and west of Río Chico and south of Colhué-Huapí.

Diagnosis: Sole species now referred to the genus. Measurements are given in tables 50 and 51.

The extremely inadequate type of (as eventually named) *Toxotemnus lophiodontoides* is markedly broader, absolutely and relative to its length, than the corresponding tooth of the type of *A. distentus*. The former type is doubtfully determinable, and the name is at least a possible synonym of *A. distentus*. The two are from different localities, but that in itself does not imply specific distinction.

The specimens in the Muséum National d'Histoire Naturelle in Paris and the American Museum of Natural History are all from a third (quite extensive) locality. They are almost surely conspecific among themselves. Measurements and morphology are in adequate agreement, and the lower dentitions in the American Museum occlude well with (a cast of) the upper dentition in Paris, if allowance be made for the obvious fact that they are of different individuals. It is not so sure that this species is *Anisotemnus distentus* and (or) *"Toxotemnus lophiodontoides."*

TABLE 50

Measurements of the Lower Teeth of the Type and Referred Specimens of *Anisotemnus distentus*

	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
M.A.C.N. No. 10588[a]	12.4	7.9	13.4	9.3	14.7	8.9	16.8	9.9	22.6	10.8	24.0	14.3	27.8	13.7
A.M.N.H. No. 28696	12.1	9.4	12.7	9.0	15.0	10.3	15.6	12.0	19.1	13.4	22.7	14.9	—	—
A.M.N.H. No. 29389[b]	—	—	—	—	13.5	8.8	14.0	10.9	18.3	12.6	19.5	13.8	—	13.7
M.N.H. Tournouër No. 26	—	—	11.8	8.5	—	—	13.6	10.1	—	—	20.5	13.6	26.4	12.7

[a] Type.
[b] Worn.

TABLE 51

Measurements of the Upper Teeth of the Type and Referred Specimens of *Anisotemnus distentus*

	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
M.A.C.N. No. 10588[a]	—	—	13.0	15.1	*ca.* 16	17.1	15.2	23.6	23.2	25.5	25.1	28.8	—	—
M.A.C.N. No. 10615	—	—	—	—	—	—	—	—	—	—	*ca.* 26½	*ca.* 35	—	—
M.N.H. Tournouër No. 30	11.7	10.4	13.3	17.6	14.6	21.5	15.7	27.2	21.8	31.3	22.6	32.3	18.3	29.5
M.N.H. Tournouër No. 35	—	—	—	—	—	—	—	—	—	—	23.4	30.7	18.3	27.0

[a] Type.

The teeth, upper and lower, are for the most part shorter and relatively or absolutely wider than those of the type of *A. distentus.* However, the narrowness of the teeth of the latter specimen seems to be affected in part by crushing, and in any event the differences are not so great as to exclude reference to a single species.

Gaudry's composite and somewhat restored figures, mentioned above, are inaccurate as to fine detail but give a reasonably adequate impression of the teeth.

ACOELOHYRAX AMEGHINO, 1902

Acoelohyrax AMEGHINO, 1902a, p. 10; 1906, p. 467. SCHLOSSER, 1923, p. 609.

Plexotemnus AMEGHINO, 1904a, vol. 58, p. 236; 1906, p. 468. SCHLOSSER, 1923, p. 615.

TYPE: *Acoelohyrax coronatus.*

TYPE OF SYNONYM: *Plexotemnus complicatissimus.*

DISTRIBUTION: Casamayoran and Mustersan; Patagonia.

DIAGNOSIS: Crowns of cheek teeth higher than usual in other isotemnids. Upper premolar and molar ectolophs high but otherwise nearly as in *Pleurostylodon*; lingual faces long, and especially on molars somewhat concave vertically and bulging at base; posterior cingula, most noticeably on premolars but also on molars, projecting posterolingually and forming a distinct lobe; coronal pattern resembling that in *Pleurostylodon* but with numerous cristae, the complication in that region approached only by most complex variants of *Pleurostylodon* and not quite equaled by any; no distinct lingual cingula. M^3 relatively more elongate, less reduced posteriorly than in *Pleurostylodon.* Lower molars with metaconid not bifid as in *Pleurostylodon*, but with slight, crestlike, anterior projection from metalophid; protolophid with a partly separate, cusplike, lingual termination; on unworn molars a small cuspule anteromedial in the talonid, just lingual to anterior end of hypolophid.

Acoelohyrax was based essentially on a single upper tooth, which Ameghino believed to be a molar but which is almost certainly P^4. Lower molars were referred by Ameghino, but probably in error. The P^4 is distinctive in being somewhat higher-crowned than that of most isotemnids (but lower than that of typical archaeohyracids), with a complex set of cristae and associated crests, and with a projecting posterolingual cingular lobe. *Plexotemnus* was described at length but was not compared with any other genus, and the description does not include any distinction from *Acoelohyrax*, then referred to a different family. The figured M^{2-3} of *Plexotemnus* (Ameghino, 1904b, figs. 253, 312) are part of a specimen with P^4–M^3, hence directly comparable with the P^4 on which *Acoelohyrax* was based. The two are not identical, but the most distinctive characters of P^4 of *Acoelohyrax*, mentioned above, are also those of P^4 of *Plexotemnus.* Generic identity cannot be considered certain, but it is probable that the two supposed genera are closely related, and it is a reasonable working hypothesis to unite them pending further knowledge.

Ameghino referred *Acoelohyrax* to the Archaeohyracidae but considered it intermediate between *Acoelodus* and *Pseudhyrax.* The single, isolated P^4 could indeed belong to the Oldfieldthomasiidae (Ameghino's "Acoelodidae"), the Archaeohyracidae, or other groups, and lower teeth referred to *Acoelohyrax* by Ameghino probably do belong to the Oldfieldthomasiidae. However, those lower teeth probably do not belong to *Acoelohyrax.* I long wavered between placing the single tooth surely referable to that genus in the Oldfieldthomasiidae, the Archaeohyracidae, or the Isotemnidae. *Plexotemnus* also has resemblances to all three families and even, although in less degree, to the Notohippidae, but on balance it is closest to the Isotemnidae, particularly to *Pleurostylodon* of which its cheek teeth could be simply a somewhat more complex and higher-crowned version. *Plexotemnus*, then, is at least tentatively acceptable as isotemnid. It is not certain that *Acoelohyrax* is the same genus, but that it is gives us a hypothesis to go on, and *Acoelohyrax* is therefore also tentatively considered isotemnid. Unfortunately the less-known and generally more dubious name has priority.

The type of *Plexotemnus complicatissimus* is from the Casamayoran ("Notostylopense") of Colhué-Huapí. *Acoelohyrax* was specified as from the upper Casamayoran ("Partie supérieure des couches à Notostylops"), with no locality given. The American Museum of Natural History has a series of specimens, discussed below as *Acoelohyrax ?coronatus*, of unfortunately dubious origin but probably Casamayoran. There is, however, a specimen collected by me in the Mustersan of Cerro Blanco (near Colhué-Huapí) that is specifically distinct but otherwise very close to *Acoelohyrax* and its probable synonym *Plexotemnus*: A.M.N.H. No. 29487, discussed below under *?Acoelohyrax* spp. indet. There are also specimens from the Mustersan in the Ameghino Collection that resemble that specimen as well as (but less closely) Casamayoran *Acoelohyrax-Plexotemnus*. Those Mustersan specimens were referred to *Trimerostephanos* by Ameghino.

The type of *Trimerostephanos*, *T. scabrus* Ameghino, 1895, and at least one other supposed species, *T. scalaris* Ameghino, 1897, are almost certainly Deseadan in age.[1] In 1901 Ameghino named four other supposed species, *T. coalitus*, *coarctatus*, *sigma*, and *ultimus*, from the Mustersan. The unfigured type and presumably only specimen of "*T.*" *ultimus* has been lost or mislaid, and the description is inadequate for conclusion. The other Mustersan specimens referred to *Trimerostephanos* resemble *Acoelohyrax* and its probable synonym *Plexotemnus* much more closely than they resemble Deseadan *Trimerostephanos*. The latter reference would be suspect in any case, because there are no adequately substantiated cases of genera common to the Mustersan and Deseadan. There is also doubt about supposed cases of genera common to the Casamayoran and Mustersan, and there are no species common to the two, but there are species so similar that their generic separation is dubious at least. Casamayoran *Thomashuxleya* versus Mustersan *Periphragnis* and Casamayoran *Anisotemnus* versus Mustersan *Rhyphodon* are examples in the present family (discussed below).

Mustersan "*Trimerostephanos*," surely distinct from true *Trimerostephanos*, may also prove to be generically distinct from *Acoelohyrax* or *Plexotemnus*. At present, however, I cannot provide an objective diagnosis reasonably placed at the generic level, and I therefore refer the Mustersan specimens in question to *?Acoelohyrax*.

Acoelohyrax coronatus Ameghino, 1902

Plate 25, figure 10

Acoelohyrax coronatus Ameghino, 1902a, p. 10; 1904b, p. 309, fig. 411.

Type: M.A.C.N. No. 10781, isolated left P^4, type or lectotype; also three isolated lower molars, possibly syntypes but probably not of this genus.

Hypodigm: Lectotype only.

Horizon and Locality: Late Casamayoran, Patagonia, *fide* Ameghino. No closer locality given.

Diagnosis: P^4 of type measuring 8.3 by 10.3 mm.; smaller and less transverse than P^4 of the type of *A. complicatissimus*. Metacone fold nearly as prominent as paracone fold. Posterolingual cingular lobe moderate.

Acoelohyrax ?coronatus

A.M.N.H. Nos. 29370–29381, inclusive, are upper and lower jaw fragments and teeth, most if not all of which belong to this general group although of dubious origin and specific, perhaps also generic, assignment. In addition to the collections on which this study is essentially based, as elsewhere enumerated, the American Museum of Natural History has various Argentine fossil mammals acquired by gift, exchange, or purchase through the years from the Ameghinos onward. For the most part the early Cenozoic specimens in these odd lots add nothing to what is known from the more basic materials for

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[1] The collection described in 1895 probably included no pre-Deseadan mammals. That described in 1897 did include Casamayoran and Mustersan as well as Deseadan mammals, but the faunas were not then distinguished. *Trimerostephanos scalaris* was not subsequently considered Mustersan when the distinction was made. Loomis (1914, pp. 130–131) treated *T. augustus* Ameghino, 1897, and *T. biconus* Ameghino, 1897, as Deseadan, ignoring the fact that Ameghino had later stated that those species are Casamayoran ("Notostylopéen") and had removed both from *Trimerostephanos*. The former was made type of *Dimerostephanos* and the latter (correctly) referred to *Pleurostylodon*. It should further be noted that the upper figure on page 140 of Loomis (1914), said to be of the type of *Asmodeus scotti* from the Deseadan, is in fact a Casamayoran specimen of *Thomashuxleya*. There are similar errors throughout Loomis' book.

TABLE 52

LOWER TEETH OF THE *Acoelohyrax* GROUP

	P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W
A. complicatissimus								
M.A.C.N. No. A35-1[a]	9.1	7.2	11.9	7.5	13.6	8.0	17.7	9.4
A. ?coronatus								
A.M.N.H. No. 29382	—	—	8.1	6.6	10.3	6.5	—	—
A.M.N.H. No. 29383	—	—	9.8	5.9	10.9	7.0	—	—
A.M.N.H. No. 29385	—	—	—	—	9.5	7.1	14.5	7.1
A.M.N.H. No. 29386	—	—	—	—	9.5	6.9	13.5	6.3
?A. coalitus								
M.A.C.N. No. 10964[a]	11.0	8.2	*ca.* 14	9.5	—	—	—	—
?A. coarctatus								
M.A.C.N. No. 10965[b]	7.8	6.7	*ca.* 8½	*ca.* 7	10.8	8.1	16.5	8.5
M.A.C.N. No. 10966[b]	7.9	6.6	—	—	—	—	—	—
?A. sigma								
M.A.C.N. No. 10967[a]	—	—	8.6	6.3	9.0	*ca.* 7	14.8	6.5

[a] Type.

[b] Syntypes.

this work and furthermore have poor data, if any. They have therefore generally not been specified here. However, there are some that do add to knowledge, even if they remain enigmatic and may raise questions that they do not answer. It then seems advisable to take some notice of them, which is true of the specimens catalogued as at the beginning of this paragraph.

These are part of a collection made at two localities, one near Cerro Talquino and one near Sierra Cuadrada in Chubut, Argentine Patagonia. The former fossil site is in fact some distance southwest of Cerro Talquino, in the southeast corner of Lote 15, some 35 kilometers north of Lake Colhué-Huapí and some 15 kilometers south-southeast of the Laguna de los Palacios. The Sierra Cuadrada locality is south of that sierra, in a barranca opposite the Guadal Colorado. Field data, including sketch stratigraphic profiles, were taken, but through later carelessness, not chargeable to the collector, the connection between these data and the individual specimens was lost. In most cases it is therefore now impossible to say from which of the two regions or from what bed in either one a particular specimen was derived. Some specimens, such as fragments of the genera *Polydolops*, *Notostylops*, and *Oldfieldthomasia*, are certainly Casamayoran; others are probably Mustersan; and a few are possibly Deseadan—the latter, at least, apparently surface drift.

These doubts are particularly annoying in the present instance, because the pied[1] collection includes more specimens of the *Acoelohyrax-"Plexotemnus"* group than all others put together. As noted above, the stratigraphic distribution of the group and its specific taxonomy were already uncertain, and this material makes them even more so. There is no certainty, but there is some probability, that these particular specimens are from the Casamayoran of Cerro Talquino.

As shown by the measurements of cheek teeth in tables 52 and 53, differences in size among all the Casamayoran specimens placed in the *Acoelohyrax* group range up to 50 per cent, and differences in proportion are equally striking. It is unlikely that only one species is present, especially as variation in length, more affected by wear, tends to be as great as in width, little affected by wear. It is possible to divide these specimens very tentatively into a smaller species, near *A. coronatus* and including A.M.N.H. Nos. 29371, 29372,

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[1] In typographic analogy.

TABLE 53

Upper Teeth of the *Acoelohyrax* Group

	P²		P³		P⁴		M¹		M²		M³	
	L	W	L	W	L	W	L	W	L	W	L	W
A. coronatus												
M.A.C.N. No. 10781[a]	—	—	—	—	8.3	10.3	—	—	—	—	—	—
A. coronatus												
A.M.N.H. No. 29371	—	—	—	—	8.2	11.2	*ca.* 10	*ca.* 12½	—	—	—	—
A.M.N.H. No. 29372	—	—	—	—	9.2	12.3	*ca.* 13½	*ca.* 15	14.6	16.3	—	—
A.M.N.H. No. 29373	—	—	—	—	—	—	—	—	14.9	16.2	—	—
A. complicatissimus												
M.A.C.N. No. A35-1[a]	—	—	—	—	*ca.* 9	15.4	14.1	15.0	16.0	18.8	16.8	18.2
?*A. coarctatus*												
M.A.C.N. No. 10966B	—	—	—	—	—	—	—	—	*ca.* 11½	16.3	14.8	15.6
?*A.* sp.												
A.M.N.H. No. 29487	6.9	8.5	7.3	8.9	7.6	10.5	11.1	12.1	12.2	13.3	—	—

[a] Type.

and 29373, and a larger, near *A. complicatissimus*. However, especially with the paucity of field data and absence of multiple faunally associated specimens, there is little confidence in the biological validity of a present attempt to define species in this group.

Although A.M.N.H. No. 29371 is near *A. coronatus* in size, it is more like *A. complicatissimus* in the weaker, almost absent metacone fold and stronger posterolingual cingular lobe. A.M.N.H. Nos. 29372 and 29373 are so closely similar that they are almost certainly of the same species. They are larger than A.M.N.H. No. 29371 and to that extent more like the type of *A. complicatissimus*, from which, however, they differ in other respects such as the less transverse P^4. They are still within the possible range of *A. coronatus*.

A.M.N.H. No. 29370 has three left upper teeth, probably dm^{2-4}, although it has not been practical to dissect the specimen in search of replacing teeth. Pertinence to this group is uncertain. The teeth are relatively long, narrow, and low-crowned, which could well be true of deciduous teeth.

A.M.N.H. Nos. 29382–29386, inclusive, are partial lower jaws referred to this group, probably from Cerro Talquino or possibly Sierra Cuadrada. Measurements of the sufficiently preserved teeth are given in table 52, along with those of the type of *A. complicatissimus*. As far as can be seen, they agree well with that better-preserved type, except in being consistently smaller, and may therefore be very tentatively referred to *A. coronatus*. Where the characters are visible they share with *A. complicatissimus* the distinctions incorporated in the generic diagnosis. Although the anterior part is not well preserved, A.M.N.H. No. 29382 seems to have had a small canine and short symphyseal region, as in (true) *Trimerostephanos*. Although adult, it also seems to have the symphysis unfused, an unusual condition for a notoungulate.

In the same collection are two partial lower jaws, A.M.N.H. Nos. 29387 and 29388, of about the same size and at first sight quite similar. Nevertheless they are clearly not congeneric and probably belong to *Eohyrax*, here placed in a different family. Among the distinctions are that aff. *Acoelohyrax* (or *Plexotemnus*) lower molars are less hypsodont, develop no fossetids or only transitory ones with wear, and have the length of the trigonid definitely less than that of the talonid rather than subequal as in *Eohyrax*. Those differences are all also distinctions between isotemnids and archaeohyracids in general and tend to comfirm the reference of the *Acoelohyrax* (or *Plexotemnus*) group to the Isotemnidae.

Acoelohyrax complicatissimus (Ameghino, 1904), new combination

Plate 26, figures 3, 4, 9, 11

Plexotemnus complicatissimus AMEGHINO, 1904a, vol. 58, p. 236; 1904b, p. 192, figs. 253, 312.

TYPE: M.A.C.N. No. A55-1, four upper and lower jaw fragments with right P^4–M^3, left M^{2-3}, right P_4–M_2, fragment of M_3, left M_3, and fragment of M_2. These are of the same individual age and occlude perfectly, so that Ameghino was probably right in considering them to be parts of a single animal. However, as a precaution the right P^4–M^3 are taken as lectotype. The cited figures are of M^{2-3} (only) of that piece. Labeled as from Casamayoran ("Notostylopense") of Colhué-Huapí.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayoran, Patagonia. Type from Colhué-Huapí.

DIAGNOSIS: Type P^4 measuring *ca.* 9 by 15.4 mm., somewhat larger and distinctly more transverse than type of *A. coronatus*. Metacone fold less prominent. Posterolingual cingular lobe prominent.

The generic diagnosis given above is in fact based on the type (or syntypes) of this species and not on the highly inadequate type specimen of the type species. If, as remains possible although I think it unlikely, it should turn out after all that *Acoelohyrax* and *Plexotemnus* are distinguishable at the generic level, then the present diagnosis of "*Acoelohyrax*" will be that of *Plexotemnus*. What, in that case, would be the diagnosis of *Acoelohyrax* is not predictable. What is known of *A. coronatus* does conform to the generic diagnosis based on *A.* (or *Plexotemnus*) *complicatissimus*. The two species probably are distinct, but are not certainly so.

Some further characteristics of teeth perhaps of this genus or group are given in connection with the following Mustersan species. Measurements are given in tables 52 and 53.

?**Acoelohyrax coalitus** (Ameghino, 1901), new combination

Plate 26, figure 12

Trimerostephanos coalitus AMEGHINO, 1901, p. 415.

TYPE: M.A.C.N. No. 10964, anterior part of right lower jaw with two teeth, probably P_4–M_1.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Mustersan, Patagonia. No more precise data.

DIAGNOSIS: P_4–M_1 of the inadequate type resembling those of *A. complicatissimus* in visible characters but larger and somewhat higher-crowned. Measurements as in table 52.

The inadequately preserved anterior part of this specimen seems to have been short, as noted above for a probably Casamayoran specimen. It was probably this characteristic, so unlike *Pleurostylodon*, for example, that led Ameghino to put this species in the Deseadan genus *Trimerostephanos*. That may be a character shared by *Acoelohyrax* and *Trimerostephanos*, which seem nevertheless to be quite distinct in the structure of the cheek teeth.

?**Acoelohyrax coarctatus** (Ameghino, 1901), new combination

Plate 26, figures 8, 10, 13

Trimerostephanos coarctatus AMEGHINO, 1901, p. 416; 1904b, p. 168, figs. 215, 216.

TYPE: Two lots of specimens, each labeled as of this species in the Ameghino Collection: M.A.C.N. No. 10965A, part of left lower jaw with deeply worn P_4–M_3, lectotype; M.A.C.N. No. 10965B, right P^{2-4}, M^{2-3} and left P^{2-4}, M^{2-3} of one individual; M.A.C.N. No. 10965C, isolated upper molar, perhaps M^1, not same individual as M.A.C.N. No. 10965B; M.A.C.N. No. 10966A, left side of symphysis and deeply worn P_{1-4}; M.A.C.N. No. 10966B, isolated left upper molar, perhaps M^2; M.A.C.N. No. 10966C, isolated left upper molar, perhaps M^1; M.A.C.N. No. 10966D, isolated left M^3.

Ameghino's original description could not have been based entirely on any one of those specimens but was probably based on M.A.C.N. Nos. 10965A and 10966A, which may therefore be considered syntypes. M.A.C.N. No. 10966 has two labels, *T. coalitus* and *T. coarctatus*, implying that one or more of M.A.C.N. Nos. 10966B, 10966C, and 10966D were referred to the supposedly distinct "*T. coalitus*."

HYPODIGM: The syntypes. M.A.C.N. No. 10965B occludes fairly well with the lectotype and probably is of the same species. It could even be of the same individual, so is also tentatively included in the hypodigm, and the similar M.A.C.N. No. 10966B is also tentatively included. The other specimens may not be of this species.

HORIZON AND LOCALITY: Mustersan, Patagonia. No more exact data.

DIAGNOSIS: Smaller than *?A. coalitus* but otherwise similar to the very limited extent that specimens are comparable. Measurements are given in tables 52 and 53.

M.A.C.N. No. 10966A has the roots of incisors and canine. The roots increase in size from I_1 to I_3. The canine root is of about the same size as I_3 or P_1, not enlarged as in all other Casamayoran and Mustersan isotemnids in which this character is known.

The original of Ameghino's illustration (1904b, fig. 215) is M.A.C.N. No. 10966B, neither type nor syntype but probably of this species. The original of Ameghino's figure 216 (1904b) is M.A.C.N. No. 10965C and probably does not belong to this species or, indeed, to this genus.

?**Acoelohyrax sigma** (Ameghino, 1901), new combination

Plate 27, figures 3, 4

Trimerostephanos sigma AMEGHINO, 1901, p. 416.

TYPE: M.A.C.N. No. 10967, part of left lower jaw with worn M_{1-3}.

HYPODIGM: Type and M.A.C.N. No. 10969, fragment of right lower jaw with poorly preserved M_{1-3}, referred by Ameghino probably correctly. Under the same label is another right lower jaw fragment with M_{1-2} and heel of P_4, which is *incertae sedis* and perhaps not this species.

HORIZON AND LOCALITY: Mustersan, Patagonia. No more exact data.

DIAGNOSIS: Type slightly smaller than type of "*T. coarctatus*"; trigonids relatively slightly longer, perhaps owing to differing wear. Measurements are given in table 52.

Synonymy with "*T.*" *coarctatus* is quite probable, but the data are so poor that it cannot be strongly affirmed. These specimens add nothing significant to knowledge of the group.

?Acoelohyrax spp. indet.

Plate 27, figures 1, 2

A.M.N.H. No. 29374, probably M^3 but possibly M^2, is one of the dubiously Casamayoran specimens probably from Cerro Talquino, as discussed above. If M^3, it is unusual but agrees with that of *A. complicatissimus* in not having the posterior part reduced. It is further unusual, in fact unique, in being longer than wide, measuring 18.2 mm. in length and about 16 mm. in width. In pattern it does closely resemble M^3 of *A. complicatissimus*.

A.M.N.H. No. 29487 is part of a right maxilla with P^2–M^2 from a Mustersan level at Cerro Blanco. Its M^2 closely resembles that of M.A.C.N. No. 10966B, referred to *?A. coarctatus*, but it is considerably narrower both absolutely and relative to its length. It could nevertheless be the upper dentition of *?A. coarctatus*. In any event, it is one of the best specimens known for this highly distinctive group of species and merits description. In general the teeth are closely similar to those known from the Casamayoran and placed in *Acoelohyrax* (or *Plexotemnus*) except for variable details and for being somewhat higher-crowned, as might be expected from its later date.

On this specimen (see pl. 27, figs. 1, 2) P^{2-4} have strong parastyle and paracone folds, but the metacone fold is vague. A metastyle fold becomes distinct toward the base of the crown. The anterior cingulum, basal on the crown, is strong and encloses a narrow basin. The outer part of the posterior cingulum is comparable in position and development, but its internal part rises on the crown and loops around to the posterolingual part of the protocone slope, forming a prominent and expanded basin. The protocones are high and subconical, not planed off to a flat coronal surface, even after considerable wear. On P^{2-3} there is no true protoloph. The anterior crest from the paracone region does not reach the protocone but is separated from it by a deep notch. This crest has the aspect of being only the most anterior member of a complex system of at least five irregular cristae. On P^4, however, the notch between this crest and the protocone is shallow, and a protoloph may be said to be present. On P^{2-4} there is a nominal metaloph along the posterior edge of the crown from the ectoloph to the posterior slope of the protocone. There is a small crochet, which unites with the most posterior crista.

This premolar pattern, although possibly derived from the basic isotemnid type, is unlike any other known to me and is the most complex that I have seen in these faunas.

M^{1-2} are closely similar. They have distinct protocone and hypocone, united nearly to their apices but with a groove between them, or slightly more anterior than the apical notch between them, on the lingual face. There is a typical oblique protoloph and an equally typical transverse metaloph. The coronal pattern between these lophs, as seen especially on M^2, which is, of course, less worn than M^1, can be considered as basically reducible to the pattern of a simple variant of the typical higher notoungulate molar, with two cristae, the first free and the second united distally (lingually) with the crochet. The actual details are, however, much more complex, and, although probably variable in different individuals, they suggest that this basic pattern may to some extent be subjective. On this particular tooth, between the simple, free first main crista and the protoloph there is a very small subsidiary crista that nearly meets but (at this level) does not fuse with a slightly larger spur (antecrochet-like) from the protoloph. Between the first and second main cristae there is a still smaller crista-like projection. The nominal second main crista is not simple but is made up of three distinct cristae, quite separate near the ectoloph but fusing with one another and with the crochet more lingually, near the middle of the crown. There is even another tiny, crista-like fold between the second and third of these subsidiary cristae forming the second major crista.

The anterior cingulum of M^{1-2} is well developed and is much like that of P^{2-4}. The posterior cingulum is high on the crown, encloses a narrow, deep fossette, and projects lingually as a small but distinct third lobe of the inner face.

"Trimerostephanos" ultimus Ameghino, 1901, *nomen vanum*

Trimerostephanos ultimus Ameghino, 1901, p. 416.

Type: Not found in the Ameghino Collection. The original description refers to M_1 and M^{1-3} in the usual (not Ameghino's) notation.

Hypodigm: For this work, none.

Diagnosis: (Translated in full from Ameghino into English and present terminology): Size very small. Upper molars with buccal face strongly undulating. Lower molars with strong basal cingula on buccal and lingual sides. Length of M_1, 6½ mm. Length of M^{1-3}, 20 mm.

Neither genus nor species is recognizable from Ameghino's description alone, which does, however, make it seem highly unlikely that the lost type is of the same genus, or even family, as other Mustersan "*Trimerostephanos*," that is, *?Acoelohyrax.*

ISOTEMNUS Ameghino, 1897

Isotemnus Ameghino, 1897a, p. 480; 1901, p. 410; 1906, p. 468. Scott, 1923, p. 615; 1937a, p. 518: Schlosser, 1923, p. 615.

Prostylops Ameghino, 1897a, p. 486; 1902a, p. 26; 1906, p. 468.

Eochalicotherium Ameghino, 1901, p. 417; 1906, p. 468. Schlosser, 1923, p. 615.

Lelfunia Roth, 1902, p. 255. Simpson, 1936d, p. 78 (as synonym of *Isotemnus*).

Dimerostephanos Ameghino, 1902a, p. 30; 1906, p. 468.

Amphitemnus Ameghino, 1904a, vol. 58, p. 234; 1906, p. 468.

Type: *Isotemnus primitivus.*

Types of Synonyms: Of *Prostylops*, *P. typus;* of *Eochalicotherium*, *E. cretaceum* (by selection hereby); of *Lelfunia*, *L. haugi;* of *Dimerostephanos*, *Trimerostephanos augustus;* of *Amphitemnus*, *A. nucleatus* (by selection hereby).

Distribution: Casamayoran, Patagonia.

Diagnosis: Dentition generally similar to that of *Pleurostylodon* but more brachydont. M^{1-2} with more distinct metacone fold, nearly equal to paracone fold, and with relatively well-separated protocone and hypocone. Lingual cingula consistently absent from upper cheek teeth. Basal paracone region on labial face characteristically flattened on upper cheek teeth. Lower molars with cusp anterior to lophoid metaconid (evidently not a true paraconid) strongly developed, bunoid, more distinct from metaconid than in *Pleurostylodon*. Entoconid somewhat less elongate transversely or lophoid than in *Pleurostylodon.*

Prostylops, named at the same time as *Isotemnus* but on a following page, was based on a single broken lower tooth, which has not been found on repeated search of the Ameghino Collection. The original description is hardly recognizable but could equally well apply to a lower molar of *Isotemnus*. In 1902 Ameghino referred upper premolars and molars to *Prostylops typus* and recharacterized the genus on that basis. The new description does not distinguish the genus from *Isotemnus*, to which the referred upper teeth belong. They were not associated with lower teeth, and the reason for reference to *Prostylops* was not given and is not evident. In the same publication, Ameghino (1902a) also transferred to *Prostylops* a species previously and, as I believe, correctly placed in *Isotemnus: I. apicatus*. In the absence of the original type specimen, *Prostylops* is of somewhat dubious affinities, but there is reason from Ameghino's own work to consider it a probable synonym of *Isotemnus*. I do so consider it, and as first reviser I select *Isotemnus* as the name for the genus, such action obviously tending to promote nomenclatural stability.

Eochalicotherium was said to have the lower molars more brachydont than in *Isotemnus*, the cusps larger, lower, blunter ("émoussés") and separated by shallow hollows. In fact at that time lower molars of *Isotemnus* had not been correctly identified, and, as far as distinctive at all, the description distinguished these teeth from those of *Pleurostylodon*. M^{1-2} of *Eochalicotherium* were also mentioned, but these have not been found in the collection, and the description does not distinguish them from *Isotemnus.* At the same time Ameghino (1901) also placed two other species in *Eohalicotherium,* both based on lower teeth. In fact he used this generic name for lower cheek teeth different from those of *Pleurostylodon* but not shown (or known) to be different from *Isotemnus.* Even now, lower teeth positively associated with upper teeth of *Isotemnus* are unknown, but there can be no serious doubt that *Eochalicotherium* is the lower dentition of *Isotemnus.* Morphology (heights of crowns, size, pattern) is congruous, frequency in collections is suitable, and specimens of *Eochalicotherium* articulate perfectly with those of *Isotemnus.*

Lelfunia was based on a single upper molar, compared by Roth with *Maxschlosseria* but not with *Isotemnus.* Although the locality (Gaiman in the Chubut Valley) and the age (Riochican) differ from those of typical *Isotemnus,* the tooth cannot be distinguished generically from *Isotemnus* and is specifically near *I. primitivus.*

Dimerostephanos was based on lower teeth originally referred to the Deseadan genus *Trimerostephanos.* The most distinctive character in the original definition was lack of differentiation among the lower incisors, canine, and P_1, which was based on fragments not containing the crowns of those teeth and was mistaken. Stereotyped primitive lower teeth belonging to at least three genera (*Isotemnus, Pleurostylodon, Notostylops*) and two families were placed here by Ameghino. The type specimen of the type species seems to belong to *Isotemnus* and was not differentiated from that genus by the original description.

Amphitemnus was based on one broken lower molar, not differentiated from *Isotemnus* or *Eochalicotherium,* to both of which synonymous supposed genera it rather clearly belongs. It was said to be intermediate between *Isotemnus* and *Albertogaudrya,* genera belonging in different orders, but the supposed comparison with *Isotemnus* was probably with *Pleurostylodon.* Neither the description nor the specimens reveal any reliable difference from lower teeth now referred to *Isotemnus.*

Although evidently close to *Pleurostylodon,* this genus is clearly distinct and readily recognized from either upper or lower molars if not too worn.

The Casamayoran upper teeth, on one hand, and lower teeth, on the other, now referred to this genus seem to fall into two size groups, although these are not clearly defined. No consistent morphological characters other than size have been noted in the few specimens involved. It is reasonable to assume that there are (at least) two specific taxa corresponding with the two apparent size groups, and that arrangement is tentatively adopted here. Some support for the arrangement is derived from the fact that upper and lower teeth in each of the size groups here distinguished occlude well. However, in the absence of associated upper and lower dentitions and in view of the small number of specimens the arrangement is decidedly provisional.

"*Isotemnus*" *emundatus* and "*Eochalocotherium*" *minutum* clearly do not belong in this genus and have been transferred to *Maxschlosseria.* "*Isotemnus*" *consumatus* has also been placed in *Maxschlosseria* somewhat more tentatively. *Lelfunia haugi* is placed in *Isotemnus* but is probably a distinct, earlier (Riochican) species. *?Isotemnus ctalego* is also retained as a separate Riochican species.

Isotemnus primitivus Ameghino, 1897

Plate 27, figures 5–8; plate 28; plate 29; plate 30, figures 1–4, 8

Isotemnus primitivus AMEGHINO, 1897a, p. 481, fig. 62; 1898, p. 193; 1904b, p. 143, figs. 177, 461.

Isotemnus conspiquus AMEGHINO, 1897a, p. 482; 1898, p. 173.

Trimerostephanos angustus AMEGHINO, 1897a, p. 484; 1898, p. 173.

Eochalicotherium cretaceum AMEGHINO, 1901, p. 417.

Amphitemnus nucleatus AMEGHINO, 1904a, vol. 58, p. 234.

Amphitemnus transitorius AMEGHINO, 1904a, vol. 58, p. 234.

Dimerostephanos angustus AMEGHINO, 1902a, p. 30.

TYPE: M.A.C.N. No. 10556, part of right maxilla with P^2–M^3. No field data.

TYPES OF SYNONYMS: Of *Isotemnus conspiquus,* M.A.C.N. No. 10583, part of right maxilla with badly worn M^{1-2} (lectotype)

TABLE 54

MEASUREMENTS OF UPPER TEETH OF *Isotemnus*

	P^2		P^3		P^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W	L	W	L	W
I. primitivus and synonyms												
I. primitivus												
M.A.C.N. No. 10556[a]	8.5	11.4	9.3	14.9	10.1	17.1	13.0	18.6	14.7	20.8	13.3	19.0
I. conspiquus												—
M.A.C.N. No. 10583[a]	—	—	—	—	—	—	—	—	16.0	23.4	—	—
A.M.N.H. No. 28650	—	—	10.4	15.1	10.7	19.0	14.5	21.1	15.6	22.4	14.2	20.4
I. latidens and synonyms												
I. enecatus												
M.A.C.N. No. 10587[a]	—	—	—	—	*ca.* 7½	—	*ca.* 10	—	*ca.* 12	—	*ca.* 12	—
I. apicatus												
M.A.C.N. No. 10614[a]	—	—	6.8	10.6	6.9	12.2	9.5	13.4	10.3	14.1	—	—
?*I. ctalego*												
A.M.N.H. No. 28576	—	—	—	—	7.8	—	9.5	—	—	—	—	—

[a] Type.

TABLE 55

MEASUREMENTS OF LOWER TEETH OF *Isotemnus*

	P_2		P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W	L	W
I. primitivus and synonyms												
Trimerostephanos angustus												
M.A.C.N. No. 10593[a]	*ca.* 8½	—	10.7	—	12.0	9.5	14.3	9.8	*ca.* 16½	—	—	—
Amphitemnus transitorius												
M.A.C.N. No. 10623[a]	—	—	—	—	—	—	—	—	—	—	19.2	10.6
A.M.N.H. No. 28666	—	—	—	—	—	—	14.5	11.0	16.9	11.8	*ca.* 22	10.4
A.M.N.H. No. 28938	—	—	—	—	—	—	—	—	*ca.* 15½	11.7	20.4	11.4
A.M.N.H. No. 28940	—	—	*ca.* 11½	*ca.* 8½	—	—	15.5	11.5	17.0	11.6	—	—
C.N.H.M. No. 13441	—	—	—	—	12.9	9.5	15.0	10.6	16.8	11.4	—	—
C.N.H.M. No. 13535	—	—	—	—	—	—	—	—	15.4	11.7	20.3	10.9
Isotemnus latidens and synonyms												
Anisolambda latidens,												
M.A.C.N. No. 10667[a]	—	—	—	—	—	—	—	—	*ca.* 13	*ca.* 10	—	—
Eochalicotherium crassidens												
M.A.C.N. No. 10601[a]	—	—	—	—	—	—	—	—	12.5	8.7	—	—
Eochalicotherium robustum												
M.A.C.N. No. 10594	—	—	—	—	—	—	—	—	*ca.* 13	*ca.* 10	—	—
?Isotemnus ctalego												
A.M.N.H. No. 28568[a]	—	—	—	—	—	—	—	—	10.0	7.7	12.4	7.7
A.M.N.H. No. 28541	—	—	—	—	—	—	—	—	11.0	8.1	—	—

[a] Type.

and probably not associated part of left lower jaw with M_{2-3}; no field data. Of *Trimerostephanos angustus*, M.A.C.N. No. 10593, part of left lower jaw with P_2–M_2, all but M_1 broken. Other fragments, not considered part of the type, were in the same lot in the Ameghino Collection. No field data. The original description gave a measurement of P^2–M^2, but neither then nor later were upper teeth described or designated as belonging to this species, and it is reasonably sure that only this lower jaw fragment was Ameghino's type. Of *Eochalicotherium cretaceum*, type not found. Ameghino's description refers to P_3–M_3 and P^4–M^3, probably not associated. The only specimen known to me labeled by Ameghino as of this species is M.A.C.N. No. 10598, a jaw fragment with left M_3 and part of M_2, from west of the Río Chico. Of *Amphitemnus nucleatus*, M.A.C.N. No. 10619, isolated, broken left M_3; Colhué-Huapí. Of *Amphitemnus transitorius*, M.A.C.N. No. 10623, associated left M_{2-3}; Colhué-Huapí.

Hypodigm: The types, as above, and A.M.N.H. No. 28666, part of right lower jaw with M_{1-3}; A.M.N.H. No. 28650, right P^3–M^3, from Cañodón Vaca; A.M.N.H. No. 28938, part of right lower jaw with broken M_{2-3}, from Casa Lopez; A.M.N.H. No. 73535, part of left lower jaw with M_{2-3}, from Punta Casamayor; A.M.N.H. No. 28940, part of right lower jaw with P_3–M_2 (P_{3-4} unerupted); C.N.H.M. No. P13441, part of left lower jaw with P_4–M_2.

Horizon and Locality: Casamayoran, Patagonia, various localities as given for types and hypodigm.

Diagnosis: Larger of the two Casamayoran species as here tentatively recognized. Measurements are given in tables 54 and 55.

Isotemnus conspiquus was distinguished from *I. primitivus* by larger size only. The difference in the types is only about 10 per cent and is not in itself sufficient to indicate specific distinction.

In the absence of the type, *Eochalicotherium cretaceum* is at best a *species inquaerenda* and probably a *nomen vanum*, but a specimen referred here by Ameghino is at least close to "*Trimerostephanos*" *augustus.*

"*Amphitemnus nucleatus*" differs from "*Trimerostephanos augustus*" in no way visible to me. "*Amphitemnus transitorius*" M_3 has the entoconid possibly less developed and a slightly more distinct internal cingulum than in "*A. nucleatus*," but is barely if at all different from the latter or from "*T. augustus*."

Synonymy for these miscellaneous fragments from widely scattered localities is perhaps more hopeful than definitive, but they do occlude well, are closely similar, and cannot be realistically defined as separate species.

Among the three names simultaneously published in 1897, as first reviser (under the definition of the Code) I give priority to *I. primitivus*, not because it was on an "earlier" page but because it was based on much the best type.

Isotemnus latidens (Ameghino, 1901)

Plate 30, figures 5–7, 9

Anisolambda latidens Ameghino, 1901, p. 384.
Isotemnus enecatus Ameghino, 1901, p. 411.
Isotemnus apicatus Ameghino, 1901, p. 412.
Eochalicotherium crassidens Ameghino, 1901, p. 417.
Prostylops apicatus: Ameghino, 1902a, p. 27.
Isotemnus cuspidatus Ameghino, 1901, p. 412.
Eochalicotherium robustum Ameghino, 1901, p. 418.

Type: M.A.C.N. No. 10667, fragment of left lower jaw with badly worn and somewhat broken M_{1-2}, evidently the type, as Ameghino's measurements can only have been made on it. With it is a better-preserved fragment, not associated, with left M_{2-3}. Colhué-Huapí, north.

Types of Synonyms: Of *Isotemnus enecatus*, M.A.C.N. No. 10587, part of right maxilla with P^4–M^3, all with labial walls broken off; west of the Río Chico. Of *Eochalicotherium crassidens*, M.A.C.N. No. 10601, fragment of right lower jaw with M_2 and broken talonid of M_1; west of the Río Chico. Of *Isotemnus cuspidatus*, not found. Of *Eochalicotherium robustum*, M.A.C.N. No. 10594, eight fragments of lower jaws with one or two cheek teeth in each, a fragment of maxilla with left P^{2-3}, and a loose P^4. Probably no two of these 10 specimens are from the same individual and at least two species, perhaps genera, are present. The specimen most nearly agreeing with Ameghino's description and measurements is a bit of left lower jaw with a probable second (perhaps first) molar, taken as lectotype. West of the Río Chico. Of *Prostylops apicatus*, M.A.C.N. No. 10614, broken right maxilla with P^3–M^2; west of the Río Chico.

Hypodigm: Known types, as above.

Horizon and Locality: Casamayoran, Patagonia, most known specimens from west of the Río Chico, as above.

Diagnosis: In size, smaller of the two Casamayoran species here recognized. Measurements are given in tables 54 and 55.

The type is the only specimen not from west of the Río Chico and is also very poorly preserved, but it seems to belong in this size group and is not specifically distinguishable from the other specimens here united.

The teeth of the type of *Isotemnus apicatus* are much worn. They are slightly smaller than those of the type of *I. enecatus* but seem to be conspecific. They are even more similar to teeth of a referred specimen of *Prostylops typus*, with which they were not compared although Ameghino transferred this species to *Prostylops*. If that referred specimen (M.A.C.N. No. 10612) really belongs to *P. typus*, for which there is no positive evidence, then *Isotemnus typus* is the prior name for the present species.

No material placed in *I. cuspidatus* by Ameghino was found, but Ameghino considered it only slightly smaller than *I. enecatus*, with a shorter metaloph on M^3. That carries a measure of probability that the specific names are in fact synonymous. Otherwise *I. cuspidatus* must be considered a *nomen vanum* at present.

"*Eochalicotherium crassidens*" and "*E. robustum*" are names for specifically indistinguishable medium-sized lower teeth of *Isotemnus*. They occlude well with upper teeth here referred to *I. latidens*.

Isotemnus typus (Ameghino, 1897), *species dubia*

Prostylops typus Ameghino, 1897a, p. 486; 1898, p. 174; 1902a, p. 26; 1904b, p. 158, fig. 197.

Isotemnus typus: Cabrera, 1935, p. 12. (Cabrera did not say that this is a reallocation of *Prostylops typus*, but it must be, because there is no other *typus* in or closely related to *Isotemnus*.)

Type: A broken right lower molar, not found. It was not figured, and the description is not diagnostic.

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

Diagnosis: Not diagnosed.

Ameghino later referred to this species M.A.C.N. No. 10612, right P^4–M^3 from Colhué-Huapí, and from 1902 onward his concept of the genus and species was based on that specimen, not on the type. The specimen belongs to *Isotemnus* and is not distinguishable from the species here called *I. latidens*. If that referred specimen were conspecific with the type of *Prostylops typus*, then *Isotemnus typus* would be the correct name for my *I. latidens*, but there seems to be no way to determine such conspecificity.

?Isotemnus colhuehuapiensis (Ameghino, 1902), new combination, *nomen vanum*

Plate 30, figure 10

Dimerostephanos colhuehuapiensis Ameghino, 1902a, p. 30.

Type: M.A.C.N. No. 10604, partial left lower jaw with P_4–M_3, lectotype. With this are two other lower jaw fragments, possibly but improbably syntypes, not of the same individual and probably not of the same species.

Hypodigm: Type (or lectotype) only.

Horizon and Locality: Casamayoran, Colhué-Huapí.

Diagnosis: Not diagnosed.

The only referable specimen is so deeply worn and badly broken and corroded that it is really unidentifiable. It could belong to *Isotemnus* but could belong to some other quite different genus, perhaps even to *Maxschlosseria*, as the lower dentition of some form like "*Isotemnus*" *consumatus* or "*Eostylops*" *obliquatus*, now referred to *Maxschlosseria*. M_3 measures approximately 12.3 by 6.3 mm.

Isotemnus haugi (Roth, 1902)

Lelfunia haugi Roth, 1902, p. 255.

Isotemnus haugi: Simpson, 1934e, p. 13; 1936d, p. 69.

Type: M.L.P. No. 12-2206, isolated left upper M^2.

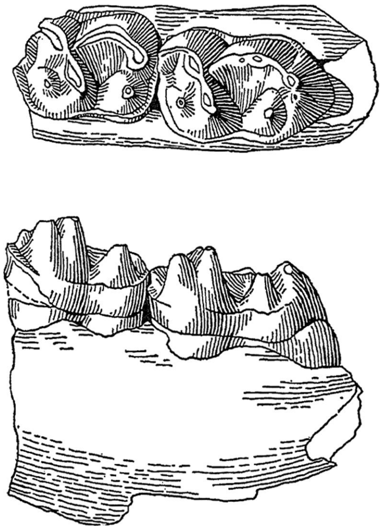

FIG. 34. *?Isotemnus ctalego* Simpson, A.M.N.H. No. 28568, type, fragment of right lower jaw with M$_{2-3}$, crown and lingual views. ×2.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Riochican, Chubut Valley near Gaiman (Roth's "Cretáceo superior del Río Chubut").

DIAGNOSIS: Intermediate between *I. primitivus* and *I. latidens* in size; type M^2 measures 13.5 by 17.5 mm. Type M^2 deeply excavated between paracone and metacone folds on buccal face; no external or internal cingula.

This species is based on inadequate material and is not well distinguished from either of the sufficiently established Casamayoran species. It is, however, from a distinctly different horizon and locality, which enhances the probability that its otherwise dubious morphological differences do have taxonomic significance.

?Isotemnus ctalego Simpson, 1935

Text figure 34

?Isotemnus ctalego SIMPSON, 1935a, p. 15, fig. 17.

TYPE: A.M.N.H. No. 28568, fragment of right lower jaw with M$_{2-3}$.[1]

HYPODIGM: Type and A.M.N.H. No. 28576, fragment of right maxilla with broken P^4–M^1; A.M.N.H. No. 28541, fragment of right lower jaw with M$_2$.

HORIZON AND LOCALITY: Riochican, Cañadón Hondo, Chubut.

DIAGNOSIS: Size in range of that of *I. latidens*, perhaps averaging slightly smaller. Measurements are given in tables 54 and 55. More brachydont than Casamayoran isotemnids. P^4–M^1 with slight external cingula. M$_{2-3}$ with slight external and internal cingula; entoconid bunoid, not transversely elongate; hypolophid with distinct hypoconid and hypoconulid.

This species is clearly allied to Casamayoran *Isotemnus* and could be directly ancestral to the latter. It is clearly and interestingly more primitive, to an extent that might justify generic separation if it were better known. The known specimens are not directly comparable with the type of *Isotemnus haugi*, which is from a distant locality and probably not quite the same age, but the two are almost certainly distinct. *?Isotemnus ctalego* is smaller, more brachydont, in general probably more primitive, *I. haugi* being closer to the Casamayoran forms.

THOMASHUXLEYA AMEGHINO, 1901

Thomashuxleya AMEGHINO, 1901, p. 409; 1902a, p. 24; 1906, p. 468. SCHLOSSER, 1923, p. 617. SCOTT, 1913, pp. 462, 485; 1937a, pp. 518, 523, figs. 332, 333. SIMPSON, 1932b, p. 2, figs. 2, 3; 1935c, p. 318, 2 figs.; 1936b, p. 1, figs. 1–2.

TYPE: *Thomashuxleya rostrata.*

DISTRIBUTION: Casamayoran, Patagonia.[2]

DIAGNOSIS: Dentition closely similar to that of *Pleurostylodon.* Teeth generally more massive. Cheek teeth chunky, subquadrate. Hypocone lobe of upper molars smaller than in *Pleurostylodon.* Continuous, small lingual cingulum on upper cheek teeth. Lower premolars without separate entoconid. Skull massive, with ear region deep and compressed anteroposteriorly as in later Toxodonta; epitympanic and hypotympanic sinuses relatively smaller than in *Pleurostylodon.* Feet ungulate, broad, digitigrade, pentadactyl. Species much larger than any other Casamayoran members of the family.

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[1] "M$^{1-4}$" in the original publication is an obvious misprint.

[2] A Mustersan species was referred to this genus in error by Roth (1901).

Ameghino referred this genus, *Anisotemnus*, and his "*Proasmodeus*" (a synonym of *Periphragnis* Roth) to the Homalodotheriidae (or "Homalotheriidae"). No comparison was made with *Pleurostylodon*, referred to the Isotemnidae, although the resemblance was noticed to the extent of placing all in the "Ancylopoda." Ameghino's description did not distinguish *Thomashuxleya* from *Pleurostylodon*, *Anisotemnus*, or *Periphragnis*. In fact the dentitions of these four genera are so alike as to be hardly distinguishable in clear-cut morphological terms, and the preceding diagnosis is provisional and somewhat ambiguous. Within the Casamayoran faunas, *Thomashuxleya* is more readily recognizable by its comparatively great size than by other characters.

Because of its relatively great size, this genus is impressive and can hardly be overlooked by even casual collectors. It is nevertheless a rather rare element in the fauna, the Ameghino Collection including only some 10 specimens and ours about 15 more, most of them from a single pocket in Cañadón Vaca. Ameghino named only five species. One, "*T.*" *principialis*, does not belong to this genus and is listed below under Isotemnidae *incertae sedis*. Of the other four, two seem to be valid, and two are tentatively reduced to synonymy.

DESCRIPTION

The dentition is so like that of other isotemnids, especially *Pleurostylodon*, described above in detail, that separate description would be merely repetitious. Several partial skulls are known, but all are poorly preserved and add little to knowledge of primitive notoungulate skulls described for other genera. This is the only Casamayoran genus in which it has been possible to restore the whole skeleton, which, as do other parts of the anatomy, proves to be closely similar to that of *Pleurostylodon* as far as comparable materials are at hand. More extensive consideration of primitive notoungulate skeletons is deferred for later special studies, but the following summary (modified from Simpson, 1936b) suffices for present purposes.

The three principal specimens here briefly recorded are the following:

A: A.M.N.H. No. 28905, including most of the vertebrae from the atlas to the anterior caudals, nearly complete right forelimb, left pelvis and femur, many ribs, and other fragments. Fragments evidently of the skull of the same individual were found nearby. The specimen, the principal basis for restoration of the whole skeleton, is referred to *Thomashuxleya externa* with reasonable probability. Found by G. G. Simpson, 1930, in the Casamayoran of the "Oficina del Diablo," Cañadón Vaca, Chubut.

B: A.M.N.H. No. 28906, 14 vertebrae, sternum, clavicle, most of both forelimbs, ribs, and other fragments. The generic ascription is uncertain. The skeleton is smaller than A, but generally similar. It may belong to a small species of *Thomashuxleya* or possibly to *Anisotemnus*. In any event it is an isotemnid. Found by C. S. Williams, 1931, in the Casamayoran (slightly below the level of A but not appreciably different in age), Cañadón Vaca, Chubut.

C: A.M.N.H. No. 28904, left humerus, radius, and ulna, both femora and tibiae, numerous foot bones, one dorsal and several caudal vertebrae, ribs, and other fragments. This is the smallest skeleton of the three, almost surely of *Pleurostylodon*, as that is the commonest genus including species of this size and as the bones agree well with fragments found in actual association with *Pleurostylodon* skull and jaw fragments. Found by G. G. Simpson, 1931, in the Casamayoran (same level as A), Cañadón Vaca, Chubut.

For brevity the three skeletons are described together and are referred to as A, B, and C. The structure is essentially the same in all, with differences apparently of not more than generic value.

Comparison is chiefly with *Homalodotherium* of the Santa Cruz, especially the skeleton found by the Field Museum party under Riggs and described by Scott (1930). *Homalodotherium* represents one extreme of toxodont specialization in the skeleton, and among the special points of interest of the Casamayoran specimens are the demonstration of the origin of its peculiarities from a structure more normal, or more primitive, and indication of the degree of evolution in a single group from Casamayoran to Santacruzian time. Where the part is unknown in *Homalodotherium*, or to suggest special resemblances, some reference is also made to Santa Cruz typotheres as described by Sinclair (1909) and toxodonts as described by Scott (1912a).

VERTEBRAE: The posterior dorsals, lumbars, sacrum, and anterior caudals were pre-

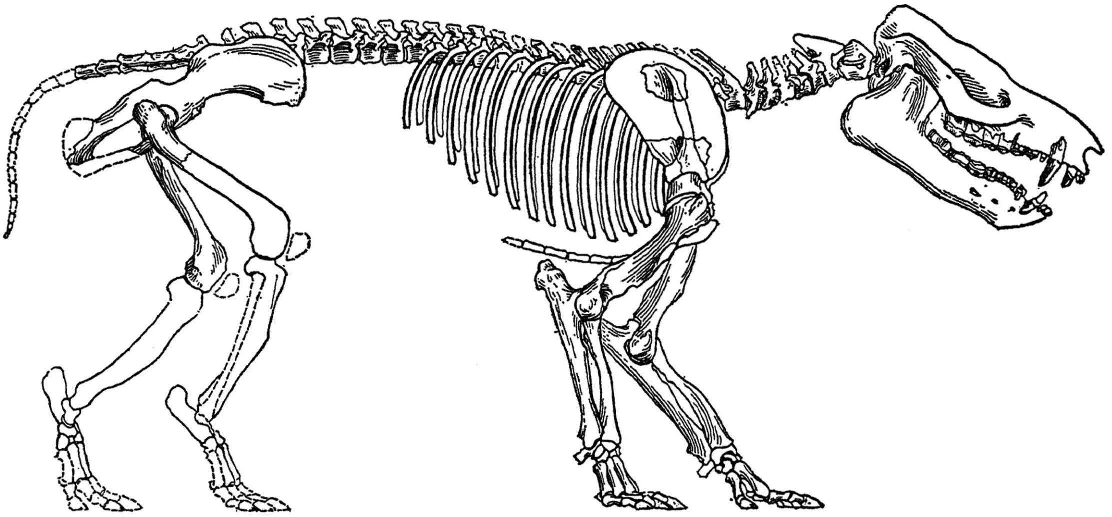

FIG. 35. *Thomashuxleya externa* Ameghino, reconstruction of skeleton. Skull and jaws based principally on A.M.N.H. No. 28698, in part also on A.M.N.H. No. 28447, not associated with postcranial skeleton but of the same species. Shaded parts of postcranial skeleton all from a single individual, A.M.N.H. No. 28905. Unshaded parts with solid outline from specimens of contemporaneous, closely related animals, scaled to size of this individual. Parts shown in broken outline hypothetical. ×1/10.

served in articulation in A, but breakage of the processes makes it uncertain exactly where the change from dorsal to lumbar occurs. There are certainly five and not more than seven lumbars, seven being the most probable number. There are preserved 11 to 13, probably 11, dorsals, but, as most of these were scattered, a few may well be missing; judged from later notoungulates it is probable that there were about 15 dorsals in the complete series. There are four sacrals in A. B and C do not contribute to knowledge of the vertebral formula.

Six cervicals are preserved in A, the missing vertebra probably being the fifth, or possibly the sixth. The atlas considerably resembles that of *Nesodon*, but is less depressed dorsoventrally and has the transverse processes relatively much smaller. The axis has a large, peglike, odontoid process. The transverse processes, although imperfectly preserved, were clearly much smaller than in *Nesodon*, and the canal through each is diminutive. The neural spine is much less expanded than in *Homalodotherium* (although relatively slightly more elongate than in *Nesodon*) and its expansion is less anteroposterior, more anteroinferior-posterosuperior, so that it extends relatively farther above the postzygapophyses behind and in a more pronounced point above the odontoid before. A prominent vertebrarterial canal is present on all the four other preserved cervicals of A, but of the three cervicals of B (all posterior to the axis) one, probably the last, lacks the canal.[1] In both specimens, so far as shown, the neural arches of cervical vertebrae 3 through 7 are similar, simple, with large normal zygapophyses and weak, simple neurapophyses directed slightly backward. The transverse process on the third cervical of A has a short anteroinferior reflection forward and a prominent, recurved production outward and backward. On the sixth or possibly fifth cervical, the process is of similar shape but is less produced, and on the seventh it is longer but less expanded, simpler, and directed downward and outward. The process on the probable seventh cervical of B is similar but relatively shorter and directed less ventrally. On the probable sixth of B, however, the process is unlike anything preserved in A (but the latter is incompletely

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[1] The probable seventh of A is here poorly preserved, and the apparent canal may be anomalous or spurious.

preserved), forming a great, hatchet-like ventral plate produced into a posterior horn, recalling the process on the sixth cervical of *Nesodon* although of different exact outline. All the centra are short, the width in each case considerably exceeding the length.

The anterior dorsals have the ordinary scalelike zygapophyses and present no marked peculiarities aside from the slenderness and small size of the spines (noted also in *Homalodotherium* by Scott), and their marked posterior inclination. There is no anticlinal vertebra, even the lumbar (and indeed the sacral) spines being slightly inclined posteriorly, an unusual character probably associated with relative inflexibility of the posterior dorsal and lumbar region. On the posterior dorsals the spine is very low, relatively lower than in *Homalodotherium*, barely rising above the prezygapophyses, but expanded anteroposteriorly, squarely truncated, and only slightly inclined backward. Its position is wholly posterior, between the postzygapophyses. The metapophyses so strongly developed in *Homalodotherium* are absent or perhaps barely indicated by a slight blunt process directed upward and outward from the prezygapophysis. On the most posterior dorsal known in *Homalodotherium* the cylindrical toxodont lumbar type of articulation is not indicated on the prezygapophyses and barely suggested on the postzygapophyses, but in *Thomashuxleya* this type is fully developed at a corresponding part of the series, the articulation being there at least as fully cylindrical as on any lumbar in *Nesodon.*

The lumbar articulations are more complex and rigidly interlocking than in Santa Cruz toxodonts or typotheres and remarkably parallel the very specialized condition in some artiodactyl lumbars (e.g., in *Odocoileus*). In addition to the cylindrical primary articulation, another lamina is developed above this so that the articular surface is strongly S-shaped in transverse section. A low, nonarticular, anteroposterior crest on the dorsal surface of the prezygapophysis represents the still poorly developed metapophysis. Anapophyses appear to be lacking. The neural spines and centra are as in the posterior dorsals, save that the latter are somewhat more elongate and the former tend (at least in A) to be bifid posteriorly. The transverse processes are long, simple, dorsoventrally compressed blades.

The sacrum, known only in A and there rather poorly preserved, seems to consist of four coalesced vertebrae, of which three articulate with the ilium. The general outline seems to be very much as in *Adinotherium* save that in the latter and most later notoungulates several caudals still free in *Thomashuxleya* have become fused into the sacral complex. The first sacral has somewhat larger metapophyses than are preserved on any of the lumbars. Posterior to this the articulations appear only as blunt, but quite distinct, processes in which the elements are not distinguishable. The first two neural spines are separate, and prominent and posterior to these is only a low, sharp, nearly undifferentiated ridge.

The anterior caudals (A and C) are large, heavy, dorsoventrally compressed bones with semicylindrical zygapophyses. The neural spines are merely sharp longitudinal ridges barely rising into free processes. The transverse processes are strong, broad plates. In C this stout structure is seen to break down rapidly, probably by about the seventh or eighth, and almost surely before the tenth, caudal, and the more distal vertebrae are short, irregular centra with no neural arches or zygapophyses. The inference is that the tail in these forms was heavy but short.

RIBS: The ribs with the three specimens are not remarkable in any way. None is strongly expanded or more than slightly slablike.

STERNUM: Most of the sternum is preserved in B, and part of the presternum in A. The latter is like that of B, as far as preserved, except for being larger and proportionately stouter. The presternum (of B) has prominent first rib articulations at the widest part of the bone, and between and anterior to them is a deep dorsal concavity or pocket. The ventral surface of this part of the bone has a very high median keel. The anterior dorsal border is not preserved. After narrowing posterior to the rib articulations, the bone expands slightly at the posterior end. It is here much wider than deep. This bone is very unlike that of *Homalodotherium*, and somewhat more but not exactly like that of *Nesodon*. In B there follow five (or possibly six) quadrate mesosternal segments, much compressed dorsoventrally, with projections at the four corners but otherwise almost featureless. It cannot be determined whether the last of these is the xiphisternum or how many other segments may have been present.

CLAVICLE: What is indubitably a clavicle is present in B. It is a well-developed but simple, slender, curved bone very unlike the element considered as a clavicle in *Homalodotherium*.

SCAPULA: The scapula is peculiar, very unlike that of later toxodonts and somewhat more like that of some typotheres, e.g., *Protypotherium*. This part is too poorly known in *Homalodotherium* for very useful comparisons to be made. The spine is very high in A, with a flattened free border. There is a single prominent metacromion at the posteroinferior end of the spine in both A and B, but no second metacromion above this. The acromion is incomplete in both these specimens, but clearly was unusually large and stout, although not wide. In A.M.N.H. No. 28878, *Pleurostylodon*, the acromion is completely preserved and is smaller and directed less anteriorly than is indicated in A and B, being very like this part in *Protypotherium*. The prespinous surface in B is much larger than the postspinous, and the coracoid process is a stout, hooklike projection.

HUMERUS: The proximal end, completely preserved only in B, has a large projecting greater tuberosity which is, however, much less prominent than in *Nesodon*, and a smaller but distinct lesser tuberosity. The deltoid crest is prominent in all three individuals, but is less so than in *Homalodotherium*, does not extend so far distally, and does not form a free projection at the distal end. The supinator crest is strong, relatively about as marked as in *Homalodotherium*, and longer proximodistally. The entepicondyle is of moderate development in A and B, about as in *Homalodotherium*. In C it is relatively larger. The entepicondylar foramen, absent from *Homalodotherium*, is present in all three of these earlier forms.

RADIUS AND ULNA: Radius and ulna are known in all three specimens and are essentially similar in all three, save that those of B and C are somewhat lighter in build as well as smaller and have the ulnar shaft and side of the olecranon more excavated. They are heavy, separate bones, more elongate than in *Nesodon* but less so than in *Homalodotherium*. The ulna is nearly straight, not so bowed as in *Homalodotherium*, although the strong olecranon is somewhat deflected to the internal side. The distal end (in A, poorly preserved in B and C) is slightly less transverse than in *Homalodotherium*. Other characters agree rather closely with those of the latter or with those of notoungulates in general. The radius is markedly arched, apparently more than in *Homalodotherium*. The proximal end is considerably more transverse than in the latter and less circular, probably indicating less power of rotation. The distal end is likewise somewhat more transverse than in *Homalodotherium*, and the scaphoid articulation, which is partly concave, seems to be relatively slightly smaller in A and B, but perhaps not in C. The dorsal notch between the two surfaces is present but somewhat less pronounced than in the later genus.

MANUS: The left carpus is perfectly preserved in B except for some breakage of the cuneiform. Most of the right carpals of A are represented, but all but the pisiform and trapezium are fragmentary, and there are a few elements from C, but the differences are important only for generic distinctions and need not be pointed out here. The following remarks are all based on B. The eight usual mammalian elements are all present and separate. On the dorsal or lateral exposures, the cuneiform, unciform, and pisiform are large, the lunar, scaphoid, and trapezium moderate, and the magnum and trapezoid small. In the carpus of *Homalodotherium*, the magnum, trapezoid, and to a slight degree the lunar are relatively larger, whereas the scaphoid is relatively smaller. In the later genus the proximal elements are relatively shorter, especially noticeable in the lunar, although the known distal elements are all relatively longer. The earlier carpus is distinctly less serial. In *Homalodotherium* the only distal articulation for the scaphoid is with the trapezoid, but in B it also has distinct facets for trapezium and magnum. The lunar-magnum articulation is much larger than the lunar-unciform in the later genus, but they are of nearly equal size in B. The facets for metacarpal II on the magnum and for III on the unciform also appear to be relatively larger in the earlier form. The pisiform of B is quite as large as any other carpal, and has a large facet for the ulna, with which it must have been constantly in contact (whereas in *Homalodotherium* the ulna has no facet for the pisiform). There is a small radial sesamoid, proximal to the trapezium.

The metacarpals are rather short and stout, not elongate as in *Homalodotherium*. The descending order of length is III-II-IV-V-I. In the articulated carpus II and IV are of nearly equal length and the foot is mesaxonic, although not markedly so. Unlike the situation in *Homalodotherium*, V is decidedly shorter and not stouter than II to IV. In B, I is nearly as long as V but more slender, and in A it is relatively much shorter, but in both it is well developed and fully functional. Its proximal articulation is far removed from that of II, and it diverges very markedly from the other metacarpals, although its articulation does not permit it to be definitely opposed to them. Each metacarpal (except possibly I, in contact with which they are not preserved) has a pair or large, distal, palmar sesamoids. Between these the articular surface is keeled, but even here the keel is very slight, and there is none on the globular, purely distal and dorsal part of the articulation which normally was all that came in contact with the proximal phalange. The pose can only have been digitigrade, with the main weight falling on and immediately anterior to the row of sesamoids. The phalanges had much freedom of motion on the metacarpals and, apparently, independent of one another. The whole structure is one of an animal that has not lost or that is secondarily acquiring a grasping manus, very unlike any typical ungulate development.

The proximal and medial phalanges are short and stout, but less so than in *Homalodotherium*, and the medial phalanges are all distinctly shorter and smaller than the proximal. The articulation between these two is about as oblique as in the later form, and that for the unguals permits a nearly equal freedom of motion. The unguals are much less clawlike than in *Homalodotherium*, although they show a possible structural beginning of such a specialization. The more medial unguals are long, depressed, and deeply fissured. The more lateral are less depressed and have the fissure much smaller or possibly absent.

PELVIS: Aside from a few scraps of no interest, the pelvis is known only in A, in which the posterior and inferior parts of the ischium and the inferior part of the pubis are missing. The whole pelvis is rather like that of *Homalodotherium*, especially the ilium which is similarly expanded into a great crescentic, nearly horizontal plate, but the obturator foramen is distinctly more oval and anteroposterior and the ischial spine is more definite and more posterior. As far as preserved, the ischium and pubis are more toxodont- or even typothere-like than in *Homalodotherium*, or, in other words, more generalized within the Notoungulata.

FEMUR: The femora (A and C but imperfect in both cases) are much more primitive than in *Homalodotherium* and remarkedly resemble those of *Hegetotherium* and *Protypotherium*, which may be assumed nearly to have retained the ancestral notoungulate structure in this part. The shaft is not notably flattened, the greater trochanter projects above the head, and the notch between these is moderately pronounced. There is a lesser trochanter and it is prominent; the third trochanter is distinct, short proximodistally, and opposite or slightly distal to the lesser trochanter, and the patellar groove is relatively long and narrow—all features so fundamentally unlike *Homalodotherium* that, on this bone alone, the two types would hardly be supposed to be related at all.

TIBIA AND FIBULA: The fibula is not known in A, B, or C, but is partly present in A.M.N.H. No. 28690, mentioned below, in which it is a slender, but complete and separate, bone of generally primitive character. The tibia, present in the specimen just mentioned and in C, is likewise primitive and altogether unlike that of *Homalodotherium*. It differs from the latter, among other ways, in being relatively longer and more slender, with the proximal and distal ends much less transverse, cnemial crest very prominent but less massive, extending farther distally, and ending more abruptly.

PES: Of the pes, only the navicular and cuboid of C are preserved and surely identifiable in the three skeletons here chiefly considered. There is, however, another specimen, A.M.N.H. No. 28690, found by me at about the same level and locality as the three principal specimens, in which the tarsus, lacking only the distal end of the calcaneum, is well preserved, and part of the metatarsus is present. The genus, or even family, is uncertain. The size is still smaller than C, but the morphology of the duplicated parts (including femur and tibia) is similar. The genus is probably not *Pleurostylodon*, but the family could well be the same (Isotemnidae), and in any event the tarsus is structurally primitive for the Notoungulata and probably also particularly for the Toxodonta. The following notes refer to this specimen.

The calcaneum is of normal proportions, and the tuberosity is much less expanded than in *Homalodotherium*. The fibular facet is not preserved, but from the calcaneal facet on the fibula it must have been small. The trochlea of the astragalus is shallow and broad. There are a large astragalar foramen and a large, strongly differentiated groove for a flexor tendon. The neck is relatively long, and the head is spherical, somewhat transverse. There is no contact with the cuboid. The navicular is markedly transverse, although less so than in *Homalodotherium*, and the cuneiforms are all distinct, but the mesocuneiform is very small. The first metatarsal is shorter than the second but is functional and was followed by phalanges. The third metatarsal is markedly larger than the second. Both second and third are much more slender than in *Homalodotherium*, and the distal articulations are nearly spherical on the dorsal side and sharply keeled on the plantar side. The cuboid articulations do not suggest enlargement of the fifth metatarsal.

When articulated with the tibia and fibula, this foot tends to incline somewhat toward the tibial border when the crus is vertical. The flexibility of the tarsus permits it to assume a normal position, whether plantigrade or digitigrade, but it seems very unlikely that the foot could be brought to rest on the fibular border as in *Homalodotherium* (in the opinion of Scott and of Ameghino). The exact posture cannot be determined, but it seems probable that the foot was semidigitigrade. The posture indicated by the pes of *Homalodotherium* is probably one of its many secondary specializations.

LIMB PROPORTIONS: A few indices for various limb elements indicate the rather generalized proportions of the Casamayoran skeletons as compared with those of later notoungulates (see table 56).

The Casamayoran specimens agree rather closely with *Phenacodus*, save that the latter has the humerus slightly shorter relative to the three other elements with which these indices compare it, probably a reflection of the somewhat more cursorial habitus of *Phenacodus*. Even on this point the difference is not marked.

The Casamayoran specimens differ little from the Santa Cruz typothere and toxodont, save for the cursorial lengthening of the tibia in the former and graviportal shortening of the metatarsus in the latter. *Homalodotherium* differs markedly in each of these indices. The

TABLE 56

LIMB INDICES FOR SOME NOTOUNGULATES

Index	Casamayor Specimens A	B	C	A.M.N.H. No. 28690	*Homalodotherium segoviae*	*Protypotherium australe*	*Nesodon imbricatus*
Radiohumeral	76	73	77	—	112	80	78
Metacarpohumeral	31	28	34	—	47	34	38
Humerofemoral	85	—	95	—	76	94	97
Tibiofemoral	—	—	88	—	60	113	87
Metatarsotibial	—	—	—	35	26	35	25

strong inference is that the proportions of the Casamayoran forms are approximately those primitive for notoungulates in general and that these proportions were little changed in Santa Cruz toxodonts and typotheres but that *Homalodotherium* is profoundly modified in limb proportions.

Thomashuxleya rostrata Ameghino, 1901

Plate 33; plate 34, figure 2

Asmodeus scotti [in error]: AMEGHINO, 1897a, fig. 57.

Thomashuxleya rostrata AMEGHINO, 1901, p. 409.

Thomashuxleya robusta AMEGHINO, 1901, p. 410.

TYPE: M.A.C.N. No. 10370, part of left lower jaw with I_2–P_4 and part of left maxilla with I^1–P^4. Probably associated, but, if they prove not to be, the lower jaw, more directly comparable with related types, is to be taken as lectotype. No field data.

TYPE OF *Thomashuxleya robusta*: Lower teeth, not found in the Ameghino Collection.

HYPODIGM: The type and the following: M.A.C.N. No. 10539, part of right lower jaw with P_4–M_3, referred to *T. rostrata* by Ameghino, probably correctly, Colhué-Huapí "Norte"; M.A.C.N. No. 10542, left M^{1-3} and fragments, referred to *T. rostrata* by Ameghino, probably correctly, Colhué-Huapí; M.A.C.N. No. 10541, right I^2, right P^{3-4}, left P^4, broken right M^1, right and left M_1, and other fragments (referred to *T. rostrata* by Ameghino, but association is uncertain and some may not belong here); Colhué-Huapí "Norte"; A.M.N.H. No. 28692, parts of lower jaws with right P_3–M_3 and left M_1 (broken), M_{2-3} (both M_3's in crypts), Colhué-Huapí (the original of this specimen is now in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" in Buenos Aires); A.M.N.H. No. 28764, fragment of right lower jaw with P_4, Colhué-Huapí.

HORIZON AND LOCALITY: Casamayoran, Patagonia, known localities as above.

DIAGNOSIS: The larger of the two species here recognized as valid. Measurements are given in tables 57–59.

Ameghino distinguished *T. robusta* from *T. rostrata* as being stronger, with relatively larger canine, and strong cingula on the cheek teeth. These are all quite variable within *T. rostrata*, even in specimens referred to that species by Ameghino. The type of *T. robusta* has been lost or mislaid, but a P_4 referred by Ameghino himself is indistinguishable from that of *T. rostrata*. Unless the type is rediscovered and indicates otherwise, it is reasonable to conclude that the supposed species are synonymous.

The type of *T. rostrata*, as were other Casamayoran specimens described in 1897 was almost surely from Colhué-Huapí, and all specimens now referred to the species and with known localities are from there or from Colhué-Huapí "Norte," which tends to support the validity of the grouping.

Thomashuxleya externa Ameghino, 1901

Plate 31; plate 32; plate 34,
figures 1, 3; text figure 35

Thomashuxleya externa AMEGHINO, 1901, p. 410; 1902a, p. 25. (This is labeled as a new species in both publications, and the descriptions differ slightly, but there is little doubt that they were based on the same type and that a second species was not intended in 1902.)

Thomashuxleya artuata AMEGHINO, 1901, p. 409.

TYPE: M.A.C.N. No. 10537, part of left lower jaw with P_4–M_2. "Este de Río Chico."

TYPE OF *Thomashuxleya artuata:* M.A.C.N. No. 10540, part of left lower jaw with alveoli of C–P_2 and much worn and broken crowns of P_3–M_3. No field data.

HYPODIGM: Types and the following: M.A.C.N. No. 10544, right M_{1-3} (referred to *T. artuata* by Ameghino but more like type of *T. externa*, now considered synonymous), no field data; M.A.C.N. No. 10369, probably associated right P_4–M_2 and left M_{2-3} (without label by Ameghino), no field data; M.A.C.N. No. 10543, isolated right M^1, left M^2, and other fragments, probably not associated (referred to *T. externa* by Ameghino), no field data; A.M.N.H. No. 28447, associated skull and jaws with most of dentition, Cañadón Vaca; A.M.N.H. No. 28697, partial lower jaws with right P_4–M_2 and left M_{2-3}, Cañadón Vaca; A.M.N.H. No. 28756, partial lower jaws with right I_3, C, P_2–M_2, left I_{2-3}, C, P_2–M_3, Cañadón Vaca; A.M.N.H. No. 28698, partial skull and associated lower jaws, with much of dentition, in poor preservation, Cañadón Vaca; A.M.N.H. No.

TABLE 57

MEASUREMENTS OF LOWER TEETH OF *Thomashuxleya*

	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
T. rostrata and synonym														
T. rostrata														
M.A.C.N. No. 10370[a]	13.7	11.8	17.5	12.7	18.1	14.8	20.9	16.6	—	—	—	—	—	—
M.A.C.N. No. 10539[b]	—	—	—	—	—	—	19.9	17.8	*ca.* 26	19.8	26.4	19.5	37.2	16.9
T. robusta														
M.A.C.N. No. 10546[b]	—	—	—	—	—	—	21.5	16.8	—	—	—	—	—	—
A.M.N.H. No. 28692[c]	—	—	—	—	19.5	16.5	—	—	26.0	16.4	28.5	18.8	—	—
A.M.N.H. No. 28764[c]	—	—	—	—	—	—	21.8	13.7	—	—	—	—	—	—
T. externa and probable synonym														
T. artuata														
M.A.C.N. No. 10540[a]	—	—	—	—	16.5	14.6	*ca.* 19	17.2	*ca.* 21	—	*ca.* 28	—	*ca.* 37	—
T. externa														
M.A.C.N. No. 10537[a]	—	—	—	—	—	—	16.3	13.0	19.5	14.0	*ca.* 23	15.5	—	—

[a] Type.
[b] Referred by Ameghino.
[c] From Colhué-Huapí.

TABLE 58

MEASUREMENTS OF LOWER TEETH OF *Thomashuxleya externa*

	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
Cañadón Vaca														
A.M.N.H. No. 28447	—	—	14.2	11.1	16.2	11.6	18.1	13.0	22.0	15.6	27.5	16.5	31.6	15.8
A.M.N.H. No. 28697	—	—	—	—	—	—	17.3	14.2	23.2	15.9	25.5	17.2	*ca.* 36	16.6
A.M.N.H. No. 28756	—	—	14.7	10.9	15.7	12.8	16.4	14.2	21.8	16.3	25.6	17.8	32.3	16.3
A.M.N.H. No. 28698	11.0	10.0	15.1	12.6	16.7	13.6	16.5	14.6	*ca.* 24	16.1	*ca.* 26	17.8	*ca.* 37	*ca.* 17
A.M.N.H. No. 28686	—	—	—	—	—	—	—	—	—	—	—	—	34.5	17.0
Colhué-Huapí														
A.M.N.H. No. 28822	—	—	—	—	—	—	—	—	*ca.* 20	16.4	*ca.* 23½	18.0	—	—

TABLE 59

Measurements of Upper Teeth of *Thomashuxleya*

	P¹		P²		P³		P⁴		M¹		M²		M³	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
T. rostrata														
M.A.C.N. No. 10370[a]	15.4	15.7	17.0	27.2	19.5	31.2	21.0	*ca.* 35	—	—	—	—	—	—
M.A.C.N. No. 10542	—	—	—	—	—	—	—	—	29.5	41.8	33.0	44.2	28.8	40.8
T. externa														
M.A.C.N. No. 10543[b]	—	—	—	—	—	—	—	—	*ca.* 24	*ca.* 34	28.5	35.9	—	—
A.M.N.H. No. 28699	—	—	17.5	22.1	16.8	26.4	18.5	32.1	23.8	35.8	26.7	*ca.* 42½	—	39.5
A.M.N.H. No. 28757	13.8	11.5	15.2	22.1	*ca.* 18½	*ca.* 26½	—	—	25.7	—	27.2	39.2	—	—
A.M.N.H. No. 28698	*ca.* 10	*ca.* 11	—	—	*ca.* 16	—	*ca.* 18	33.2	23.9	38.7	27.2	*ca.* 41	*ca.* 26½	*ca.* 41½

[a] Type.

[b] The two teeth under this number are not from the same individual.

28686, jaw fragment with left M_3, Cañadón Vaca; A.M.N.H. No. 28677, crushed left lower jaw with P_2–M_3, Cañadón Hondo; A.M.N.H. No. 28757, much of right side of skull with P^1–M^3, Cañadón Vaca (original specimen now in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" in Buenos Aires); A.M.N.H. No. 28699, facial part of skull with right I^3, C, P^{2-4}, M^3, left I^3, C, P^{2-4}, M^{1-2}, Cañadón Vaca.

HORIZON AND LOCALITY: Casamayoran, Patagonia. All definitely identified specimens of known origin from the region of the Río Chico, Chubut.

DIAGNOSIS: The smaller of the two species here recognized as valid. Measurements are given in tables 57–59.

The type of *T. artuata* is particularly poor, and its teeth are probably somewhat larger than the average of other specimens now referred to this species. It is also of unknown geographic origin. Under the provisions of the Code, as first reviser I now consider *T. externa* and *T. artuata* as synonyms, published simultaneously, and I select *T. externa* as prior because that is more likely to stabilize nomenclature. (Under the Code, the fact that *T. externa* was first printed on a later page of the same publication has no necessary bearing on priority.) The type of *T. externa* and all the now referred specimens of known origin are from the same region: Ameghino's "Este de Río Chico" was near or perhaps identical with our "Cañadón Hondo," and his "Río Chico" or "Oeste de Río Chico" was near or identical with our "Cañadón Vaca." These geographic associations tend to confirm the specific arrangement here adopted. In several instances specimens from the Río Chico indicate geographic, temporal, or both sorts of differences from other members of the same genera.

There is one specimen from Colhué-Huapí, A.M.N.H. No. 28822, a fragment with right M_{1-2}, that seems to be nearer to *T. externa* than to *T. rostrata*, but the specimen is poor and the identification doubtful.

PERIPHRAGNIS ROTH, 1899

Periphragnis ROTH, 1899, p. 387; 1927, p. 194: SCOTT, 1937a, p. 518. SIMPSON, 1936d, p. 79.

=*Ancylocoelus* [error]: AMEGHINO, 1899, p. 12.

Tehuelia ROTH, 1902, p. 253. SIMPSON, 1936d, p. 80 (as synonym of *Periphragnis*).

Proasmodeus AMEGHINO, 1902a, p. 23; 1904b, p. 116; 1906, p. 490. SCOTT, 1913, p. 462. SCHLOSSER, 1923, p. 617. SIMPSON, 1936d, p. 79 (as synonym of *Periphragnis*).

Lemudeus ROTH, 1903, p. 144. SIMPSON, 1936d, p. 81 (as synonym of *Calodontotherium*).

Calodontotherium ROTH, 1903, p. 148; 1927, p. 234, pl. 13, fig. 3. SIMPSON, 1936d, p. 81.

Eurystephanodon ROTH, 1903, p. 158. SIMPSON, 1936d, p. 80 (as synonym of *Periphragnis*).

TYPE: *Periphragnis harmeri.*

TYPES OF SYNONYMS: Of *Tehuelia*, *T. regia*; of *Proasmodeus*, *Asmodeus armatus*; of *Lemudeus*, *L. angustidens*; of *Calodontotherium*, *C. palmeri*; of *Eurystephanodon*, *E. cattanii*. (The last three genera were published with two species in each; the type species here given were designated in Simpson, 1936d.)

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: Closely similar to *Thomashuxleya*, but teeth with slightly higher crowns (although still brachydont); parastyle and paracone folds of upper molars less prominent and less sharply separate; parastyle folds of upper cheek teeth strongly interlocking with preceding teeth lingual of metastyle; P_2 more complex, with well-developed posterolingual sulcus; lower premolars generally shorter and relatively broader; incisor series less anteroposterior, more transverse.

Roth had an extensive collection from his "Lago Musters" locality, probably the same as our Cerro del Humo. He based five genera and seven species on the large isotemnids of that locality. There is indeed much variation: not surprisingly, each specimen is distinctive in some detail. However, no associations of morphological details are consistent, and analysis of measurements (see under *P. harmeri*) gives no reason or basis for recognizing more than one species from that locality. Roth's descriptions give no acceptable diagnoses of species, *a fortiori* of genera. Roth referred two specimens to Ameghino's Casamayoran genus *Thomashuxleya*. The resemblance is indeed close, but resemblance to Roth's *Periphragnis harmeri* is even closer, to the point of identity.

Ameghino, who did not have access to Roth's materials and was loath to admit that any of Roth's work was valid, at first (1899) guessed that *Periphragnis* was synonymous with *Ancylocoelus* Ameghino, a Deseadan leontiniid. At that time the Ameghinos had not distinguished the *Astraponotus* or in our terms Mustersan fauna, to which *Periphragnis* belongs. Thereafter Ameghino simply ignored all of Roth's names, and when he came to describe the large Mustersan isotemnids he named them *Proasmodeus*, without comparison with or diagnosis against *Periphragnis*. With considerable doubt, one of Ameghino's species may be distinct from Roth's, but they are extremely similar, and generic separation cannot be sustained.

Periphragnis is so closely similar to *Thomashuxleya* that the generic diagnosis is not clear-cut and if the two were of the same age they would perhaps be considered generically identical. Indeed *Pleurostylodon*, *Anisotemnus*, *Thomashuxleya*, and *Periphragnis* are more readily distinguished by the sizes of their typical species, increasing in the order named, than by more reliable generic criteria. Nevertheless there are some slight differences in comparatively well-preserved specimens. *Periphragnis*, almost certainly directly derived from *Thomashuxleya*, is slightly more advanced, as suggested in the diagnosis. The degree of advance, hence the rate of evolution as well, is nevertheless less than in most lineages known in both Casamayoran and Mustersan. As shown below, however, it is comparable to the rate in the closely related *Anisotemnus-Rhyphodon* line.

In the other direction, *Periphragnis* resembles *Asmodeus* of the Deseadan, as Ameghino's name *Proasmodeus* correctly suggests. The sequence *Thomashuxleya-Periphragnis-Asmodeus-Homalodotherium* may represent direct ancestry and descent, but the difference between *Periphragnis* and *Asmodeus* is considerable, and the genetic continuity may be broken there. *Asmodeus* is much more like *Homalodotherium* both in dentition and in limb structure. In fact *Periphragnis* does not have any of the peculiarly homalodothere characters, and, even though it is a possible ancestor, its reference to the antecedent Isotemnidae and reference of *Asmodeus* to the subsequent Homalodotheriidae are justified.

TABLE 60

ARTICULATIONS BETWEEN PROXIMAL AND DISTAL CARPALS IN SOME ISOTEMNIDS AND A HOMALODOTHERE

Proximal	Distal	Casamayor Isotemnid and *Periphragnis*	*Homalodotherium*
Scaphoid	Trapezium	Moderate	None
	Trapezoid	Large	Large (exclusive)
	Magnum	Small	None
Lunar	Trapezoid	None	None
	Magnum	Moderate	Large
	Unciform	Large	Moderate
Cuneiform	Magnum	None	None
	Unciform	Large	Large

There is a left front foot in the Roth Collection, M.L.P. No. 12-1711, almost certainly of *Periphragnis* and comparable to the front foot of A.M.N.H. No. 28906, a partial skeleton of a Casamayoran isotemnid discussed above. The later and larger animal has a stockier, stouter foot, as would be expected, but the structure is essentially the same. In the homalodotheres, as in some other groups and contrary to an early hypothesis, specialization has involved evolution of a more, not less, serial carpus, as can be seen in table 60.

Periphragnis harmeri Roth, 1899

Plate 34, figure 4; plate 35; plate 36;
plate 37, figures 1, 3, 4

Periphragnis Harmeri ROTH, 1899, p. 387; 1927, p. 234, pl. 13, fig. 2.

=*Ancylocoelus frequens* [error]: AMEGHINO, 1899, p. 12.

Periphragnis harmeri: SIMPSON, 1936d, p. 67.

Tehuelia regia ROTH, 1902, p. 253.

Periphragnis regia: SIMPSON, 1936d, p. 67.

Thomashuxleya Rankei ROTH, 1902, p. 253.

Periphragnis rankei: SIMPSON, 1936d, p. 67.

Asmodeus armatus AMEGHINO, 1901, p. 408.

Proasmodeus armatus: AMEGHINO, 1902a, p. 24; 1904b, p. 116, figs. 131, 384–387.

Lemudeus angustidens ROTH, 1903, p. 144.

= *Calodontotherium varietatum:* Simpson, 1936d, pp. 67, 81.

Periphragnis cristatus Roth, 1903, p. 148. Simpson, 1936d, p. 80.

Periphragnis cristata [misprint]: Simpson, 1936d p. 67.

Calodontotherium varietatum Roth, 1903, p. 149. Simpson, 1936d, p. 69 (as a possible synonym of *Periphragnis harmeri*).

Type: M.L.P. No. 12-1769, a palate and left zygoma, with left P^2–M^3 and right P^2–M^2.

Types of Synonyms: Of *Tehuelia regia:* M.L.P. No. 12-1771, much of the skull with no teeth but canines and a lower jaw with right C–M_2 and left C, P_3–M_3. Probably of one individual, but in case of doubt the lower jaw is taken as lectotype.

Of *Thomashuxleya rankei:* M.L.P. No. 12-1715, a lower with left I_3, C, P_2–M_3, and right P_2, P_4–M_3. The missing anterior teeth have been restored and the right P_2 has been inserted in the position of the missing right P_3. Under the same number is a poorly preserved skull, probably not associated, possibly a syntype but not Roth's essential basis for the species. In any case, the lower jaw is taken as lectotype.

Of *Asmodeus armatus:* The original description was based primarily on the lower dentition. The only lower dentition found in the Ameghino Collection and labeled only as of this species, but not as its type (M.A.C.N. No. 10928), does not agree well with Ameghino's description and is probably not a syntype or type. Another is labeled both as *Asmodeus armatus* and as *Proasmodeus exauctus* and is the type of the latter species. The respective descriptions would not exclude the possibility that this was the lower jaw on which "*A.*" *armatus* was for the most part originally based, but the measurements given for M_1 do not agree. The original publication of "*A.*" *armatus* described no upper teeth but gave measurements for length of P^2–M^3 and length and width of M^1 Those were evidently based on M.A.C.N. No. 10925, P^2–M^3 of both sides from a single individual, labeled "*Asmodeus armatus*" by Ameghino, but not "Tipo." (However, few of Ameghino's types are labeled as such.) One of the premolars is the original of figure 387 of Ameghino (1904b). (Originals of other figures labeled as of this species in Ameghino, 1904b, were not found in the collection.) This specimen was clearly before Ameghino when he named the species and is essentially a syntype even though it was not the principal basis for the name. The syntype lower dentition would be the more desirable lectotype, but, since that is not at hand or not identifiable, I designate M.A.C.N. No. 10925 as lectotype.

Of *Lemudeus angustidens:* M.L.P. No. 12-2208, an isolated P^4.

Of *Periphragnis cristatus*: M.L.P. No. 12-1705, part of left maxilla with P^2–M^1 and of left lower jaw with P_3–M_3. They may not be associated, and the lower jaw is taken as lectotype.

Of *Calodontotherium varietatum:* M.L.P. No. 12-2197, two fragments with right P^{3-4} and M^{1-2}. The two pieces do not make contact, but are probably associated as Roth believed. In case of doubt, the piece with M^{1-2} is taken as lectotype.

Of *Eurystephanodon cattanii:* M.L.P. No. 12-2224, a badly broken skull with remnants of possibly deciduous and permanent teeth, including fairly well-preserved, probable M^2 (believed by Roth to be M^3).

Hypodigm: The types, as above, and numerous other specimens from Roth's Lago Musters and our Cerro del Humo; numbers and measurements are given in tables 61–63.

Horizon and Locality: Mustersan, Patagonia. The specimens basic to the present concept are from Roth's Lago Musters or our Cerro del Humo (probably the same locality), but the species almost certainly occurs at Roth's Cañadón Colorado, and some specimens from other localities are doubtfully or not separable.

Diagnosis: Typical of the genus. Distinguished from other possible species by sizes and proportions of teeth, as shown in tables 61–63.

The Roth collection from his "C.s.M.," "Cretáceo superior de Lago Musters," which is probably the Mustersan of Cerro del Humo (see Simpson, 1936d), consists largely of specimens now referred to this species. They are highly variable and at first sight give the impression of including more than one (but surely not so many as seven) species. On

TABLE 61

MEASUREMENTS OF LOWER TEETH OF *Periphragnis harmeri*

	P_2		P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W	L	W
Roth Collection, "Lago Musters"[a]												
M.L.P. No. 12-1708	17½	13	19	15	20½	15½	25	15	26	16½	35	16
M.L.P. No. 12-1762	17	14	18	16	19½	17	25½	15	25½	16	35½	15
M.L.P. No. 12-1759	16	13½	18½	14½	19	15½	24	15½	26½	16	35	15½
M.L.P. No. 12-1754	—	—	18½	15½	20	16	24½	16	25½	16	—	—
M.L.P. No. 12-1753	—	—	—	—	19	16	23	15½	25½	16	34½	15
M.L.P. No. 12-1709	—	—	—	—	20	16½	24½	16	26	17	37	16
M.L.P. No. 12-1745	—	—	—	—	—	—	23½	14½	26	15	37½	14½
M.L.P. No. 12-1757	—	—	—	—	—	—	23	16	24	17	36	17½
M.L.P. No. 12-1716	16½	13½	16	13	19	14½	22	15½	24	16	32	15½
M.L.P. No. 12-1705[b]	—	—	20½	17	20	18½	24	19	28	19½	34	18
M.L.P. No. 12-1771[c]	14	12	16	13	18½	14½	22	15	25	16	38	17
M.L.P. No. 12-1715[d]	16	14	17½	15	21	16	22	16	25	17	35	15
Scarritt Collection, Cerro del Humo												
A.M.N.H. No. 29403	—	—	16.8	14.6	18.8	16.2	23.2	17.7	28.2	20.5	40.7	19.4
A.M.N.H. No. 29416	17.5	14.4	18.6	16.0	19.1	16.8	23.2	16.6	25.6	17.6	34.1	16.8
A.M.N.H. No. 29421	18.9	15.5	19.5	16.4	20.3	17.0	25.0	19.6	26.5	20.3	*ca.* 34½	*ca.* 18½
A.M.N.H. No. 29417	—	—	19.3	14.2	21.6	16.0	23.4	15.9	26.5	16.5	37.3	16.6

[a] Measurements to half millimeters. Changes with wear and other inadequacies make more precise measurement of doubtful or no significance.

[b] "*Periphragnis cristatus.*"

[c] "*Tehuelia regia.*"

[d] "*Thomashuxleya rankei.*"

TABLE 62

STATISTICAL DATA ON SPECIMENS OF *Periphragnis* COLLECTED BY ROTH AT HIS "LAGO MUSTERS" LOCALITY

		N	OR[a]	$\bar{X}$	s	V
P_2						
	L	6	14 –17½	16.17±.49	1.21±.35	7.5±2.2
	W	6	12 –14	13.33±.31	0.75±.22	5.6±1.6
P_3						
	L	8	16 –20½	18.00±.62	1.51±.44	8.4±2.1
	W	8	13 –17	14.88±.49	1.38±.34	9.3±2.6
P_4						
	L	10	18½–21	19.65±.25	0.78±.17	4.0±0.9
	W	10	14½–18½	16.00±.37	1.18±.26	7.4±1.7
M_1						
	L	12	12 –25½	23.58±.35	1.20±.24	5.1±1.0
	W	12	14½–19	15.75±.33	1.14±.23	7.2±1.5
M_2						
	L	12	24 –28	25.58±.30	1.04±.21	4.1±0.8
	W	12	15 –19½	16.50±.32	1.11±.23	6.7±1.4
M_3						
	L	11	32 –38	35.41±.51	1.70±.36	4.8±1.0
	W	11	14½–18	15.90±.34	1.14±.24	4.4±0.9

[a] Specimens were measured to the closest half millimeter. Size and preservation are such that more refined measurement would not improve the statistics.

closer study, however, all extremes are found to be connected by intermediates, no measurable distributions are bimodal (or polymodal), and there is no objective way to distinguish separate species. Lower cheek teeth are sufficiently numerous to permit calculation of estimates of normal parameters (given in table 62). Some of the coefficients of variation are indeed somewhat above average for mammal teeth (the highest, 9.3), but none is higher than have been found within well-defined single species, and the mean of the 12 coefficients, 6.2, is virtually at the mean for homologous measurements in single species of mammals. When it is also noted that these specimens include greatly different stages of wear and various postmortem distortions, the figures are clearly consistent with pertinence to one species. Upper teeth in the same collection are not numerous enough for worth-while estimates of parameters, but their considerable variation is likewise within that likely for a single species under comparable conditions of wear and preservation (table 62).

Four lower jaws in the American Museum collection from Cerro del Humo provide 22 measurements homologous with those included in the statistics for the Roth Collection (table 61). The greatest observed deviation (for WM_2) could occur by chance once in 22 times in a normal population with this estimated variability. As might be expected, specimens from other localities and (in all probability) exact levels do not agree so well, and they are very tentatively placed in other species, as follows.

The only Roth specimen now definitely referred to this species and probably not from Roth's Lago Musters or our Cerro del Humo is Roth's type of *Eurystephanodon cattanii*. In publication (Roth, 1903, p. 50) this was said to be from Lago Musters, but the specimen itself is labeled "C.s.C.C.," that is (in Roth's system) "Cretáceo superior del Cañadón Colorado," a different Mustersan locality. The preservation also is like that of Roth's "C.s.C.C." specimens and different from his "C.s.M." specimens. The poorly preserved skull has no evident differences from a skull of *P. harmeri* from "C.s.M." The only measurable tooth is M^2, 28 mm. in length and 24+ in width, not significantly different from tooth dimensions of "C.s.M."

TABLE 63

Measurements of Upper Teeth of *Periphragnis harmeri* and Synonyms

	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. 12-1769[a]	19.3	24.4	19.2	27.5	20.1	34.4	29.0	33.7	29.3	38.3	29.4	36.1
M.L.P. No. 12-1705[b]	*ca.* 19	*ca.* 27	*ca.* 18½	*ca.* 29	*ca.* 19½	*ca.* 33½	*ca.* 27½	*ca.* 39½	—	—	—	—
M.L.P. No. 12-1714	—	—	*ca.* 18½	*ca.* 30½	—	—	*ca.* 22	—	*ca.* 27	*ca.* 39	*ca.* 28	*ca.* 36½
M.L.P. No. 12-1712	*ca.* 19	*ca.* 28	*ca.* 16	*ca.* 29	*ca.* 18	*ca.* 33	*ca.* 25½	*ca.* 39½	*ca.* 29	*ca.* 42½	—	—
M.L.P. No. 12-2197[c]	—	—	*ca.* 18½	*ca.* 27	*ca.* 19	*ca.* 30½	*ca.* 24	*ca.* 32½	*ca.* 29	*ca.* 36½	—	—
M.L.P. No. 12-2208[d]	—	—	—	—	*ca.* 17½	*ca.* 31	—	—	—	—	—	—
M.A.C.N. No. 10925[e]	19.0	29.0	20.0	31.0	20.8	35.9	25.5	37.0	29.2	38.4	26.2	38.0

[a] Type of *P. harmeri.*
[b] Type of *P. cristatus.*
[c] Type of "*Calodontotherium varietatum.*"
[d] Type of "*Lemudeus angustidens.*"
[e] Lectotype of *P.* "*armatus.*"

specimens. There is also an undescribed right lower jaw with P_2–M_3 from "C.s.C.C." in the Roth Collection, M.L.P. No. 12-1568. All of its 12 tooth dimensions are within the observed range of Roth's "C.s.M." sample (see table 65). It is thus highly probable that *P. harmeri* does occur at "C.s.C.C." and also that *Eurystephanodon cattanii* is a synonym of that name.

The status of "*Asmodeus armatus*" is extremely unsatisfactory. The problem of its type specimen is summarized above. The dimensions given by Ameghino for M_1, 20 by 15 mm., are so small as to exclude occlusion with the syntype upper teeth and are apparently inconsistent with reference by Ameghino of M.A.C.N. No. 10928 to this species, as its M_1 measures 26.8 by 19.2 mm. The figures 20 by 15 mm. could conceivably be a misprint or *lapsus*, but in any case that lower jaw is decidedly *incertae sedis* until found or identified. The upper teeth here made lectotype, and at least part, if not the main basis, of Ameghino's later concept of *Proasmodeus armatus*, are not clearly separable from the Lago Musters-Cerro del Humo samples of *Periphragnis harmeri*, and on that basis the two names are synonymized, but there is considerable persisting doubt. The lectotype locality of *Proasmodeus armatus* is unknown. It could be the same as Roth's Lago Musters and our Cerro del Humo, because Carlos Ameghino also collected near that locality, at what he called "Coluapi [Colhué-Huapí] Norte."

Periphragnis exauctus (Ameghino, 1901),
new combination

Plate 37, figure 2; plate 38, figures 1, 2

Proasmodeus exauctus AMEGHINO, 1902a, p. 24.

TYPE: M.A.C.N. No. 10926, part of a mandible with toothless symphysis and left P_2–M_3. An astragalus with this specimen is unlikely to be of this individual and may not be of this species or genus. As noted above, this specimen is labeled both "*Asmodeus armatus*" and "*Proasmodeus exauctus*" and may just possibly be the principal syntype of the former species as well as type of the latter species, but that is improbable.

HYPODIGM: With certainty, only the type. The following are doubtfully referred: M.A.C.N. No. 10928, right P_2–M_3 and left M_{2-3} of one individual; A.M.N.H. No. 29420, lower jaw with dentition complete except right P_1; A.M.N.H. No. 29422, lower jaw with right P_1–M_3 and left P_3–M_3. A.M.N.H. No. 28752, fragment of right lower jaw with M_{2-3} and stumps of P_{3-4}.

HORIZON AND LOCALITY: Mustersan, Patagonia. No other data on specimens in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; American Museum specimens are from Cerro Blanco.

DIAGNOSIS: Doubtfully distinct from *P. harmeri*, but lower premolars slightly longer absolutely and relative to the molars. Measurements are given in table 64.

Periphragnis exauctus is quite likely the same as *P. harmeri*, but our small series from Cerro Blanco does show minor but fairly consistent differences in the premolar dimensions and proportions, in which they more nearly resemble the type of *P. exauctus*. That name can therefore be very tentatively retained. M.A.C.N. No. 10928 was referred by Ameghino to "*Asmodeus armatus*," but it does not agree well with his description of the lost or unidentified syntype lower dentition of that species and does not occlude well with the syntype-lectotype upper dentition. It does agree better with the doubtfully distinct type of *exauctus* and with our Cerro Blanco series. Cerro Blanco, essentially an extension of the main Colhué-Huapí locality, was known to Carlos Ameghino, and the two Ameghino specimens of *P. exauctus* could have come from there.

?Periphragnis circunflexus[1] (Ameghino, 1901),
new combination

Asmodeus circunflexus AMEGHINO, 1901, p. 408; 1904b, p. 283, fig. 383.

TYPE: Lectotype, M.A.C.N. No. 10896, associated right P_4–M_1. The original description also gives measurements but not descriptions of P^2–M^3, not found, here excluded from lectotype.

HYPODIGM: Type and M.A.C.N. No.

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[1] "Circunflexus" is an incorrect spelling, but, since there is no evidence that it was inadvertent or misprinted, it is nevertheless valid under the Code.

TABLE 64

Measurements of Lower Teeth of *Periphragnis exauctus* and *P. circunflexus*

	P_2		P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W	L	W
P. exauctus												
M.A.C.N. No. 10926[a]	19.0	17.0	21.0	17.2	21.2	17.7	26.0	18.1	27.1	20.0	34.7	18.7
M.A.C.N. No. 10928	21.0	16.7	20.4	17.6	21.8	18.2	26.8	19.2	28.0	19.3	39.4	19.3
A.M.N.H. No. 29420	20.0	16.2	22.5	17.4	22.5	17.5	23.9	17.6	27.1	17.7	38.8	18.3
A.M.N.H. No. 29422	19.5	15.7	19.7	17.7	21.9	18.5	22.2	19.4	24.9	19.8	37.7	19.2
A.M.N.H. No. 28752	—	—	—	—	—	—	—	—	26.6	19.9	38.2	18.1
P. circunflexus												
M.A.C.N. No. 10896[a]	—	—	—	—	27.5	23.7	36.5	25.5	—	—	—	—
M.A.C.N. No. 10894[b]	(24.5	20.0)	(23.5	21.5)	(29.2	24.0)						
	(24.1	20.6)	(25.5	23.5)								

[a] Type.

[b] Isolated teeth of different individuals.

10894, numerous isolated teeth of a number of different individuals but probably conspecific.

Horizon and Locality: Mustersan, Patagonia, but see below. Type from Colhué-Huapí.

Diagnosis: Significantly larger than *Periphragnis harmeri* or *exauctus*. Metaconid extended posteriorly along lingual rim, enclosing a talonid basin on P_4. P_2 more complex than usual in other forms referred to *Periphragnis*, heavier, and with large accessory tubercle at posterior end of proximal groove. Measurements are given in table 64.

This species is clearly distinct from *P. harmeri* or *exauctus* and does indeed approach *Asmodeus*, to which Ameghino referred it. At the type locality the boundary between Deseadan and Mustersan is not everywhere clear, and also drift specimens from the Deseadan may occur on the surface of the Mustersan. There is, then, some possibility that the type is a Deseadan specimen of *Asmodeus*, although it is unlikely. Carlos Ameghino rarely made such errors. As far as I have been able to compare, these lower teeth (less distinctive than upper teeth) are not exactly like any known to belong to *Asmodeus*. The various loose teeth under M.A.C.N. No. 10894 are, for the most part at least, near those of the type, and repetition of the confusion of levels is even less likely. Roth's *Calodontotherium palmeri* (see below) is also probably Mustersan, could be the upper dentition of *circunflexus*, and is at least closer to *Periphragnis* than to *Asmodeus*.

It is thus probable that *circunflexus* is a large and rather advanced Mustersan species of (or closely allied to) *Periphragnis*.

Periphragnis palmeri (Roth, 1903), new combination

Plate 38, figure 4

Calodontotherium Palmeri Roth, 1903, p. 148.

Calodontotherium palmeri: Simpson, 1936d, p. 67 (as a probable species of *Periphragnis*).

Type: M.L.P. No. 12-1737, fragment of right maxilla with M^{1-2} and alveoli of P^{3-4}.

Hypodigm: Type only.

Diagnosis: Larger than *P. harmeri;* measurements (to the nearest half millimeter) of the type are: P^3, length, 18½, width, 27; P^4, length, 19, width 30½; M^1, length, *ca.* 24, width, 32½; M^2, length, 29, width, 36½. Upper molars with distinct but not very sharp paracone folds, cingulum not crossing lingual face of hypocone, lingual face of "entoloph" flattened, no groove between protocone and hypocone.

Except for the larger size, the characters given are not necessarily distinctive from those of *P. harmeri*, in which they are approached by variant specimens, and they are not known to be constant or typical in *P.*

TABLE 65

MEASUREMENTS OF LOWER TEETH OF *Periphragnis* sp.

	P_2		P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W	L	W
A.M.N.H. No. 29423	—	—	—	—	—	—	—	—	24.6	15.7	31.6	15.4
A.M.N.H. No. 29404	16.7	12.2	*ca.* 16	12.3	*ca.* 16½	13.8	*ca.* 22½	15.0	*ca.* 24	15.3	31.5	16.0
C.N.H.M. No. P13317	—	—	—	—	15.0	12.6	17.8	12.8	27.1	15.1	35.5	16.9
C.N.H.M. No. P13531	—	—	—	—	—	—	—	—	25.6	20.8	35.6	19.5
C.N.H.M. No. P13300	—	—	—	—	—	—	—	—	26.1	19.9	35.6	17.5
C.N.H.M. No. P13303	*ca.* 17	15.5	—	—	—	—	26.4	20.1	26.6	20.7	37.9	19.0
M.L.P. No. 12-1568[a]	17½	13	18½	15	19½	16½	23	15	25	15	36	14½

[a] Measured to nearest half millimeter.

palmeri. The one known specimen is close to *P. harmeri* in morphology, and there is no justification for placing it in a different genus. This could be the upper dentition of *?P. circunflexus*, but the association cannot be positively affirmed.

Periphragnis sp.

The variability in this group is further exemplified by a number of lower jaws that cannot assuredly be referred to one or another of the more or less established species. Dimensions of their teeth are given in table 65. The American Museum and Field Museum specimens are from Colhué-Huapí, and the Museo de La Plata specimen is from Cañadón Colorado (Roth's "C.s.C.C."). The latter is indistinguishable from *P. harmeri* and was mentioned under that species. The American Museum and Field Museum specimens could also be variants of *P. harmeri*, but are enough different from the Musters-Cerro del Humo series to raise some doubts.

RHYPHODON Roth, 1899

Rhyphodon Roth, 1899, p. 388. Simpson, 1933f, p. 13, fig. 3; 1936d, p. 78. Scott, 1937a, p. 518.

Setebos Roth, 1902, p. 253. Simpson, 1933f, p. 13 (=*Rhyphodon*); 1936d, p. 79 (=*Rhyphodon*).

Pehuenia Roth, 1902, p. 254; 1927, p. 236, pl. 5, fig. 13. Simpson, 1933f, p. 13 (=*Rhyphodon*); 1936d, p. 79 (=*Rhyphodon*).

Type: *Rhyphodon lankesteri.*

Types of Synonyms: Of *Setebos*, *S. terribilis;* of *Pehuenia*, *P. wehrlii.*

Distribution: Mustersan, Patagonia.

Diagnosis: Similar to *Periphragnis*, but upper and lower cheek teeth more transverse; hypocone better developed and relatively lingual on upper cheek teeth, including M^3; metacone fold slightly more definite; premolar protoloph notched and incomplete when unworn; P_2 more molariform, single crescent on trigonid, talonid lophid abutting against middle of metalophid, not at lingual end; I_3 not enlarged, and I^3 less enlarged than in *Periphragnis*. Even more closely similar to *Anisotemnus*, but upper premolars more transverse, less quadrate; ectoloph folds less distinct; more nearly hypsodont.

Roth compared *Setebos* with *Periphragnis*, and the differences noted are just those that also distinguish *Rhyphodon* from *Periphragnis*. *Rhyphodon* and *Setebos* were evidently based on the same species. Roth's description of *Pehuenia* was not comparative and contains nothing not also true of *Rhyphodon*. *Pehuenia* was also based on the same species as *Rhyphodon.*

Rhyphodon is closely similar to the Casamayoran *Anisotemnus* to the point of being rather doubtfully separable, but the later genus does seem to show some slight advance in dental structure. The relationship is like that of *Periphragnis* to *Thomashuxleya* and is likewise almost certainly one of direct descent in a very slowly evolving line. In the case of *Rhyphodon lankesteri* and *Anisotemnus distentus* the later species is not even larger than the earlier.

Although *Rhyphodon* is well represented in Roth's Lago Musters Collection, we found only a skull without teeth and a few isolated teeth at Cerro del Humo, believed to be the same locality. The genus has not been recognized in the Ameghino Collection, and this is an exceptional case in which Ameghino and Roth apparently did not apply different names to the same genus.

Our skull, A.M.N.H. No. 29414, although without teeth, is clearly identifiable as *Rhyphodon lankesteri* by comparison with Roth's specimens from (in all probability) the same locality. It has provided a brain cast described by Simpson (1933f). The following is a somewhat modified version of that description:

The total length of the skull (slightly crushed and tip of premaxilla missing) was about 230 mm., and of the brain, exclusive of the medulla, about 85. The index is thus 37. When the large size (tending to give a small index) and the short rostrum (tending to give a large index), and the general proportions of the brain itself, are allowed for, this probably indicates an effective brain size not significantly different from *Notostylops* (48, made large by small size and short rostrum) or *Phenacodus* (30, made small by large size and long rostrum), so far as such a necessarily very rough estimate can be made.

The arrangement seems to be about as serial as in *Phenacodus* or *Notostylops*, and the flexure about as in the latter, except that the olfactory bulbs are bent downward (they are overlain by large frontal sinuses absent from the other genera mentioned). The ratio of olfactory bulbs to cerebrum to cerebellum is roughly 3/8/6, rather closely paralleling that in *Phenacodus* or *Notostylops*, but with relatively somewhat smaller olfactory bulbs. The maximum cortical width is contained almost exactly twice in the length, making the brain as a whole relatively more elongate than in *Phenacodus* and less than in *Notostylops*. The most unusual feature of the general proportions is that the cerebellum is almost as wide as the cerebrum.

The olfactory bulbs, fully exposed and large, although relatively smaller than in *Notostylops*, are of almost equal width, length, and depth. They are completely separated by a deep narrow fissure, which does not, however, split the strong peduncles. The olfactory tubercles are visible but not prominent and are more poorly defined than in *Notostylops*. The pyriform lobes are about as prominent as in *Phenacodus* or *Notostylops*, or possibly slightly weaker relatively, and are visible in dorsal view, extending laterally to the neopallium as in *Phenacodus* rather than posteriorly as in *Notostylops*.

The neopallium, although longer and narrower than in *Phenacodus*, has the less strongly triangular outline of that genus, the anterior and posterior widths being less disparate than in *Notostylops*. The rhinal fissure is nearly straight, continuous, and horizontal. The fossa sylvii is placed as in *Notostylops*. Imperfections of the bones make it impossible to say whether it is produced into a fissure, but, if present, this must have been shallow and short. The neopallium is almost perfectly smooth, the only evidence of a sulcus being a short, straight, very shallow and vague, longitudinal depression 6 mm. above the rhinal fissure and about 15 mm. from the midline. If this is a sulcus, it seems to correspond more nearly with the (nominally) suprasylvian sulcus of *Notostylops*. If so, its development without a sulcus lateralis is unusual, and, if it is the sulcus lateralis, its very lateral position is even more extraordinary. The region of the hypophysis is imperfect, but it is evident that the fossa hypophyseos was even smaller and shallower than in *Phenacodus*.

There is a depressed dorsal area between cerebrum and cerebellum, and the midbrain may have been exposed, but, if so, the exposure was small.

The whole cerebellar region is vague and lacks definite character, partly owing to the imperfection of the bone surface, but even where this is completely preserved the sculpture is slight and indefinite. The occipital exposure is strongly inclined forward and not distinctly differentiated from the dorsal exposure, as it is in *Phenacodus*, *Notostylops*, or indeed most other mammals. Near the junction of these two planes, a division into a large vermis and smaller hemispheres is vaguely seen, but otherwise these surfaces lack definite characters. In lateral view there is a very marked difference from *Phenacodus*, *Notostylops*, and most other primitive ungulates in that there is a lobe of the cerebellum lodged in a fossa of the petrosal posterior and slightly ventral to the internal auditory meatus but very little or probably none dorsal or dorsoanterior to the meatus in the region of the flocculus. I am unable to homologize or interpret this condition, but it seems to be indicated by unbroken bone surface in the skull. As in *Phenacodus* and, less markedly, *Notostylops*, another descending lobe or fissure filling curves to the foramen lacerum posterius around the posterior margin of the petrosal fossa.

The cranial exits are remarkable. There is no definite indication of the optic chiasma, and no trace of an optic canal or foramen can be seen. The optic nerves must have left the brain in a common tunnel with the other nerves destined for the orbit, III, IV, V_1, and VI. In *Pleurostylodon* there is a separate optic foramen. The condition in *Homalodotherium* and related later forms is unknown to me.

The paired projections leading to the anterior lacerate foramina are of enormous size. They carried a complex of nerves, certainly III, IV, V_1, and VI, and almost surely also II and V_2. Their compound nature is indicated by a longitudinal groove on the ventral face of each. The stalks representing the median and posterior lacerate foramina are larger on the cast than they would be had not the tympanic bulla been destroyed and a large postmortem gap been created between the periotic and the basioccipital-basisphenoid. V_3 clearly passed out through the gap now confluent with the median lacerate foramen, but doubtless had a more exclusive exit when the bone was complete. As usual, IX, X, and XI undoubtedly left through the posterior lacerate foramen. The internal auditory meatus, VII and VIII, is at a relatively high position, more on the lateral than on the ventral surface of the cast; XII is large and is immediately posterior to the posterior lacerate foramen.

In the region of the fossa sylvii on the left side is a heavy stalk, representing a skull canal which branches in the bone and appears externally as two foramina, a smaller one immediately above the anterior lacerate foramen and a larger dorso-postero-external to this. On the right side there are similar foramina on the external surface of the skull, but the canal fillings have separate origins on the cast. This asymmetry may be, but does not seem to be, due to breaking away of the common part of the canal on the right side. These prominent canals are probably of vascular origin. There are similar but variable openings in this region in *Pleurostylodon* and some other early notoungulates that can hardly be interpreted as anything but vascular. The possible (but uncertain) occurrence of a very much smaller single opening in the same region in *Notostylops* suggests correlation with this condition, but on such poor data as to be only a suggestion. In any case the difference between the two is marked. The prominent posterolateral vascular passage from the cerebral chamber in *Notostylops* (and some typotheres) is absent from *Rhyphodon*.

Skull structure is much as in *Pleurostylodon*, but with some striking differences additional to those noted above. The postglenoid process, so prominent in *Pleurostylodon*, barely exists in *Rhyphodon*, and a postglenoid foramen has not been identified. The porus is relatively smaller, and the ventral tympanic plate is massive, without a clear crista meatus. Hypotympanic and epitympanic sinuses are present, as in all notoungulates, but are relatively quite small.

The general uniformity of isotemnid tooth structure makes detailed description for this genus superfluous.

Rhyphodon lankesteri Roth, 1899

Plate 39; plate 40, figure 1

Rhyphodon Lankesteri ROTH, 1899, p. 388.

Rhyphodon lankesteri: SIMPSON, 1932b, p. 1, fig. 1; 1936d, p. 66.

Setebos terribilis[1] ROTH, 1902, p. 253: SIMPSON, 1936d, p. 67 (as synonym of *R. lankesteri*).

Pehuenia werhlii ROTH, 1902, p. 254. SIMPSON, 1936d, p. 66 (as synonym of *R. lankesteri*).

Pehuenia insigna ROTH, 1903, p. 144. SIMPSON, 1936d, p. 66 (as synonym of *R. lankesteri*).

Lemudeus proportionalis ROTH, 1903, p. 144. SIMPSON, 1936d, pp. 67, 81 (as synonym of *R. lankesteri*).

TYPE: M.L.P. No. 12-1717, a partial skull with left P^2–M^3 and a lower jaw with both canines, left P_2–M_3 and right P_2, P_4–M_3. These are of the same species but not the same individual, and I therefore take the partial skull as lectotype.

TYPES OF SYNONYMS: Of *Setebos terribilis*, M.L.P. No. 12-1744, a poorly preserved but nearly complete skull with remnants of M^3. Of *Pehuenia wehrlii*, M.L.P. No. 12-2186, palate and part of the face with right P^2–M^1 and left P^2–M^2. Of *Pehuenia insigna*, M.L.P. No. 12-1575, fragments of palate and tips of nasals, without teeth; Roth mentioned a tooth as attributed to the species, hence not part of the type or a syntype. Of *Lemudeus proportionalis*, M.L.P. No. 12-2212, an isolated right P^3; Roth mentioned two premolars, but only this one was identified in his collection, and it is taken as lectotype.

HYPODIGM: The types, and M.L.P. No. 12-1718, partial jaw with P_2–M_1; M.L.P. No. 12-1729, partial jaw with P_3–M_3; M.L.P. No. 12-1720, partial jaw with P_3-M_2; M.L.P. No. 12-1719, partial jaw with P_{3-4} and M_{2-3}; M.L.P. No. 12-1721, partial jaw with P_2–M_3; A.M.N.H. No. 29414, partial skull without teeth.

HORIZON AND LOCALITY: Mustersan, Patagonia, all known specimens from Roth's Lago Musters ("C.s.M."), our Cerro del Humo.

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[1] This means roughly "the terrible Patagonian pagan god." It was a strange conceit on Roth's part to give so horrific a name to a mild herbivore smaller than a sheep and probably less terrible than a lamb.

TABLE 66

MEASUREMENTS OF LOWER TEETH OF *Rhyphodon lankesteri*[a]

	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. 12-1717	11½	10	13	10½	15	12	18½	12½	20	13½	25½	13
M.L.P. No. 12-1718	11	8½	13	9	14½	10½	17½	12½	—	—	—	—
M.L.P. No. 12-1729	—	—	13	10½	14	11½	19	12½	20½	13	26	12½
M.L.P. No. 12-1720	—	—	13½	10	14½	11½	18½	13½	21	14	—	—
M.L.P. No. 12-1719	—	—	12½	9½	15½	11	—	—	20	13½	—	13
M.L.P. No. 12-1721	10½	9	12½	9	14½	10½	17	11	19	12½	26	12

[a] Measured to nearest half millimeter.

DIAGNOSIS: Only species surely distinct and referable to this genus. Measurements as are given in tables 66 and 67.

Roth strangely neglected to compare his skulls of *Rhyphodon lankesteri* and "*Setebos terribilis*" from the same locality. The latter is a bit more robust, but the difference in any one dimension is less than 10 per cent. The one badly preserved tooth of the latter type provides no means of diagnosis. The type of "*Pehuenia wehrlii*" is also almost identical in structure and size with that of *R. lankesteri*, and there is no reason to suspect possible specific distinction.

The skull fragments on which Roth based "*Pehuenia insigna*" were said to differ in being smaller than "*P. wehrlii*," with more elongate and rounded premaxilla, the canine offset, and the maxilla strongly curved outward. The canine was slightly farther from P^1, an insignificant difference. The other supposed distinctions seem to me to be non-existent.

The isolated P^3 type of "*Lemudeus proportionalis*" is almost exactly as in *Rhyphodon lankesteri*. Its most distinctive character is a notched protoloph, but that, too, is usual even if not universal in *R. lankesteri*.

The syntype (not lectotype) lower jaw of *R. lankesteri* is pathological, as described by Simpson, (1932b). Although interesting in itself, the pathology has no bearing on systematics or normal morphology and therefore is not redescribed here.

?Rhyphodon angusticephalus (Roth, 1903)

Eurystephanodon angusticephalus ROTH, 1903, p. 151.

?Rhyphodon angusticephalus: SIMPSON, 1936d, p. 69.

TYPE: M.L.P. No. 12-2284, a poorly preserved skull fragment with somewhat doubtfully identified and likewise poorly preserved right P^2, P^4, and M^{1-2}. With it but not part of the same individual and not syntypes are a jaw fragment with three teeth, either dm_{3-4} M_1 or dm_4 M_{1-2}, unidentifiable but perhaps *Periphragnis*, and an isolated right upper

TABLE 67

MEASUREMENTS OF UPPER TEETH OF *Rhyphodon lankesteri*[a]

	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. 12-1717[b]	14½	18	15	20	15	25	20	27	23½	31	19	27½
M.L.P. No. 12-2186[c]	14	17	14	19½	15½	24	21½	27½	24	31½	—	—
M.L.P. No. 12-2212[d]	—	—	13½	19½	—	—	—	—	—	—	—	—

[a] Measured to nearest half millimeter.

[b] Lectotype.

[c] Type of "*Pehuenia wehrlii.*"

[d] Type of "*Lemudeus proportionalis.*"

molar, perhaps M^2, possibly of *R. lankesteri.*

HYPODIGM: Type only.

HORIZON AND LOCALITY: Mustersan, Patagonia, Roth's Cañadón Colorado ("C.s.C.C.").

DIAGNOSIS: Probably close to and perhaps identical with *R. lankesteri,* but molars possibly significantly smaller, M^2 (not surely identified as to position) measuring about 19 by 27 mm.

DISTYLOPHORUS AMEGHINO, 1902

Stylophorus ROTH, 1902, p. 252, *nec* Hesse, 1870.

Distylophorus AMEGHINO, 1902a, p. 19 (to replace *Stylophorus* Roth, "nom préoccupé par plusieurs auteurs"). ROTH, 1927, p. 233, pl. 2, fig. 1. SIMPSON, 1936d, p. 88.

TYPE: *Stylophorus alouatinus.*

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: I_{1-2} subequal, I_3 larger; apices of lower incisors trilobed, labial faces convex, with shallow vertical grooves, lingual faces excavated and with strong vertical lateral and medial ridges. C slightly larger than I_3 or P_1. P_1 smaller than C but more caniniform than molariform. P_{2-4} progressively molariform, about as in *Rhyphodon* but relatively longer and narrower. P_4 with distinct transverse entoconid. M_{1-3} about as in *Rhyphodon,* but metaconids simpler, hypolophid flatter, especially on M_3, and hypoconulid end fully labial, a small distinct cuspule on its lingual slope.

The definition of this genus depends on doubtful identifications and interpretations of specimens, discussed under the species. According to my interpretation, the genus is distinctive from any in which principal comparable parts are known and hence is considered valid. The lower dentition is a unique but moderate variation on the simplest sort of notoungulate pattern, marked especially by the peculiar incisors, the progressive molarization of premolars, and the likewise simple molars. The lack of distinctively divergent characters makes classification doubtful, but on the whole such a prototypal toxodont-like dentition makes provisional reference to the Isotemnidae satisfactory.

As noted under the species, an upper dentition assembled and referred to this genus by Roth is peculiar and would emphasize both the validity of the genus and its doubtful place in classification. There is, however, some doubt as to whether that dentition is correctly assembled and does belong to this genus.

As indicated by the specific name, Roth compared this genus with primates, whereas Ameghino, who probably had not seen either figures or originals, believed it to be a phenacodontid. Both were remarkably poor guesses.

Distylophorus alouatinus (Roth, 1902)

Stylophorus alouatinus ROTH, 1902, p. 252.

Distylophorus alouatinus: AMEGHINO, 1902a, p. 19. ROTH, 1927, p. 194, pl. 3, fig. 10, pl. 13, fig. 1. SIMPSON, 1936d, p. 67.

Type: No specimen labeled as belonging to this species or genus was found in the Roth Collection when I studied it. The original description was based essentially on the lower dentition (incisors, premolars, molars) but also mentioned upper teeth. Roth later (1927) figured upper teeth as of this species, and those may have been syntypes, but were not the main basis for the definition. They were not found in the collection, although photographs of them are available. There is an unlabeled specimen, M.L.P. No. 12-2210, in the collection that does not belong to any of Roth's other genera and that is consistent with (but not absolutely identified by) Roth's summary description of lower teeth. It does represent an otherwise unnamed genus and species. I think it likely that this was Roth's type or principal syntype, and in any event believe that it can justifiably be designated as lectotype or, if need be, neotype. This specimen consists of the entire right lower dentition, I_{1-3}, C,P_{1-4}, M_{1-3}. The teeth are not in a jaw[1] but were loose and have been assembled and mounted in plaster. A further element of doubt is thus introduced, but I believe that these teeth did belong to one individual and have been placed in correct sequence. Where they are appressed (especially P_4–M_3), the facets fit, the morphology is consistent, and so are the degrees of wear on the various teeth.

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[1] The contrary statement in Simpson (1936d, p. 88. line 14) was due to misunderstanding on the part of an editor.

TABLE 68

MEASUREMENTS OF LOWER TEETH OF *Distylophorus alouatinus*[a]

		M.L.P. No. 12-2210[b]	A.M.N.H. No. 29472
Maximum crown diameters			
	I_1	8½	—
	I_2	9	—
	I_3	11½	—
	C	14½	—
P_1			
	L	12½	—
	W	8	—
P_2			
	L	13	—
	W	9	—
P_3			
	L	14½	—
	W	9½	—
P_4			
	L	15	16
	W	9½	10½
M_1			
	L	19	17½
	W	11½	12
M_2			
	L	21½	21½
	W	13	13½
M_3			
	L	27½	29
	W	14½	11½

[a] Measurements to nearest half millimeter.

[b] Lectotype.

The upper dentition, apparently I^3–M^2, much later figured by Roth (1927, pl. 3, fig. 10, and pl. 13, fig. 1) was also assembled from loose teeth and mounted in plaster. It is also of the right side, and the teeth could have belonged to the same animal as the lower teeth, M.L.P. No. 12-2210, but the sequence looks awkward, and I suspect that one or more of the teeth are incorrectly placed if, indeed, they do belong together. This was possibly a syntype, but that is uncertain, and the specimen was not found at the time of my study. It therefore seems unwise and unnecessary to take this as type or lectotype.

HYPODIGM: The lectotype, as above, with doubt also the lost but figured upper teeth, and A.M.N.H. No. 29472, part of right lower jaw with P_4–M_3.

HORIZON AND LOCALITY: Mustersan, Patagonia. Lectotype from Colhué-Huapí.

DIAGNOSIS: Only known species of the genus as here defined. Measurements are given in table 68.

Our specimen from Colhué-Huapí is not significantly different in size or most characters but does have the trigonids relatively somewhat shorter and the hypolophid of M_3 more curved. It may possibly, but probably does not, represent a somewhat different taxon.

The figured but mislaid upper teeth probably do belong to this species, whether or not correctly associated and assembled. The premolars are apparently progressively molariform but without evident hypocones. The molar hypocones also are relatively small and rather posterolabial than posterior to the protocones, which have a decidedly rounded labial face, not flattened as in *Periphragnis*, for example. The main fossettes of (doubtfully) P^2–M^2 are unusually large and deep and not so elongate anterolabio-posterolingually as in typical isotemnids.

?ISOTEMNIDAE INCERTAE SEDIS

LAFKENIA Roth, 1902, NOMEN DUBIUM

Lafkenia ROTH, 1902, p. 254; 1927, p. 235, pl. 13, fig. 5. SIMPSON, 1936d, p. 82 (as probable synonym of *Rhyphodon*).

TYPE: *Lafkenia sulcifera.*

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: Based on probable deciduous molars of an isotemnid, perhaps *Rhyphodon.*

The two specimens placed here (as representative of two new species) by Roth are distinctive enough in their own terms but are almost certainly deciduous molars of a genus and species known by permanent teeth under another name. Discovery of associated deciduous and permanent teeth is needed to determine the affinities and, if such it prove to be, synonymy.

Lafkenia sulcifera Roth, 1902, *nomen dubium*

Plate 41, figure 1

Lafkenia sulcifera ROTH, 1902, p. 254; 1927, p. 195, pl. 4, fig. 9.

Type: M.L.P. No. 12-1461, an isolated right upper cheek tooth.

Hypodigm: Type only.

Horizon and Locality: Mustersan, Patagonia. Roth's Lago Musters.

Diagnosis: Probably a milk tooth of an otherwise named species. Type measuring 17 by 19 mm.

Lafkenia schmidti Roth, *nomen dubium*

Plate 41, figure 5

Lafkenia Schmidti Roth, 1902, p. 254.

Type: M.L.P. No. 12-2188, fragment of right maxilla with two successive teeth, probably either dm$^{2-3}$ or dm$^{3-4}$.

Hypodigm: Type only.

Horizon and Locality: Mustersan, Patagonia. Roth's Lago Musters.

Diagnosis: Probably milk teeth of an otherwise named species. Successive teeth measure 13½ by 13 and 16 by 15½ mm.

COLHUELIA Roth, 1902, nomen dubium

Colhuelia Roth, 1902, p. 254. Simpson, 1936d, p. 82 (as possible synonym of *Periphragnis*).

Type: *Colhuelia fruhi.*

Distribution: Mustersan, Patagonia.

Diagnosis: Based on probable deciduous molars of an isotemnid, perhaps *Periphragnis.*

Roth's three specimens all seem to be upper milk molars similar to those of "*Lafkenia*" but from a larger animal, which suggests *Periphragnis.* Again only discovery of associated deciduous and permanent teeth can settle the matter.

Colhuelia fruhi Roth, 1902, *nomen dubium*

Plate 41, figure 2

Colhuelia Frühi Roth, 1902, p. 254.

Type: The following teeth, all deeply worn, were probably syntypes: M.L.P. No. 12-2216, left upper tooth, perhaps dm^{2}, lectotype; M.L.P. No. 12-2215, right upper tooth, more transverse, probably more posterior; M.L.P. No. 12-2214, left upper tooth, similar to lectotype in form but slightly smaller.

Hypodigm: Types only.

Horizon and Locality: Mustersan, Patagonia. Roth's Lago Musters.

Diagnosis: Probably milk teeth of an otherwise named species. The lectotype measures 19 by 19 mm., the other syntypes 20 by 21½ and 17½ by 16½.

COLHUAPIA Roth, 1902, nomen dubium

Colhuapia Roth, 1902, p. 255. Simpson, 1936d, p. 82.

Type: *Colhuapia rosei.*

Distribution: Mustersan, Patagonia.

Diagnosis: Based on probable deciduous molars of an isotemnid, perhaps *Periphragnis.*

The two deeply worn teeth on which Roth based this "genus" are unidentifiable and could well belong to "*Colhuelia fruhi,*" hence perhaps to some (probably already named) species of *Periphragnis.*

Colhuapia rosei Roth, 1902, *nomen dubium*

Plate 41, figure 6

Colhuapia Rösei Roth, 1902, p. 255.

Type: Two teeth placed together and labeled as of this species in the Roth Collection were perhaps syntypes, but M.L.P. No. 12-2221, isolated right upper cheek tooth, perhaps dm^{3}, is closer to Roth's measurements, so is probably the type and in any case is made lectotype. The other specimen is M.L.P. No. 12-2222, also a right upper cheek tooth, perhaps dm^{4}.

Hypodigm: Type only.

Horizon and Locality: Mustersan, Patagonia. Roth's Lago Musters.

Diagnosis: Probably milk teeth of an otherwise named species. Type measuring 19½ by 22½ mm.

"Trigonolophodon" modicus Roth, 1903, *nomen dubium*

Plate 41, figure 3

Trigonolophodon modicus **Roth, 1903, p. 147.**
"*Trigonolophodon*" *modicus:* Simpson, 1936d, p. 90.

Type: M.L.P. No. 12-2190, left upper molar. Roth also mentioned a lower jaw with P_4–M_3, but this was not found in the collection.

Hypodigm: Type only.

Horizon and Locality: Mustersan, Patagonia. Roth's Lago Musters.

Diagnosis: Labial face of upper molar nearly plane, parastyle and paracone folds slight. Upper molar (perhaps M^3) with large protocone and vestigial hypocone; well-developed cingula. Type measuring $25\frac{1}{2}$ by 34 mm.

In the absence of the possibly syntype lower jaw, all that can be said of this supposed species is that it is a virtually undeterminable notoungulate and could belong to *Periphragnis*. It is highly unlikely that it belongs to the Deseadan genus *Trigonolophodon.*[1]

"Pehuenia" magna Roth, 1903, *nomen dubium*

Plate 41, figure 4

Pehuenia magna Roth, 1903, p. 145. Simpson, 1936d, pp. 67, 79 (not this genus).

Type: M.L.P. No. 12-2189, isolated left upper molar.

Hypodigm: Type only.

Horizon and Locality: Mustersan, Patagonia. Roth's Lago Musters.

Diagnosis: Parastyle and paracone folds on type upper molar moderately prominent, subequal; broad medial excavation of labial face, then rounded posterior metacone fold; inner face flattened, large protocone and small hypocone separated from metaloph. Type measuring $31\frac{1}{2}$ by 39 mm.

This could be a variant form of *Periphragnis*, but it is rather peculiar and highly dubious. It does not belong to *Pehuenia* (=*Rhyphodon*).

"Eurystephanodon" crassatus Roth, 1903, *nomen dubium*

Eurystephanodon crassatus Roth, 1903, p. 151. Simpson, 1936d, p. 67 (as *incertae sedis*).

Type: M.L.P. No. 12-1600, isolated broken right upper molar, lectotype or type. Under the same number is a jaw fragment with left M_{1-2}, syntype or referred.

Hypodigm: Lectotype only.

Horizon and Locality: Mustersan, Patagonia. Roth's Lago Musters.

Diagnosis: A practically indeterminate isotemnid. Type upper molar about 22 mm. in length.

This could be a somewhat variant *Rhyphodon*, but does not seem really identifiable. It probably does not belong to *Eurystephanodon* (=*Periphragnis*).

"Thomashuxleya" principialis Ameghino, 1902, *nomen dubium*

Thomashuxleya principialis Ameghino, 1902a, p 25.

Type: M.A.C.N. No. 10937, jaw fragment with M_{2-3}.

Hypodigm: Type only.

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

Diagnosis: A probable isotemnid of moderate size, not more closely identifiable. M_2 of type measuring 13.5 by 9.0 mm.; M_3, about $18\frac{1}{2}$ by 8.8 mm.

This specimen probably does not belong to *Thomashuxleya*. I could not closely match it among other isotemnids, but it is hardly determinate as to genus or even family.

FAMILY **NOTOHIPPIDAE** AMEGHINO, 1895

Notohippidae Ameghino, 1895.
Rhynchippidae Loomis, 1914.

Definition: Notoungulates of moderate size, early becoming hypsodont and fully lophodont, latest members with cement-covered molars adapted to grazing and functionally comparable to those of the most advanced Equidae but still with only slightly modified basic toxodont pattern. Dentition complete and closed but with C's reduced in size, more or less incisiform, and P^1_1 persistently small. Incisors variously enlarged, arranged in a broad, somewhat flattened arch. Upper premolars primitively with metaloph but no protoloph, or a deeply notched protoloph; P^{3-4}_{3-4} becoming almost fully molariform in later forms. Upper molars (and molariform premolars) with two cristae soon united with each other and with the crochet by wear; three labial fossettes, another enclosed by a cingulum posterior to the metaloph, and a lingual fossa—pattern variable with wear and also systematically by dif-

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[1] The only available purported review of the Deseadan fauna, Loomis (1914), omits all of Roth's numerous Deseadan taxa.

ferent levels of union of the various lophs. Lower molars with very short trigonids, without fossettids, and long talonids, developing one, two, or three transient fossettids.

KNOWN DISTRIBUTION: Mustersan to Santacrucian, Patagonia.

Ameghino (1895) based this family on one of its latest, most specialized members but later (e.g., his definitive arrangement of 1906) also placed older (back to Mustersan) genera here. Loomis (1914) incorrectly referred *Notohippus* itself and other relatively specialized genera to the family Toxodontidae. He therefore proposed a then new family, Rhynchippidae (with an almost completely erroneous definition), for the comparatively less-specialized, clearly non-toxodontid genera. I (Simpson, 1932f) returned to Ameghino's concept of special relationship between, e.g., *Rhynchippus* and *Notohippus*, and nonreference of the latter to the Toxodontidae, but recognized as separate families Rhynchippidae and Notohippidae. Patterson (1934b) argued that the supposed family distinction is invalid or exaggerated, and I (Simpson, 1936e) accepted that view, referring the "rhynchippid" *Pseudostylops* to the Notohippidae. Still later (Simpson, 1945) I continued to recognize only one family, but divided it into Rhynchippinae and Notohippinae. The two groups thus designated are morphologically separable, but whether such separation is justified either by phylogeny or or by convenience remains decidedly moot. Decision will depend largely on the post-Mustersan forms, and I therefore do not pursue the matter further here, where it suffices simply to place the Mustersan species in the Notohippidae.

Although Ameghino recognized the essential unity of this family, he referred one supposed genus, *Pseudostylops*, now known certainly to be a notohippid, to the Trigonostylopidae, which belong to a different order, as Ameghino also recognized in different terms. He believed the Notohippidae to be related or ancestral to true horses and placed them in his order Hippoidea.

Roth (1902) named two probably synonymous genera (*Eurvstomus*. *Lonkus*) now referred to the Notohippidae. For one of these he vaguely recognized relationship with a notohippid: "Los molares superiores [de *Eurystomus*] se parecen algo al *Morphippus*." The other, *Lonkus*, was not compared with anything or classified in any way. Ameghino (1902a) also noted the resemblance of *Eurystomus* to notohippids and suggested that it might be synonymous with the Deseadan *Eurygeniops*.

Loomis (1914) placed this group in the order Notoungulata, suborder Toxodonta (or Toxodontia), an action that still seems to be correct, although relationship to the Toxodontidae is probably not so close as he thought.

Among earlier and contemporary forms, the Mustersan notohippids are unique but do have some possibly significant resemblance to the group here somewhat tentatively united under the name *Acoelohyrax* in the Isotemnidae. *Acoelohyrax* also has a tendency (to less degree) toward hypsodonty, upper premolars with notched or interrupted protolophs, similar upper molars except for being less hypsodont and with more complex arrangement of cristae, lower molars with short trigonids and long talonids with a tendency (less pronounced than in notohippids) to develop fossettids, and probably (but not quite surely) small canines and a transverse incisor series. It is possible but it seems unlikely that these rather peculiar resemblances are entirely convergent. The two groups are nevertheless quite distinct when undoubted notohippids first appear in the Mustersan. If not convergent, the resemblance could be taken as evidence either that *Acoelohyrax* is an early offshoot of the Notohippidae or that the Notohippidae arose from earlier Isotemnidae and that *Acoelohyrax* evolved with some parallelism from that ancestry. The latter interpretation seems somewhat more likely, but in fact the difference between the two interpretations is rather formal and not very important.

This group is very rare at the Mustersan localities worked by Carlos Ameghino or the Scarritt Expeditions and can be considered fairly well represented in only one deposit, at an unknown locality, worked by Roth. The poverty of specimens and the radical changes in measurable dimensions and observable morphology with wear make the classification of these Mustersan forms difficult and dubious, to an even greater degree than most other families in these early faunas. At present I recognize only one Mustersan genus, *Eomorphippus*. "*Interhippus*," clearly distinct from *Eomorphippus*, is apparently synonymous with Deseadan *Coresodon* and, although recorded as Mustersan, is probably Deseadan, only, in age. Ameghino (1906, p. 469) once listed the otherwise Deseadan *Nesohippus* in the Mustersan ("Astraponotéenne") fauna, almost certainly by mistake, because no Mustersan species was ever described, there are no Mustersan specimens in the Ameghino Collection labeled as of this genus, and there is no other mention of its occurrence in the Mustersan.

EOMORPHIPPUS AMEGHINO, 1901

Eomorphippus AMEGHINO, 1901, p. 373; 1906, p. 469. SCHLOSSER, 1923, p. 611. SCOTT, 1937a, p. 504.

Pseudostylops AMEGHINO, 1901, p. 395; 1906, p. 470. SCHLOSSER, 1923, p. 611. SCOTT, 1937a, p. 504.

Lonkus Roth, 1902, p. 256.

Eurystomus ROTH, 1902, p. 256, *nec* Vieillot, 1816.

Pleurystomus AMEGHINO, 1902a, p. 14, substitute for *Eurystomus* Roth "préoccupé par plusieurs auteurs."

TYPE: *Eomorphippus obscurus*. *Eomorphippus obscurus* and *E. rutilatus* were published simultaneously. I here select *E. obscurus* as type.

TYPES OF SYNONYMS: Of *Pseudostylops*, *P. subquadratus;* of *Lonkus*, *L. rugei;* of *Eurystomus*, *E. stehlini.*

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: Hypsodonty moderate, less than in later forms. No cement on teeth. I^3 enlarged. P^{1-3} with notched or incomplete protoloph. P^4 more, but not fully, molariform, without distinct hypocone. Upper molars with lingual hypocones, a variable but deep cleft between protocone and hypocone, blocked by a medial projection which is probably the anterior end of the crochet. Fossettes, as distinct from the persistent major fossa, rapidly obliterated by wear. Lower molars with clefts anterior and posterior to the entoconid, which may variably develop with wear into evanescent fossettids.

In describing a specimen of this genus (Simpson, 1936e), I called it *Pseudostylops* but considered it possible that some specimens placed by Ameghino in *Eomorphippus* belong here. I believed that as of then *Pseudostylops* was certainly identifiable and *Eomorphippus* was not or was only doubtfully so, and I considered it "very unlikely" that the two generic names are synonymous. I therefore gave precedence to *Pseudostylops*, published at the same time but on a succeeding page. Of Ameghino's two species of *Eomorphippus*, also published simultaneously, "*E.*" *rutilatus* now proves to be not a notohippid but an archaeohyracid and is here removed to the latter family and to the new genus *Bryanpattersonia*. The more extensive materials now available make the other species, *E. obscurus*, identifiable and show that it is congeneric with *Pseudostylops*. Choice of *E. obscurus* as type of *Eomorphippus* thus makes that name and *Pseudostylops* synonymous after all. Under the current Code [Stoll and others, 1964, Article 24 (a) (i)] my giving priority to *Pseudostylops* (Simpson, 1936e) does not determine relative priority because I did not "[make] it clear that [I believed] them to represent the same taxonomic unit," and in fact expressed the opinion that that was very unlikely. I now do positively state that I believe the two names to represent the same genus, and, thus qualified as first reviser, I choose *Eomorphippus* as the name of that taxon. Such choice is not made on the basis of page priority, which, as in 1936, I still consider ridiculous and which is expressly excluded by the present Code. There is little or nothing to choose on the basis of adequacy (inadequacy, in fact) of types or usage. *Eomorphippus* is a preferable name because it correctly suggests relationship to *Morphippus*, a Deseadan notohippid, whereas *Pseudostylops* incorrectly suggests relationship to the other *-stylops* genera, most of which are notostylopids and none of which are notohippids.

Ameghino did not compare *Pseudostylops* and *Eomorphippus*, having referred them to different orders and based them on specimens with no parts in common. Now that specimens simultaneously comparable with both types are known, there is little doubt that the names were applied to the same genus, and they may have been based on the same species.

Roth published *Eurystomus stehlini* and *Lonkus rugei* as from "Formación terciaria inferior," which generally means what we call Deseadan. (Like Ameghino, Roth thought that the Mustersan was Cretaceous in age, but he believed the Deseadan to be Tertiary.) I therefore omitted those supposed genera and species from my study of pre-Deseadan mammals in the Roth Collection (Simpson, 1936d) and from preparations for the present monograph. However, Bryan Patterson, preparing similar studies on the Deseadan and Colhuehuapian faunas, found that Roth's collection from the "Terciario inferior de Cañadón Blanco" includes not only Deseadan but also some Casamayoran and Mustersan mammals. *Eurystomus* and *Lonkus* so closely resemble each other and Ameghino's *Eomorphippus* and *Pseudostylops* that Patterson considers the four names synonymous and considers Roth's specimens of this genus to be from a Mustersan deposit. (Roth's "Cañadón Blanco" was in Chubut, but has not been more precisely located.) I am much indebted to Patterson for this information. The Roth specimens provide the best knowledge of the dentition, and I am further indebted to Patterson for the following description. I have inserted a few remarks in square brackets.

THE DENTITION OF *Eomorphippus*

BY BRYAN PATTERSON

The upper incisors are arranged in a nearly transverse line across the muzzle. When unworn, there is a prominent semicircular internal cingulum that, with wear, isolates a very transitory cup and a rather blunt, median, internal ridge. The ridge is most pronounced on I^3. There are no external cingula. The teeth, particularly I^{1-2}, decrease in transverse diameter with wear. The canine is similar in structure to I^3 but much smaller, and is situated posterior to it. The muzzle is wide, and the palate pinches in notably across C–P^1, about as in *Morphippus* [a Deseadan notohippid]. The incisors are approximately one-half of the height of those of *M. imbricatus*, and are less curved.

P^1 is a small, subquadrangular, single-rooted tooth. The ectoloph is complete, with a small parastyle ridge, separated by a vertical groove from the large and prominent paracone ridge, and with a faint, posterior, vertical ridge. The extremities of the ectoloph are joined by cingula to the median, internal protocone, and this cusp is connected to the center of the ectoloph by a transverse crest that divides the crown into shallow anterior and posterior basins. A branch from this crest connects posterointernally with the posterior cingulum, isolating a small fossette. P^2 is considerably wider than P^1; the protocone is compressed anteroposteriorly; the transverse crest occupies the position of the metaloph on the molars; the anterior cingulum fails to reach it, and the posterior cingulum extends to a lower point on the crown. The posterointernal, cup-shaped fossette is prominent, and there is no trace of a protoloph. The anterior basin is deepest at the center; extreme wear would isolate a small, median fossette. On P^3 the protocone has a prominent anteroexternal spur that falls a little short of the ectoloph and would not unite with it until wear had reached a very advanced stage. The median valley, here partially isolated, is very deep at the center. The anterior cingulum is high on the crown but fairly prominent, with a freely projecting inner extremity. The protoloph is complete on P^4; the parastyle ridge is more external, and the paracone ridge relatively smaller, than on the preceding premolars; an external swelling is present in the region of the metacone; there is a faint, median internal groove; and the anterior cingulum is less prominent internally.

M^1 is broken internally on both sides [in M.L.P. No. 12-1508, the only Roth specimen with upper molars; other specimens show that M^1 is virtually identical with M^2 in structure]. The ectoloph resembles that of M^2, and the internal cleft between protocone and hypocone appears to have been about as deep. M^2 is but little worn [in M.L.P. No. 12-1508] and, at its present state of wear, considerably longer than wide. The ectoloph is gently undulating, the parastyle projecting a little anteriorly and separated by a slight, very shallow depression from the paracone ridge. A slight swelling at the metacone is present, and there is no posterior vertical

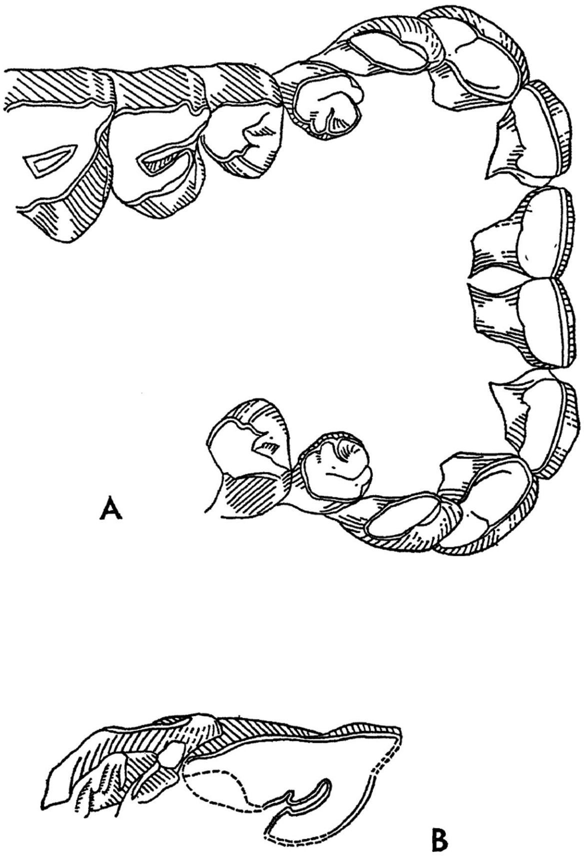

FIG. 36. *Eomorphippus obscurus* Ameghino, M.L.P. No. 12-1508, type of *Eurystomus stehlini*. A. Reconstruction of anterior upper dentition; right I^1–C and left P^{1-2} are reversed from the other side. B. Broken right M^{2-3}. Drawn by M. T. Cabrera for B. Patterson. ×1.5.

ridge. The protoloph is decidedly oblique and forms more than half of the internal face. A deep, narrow cleft between protocone and hypocone persists to within a few millimeters of the base of enamel; a slight cingulum is present below it. [The cingulum seems to be absent from M^1 and from some other specimens of M^2.] At least two cristae projected from the ectoloph into the central valley, and there may have been a small one anterior to them in the unworn crown. [That is unlikely; a third, anterior crista is not shown by any specimen, including unworn M^3 of A.M.N.H. No. 29462.] The metaloph is short, thin, and transverse; it is joined to the posterior crista. The posterior cingulum runs from the posterior extremity of the ectoloph to the hypocone, enclosing a shallow, nearly circular fossette, as in later notohippids. An anterior cingulum is present at the base of the tooth. M^3 has a rather more convex ectoloph with less distinction between parastyle and paracone ridges and a more prominent metacone swelling than in the other molars; a distinct posterior vertical ridge is present. [M^3 of A.M.N.H. No. 29462 does not have a distinct metacone swelling.] The protocone-protoloph forms a greater part of the internal face than in M^2, and the cleft between protocone and hypocone does not extend quite so near to the base of the tooth. Cristae and crochet are united

FIG. 37. *Eomorphippus obscurus* Ameghino, M.L.P. No. 12-1508, type of *Eurystomus stehlini*. A. Anterior lower teeth. B. Right P_2–M_3. Drawn by M. T. Cabrera for B. Patterson. ×1.5.

to form a crenulated crest running between protoloph and ectoloph. [Unworn M^3 of A.M.N.H. No. 29462 shows that the crochet is remarkably large, perhaps a family character; it is the crochet and not, as might appear on worn teeth, the second crista that forms the mass visible through the labial cleft.]

The lower incisors and canines are arranged in a nearly transverse line across the symphysis, I_1–C, engaging I^{1-3}, as in other notohippids. The incisors bear a conspicuous ridge on their internal faces, which lower down on the crown joins a ridge on the internal (medial) edge. On the canine this ridge is small and inconspicuous. There are no external cingula.

P_1 is only partially visible [in M.L.P. No. 12-1508]. It bears a prominent, external vertical ridge, the protoconid ridge, and a wavy crest that, externally, is convex anteriorly and concave posteriorly behind the vertical ridge. P_2 differs in the greater sinuosity of the crest and the deeper external valley behind the protoconid ridge; P_3 is submolariform; an entoconid is present, and there is a rudimentary paraconid ridge, but the crista obliqua is joined to the metaconid and not to the center of the metalophid. P_4 is nearly molariform, differing from the molars only in the less prominent paraconid and in the deeper external cleft between the trigonid and talonid. [In some other specimens, at least, the talonid of P_4 is not so long relative to the trigonid as it is in the molars.]

In the molars the trigonid is considerably smaller than the talonid, as in notoungulates generally, the paraconid prominent and anterointernal in position, separated from the metaconid by a well-developed internal cleft. The hypolophid is gently curved inward posteriorly in M_{1-2}, very long and straighter in M_3. On the internal side of the talonid, the entoconid pillar is very large and prominent, connected to the hypolophid and set off anteriorly and posteriorly by deep clefts opening internally. As a rule, the cleft between the metalophid and entoconid is the deeper of the two on M_{1-2}, and that between the entoconid and the posterior end of the hypolophid is invariably the deeper on M_3. In some individuals, e.g., M.L.P. No. 12-1523, the entoconid is expanded anteroposteriorly, and its base unites with that of the metaconid higher on the tooth than usual, causing the cleft between these pillars to be shallower than the posterior cleft on M_{1-3}. Exactly comparable variations occur among the various lower molars attributed by Ameghino to *Eomorphippus obscurus.*

The Roth specimens show, even better than the specimen found by Feruglio and described by Simpson (1936e) as *Pseudostylops*, that the essential characters of the Notohippidae, and the included Rhynchippinae, were established by Mustersan time. *Eomorphippus* represents, structurally at least, the ancestry of *Morphippus Eurygenium*, and *Rhychippus* [of the Deseadan]. With the exception of the Archaeohyracidae, which are even more advanced, the Notohippidae appear to have been, at this time, the most progressive of the various toxodont families that survived to the Deseadan or later.

I have made a direct comparison with the cast in the Museo Argentino de Ciencias Naturales of Feruglio's specimen [described in Simpson, 1936e] and, allowing for some difference in age, the only distinction seems to be that I^3 is slightly smaller in Roth's type of *Eurystomus stehlini.* P^{2-4} of both agree almost perfectly. M^1 of the Feruglio specimen is at the same stage of wear as M^2 of Roth's type, and the resemblance is very close.

Ameghino's syntypes of *Eomorphippus obscurus* (three upper molars) vary somewhat in the depth of the cleft between protocone and hypocone. In the left M^2 [perhaps M^1] this persists almost to the base of the enamel, as in Roth's type, where there is a prominent, rounded, cingular area. In the right M^2 [or perhaps M^1] syntype the cleft had closed more than 7 mm. above the base. As far as I can judge from the cast, Feruglio's specimen may have been closer to the right M^2 than to the left M^2 and Roth's type in this respect. In left M^3 [lectotype] of *E. obscurus*, the cleft closes 11 mm. above the base, and in Roth's type about 6 mm. These differences here appear to be individual variations, but they later become segregated and taxonomically significant in *Morphippus-Eurygenium* (slight cleft) on one hand, and *Rhynchippus* (deeper cleft) on the other.

[End of section by Bryan Patterson.]

Eomorphippus obscurus Ameghino, 1901

Plate 41, figures 7–12; text figures 36–38

Eomorphippus obscurus AMEGHINO, 1901, p. 373.
Pseudostylops subquadratus AMEGHINO, 1901, p. 395; 1904b, p. 282, fig. 381. SIMPSON, 1936e, p. 1, unnumbered text fig.
Eurystomus Stehlini ROTH, 1902, p. 256.
Pleurystomus (*Eurystomus*)[1] *Stehlini:* AMEGHINO, 1902a, p. 14.
Lonkus rugei ROTH, 1902, p. 256.

TYPE: M.A.C.N. No. 10917, two left and one right upper molars, syntypes. The measurements given were from the slightly broken left M^3, which is taken as lectotype. Lower molars were also mentioned in the type description, probably those under M.A.C.N. No. 10914, but as Ameghino labeled M.A.C.N. No. 10917 "tipo," the lower molars should probably not be considered syntypes.

TYPES OF SYNONYMS: Of *Pseudostylops subquadratus*, M.A.C.N. No. 10904, an isolated upper premolar, probably P^3; of *Eurystomus stehlini*, M.L.P. No. 12-1508, palate with partly broken but full dentition and associated symphysis and right ramus with left I_1–P_1, right I_{1-3}, and P_2–M_3; of *Lonkus rugei*, M.L.P. No. 12-1515, fragment of right lower jaw with P_{2-3} and alveoli or roots of I_1–P_1. (Roth's diagnosis was based on more than one specimen and also gave measurements of M_1, but Patterson, personal communication, takes this specimen as lectotype.)

HYPODIGM: The types and the following: M.A.C.N. No. 10914, 16 isolated, nonassociated, partly broken teeth, not all of this species or genus (of these, two right M_1's, two left M_2's, one right M_2, and two right M_3's probably are of this species; the whole lot labeled by Ameghino "Probablemente de un solo género," contrary to my judgment of probability); M.L.P. No. 12-1512, jaw fragment with right P_4–M_3; M.L.P. No. 12-1519, jaw fragment with left M_{2-3}; M.L.P. No. 12-1523, jaw fragment with left M_2; M.L.P. No. 12-1520, jaw fragment with left M_3; M.L.P. No. 12-1523, jaw fragment with right M_{2-3}; M.L.P. No. 12-1536, isolated right I^2 and left I^3; M.L.P. No. 12-1538, isolated and broken right and left M_3's; M.L.P., uncatalogued, jaw fragment with left M_{1-3}; A.M.N.H. No. 29462, fragment

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[1] The form in which Ameghino wrote this name was intended to indicate that *Eurystomus* Roth, preoccupied, is synonymous with *Pleurystomus* Ameghino, and not, as would now be indicated by use of this form, that *Eurystomus* was considered a subgenus of *Pleurystomus.*

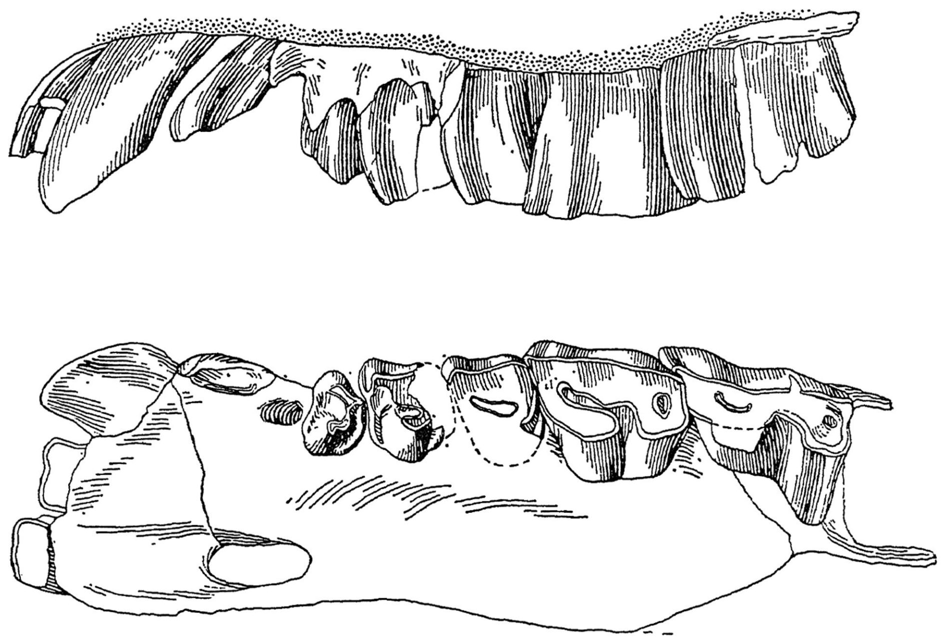

FIG. 38. *Eomorphippus obscurus* Ameghino, Feruglio Collection, University of Padua, partly broken left I$^{1-3}$, C, and P^2–M^2, buccal and crown views. ×1.25.

of maxilla with right M$^{2-3}$, not exactly measurable and somewhat doubtfully included in the hypodigm, but of special interest as having M^3 virtually unworn.

HORIZON AND LOCALITY: Mustersan, Patagonia. No field data with Ameghino specimens. Roth specimens from "Cañadón Blanco," but that is an unknown locality. American Museum specimen from Colhué-Huapí.

DIAGNOSIS: Structure essentially as described for the genus. Cheek teeth slightly larger, more hypsodont, than those of only other species now recognized in the genus. Measurements are given in tables 69 and 70.

?Eomorphippus pascuali,[1] new species

Plate 41, figures 13–15

TYPE: A.M.N.H. No. 29405, maxillary fragment with left P^2–M^2, collected by C. S. Williams on the first Scarritt Expedition, November 19, 1930.

HYPODIGM: Type only, but A.M.N.H. No. 29474, jaw with right I$_3$–M$_3$, is doubtfully referred.

HORIZON AND LOCALITY: Mustersan, Patagonia. On line of section M in Simpson field book for 1930 in the American Museum of Natural History, level marked on section, just below the erosional base of upper channel bed.

DIAGNOSIS: Type with P^3–M^2. Somewhat, probably not significantly, smaller than specimens now referred to *E. obscurus*. Crowns relatively lower. Protocone-hypocone cleft nearly to base, and all labial fossettes disappearing before cleft is closed by wear. P$^{3-4}$ with continuous protoloph. P^2–M^2 with relatively clear metacone swellings on labial faces. Measurements are given in tables 69 and 70.

This type specimen is evidently similar to *Eomorphippus obscurus*, but it is almost impossible that it belongs to that species. It was found at the same locality and level as A.M.N.H. No. 29462, which surely belongs to *Eomorphippus* and probably to *E. obscurus*. On that specimen the distance from the bottom of the protocone-hypocone cleft to the base of M^2 is greater than 14.2 mm. (the base is not quite complete). On the type

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[1] Named for Dr. Rosendo Pascual of the Museo de La Plata, an able student of Argentine fossil mammals.

TABLE 69

Measurements of Upper Teeth of Mustersan Notohippidae

	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
Eomorphippus obscurus														
M.A.C.N. No. 10914[a]	—	—	—	—	—	—	—	—	—	—	—	—	21½	18
M.L.P. No. 12-1508[b]	5.8	5.8	7.0	9.9	9.4	12.7	10.5	14.4	14.4	—	16.3	17.7	18.8	15.4
M.A.C.N. No. 10904[c]	—	—	—	—	9	10½	—	—	—	—	—	—	—	—
A.M.N.H. No. 27885[d]	—	—	6.9	9.0	—	11.0	—	—	18.1[e]	14.7	—	—	—	—
?*Eomorphippus pascuali*														
A.M.N.H. No. 29405[f]	—	—	7.4	9.9	7.9	11.0	9.2	12.5	13.5	13.2	15.1	14.8	—	—
Interhippus deflexus														
M.A.C.N. No. 10916[f]	—	—	—	—	—	—	—	—	—	—	16½	15	—	—

[a] Lectotype of *Eomorphippus obscurus.*

[b] Type of *Eurystomus stehlini.* Measurements from Bryan Patterson.

[c] Type of *Pseudostylops subquadratus.*

[d] Specimen described by Simpson (1936f). The original is in the Feruglio Collection at the University of Padua, Italy. The catalogue number is that of a cast in the American Museum of Natural History, but the measurements were taken on the original specimen.

[e] Misprinted in Simpson (1936f, p. 10).

[f] Type.

TABLE 70

MEASUREMENTS OF LOWER TEETH OF MUSTERSAN NOTOHIPPIDAE

	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
Eomorphippus obscurus														
M.L.P. No. 12-1508[a]	—	—	7.1	5.1	8.9	6.3	10.7	7.0	12.0	7.3	16.1	8.4	20.9	—
M.L.P. No. 12-1515[b]	—	—	7.6	5.1	8.9	6.0	—	—	—	—	—	—	—	—
M.L.P. No. 12-1512[c]	—	—	—	—	—	—	9.6	6.4	—	6.7	15.1	7.9	22.6	8.4
M.L.P. No. 12-1519[c]	—	—	—	—	—	—	—	—	—	—	14.4	7.7	19.1	8.3
M.L.P. No. 12-1523[c]	—	—	—	—	—	—	—	—	—	—	14.7	7.3	—	—
M.L.P. No. 12-1520[c]	—	—	—	—	—	—	—	—	—	—	—	—	18.5	7.8
M.L.P. (not catalogued)[c]	—	—	—	—	—	—	—	—	12.0	7.2	16.3	7.8	21.7	8.0
M.L.P. No. 12-1523[c]	—	—	—	—	—	—	—	—	—	—	—	—	17.0	8.5
M.L.P. No. 12-1523[c]	—	—	—	—	—	—	—	—	—	—	—	7.2	19.4	—
M.A.C.N. No. 10914[d]									(13.1	8.2)	(15.8	9.2)	(21.1	10.0)
											(16.3	8.9)	(21.8	8.3)
?E. ?pascuali	7.3	5.1	7.1	5.9	7.6	6.0	9.1	—	11.7	7.2	14.4	9.2	23.1	9.4
A.M.N.H. No. 29474														

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[a] Type of *Eurystomus stehlini.* Measurements from Bryan Patterson.

[b] Lectotype of *Lonkus rugei.* Measurements from Bryan Patterson.

[c] Measurements from Bryan Patterson.

[d] Unassociated single teeth.

of *?E. pascuali* the homologous measurement is only 4.0 mm. Even though this feature is quite variable in *Eomorphippus*, as noted by Patterson (above), such a difference, implying also a marked difference in hypsodonty, would be almost incredible within one species. The other noted distinctions, although minor, tend to confirm the separation. It is, indeed, possible that *?E. pascuali* represents a different, but related, genus.

A.M.N.H. No. 29474, the lower jaw mentioned above under Hypodigm, was found at the same locality and only 2 feet higher in the section, but above the erosional base of the upper channel bed. That erosion surface, however, does not represent a detectable hiatus; as far as observable the Mustersan fauna is the same above and below it. The lengths of P_3–M_2, but not the widths and not the lengths of P_2 and M_3, are slightly below those of specimens referred to *E. obscurus*, and this jaw would occlude reasonably well (for a different individual) with the type of *?E. pascuali*. Although the teeth are all deeply worn, they seem to have been about as hypsodont as those of *?E. pascuali*, less than those of *E. obscurus*. P_{1-2} seem to be more molariform than in *E. obscurus* and to have the protoconid labial convexity sharply reflected posteriorly. If this is *?E. pascuali* and if the difference in lower premolars were fully confirmed, reference to a different genus would be supported, but there are too many uncertainties for one to take this step, especially in a fauna already burdened with such a plethora of synonymous and doubtful names.

INTERHIPPUS AMEGHINO, 1902, NOMEN DUBIUM

Interhippus AMEGHINO, 1902a, p. 13; 1906, pp. 469, 471. LOOMIS, 1914, p. 127. SCHLOSSER, 1923, p. 611. SCOTT, 1937a, p. 504.

TYPE: *Interhippus deflexus*.

DISTRIBUTION: According to Ameghino, uppermost Mustersan ("Partie la plus supérieure des couches à Astraponotus"), but probably Deseadan (see below), Patagonia.

DIAGNOSIS: Probably synonymous with *Coresodon*. Upper molar rooted but very hypsodont; subquadrate with labial side a little longer than lingual side; lingual face deeply cleft between subequal protocone and hypocone; lingual fossa (or external extension of cleft) bifurcated, with small posterolabial and long, curving, anterolabial extensions; moderately worn molar with closed, small, posterolingual fossette and two similar mediolabial fossettes; cleft, fossettes, and whole crown deeply covered with cement. (The syntype lower molar probably is of the same genus and has concordant characters.)

This is clearly distinct from *Eomorphippus* or any other known Mustersan genus and is by far the most advanced notoungulate yet recorded as from the Mustersan. It is quite as advanced as any Deseadan notohippid. Ameghino's painstaking note that the type is from the very top of the Mustersan lends some likelihood to the suspicion that it was in fact derived from the Deseadan.[1] Ameghino made no comparison with Deseadan *Coresodon*, and Patterson (personal communication) finds the supposed genera inseparable. The supposed species "*Interhippus deflexus*" and *Coresodon scalpridens* are also closely similar and doubtfully separable. No Mustersan and Deseadan specimens of surely determined age are anything like so similar, and it seems virtually certain that "*Interhippus*" and "*I. deflexus*" are Deseadan. Ameghino named a supposed second species, *I. phorcus* as from the Deseadan. Patterson (personal communication) considers this a synonym of *Coresodon scalpridens*.

"Interhippus" deflexus Ameghino, 1902, *nomen dubium*

Interhippus deflexus AMEGHINO, 1902a, p. 13; 1904b, p. 136, figs. 162, 241, 242.

TYPE: M.A.C.N. No. 10916, upper right M^1 or M^2 (lectotype) and lower left M_3 (syntype).

HYPODIGM: Types only.

HORIZON AND LOCALITY: Recorded as Mustersan but probably Deseadan, Patagonia. No locality data.

DIAGNOSIS: Doubtfully distinct from *Coresodon scalpridens*. Measurements of lectotype are given in table 69.

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[1] Loomis (1914, p. 128) recorded *I. deflexus* as from the Deseadan, but without comment or explanation; this was probably just a careless overlooking of the fact that Ameghino ascribed it to the Mustersan.

TABLE 71

MEASUREMENTS OF TEETH OF *Puelia plicata*

	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
M.L.P. No. 12-1536[a]	—	—	5.8	8.6	7.7	9.8	—	—	—	—	—	—	—	—
M.L.P. No. 12-1534	5.8	6.1	6.0	8.4	6.6	9.3	7.9	10.5	10.0	12.4	10.0	12.5	11.9	11.7
M.L.P. No. 12-1533	—	—	5.9	—	—	—	7.8	10.4	8.9	11.2	—	—	—	—

[a] Type.

NOTOUNGULATA INCERTAE SEDIS

Here is presented a mixed batch of names which were probably based on specimens of notoungulates but which for one reason or another have no real meaning at present. They vary from names like *Puelia*, probably classifiable and perhaps even valid with further study, to some that are unlikely ever to acquire any meaning or value. It is vexatious that there is no way to jettison the latter permanently and thus clear up accumulated clutter in this science. However, one can never be absolutely certain which names may be and which are not salvageable. Whoever thinks he has discovered a new taxon in these faunas is ethically obliged to consider the possible applicability of one of these names. Others are well advised to ignore them.

These are all *taxa inquirenda*, *nomina dubia*, or *nomina vana*,[1] and many of them are *nomina oblita*. I therefore here list the names without such tags, but with the understanding that in my opinion none of the names under this heading has currently established *zoological* significance. Since these names are not here treated as designating definable taxa, publication here does not affect status as *nomina oblita*, if such they are or would be except for this publication.

It is not certain that all the names here listed were applied to specimens of notoungulates, and some perhaps should be treated as Mammalia *incertae sedis*. Conversely, it is possible that some names later listed as Mammalia *incertae sedis* were applied to notoungulates.

PUELIA ROTH, 1902

Puelia ROTH, 1902, p. 252. SIMPSON, 1936d, p. 89.

TYPE: *Puelia plicata*.

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: Uncertain, but see description of specimens, below.

Puelia plicata Roth, 1902

Plate 42, figures 3, 5

Puelia plicata ROTH, 1902, p. 252. SIMPSON, 1936d, pp. 67, 89.

TYPE: M.L.P. No. 12-1536, part of left maxilla with alveoli of C–P^1 and crowns of P^{2-3}.

HYPODIGM: The type and, with some doubt, the following: M.L.P. No. 12-1534, part of left maxilla with deeply worn P^1–M^3; M.L.P. No. 12-1533, part of right maxilla with P^2–M^1, worn and broken.

HORIZON AND LOCALITY: Mustersan of Patagonia. Roth's "Lago Musters."

DIAGNOSIS: Uncertain; see description below. Measurements are given in table 71.

* * *

This taxon is almost certainly identifiable on the basis of the specimens listed above, but unfortunately when I studied those specimens no well-comparable material was at hand, and I have been unable to make a proper restudy or new first-hand comparisons.

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[1] The term *nomen vanum* is not defined or mentioned in the International Code. It has sometimes been used to mean a name that is an intentional but invalid change in spelling. That meaning is not supported by convenience, usage, or etymology. I shall continue to call such names quite plainly "invalid emendations" and, as in Part 1 of this monograph, shall use *nomen vanum* for a name that has standing in nomenclature (is not a homonym, known synonym, or *nomen nudum*) but none in zoology (it is not known to what taxon, if any, the name applies).

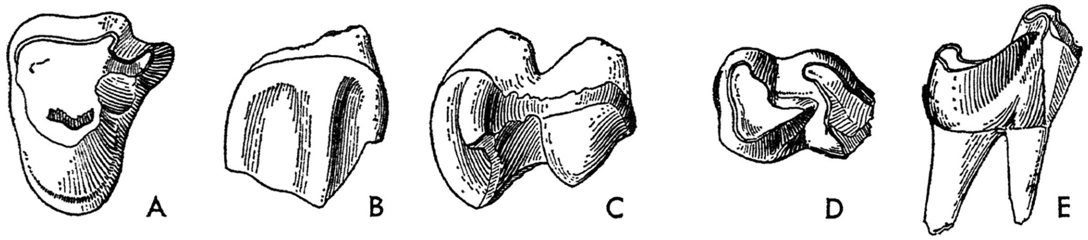

FIG. 39. *Brandmayria simpsoni* Cabrera. A–C. M.L.P. No. 34-V-22-3, type, right upper premolar. A. Crown view. B. Labial view. C. Anterior view. D, E. M.L.P. No. 34-V-22-5, lower cheek tooth. D. Crown view. E. Labial view. After Cabrera. ×4.

The maxillary teeth have the full placental number and are closely crowded, rather high brachydont to mesodont. The canine alveolus is as small as that of P^1. P^1 has a single root and a subtriangular crown. P^{2-4} have a strong ectoloph, weak parastyle fold, strong paracone fold, no mesostyle fold, very weak metacone and metastyle folds. The protoloph is feebly developed and has a notch opening into the central fossette. The metaloph is strong and complete. The hypocone is stronger and more lingual than the protocone. There are strong anterior and less strong posterior cingula. M^{1-2} have a moderate paracone fold; other buccal folds are slight or absent. The protocone is lingual and larger than the hypocone. On the worn available specimens the cristae cannot be made out as separate structures, and the preserved external fossettes are obliterated. M^3 is regularly triangular, the length and width are nearly equal, the hypocone is reduced or absent, and the metaloph is reduced.

These specimens considerably resemble those of *Acoelohyrax* (or *Plexotemnus*) described under the Isotemnidae above. If they do indeed belong to that group and if generic distinction can be made between Casamayoran and Mustersan specimens, then *Puelia* might be a valid generic name for the latter. Those are, however, highly doubtful conditional statements. There are apparent differences between *Puelia* and that group, such as the apparently simpler buccal or crista pattern in *Puelia* and, more certainly, the apparently quite different shape and structure of M^3.

BRANDMAYRIA CABRERA, 1935

Brandmayria CABRERA, 1935, p. 13.

TYPE: *Brandmayria simpsoni.*

DISTRIBUTION: Riochican, Patagonia.

DIAGNOSIS: Uncertain at generic level. See species, below.

Brandmayria simpsoni Cabrera, 1935

Text figure 39

Brandmayria simpsoni CABRERA, 1935, p. 13.

TYPE: M.L.P. No. 34-V-22.3, isolated right upper premolar.

HYPODIGM: Essentially the type. Cabrera also referred to this species M.L.P. No. 34-V-22.5, an isolated right lower premolar found with the type.

HORIZON AND LOCALITY: Upper Riochican,[1] Bajo de la Palangana, north of Pico Salamanca, Chubut.

DIAGNOSIS: Translated from Cabrera: "This tooth is similar, more than to anything else, to the homologous premolar of *Entostylops* [presumably a misprint for *Entelostylops*], but it is less rounded and more angular on the lingual side and has the metastyle almost effaced as well as the parastyle, which is decidedly low, to such a degree that it really forms part of the anterior cingulum or margin. Dimensions: length 6 mm., width 7½ [given as 7.5 but it appears that measurements were to half millimeters], maximum height of crown (on the mesostyle [paracone fold in my terminology]) 5."

Both the type and the referred lower premolar are those of a small, primitive notoungulate. They seem to me to lack any really

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[1] Cabrera (1935) did not accept the nomenclature here used and argued at some length about the stratigraphy and nomenclature of beds which he had never seen and about which he unfortunately had quite confused and erroneous ideas. My great admiration and affection for my late colleague must not be permitted to exclude keeping the record straight.

diagnostic generic characters, although they would probably be identifiable if more complete specimens including homologous teeth were found. They do not have definitely notostylopid characters, and I think it unlikely that they have a special relationship with "*Entelostylops*" (a synonym of *Notostylops*). I have not studied the specimens at first hand.

EDVARDOCOPEIA Ameghino, 1901

Edvardocopeia Ameghino, 1901, p. 395; 1906, p. 470. Scott, 1913, p. 509: Schlosser, 1923, p. 617.

Type: *Edvardocopeia sinuosa.*
Distribution: Casamayoran, Patagonia.
Diagnosis: Uncertain.

Edvardocopeia sinuosa Ameghino, 1901

Edvardocopeia sinuosa Ameghino, 1901, p. 345; 1904b, p. 283, fig. 382.

Type: Not found by me in the Ameghino Collection. The original description mentioned an upper premolar and a (lower) symphysis. The type (or lectotype) may be the original of Ameghino's figure, cited above.
Hypodigm: Type (?) figure only.
Horizon and Locality: Mustersan, Patagonia. No other data.
Diagnosis: Uncertain.

Ameghino's figure shows a right upper premolar measuring 9.3 by 14.2 mm., if the stated enlargement is accurate. There is no developed protoloph and there is only one internal cusp, bulging anteriorly from the apparent but somewhat anterior metaloph. There are strong, basin-forming anterior and posterior cingula. The labial face is strongly but simply swollen.

Ameghino referred this specimen to the Trigonostylopidae, but it is very different from any known teeth of that family. It may rather be a notoungulate, but I am at a loss to place it more exactly than that.

CAROLODARWINIA Ameghino, 1901

Carolodarwinia Ameghino, 1901, p. 406; 1906, p. 470: Schlosser, 1923, p. 616.

Type: *Carolodarwinia pyramidentata.*
Distribution: Mustersan, Patagonia.
Diagnosis: Uncertain.

Carolodarwinia pyramidentata Ameghino, 1901

Plate 42, figures 1, 2

Carolodarwinia pyramidentata Ameghino, 1901, p. 406; 1904b, p. 281, fig. 380.

Type: M.A.C.N. No. 10900, isolated right upper premolar.
Hypodigm: Type only. Ameghino also mentioned canines ("Canines très fortes") in his description, but these were not found in the collection, and it is highly uncertain whether they were correctly referred to the species. (If they did belong here, Ameghino's reference of the genus to a family that never has large canines would be anomalous.)
Horizon and Locality: Mustersan, Colhué-Huapí.
Diagnosis: Uncertain. Described below.

This probably posterior upper premolar measures 24 by 38 mm. and is mesodont in height. The labial wall has strong, approximated parastyle and paracone folds and a smooth, gently undulant wall posterior to them; there is a low labial cingulum. There is no protoloph, and the chunky, pyramidal internal cusp is continuous with what appears to be a metaloph. Strong continuous cingula run around anterior, lingual, and posterior sides.

Ameghino referred this tooth to the Leontiniidae; such ascription is not impossible, although no (other?) teeth quite like this are known in that family. Leontiniids are not surely known before the Deseadan, and this dubious specimen does not warrant recording the family in the Mustersan, although, of course, its occurrence there in primitive form would not be wholly surprising. On the other hand, derivation of this specimen of a relatively advanced notoungulate from the immediately overlying Deseadan is possible.

PLEUROSTYLOPS Ameghino, 1901

Pleurostylops Ameghino, 1901, p. 394; 1904b, p. 109; 1906, p. 467. Schlosser, 1923, p. 617.

Type: *Pleurostylops glebosus.*
Distribution: Casamayoran, Patagonia.
Diagnosis: Uncertain.

Pleurostylops glebosus Ameghino, 1901

Pleurostylops glebosus Ameghino, 1901, p. 394; 1904b, p. 109, figs. 122, 481.

TYPE: M.A.C.N. No. A55-5, isolated, broken left upper molariform tooth.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayoran, west of the Río Chico.

DIAGNOSIS: Uncertain.

This is a very brachydont molariform tooth, about 15½ mm. in length, longer than wide, with cusped parastyle, paracone, and metacone in a row, protoloph and metaloph ending in well-separated protocone and hypocone, and no evident cristae.

It is unlikely that this is a trigonostylopid as Ameghino thought. It is probably a milk molar of a notoungulate, but I cannot place it more closely.

ORTHOLOPHODON ROTH, 1902

Ortholophodon ROTH, 1902, p. 253. SIMPSON, 1936d, p. 90.

TYPE: *Ortholophodon prolongus.*

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: Uncertain.

Ortholophodon prolongus Roth, 1902

Plate 42, figure 4

Ortholophodon prolongus ROTH, 1902, p. 253: SIMPSON, 1936d, pp. 67, 90.

TYPE: M.L.P. No. 12-2205, isolated lower premolar.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Mustersan, Roth's "Lago Musters."

DIAGNOSIS: Uncertain.

This seems to be a notoungulate premolar, but it has no really diagnostic characters.

TONOSTYLOPS AMEGHINO, 1902

Tonostylops AMEGHINO, 1902a, p. 32; 1906, p. 468.

TYPE: *Tonostylops spissus.*

DISTRIBUTION: Casamayoran, Patagonia.

DIAGNOSIS: Uncertain.

Tonostylops spissus Ameghino, 1902

Tonostylops spissus AMEGHINO, 1902a, p. 32.

TYPE: M.A.C.N. No. 10483, fragment of right lower jaw with ?M_{2-3}, heavily coated with manganese; type or lectotype. With it is an isolated lower molar, probably not of this individual or species.

HYPODIGM: Type only. Ameghino referred M.A.C.N. No. 10480, three lower jaw fragments representing two or three individuals, probably not this species.

HORIZON AND LOCALITY: Casamayoran, Patagonia. Type from Colhué-Huapí.

DIAGNOSIS: Uncertain.

?M_3 is peculiar in having the talonid short, hypolophid buccal, entoconid posterolingual and conical. ?M_2 measures 9.1 by *ca.* 6 mm. and ?M_3 10.0 by 6.1. It is possible that the teeth present are M_{1-2}, in which case the second preserved is not so peculiar as if it were M_3. In either case, this is certainly not a notostylopid. It is probably, but not surely, a notoungulate *incertae sedis.*

LOPHIODONTICULUS AMEGHINO, 1902

Lophiodonticulus AMEGHINO, 1902a, p. 17; 1906, p. 467.

TYPE: *Lophiodonticulus patagonicus* (hereby selected).

DISTRIBUTION: Casamayoran, Patagonia.

DIAGNOSIS: Uncertain.

Lophidonticulus patagonicus Ameghino, 1902

Plate 42, figure 6

Lophiodonticulus patagonicus AMEGHINO, 1902a, p. 17.

TYPE: M.A.C.N. No. 10637, fragment of right lower jaw with M_{1-2} (lectotype), two other jaw fragments, and an isolated premolar.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayoran ("Partie supérieure"), Patagonia.

DIAGNOSIS: Uncertain.

These poorly preserved teeth represent a slight variation on the primitive notoungulate pattern. The metaconid is simple, the hypolophid strictly buccal, and the transverse entoconid crest is virtually continuous with the posterior end of the hypolophid. These characters are also somewhat suggestive of trigonostylopids. The specimen certainly does not belong to the European family Lophiodontidae, but it is otherwise *incertae sedis*. M_1 measures approximately 6 by 4½ mm.

Lophiodonticulus retroversus Ameghino, 1902

Plate 42, figure 7

Lophiodonticulus retroversus AMEGHINO, 1902a, p. 17.

TYPE: M.A.C.N. No. 10636, fragment of right lower jaw with M_{1-2}.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayoran ("Partie supérieure"), Patagonia.

DIAGNOSIS: Uncertain.

This specimen resembles the preceding, but generic or specific identity is doubtful. M_1 measures about 5½ by 4 mm. The slightly smaller size, principal basis of Ameghino's specific distinction, does not necessarily exclude this specimen from *L. patagonicus*.

"Ultrapithecus" robustus Roth, 1902

Ultrapithecus robustus ROTH, 1902, p. 251.

TYPE: Not found.

HYPODIGM: None.

HORIZON AND LOCALITY: Presumably Mustersan, Patagonia.

DIAGNOSIS: None.

Roth's description may be translated as follows: "This species is much larger than *U. rutilans* and *rusticulus*. The length of M^1 is 11 mm. as against 6 in *U. rutilans*. The protoloph and metaloph have nearly the same [transverse] width and are not separated on the labial face; on M^2 a superficial groove is barely visible."

It is extremely unlikely that this specimen belonged to *Ultrapithecus*. In the absence of the specimen, figures, or more distinctive description, its affinities are unguessable.

"Degonia" sympathica Roth, 1902

Degonia sympathica ROTH, 1902, p. 252.

TYPE: Presumably an upper molar, not found in the Roth Collection.

HYPODIGM: None in hand.

HORIZON AND LOCALITY: Probably Mustersan, Roth's "Lago Musters," Patagonia.

DIAGNOSIS: None.

The type was not figured, and Roth's brief description distinguishes it from "*D. kollmanni*" by smaller size, much lower crown, and strong median and posterior labial crests. This description makes it extremely unlikely that the tooth in question belonged to "*Degonia*" (i.e., *Pseudhyrax*) but gives no real evidence as to what genus it did represent. Roth said that M^1 was 9 mm. long and 7 wide, which is curious because upper molars of this and allied groups are almost invariably wider than long. The name is meaningless at present.

"Notopithecus" summus Ameghino, 1897

Notopithecus summus AMEGHINO, 1897a, p. 421; 1898, p. 150.

TYPE: A humerus, not found in the collection.

HYPODIGM: None in hand.

HORIZON AND LOCALITY: Not given, but probably Casamayoran, Patagonia.

DIAGNOSIS: None.

The great size of the type and the radical discrepancy in proportions of proximal and distal ends as stated by Ameghino make it highly improbable that this specimen really belonged to *Notopithecus* or to the Notopithecidae. Even were the specimen at hand, it could not be compared with any other type, and there is little possibility that a specific diagnosis could be derived from it.

ISOTYPOTHERIUM AMEGHINO, 1904

Isotypotherium AMEGHINO, 1904c, p. 421; 1906, p. 467.

TYPE: *Isotypotherium annulatum*.

DIAGNOSIS: None.

In 1904 Ameghino published a characteristically polemic study of the astragali of early, mainly South American mammals of several different orders. He referred these to genera and in most instances species that had been based on jaws and teeth. At least among the specimens considered notoungulate (in our sense; Ameghino never used that name or concept) there was no known individual association of astragali with teeth. The specific ascriptions must be considered completely unreliable and the generic hardly less so. For example, astragali referred by Ameghino to *Trigonostylops*, *Prostylops*, *Pleurostylodon*, *Thomashuxleya*, and *?Claenodon*, representing three orders and three (or in Ameghino's own classification four) families seem to me to be closely related, probably all Toxodonta (of the present classification), and most if not all Isotemnidae. To add to the confusion, some of these really unidentified astragali were used as a basis for listing in the Casamayoran and Mustersan families not otherwise known in those faunas and almost certainly not present in them: Arctocyonidae, Eutrachytheriidae (=Mesotheriidae), Colpodontidae (=Leontiniidae).

The study of these astragali is of great interest, and I hope to go on with it elsewhere. For present purposes, however, they should be set aside as contributing nothing but confusion to the systematics of these faunas. No generic, and few if any family, ascriptions are reliable. Even ordinal ascriptions cannot be accepted without considerable further study. Taxa inferred from astragali are all *incertae sedis* and will almost certainly turn out to be the same as taxa with other names based on jaws and teeth.

Isotypotherium annulatum Ameghino, 1904

Isotypotherium annulatum AMEGHINO, 1904c, p. 421, fig. 69.

TYPE: M.A.C.N. No. 10693, an isolated right astragalus.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayoran, Patagonia. "Pico Sasamanca."[1]

DIAGNOSIS: None.

EPITYPOTHERIUM AMEGHINO, 1904

Epitypotherium AMEGHINO, 1904c, p. 422; 1906, p. 467.

TYPE: *Epitypotherium cancellatum*.

DISTRIBUTION: Casamayoran, Patagonia.

DIAGNOSIS: None.

Epitypotherium cancellatum[2] Ameghino, 1904

Epitypotherium cancellatus AMEGHINO, 1904a, p. 422, fig. 70.

TYPE: M.A.C.N. No. 10699, isolated right astragalus.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayoran ("Partie supérieure"), Patagonia. Locality not more closely given.

DIAGNOSIS: None.

PROCOLPODON AMEGHINO, 1904

Procolpodon AMEGHINO, 1904c, p. 438.

TYPE: *Procolpodon foratus*.

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: None.

Procolpodon foratus Ameghino, 1904

Procolpodon foratus AMEGHINO, 1904c, p. 438, fig. 87.

TYPE: A left astragalus, not found in collection.

HYPODIGM: None in hand.

HORIZON AND LOCALITY: Mustersan, presumably Patagonia. No other information.

DIAGNOSIS: None.

"?Claenodon" patagonicus Ameghino, 1904

?Claenodon patagonicus AMEGHINO, 1904c, p. 404, p. 50 (not here stated to be a new species, but no previous publication found); also cited in Ameghino, 1906, p. 467, as *"?Claenodon"* without specific name.

TYPE: M.A.C.N. No. 10704, isolated astragalus.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayoran, Patagonia. "Río Chico frente a Malaspina."

DIAGNOSIS: None.

This specimen certainly does not belong to *Claenodon* or to the Arctocyonidae. It is probably a notoungulate and possibly an isotemnid. It is virtually identical in size and structure with M.A.C.N. No. 10536, illustrated by Ameghino (1904c, fig. 28) and re-

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[1] A curious fact for which I have no explanation is that, although in the Ameghino Collection in general most specimens labeled as to origin are from Colhué-Huapí (i.e., the great barranca south of that lake), of the 25 astragali identified by Ameghino and labeled as to locality, only six are from Colhué-Huapí and the others are from widely scattered localities, including some where few other specimens were found. The problem of associating the astragali with otherwise known taxa is thereby intensified.

[2] *Cancellatus* in the original publication, an error correctable under the International Code.

ferred by Ameghino to *Thomashuxleya*. Except for being slightly larger, it is also very like M.A.C.N. No. 10613 (Ameghino, 1904c, fig. 21), referred to *Prostylops typus*, and the almost identical M.A.C.N. No. 10640 (Ameghino, 1904c, fig. 8), referred to *Trigonostylops wortmani*. This confusion, specified by way of example, is characteristic of identifications of astragali in Ameghino (1904c).

Other *Nomina Vana* in Roth, 1902, 1904

As mentioned on previous pages, specimens published by Roth as from "Formación terciaria inferior" and labeled "T.i.C.B." (for "Terciario inferior de Cañadón Blanco") have been found by Patterson to be a mixture apparently including Casamayoran, Mustersan, and Deseadan fossils. Types of four supposed species (three of them types of genera) were not found in the collection. They were not figured, and Roth's descriptions are not recognizably diagnostic beyond suggesting the Notoungulata. These forms are thus of unknown identity and are also of unknown age, although possibly Casamayoran or Mustersan (or Deseadan), and unknown locality within Chubut. They have no present meaning and are only listed here for the sake of completeness:

Orthogenium ameghinoi Roth, 1902 (type of supposed genus).

Pyramidon klaatschi Roth, 1902 (type of supposed genus).

Trigonolophodon elegans Roth, 1904 (the type of the genus, *T. inflatus*, is probably Deseadan, but it is highly dubious whether "*T.*" *elegans* belongs to that genus).

Archaeotypotherium transitum Roth, 1904 (type of supposed genus).

Order **ASTRAPOTHERIA** Lydekker, 1894

Definition: An Eocene to Miocene order of individually large, extinct South American ungulates. Upper incisors lost, at least in later forms. Three pairs of strongly bilobed lower incisors. Upper and lower canines greatly enlarged, becoming rootless tusks, followed by long diastemata. Premolars becoming reduced to $\frac{2}{1}$. Cheek teeth brachydont to mesodont, invariably rooted. Upper molars trapezoidal; without distinct metacone fold; protoloph strong; hypocone merging into metaloph; a single crista present in later forms; no other secondary crests. Lower molars lophodont; bicrescentic; anterior wing of trigonid crescent strong; entoconid distinct, transversely crested, attached to hypolophid and becoming part of it. In later forms a secondary pillar developing on anterior part of trigonid. Infraorbital foramen single, near orbit. Palate and choanae normal. Sagittal crest present, becoming short; temporal crests becoming very strong. Auditory notch deep and narrow; tympanic loosely attached; posttympanic process strong; no occipital exposure of mastoid. Condylar foramen large and separate. Skeleton in later forms graviportal, pentadactyl. Scaphoid resting on trapezium and trapezoid, not reaching magnum; lunar overlapping unciform. No fibulocalcaneal or naviculo-cuboid contacts. Astragalus short, broad, with very short neck, cuboid facet on neck rather than head. Calcaneal facet on fibular side of cuboid. Pes with large first and fourth, reduced second and third, digits.

The foregoing definition is intended especially to distinguish the astrapotheres from other South American ungulates and especially from notoungulates and trigonostylopoids. Skull and skeletal characters refer almost entirely to advanced forms, especially *Astrapotherium*, and in these respects the more primitive Casamayoran and Mustersan genera will probably prove to be less distinctive.

Lydekker (1894b) proposed the name Astrapotheria for a suborder of Ungulata, hence an order by present ranking which gives ordinal status to the basic divisions of the hoofed mammals. He included the two genera *Astrapotherium* and "*Homalodontotherium*" (*Homalodotherium*). Ameghino (e.g., in his definitive arrangement, 1906) correctly removed *Homalodotherium* from the vicinity of *Astrapotherium*. He placed the astrapotheres and trigonostylopoids in the Amblypoda (a now obsolete name for a composite group of Holarctic archaic ungulates). His phylogenetic diagram (Ameghino, 1906, p. 328) shows the Trigonostylopidae and Albertogaudryidae as independently derived from the "Pantostylopidae," which Ameghino classified as condylarths but which are now believed to belong to the Henricosborniidae, primitive notoungulates. The Albertogaudryidae were shown as giving rise to: Lophiodontidae (European perissodactyls); Coryphodontidae (Holarctic "amblypods," now Pantodonta) and hence Uintatheriidae (Holarctic "amblypods," now Dinocerata); Amynodontidae (Holarctic rhinoceroses); and Astrapotheriidae proper, and hence "Plicatodontidae" (a Pleistocene South American group of doubtful affinities, not astrapotheres).

Ameghino's supposed connections of Albertogaudryidae and Astrapotheriidae with lophiodonts, "amblypods," amynodonts, and "plicatodonts" were certainly erroneous, were not adopted by any other student of the group, and require no further discussion here. Since 1906 the Astrapotheria have been generally accepted as a distinct, aberrant group, ancestral to no other, either as a suborder of the Notoungulata (e.g., Loomis, 1914) or usually, and in recent years universally, as a separate order (e.g., Scott, 1913, 1928a, 1937a; Simpson, 1945). The order has been shown as including Ameghino's three families Trigonostylopidae, Albertogaudryidae (usually as a synonym or subfamily of the Astrapotheriidae), and Astrapotheriidae. The discovery of a skull of *Trigonostylops* (Simpson, 1933c) showed that it is quite unlike *Astrapotherium.* It was tentatively retained in the Astrapotheria but given subordinal distinction (Simpson, 1934d; 1945).

A connection between the trigonostylopids and astrapotheres still seemed to be indicated by *Albertogaudrya*, considered by all students to be the Casamayoran ancestor of the astrapotheres and yet in the few known parts rather similar to *Trigonostylops*. Then (Simpson, 1957) a much more astrapothere-like form, *Scaglia*, was found in the Casamayoran. It now appears that *Albertogaudrya* is a trigonostylopid, not an astrapotheriid, and that already in the Casamayoran the two families had been divergent for some time. In fact a common ancestry would almost have to be on the evolutionary level of the Condylarthra, and it is possible that the immediate condylarth origin of true astrapotheres was nearer that of the Notoungulata than that of the Trigonostylopoidea—a view not far from that of Ameghino. (Again it appears that Ameghino was often prescient about ancestral relationships of his Patagonian groups but usually badly mistaken about descendent relationships.) It thus becomes virtually mandatory to recognize the Trigonostylopoidea as ordinally distinct. That step is taken in succeeding pages of this work, where the affinities of that group, including *Albertogaudrya*, are further discussed.

As thus revised, the order Astrapotheria includes only the family Astrapotheriidae, and in the faunas here being described the Casamayoran *Scaglia* and Mustersan *Astraponotus* are the only probably valid genera, although the latter has various established and possible synonyms. Both genera are so poorly known that the affinities of the Astrapotheria must be determined mainly on the evidence of post-Mustersan forms. However, something may here be said on that subject, especially as regards the moot point of relationships with the Notoungulata.

Ameghino (e.g., 1906) did not recognize the Notoungulata as a natural group, so that he can hardly be said to have an opinion on this score. Roth (1903) excluded the astrapotheres by definition from the Notoungulata, which he named. Scott (1913 and thereafter) believed that astrapotheres were probably related to his "Toxodontia" (=Notoungulata) but held that knowledge was insufficient to prove it and that meanwhile they should be kept separate, and he maintained an order Astrapotheria. Other authorities, with less first-hand knowledge of the material, such as Schlosser (1923), Osborn (1910), and Gregory (1910), made the Astrapotheria a suborder of the Notoungulata, whereas the views of Lydekker (1894b) and of Winge (1923–1924), although expressed in different terms, would make them less than subordinally distinct in such a classification as that here used.

Although Scott considered the two groups as related, he has also shown that the resemblances are confined largely to the dentition and that the skull and skeleton are very unlike (Scott, 1928a, 1932, 1937b). He did not point out any typical notoungulate characters in the skull, nor have I been able to find any in reviewing the published evidence and good original specimens. In the skeleton of *Astrapotherium* Scott noted the following resemblances: 1. The arrangement of the canals of the atlas is about as in *Nesodon*, although otherwise the bones are dissimilar. 2. The axis was said to be generally like that of *Nesodon*, but several distinctions were pointed out. 3. The external tuberosity, deltoid crest, and trochlea of the humerus were said to resemble those of *Nesodon*, although the head of the radius was signalized as particularly unlike that of *Nesodon*, and the deltoid crest is much less like that of *Homalodotherium* than like that of *Nesodon*. 4. The elbow joint of *Astrapotherium* in general was said to be more like that of *Nesodon* than like that of *Uintatherium*. 5. The femur was at first said to resemble that of *Homalotherium* in general, but it was later found that the femur supposedly of the latter genus is also of an astrapothere.

None of these resemblances is striking as an indication of affinities. Against them are to be set very marked differences throughout the skeleton, and notably the fact that the feet of *Astrapotherium* and *Homalodotherium* "have hardly anything in common and that in the whole series of Santa Cruz ungulates there are no groups in which the feet are more unlike" (Scott, 1932, p. 235).

Perhaps the most important osteological characters uniting the various notoungulates are those of the ear region, and it is instructive to list these (cf. Patterson, 1932) and contrast them with those of the Astrapotheria and, with some anticipation of later discussion, those of the Trigonostylopoidea (see table 72).

Neither in the ear region nor in any other known part of the skull or skeleton is there convincing evidence of special affinity between notoungulates and astrapotheres.

The dentition presents a perplexing problem. The cheek dentition of *Astrapotherium* itself, as Scott has shown and as Lydekker already had noted, is strikingly like that of *Homalodotherium* and some other notoungulates. The formation of canine tusks, the loss

TABLE 72

COMPARISON OF THE CHARACTERS OF THE EAR REGION IN THE NOTOUNGULATA, ASTRAPOTHERIA, AND TRIGONOSTYLOPOIDEA

Notoungulata	Astrapotheria	Trigonostylopoidea
Tympanic forming a large, inflated bulla	Tympanic unknown, because loosely attached to skull, but certainly not large or inflated	Tympanic not inflated and of very different form
Epitympanic sinus above and behind auditory meatus	Epitympanic sinus much smaller and not homologous, in quite a different part of the squamosal	Cf. Astrapotheria
Ossified tubular auditory meatus	Auditory meatus not ossified	Meatus incompletely ossified, very short, not tubular
Deep vagina process hyoidei at posteroexternal corner of bulla	Hyoid process not in quite the same position, of very different character, no deep vagina	Cf. Astrapotheria
Stylomastoid foramen between porus acusticus and vagina processus hyoidei	Stylomastoid foramen immediately external to hyoid process	Cf. Astrapotheria
Frequently, but not invariably, with styliform process	(No styliform process)	Small styliform process
Mastoid poorly exposed or hidden, save in some primitive and a few later genera	Not exposed	Exposed on occiput, but structure very different from that of notoungulates with exposed mastoids
Prominent crest on lower surface of meatus (except in some typotheres)	(No meatus)	Meatus without crest

of upper incisors, bilobed lower incisors, and the extreme reduction of the premolars are points of difference from any known notoungulates, but the molar patterns are suggestively notoungulate-like.

There are certain basic molar characters that are found in all primitive notoungulates and are seldom completely lost in their descendants. Among the most obvious of these are the presence of a large hypocone, invariably forming a characteristic metaloph, the presence of accessory lophs in the upper molar basin (usually a characteristic crochet in primitive forms, and never wholly lacking), and the presence of an accessory column in the talonid formed (in its most primitive condition) by a transversely crested entoconid. These characters, and others which accompany them, are not all confined to the Notoungulata, but are highly characteristic of them and are already established in their earliest known members. As the homalodothere or leontiniid pattern is traced back through its abundant and now well-known direct or structural ancestry into the Casamayor, the tooth structure becomes simpler, but these notoungulate characteristics not only do not disappear but really become more obvious because they are not obscured by complication. If the *Astrapotherium* molars are really of common origin with those of *Homalodotherium*, which they resemble, the resemblance should clearly become closer and closer as the lines are followed back toward their point of origin. But if it is correct to consider *Astraponotus* and *Scaglia* as ancestral astrapotheres, and all the evidence seems to point that way, then this does not occur. On the contrary the difference in upper molar pattern between *Scaglia* and contemporaneous allies of the homalodotheres is at least as great as that between *Astrapotherium* and *Homalodotherium*. For the lower molars, the same may be said of *Astraponotus*.

If this history is correctly interpreted, then the resemblance in molar pattern between *Astrapotherium* and the Notoungulata is convergent, and the ancestral types of the two groups were unlike even in this respect. Such a degree of convergence is unusual, but not unique. For instance, it has been repeatedly pointed out that the astrapothere molars are also remarkably like those of some rhinoceroses.

It still is quite possible, and even probable on theoretical grounds although the evidence is suggestive rather than concrete, that astrapotheres and notoungulates are more closely related to each other than either is to any northern group. If so, their point of divergence must lie further back than the existence of either group as such. To reduce this conclusion to taxonomic terms, the Astrapotheria and Notoungulata must be maintained as quite distinct orders on present evidence.

FAMILY **ASTRAPOTHERIIDAE** AMEGHINO, 1887

In the present arrangement, this is the only family of the Astrapotheria, and it requires no separate diagnosis. The known and probably valid genera are few and form a rather simple sequence, and it would be pointless to designate taxa between family and genus.

SCAGLIA SIMPSON, 1957

Scaglia SIMPSON, 1957, p. 11.

TYPE: *Scaglia kraglievichorum.*

DISTRIBUTION: Casamayoran, Patagonia.

DIAGNOSIS: A primitive astrapothere. Three upper premolars on each side. M^1 with short, simple metaloph; no discrete hypocone; no trace of a crista; buccal face of crown lower than in *Astraponotus*. Face and cranium comparatively long; nasals normal (not retracted).

The most nearly comparable genus is *Astraponotus*. Points of comparison in available specimens are few, but the higher upper molar crowns and presence of a distinct crista in *Astraponotus* demand generic separation. *Scaglia* may be the immediate ancestor of *Astraponotus*, but the evidence is inadequate. The comparatively recent discovery of *Scaglia* and the fact that only a single specimen is known show that even this large, repeatedly worked fauna is still quite inadequately known.

Scaglia kraglievichorum Simpson, 1957

Text figures 40, 41A

Scaglia kraglievichorum SIMPSON, 1957, p. 11, figs. 1, 2, pls. 1, 2.

TYPE: Museo Municipal . . . de Mar del Plata, No. 207, poorly preserved partial skull.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayoran, Cañadón Vaca, Chubut, Patagonia.

DIAGNOSIS: Sole known species of the genus. Ectoloph length of M^1 of type, 20.5 mm.; maximum width, 22.9 mm.

This very young individual still had most, if not all, of its deciduous teeth. M^1 is almost fully erupted but is completely unworn and had not yet come into occlusion with the lower teeth. The capsule posterior to M^1 is broken, but it is clear that M^2 had not erupted and there is no evidence that it was calcified or that M^3 had begun to take form.

At the anterior end of the specimen as preserved there is a caniniform deciduous tooth, short-crowned and long-rooted. The somewhat recurved crown, fully covered with thin enamel except where worn, is long-oval in cross section, crested posteriorly. Strongly oblique wear has formed a facet on the anterior face. Immediately above this tooth, slightly anterior to its curving root, is the tip of a much larger, unerupted, permanent tooth that was about to replace the deciduous tooth when the animal died. It is a laterally compressed, saber-like tooth, not crested at the tip. The tip is well enameled. The enamel extends well up the tooth and was apparently still forming on most or all of its preserved portion within the alveolus (or capsule). This curves upward and backward within the bone for at least 35 mm. from the tip. There is no sign of a root, and the tooth evidently would have continued to grow and to move downward in the socket for some time, finally forming a strong tusk.

It is natural to assume, and is probably correct, that these teeth are dc and C, the latter homologous with the large tusks of later astrapotheres. There is, however, a difficulty of interpretation. The bone is so cracked that I cannot certainly make out sutures in this region. The teeth are probably in the

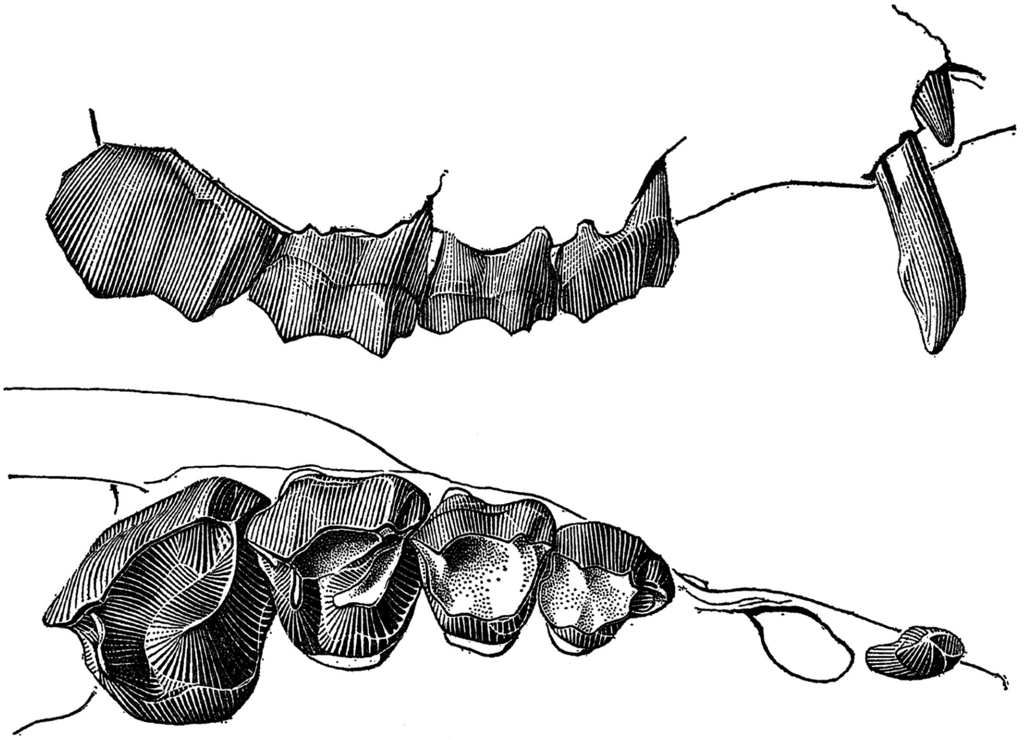

FIG. 40. *Scaglia kraglievichorum* Simpson, Museo . . . Mar del Plata No. 207, type, partial skull, right dc, dm^{2-4}, and M^1, buccal and crown views. ×1.5.

maxilla, but there is a possible suture just posterior to them, and it is barely possible that they are in the premaxilla. This possibility would not be very seriously considered were it not for the fact that immediately posterior to the dc(?) on each side there is a large pit that resembles a canine alveolus. The pits are slightly ellipsoidal, too distorted for close measurement but about 10 mm. in length and 9 in width. The right pit has been cleaned out and seems to have a shallow, entire bottom. Further excavation was made through a large crack here, and no tooth forming above the pit was found. The left pit still contains matrix with finely comminuted fragments of what could represent a crushed tooth. The pits are quite separate from and much larger than the alveoli for the dc's(?). They cannot be the locus for protrusion of the large permanent tusks.

The specimen was X-rayed at the American Museum, and a number of films were taken. These are rather unsatisfactory because of the thickness of the specimen and the presence of many fractures and irregularities in internal matrix. Nevertheless, they show no tooth forming above the pit on either side and make it improbable that such a tooth is there.

There are three possibilities: (1) the pits are not alveoli; (2) they held dm^1, which may or may not have had a successor; (3) they held dc, with or without a successor, and the teeth preserved anterior to them are di^3 and I^3. None of the three hypotheses is completely satisfactory. Later (Deseadan and Santacrucian) astrapotheres do have a comparatively shallower and more poorly defined pit in the diastema between the cheek teeth and the tusks, and this pit seems not to be a vestigial alveolus. Yet in *Scaglia* the pits resemble alveoli. A dm^1 (or P^1) thus separated from dm^2 (and P^2) would be highly unusual, so must have been its shape if it really occurred here. Moreover, the upper tusks of all later astrapotheres are certainly canines, and it seems extremely improbable that this evidently related animal would have nonhomologous tusks. Whatever these pits or alveoli may have lodged, I think it probable that the teeth preserved anterior to them are dc and the permanent canine tusk. The specimen is too broken anteriorly for one to determine whether incisors occurred anterior to the tusks. Upper incisors were already absent from Deseadan astrapotheres. The Mustersan condition (in *Astraponotus*) is unknown.

Posterior to the pits is a short diastema (about 7½ mm.) and then follows the tightly continuous cheek tooth series dm^2–M^1.

Dm^2 is irregularly triangular, with a long buccal wall and a well-developed but not expanded protocone region. The parastyle region is large and is expanded into an anterobuccal lobe. There are weak but distinct and subequal paracone and metacone convexities on the buccal wall. There is some suggestion that there were a protoloph and a metaloph but coronal details are obliterated by wear.

Dm^3 is more quadrate, the parastyle strong but not forming a lobe as on dm^2, the paracone fold also strong but the metacone fold weaker. Wear is also heavy on this tooth, but there is a suggestion that it had a large, curving protoloph and a short straight metaloph like the following two teeth.

Dm^4 is fully molariform, but it is smaller than M^1, is more quadrate (the buccal wall of the ectoloph not so oblique), and is much more brachydont. It may also be mentioned that the enamel, as fossilized, is distinctly lighter in color on the deciduous than on the permanent teeth. Such a color difference is a general rule for fossil mammals and often permits the rapid sorting of deciduous and permanent teeth from the same deposit, but so far as I know its cause has not been investigated. It may merely indicate that the enamel is thinner on deciduous teeth.

M^1 is irregularly trapezial rather than quadrate. Anterior and lingual sides are nearly at a right angle, but the internal side is shorter. Anterior and buccal sides are nearly equal but form an acute angle, the buccal side being strongly oblique with reference to the long axis of the skull. The posterior side is at an obtuse angle to both buccal and lingual sides, about equal to the latter in length and shorter than anterior or buccal sides, a fact correlated with the metaloph's being decidedly shorter than either protoloph or ectoloph.

All three lophs are simple, sharp, and well defined. The protoloph abuts buccally against the parastyle, which is sharply differentiated although comparatively smaller than on the deciduous molars. The paracone forms a distinct elevation on the ectoloph and is marked by a distinct ridge on the buccal face of the tooth. In buccal profile there is also a distinct metacone elevation, well anterior to the posterobuccal corner of the tooth and somewhat anterior to the buccal end of the metaloph. There is a lesser, poorly pronounced angulation of the profile anterior to the metacone and a broad notch between paracone and metacone. The buccal face of the ectoloph posterior to the paracone is almost smooth, with only slight ridges below the metacone, and the metastyle at the extreme posterior end of the wall.

The protoloph swings posterolingually into the poorly differentiated but large protocone, the cresting of which is almost anteroposterior and vaguely crescentic. The metaloph is low and simple, short, almost straight, and almost directly buccal-lingual. It abuts at a low (i.e., relatively basal) point against the ectoloph between metacone and metastyle. Its slightly elevated inner end is separated from the protocone by a deep notch. The central valley is open through that notch and is a broad, almost featureless basin even in this completely unworn state. There is no trace of a crista or of other secondary crests.

There are a very slight buccal basal cingulum and a stronger cingulum continuous on the anterior and lingual sides across the protocone but not across the inner end of the metaloph. A cingulum-like structure tends to enclose a small but sharply defined posterobuccal fossette, posterior to the metaloph and lingual to the metastylar part of the ectoloph.

The buccal side of the tooth is distinctly higher than the lingual, but both are lower than in *Astraponotus* or later astrapotheres.

The skull is so badly crushed and fragmented that many characters are uncertain, but some interesting points can be made out. The nasals are long, with none of the retraction so prominent in Deseadan and later astrapotheres. Each nasal is about 6 mm. wide anteriorly and expands to about 13 mm. at the anterior edge of the frontals, then narrows to the rounded insertion between the frontals. In this young animal the posterior end of the nasals is about on a level (anteroposteriorly) with the middle of the orbits.

The broad, slightly domed frontals do not form distinct postorbital processes, but each does here form a strong ledge above the posterior part of the orbit, similar to but much less prominent than that present in later astrapotheres. Posteriorly the frontals taper to a sharp point clasped between the parietal crests that converge backward into a sagittal crest, already prominent in this juvenile and presumably more so in an adult of the species.

The infraorbital foramen is not identified with certainty, but it seems to be single, of moderate size, about in line with the lower border of the orbit but some 15 to 20 mm. anterior to the orbit, above the anterior part of dm^2. The anterior orbital rim is probably notched, with the lacrimal foramen within the orbit posteromedial to the notch. No facial expansion of the lacrimal is recognized, and that bone is probably entirely within the orbit. The zygoma is little expanded laterally and rises above dm^4–M^1. There is a zygomatic process of the maxilla, visible ventrally in lateral view but almost entirely overlain by the jugal, which extends well forward into the lower rim of the orbit.

This region is much cracked and defective, but it seems fairly clear that there are, as in later astrapotheres, a confluent foramen lacerum anterius and foramen rotundum at the posterior point of the orbitosphenoid and covered externally by a wing of the alisphenoid. The foramen lacerum medium was apparently in its usual position between the basisphenoid and the sinking crest running posteriorly from the pterygoid wing of the alisphenoid. What seems to be a foramen ovale is lateral to that crest, in the alisphenoid and distinctly separated from the foramen lacerum medium. The rest of the basicranium is not preserved, nor is the occiput.

The choanae are narrow, and the anterior rim is at the level of about the middle of M^1. It would evidently be more posterior in an adult. The choanae are not particularly tubular, and there is no evidence of a bony median septum (which occurs in *Trigonostylops* but is not known in true astrapotheres). There is a slight tubercle on the ventral aspect of the palatine at each side of the rim of the choanae.

There are symmetrical vascular foramina

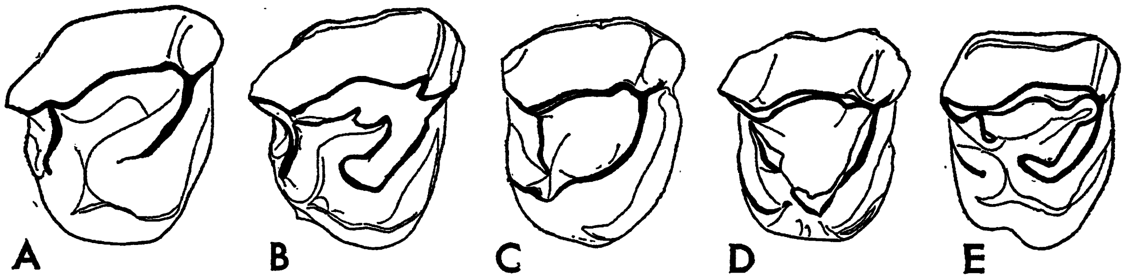

FIG. 41. Comparative series of crown views of right M¹ of astrapotheres and trigonostylopoids. A. *Scaglia kraglievichorum* Simpson. B. *Astraponotus holdichi* (Roth). C. "*Trigonostylops*" *apthomasi* Paula Couto. D. *Trigonostylops wortmani* Ameghino. E. *Albertogaudrya unica* Ameghino. Not to scale; brought to same size for comparison.

on each side of the midline near the middle of the frontals. On the right, but not the left, frontal, there is a large hole with an apparently non-broken rim posterolateral to the vascular foramen. If it is really an original feature this must be pathological or traumatic. Supraorbital foramina are apparently absent. There are prominent, scattered, vascular foramina in the posterolateral parts of the parietals and the squamous processes of the squamosals.

AFFINITIES

Scaglia is quite clearly an astrapotheriid. The only possibly contrary indications are the pits or alveoli that make homology of the tusks not completely certain and numerous characters that are much more primitive than those of any Deseadan or later astrapotheriid. But the tusks probably are homologous, after all, and a Casamayoran genus is sure to be much more primitive than related or descendent forms from the much later Deseadan.

The pattern of M¹ is unique and clearly distinct from any other known South American genus in spite of (or in part because of) its simplicity (see text fig. 41). The closest approach to this pattern is in *Astraponotus*, M¹ of which differs only in being larger, more hypsodont, and having a small crista. In these respects *Scaglia* is merely more primitive, as befits its age, and the degree of advance from *Scaglia* to *Astraponotus* is comparable with that in some other Casamayoran-Mustersan lineages. M¹ in Deseadan and later astrapotheres (especially *Parastrapotherium* and *Astrapotherium*) differs in being, as a rule, still larger than in *Astraponotus*, in having further complications of secondary crests, and in being still more hypsodont (on the buccal side, at least). In other words, they simply continue the trend seen from *Scaglia* to *Astraponotus*, and again the degree of advance is comparable with that in other lineages through the same time span.

The number of upper premolars in *Astraponotus* is not surely known but was probably three. The number is later reduced to two, in line with a strong progressive trend toward concentration of grinding on the molars. Again *Scaglia* is just what one would expect if this trend were projected back into the Casamayoran.

The skull is completely unknown in *Astraponotus*, but skulls of *Parastrapotherium* and *Astrapotherium* are available for comparison in the American Museum collections. The closely similar skulls of the latter two genera are remarkably specialized (see especially Scott, 1928a). Most of their peculiarities are functionally related to emphasis of the frontal and molar segment of the skull. This segment is extremely heavy and broad, whereas both the face and the posterior cranial region are shortened, appearing almost as if they had been forcibly compressed against the emphasized middle segment. The frontals are broad and domed. All three molars, but especially the second, are enormous, but the rest of the dentition is strongly reduced except for the likewise enormous tusks, which add their bit to the peculiar modeling of the skull.

The skull of *Scaglia* is very different at first sight, but it is merely more primitive, to much the same degree that the upper molar structure is more primitive. The face and cranium are still moderately long, although apparently less so than in *Trigonostylops* or *Phenacodus*. The frontals are broader and more domed than in the most primitive ungulates. Although the point is difficult to judge in so young a skull, the emphasis on the molars and on the molar-frontal segment of the skull seems already to be under way. In all respects the skull is just what would be expected in a primitive astrapothere. The adult would have fully developed tusks and stronger muscular attachments and would probably resemble later astrapotheres still more closely.

With slight reservations because of the doubtful interpretation of the postcanine(?) pits or alveoli, I see no reason why *Scaglia* could not be directly ancestral to any or all of the later astrapotheres.

ASTRAPONOTUS Ameghino, 1901

Plate 42, figures 8, 10

Astraponotus Ameghino, 1901, p. 401; 1904b, p. 102; 1906, p. 470. Scott, 1913, pp. 509, 512; 1937a, pp. 530, 542. Schlosser, 1923, p. 619.

Notamynus Roth, 1903, p. 133. Ameghino, 1904b, p. 102 [as synonym of *Astraponotus*]; 1906, p. 470 [separate from *Astraponotus*]. Simpson, 1936d, p. 91 [as synonym of *Astraponotus*].

Notaminus [error]: Roth, 1927, pp. 196, 211, 214.

Megalophodon Roth, 1903, p. 136; 1927, pp. 196, 211, 214, 236. Simpson, 1936d, p. 59 [as synonym of *Astraponotus*].

Type: *Astraponotus assymmetrus* Ameghino, 1901.

Types of Synonyms: Of *Notamynus*, *N. holdichi* Roth, 1903; of *Megalophodon*, *M. thompsoni* Roth, 1903.

Distribution: Musters Formation, Patagonia.

Diagnosis: Primitive astrapotheres with greatly enlarged but rooted canines; cheek teeth with higher crowns that in *Scaglia;* small, simple crista on each upper molar. Lower molars simply bicrescentic, with entoconid crests as spurs from hypoconulid region.

Roth did not compare *Notamynus* with *Astraponotus*, which had not been illustrated when he wrote. Ameghino quickly recognized the synonymy, of which there can now be little doubt. The types are not directly comparable, since *Notamynus* is based on upper molars and *Astraponotus* on various fragments without any fully characteristic parts of upper molars, but the general congruity of the material referred to both and the identity in structure of parts that are homologous and that occur at the horizons and localities of the types and almost surely belong to the same genera are sufficient proof of synonymy.

In defining *Megalophodon* Roth recognized its close resemblance to *Notamynus*, but remarked that "se diferencia en los molares superiores por tener en la parte interna un solo lofo" (that is, only a protoloph in place of both protoloph and metaloph in *Notamynus*). In fact a metaloph is also present, and the distinctions are only that this crest is slightly shorter than in the teeth referred to *Notamynus* and that the protocone is slightly more expanded posteriorly. Otherwise the structure is the same. Roth wrote that the type of the genotype "seguramente corresponde al M^2," but I see no evidence for this. The tooth has all the characters that would be expected in M^3 of *Astraponotus*, and its differences from "*Notamynus*," which probably is based on M^2, are like those between M^3 and M^2 of many genera. The probability of synonymy is so great as to demand reducing the two names to one.

It is curious that Ameghino selected this genus to typify his *Astraponotus* beds or "Astraponotense," our Mustersan. It is one of the rarest genera in the fauna, and particularly so in the Ameghino Collection, which has only one lot of isolated teeth. (The Roth and Scarritt collections each include about a dozen more isolated teeth.) Moreover, the genus is not related (and was not believed by Ameghino to be related) to those the names of which were applied to other beds in the Patagonian sequence.

The specific synonymy and true specific characters within this genus cannot now be worked out in any satisfactory way, since the types are from different parts of the dentition, associated teeth of one individual are not available, and the degree of variation is indeterminable. Several widely different localities are represented, and whether or not more than one species is present in the known material cannot now be determined. The various species proposed by Roth are listed below, but none has any clear value at present. As far as possible the general characters of the whole dentition are here described for the genus.

The dental formula is unknown.[1] Roth (1903, p. 135) described incisors referred provisionally to this genus (that is, to "*Notamynus*") as generally similar to those of *Astrapotherium*. I did not certainly identify these in his collection. With Ameghino's type there are two incisors, perhaps of this genus, that are much less distinctly or symmetrically bilobed than in later forms. They have very long roots and short crowns with a central cusp and a lesser expansion or second lobe on one side. The outer side is convex and the inner excavated and with a cingulum.

In the pied collection from Sierra Cuadrada and Cerro Talquino, mentioned above, which includes specimens probably of three ages (Casamayoran, Mustersan, Deseadan), there is a symphysis, A.M.N.H. No. 29390, which may belong to *Astraponotus*. It is broad, long, strongly procumbent, flat below, and guttered above between the canines. Roots and alveoli show that there were three incisors on each side, I_2 largest, I_3 smallest, and so pressed against the canines that their alveoli are partly confluent. The relatively immense canines have long curving roots which in this individual had not yet closed. Isolated tusks, in the same collection, otherwise closely resembling miniature tusks of *Astrapotherium*, are perhaps of this genus and suggest that the roots did finally close.

In the Roth Collection there are well-preserved upper and lower canines, M.L.P. No. 12-2187, perhaps associated, and there are a less perfect pair with Ameghino's type and most of a lower canine in our collection, A.M.-N.H. No. 29460. The lower canine is almost perfectly circular in transverse section, the upper canine being oval. The upper canine has a nearly straight root and slightly curved crown, with short external and internal enamel bands. The lower canine, both root and crown, is more curved. The mode of wear is about as in later forms.

Blastoconus and *Grypolophodon* may represent or include upper premolars of *Astraponotus*, but the possibility is so uncertain that they are here kept separate and described on pages below. The most anterior premolars referable to the genus with some confidence are represented by three teeth associated by Roth with the types of *Grypolophodon morenoi* and *G. imperfectus* and one found by us at the Cerro del Humo, A.M.N.H. No. 29472, almost identical in character with one of Roth's "*G. morenoi*" specimens. This has three well-separated roots. The labial face is convex and strongly arched, with vague and closely approximated paracone and metacone folds and a narrow, sharp cingulum turning up the anterior and posterior borders. The ectoloph is a sharp crest, with very vague paracone and metacone apices of about equal height. The protocone is much lower and is a sharply crested crescent, its wings imperfectly joined to the base of the ectoloph. There are small anterointernal and posterointernal cingula. The basal dimensions are 17.7 by 24.5 mm. Roth's other two specimens are less transverse and have more conical protocones.

The type of *Notamynus holdichi* may be taken as a typical upper molar of *Astraponotus*, probably M^2. It has been well figured by both Ameghino and Roth, and its probable phyletic characters are discussed above, so that a detailed description is unnecessary. A swelling in the position of the crista is well distinguishable, but is short and quite separate from the metaloph. The metaloph is sharp and continuous with the ectoloph, but is short, not reaching the inner border of the tooth, and is sharply separated from the protocone by the deep entrance to the central fossa. The posterior cingulum is small and confined to the outer part of the tooth.

The teeth called *Megalophodon* by Roth are to be identified with considerable assurance as M^3 of the same genus as *Notamynus* and *Astraponotus*. Its distinctions are mentioned above and are, principally, that it is relatively shorter than the "*Notamynus*" type, with the metaloph smaller and the expanded protocone occupying most of the inner part of the tooth.

None of the genera or species is based pri-

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[1] Scott (1913) wrote that the premolars were present in full series, Schlosser (1923) that the dental formula was apparently complete, and others have repeated similar statements, but as far as I have been able to observe these are assumptions that lack evidence and are rather improbable.

marily on lower cheek teeth, but a number of these were referred to synonyms of *Astraponotus* by Roth, and we found five more, two south of Colhué-Huapí and three at the Cerro del Humo. These various specimens probably include P_3, P_4, M_1, and M_2. The probable P_3, exemplified by A.M.N.H. No. 29428, has trigonid and talonid of about equal size, the former distinctly higher, both crescentic and fully lophodont, the anterior trigonid wing descending steeply and poorly developed, the entoconid little or not distinguishable, and the two basins fully open on the inner side. Probable P_4, exemplified by A.M.N.H. No. 29426, is larger, has the talonid relatively slightly larger, the anterior trigonid crest better developed, an obscure entoconid as an anterointernal spur from the hypoconulid, and the very bottom of the basins, at the internal border, tending to close by the growth of very small enamel dams across their exits.

Molars, probably both first and second, are seen in the two lower molars referred by Roth to *Notamynus holdichi* as well as A.M.-N.H. No. 29449a and a few others. They differ from the tooth just described in being more elongate, the elongation being in the talonid which is here considerably larger than the trigonid, especially when seen from the outer side, and in the similar but greater development of an entoconid spur. In at least one case, an uncatalogued tooth in the Roth Collection, there is a small swelling on the inner side of the hypoconid crescent near its anterior end, in the position where a crest or "internal pillar" develops in later astrapotheres. It is entirely distinct and distant from the structure that seems surely to represent the entoconid, and it evidently is not homologous with the entoconid structure sometimes called "internal pillar" in the notoungulates.

Astraponotus assymmetrus[1] Ameghino, 1901

Plate 42, figures 9, 11, 12

Astraponotus assymmetrus AMEGHINO, 1901, p. 401.

Astraponotus asymetrum: AMEGHINO, 1904b, p. 294, figs. 395, 396.

Astraponotus assymetrus: AMEGHINO, 1904b, p. 102.

Astraponotus asymetrus: AMEGHINO, 1904b, p. 524.

TYPE: M.A.C.N. No. 10971, a large lot of material, evidently of more than one individual, including an imperfect upper canine, one broken lower canine and a fragment of another, two incisors, an anterior upper premolar, a fragment of the inner side of another, the outer part of a posterior upper premolar, a fragment of another upper premolar, the anteroexternal corner of an upper molar, and a fragment of a maxilla without teeth. Ameghino also had another upper premolar which he described and figured but which is not now with the type lot (or syntypes). This lot is, however, his type, for all the rest of his description applies accurately to specimens in the lot and it has a slip of paper saying in Ameghino's hand "gen[er]o nuevo." The figured tooth was not his essential type, since it provides only a small part of the type description, and should not be made lectotype, not only because it is now lost but also because it is not absolutely certain that it belongs to the genus *Astraponotus* as later conceived by Ameghino and now universally received. For the present I select no lectotype. It is important that a lectotype be congeneric with Roth's *Notamynus*, since it was really the latter on which the later views of Ameghino regarding *Astraponotus*, and of all others following him, were based. It is certain that Ameghino's type or types did include some material congeneric with *Notamynus*, but it is only probable that all of it was congeneric, and a wrong selection of a lectotype might seriously upset not only the nomenclature of this important and widely known genus but also the older names for the beds and the fauna in which it occurs.

HYPODIGM: Syntypes, as above. Probably most or all known specimens of this genus are of this species, but no species is properly defined.

HORIZON AND LOCALITY: "Colhué-Huapí Norte," Casamayor Formation, Chubut, Argentina.

DIAGNOSIS: Imperfectly comparable with other supposed species. In the type material, an upper canine has, at the base of the enamel, maximum diameter 27, and minimum

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[1] None of the four forms used by Ameghino is etymologically good. No greater emendation than I have used seems to be permitted by the Code.

21, mm., a lower canine similarly 27.5 and 25 mm., two incisors have maximum diameter of 29 and 28 mm., and an anterior upper premolar measures 22.5 by 20 mm.

The anterior upper premolar figured by Ameghino, and also the similar unfigured tooth still preserved, differ from that described above chiefly in being longer and narrower, the length exceeding the width, and having a more conical protocone. If they belong to *Astraponotus*, they probably represent the first premolar in the series, either P^1 or P^2.

At present there is no really practical way of comparing any other species with this, but such a comparison will become possible when associated upper dentitions are discovered. Any or all of the following nominal species may be synonymous with the genotype. They are from the same region but probably from a different locality.

Astraponotus holdichi (Roth, 1903)

Plate 43, figure 1; text figure 41B

Notamynus Holdichi Roth, 1903, p. 133; 1927, pl. 5, fig. 7.

Astraponotus (*Notamynus*)[1]*Holdichi:* Ameghino, 1904b, p. 102, fig. 115 [also said to be = *Astraponotus "assymetrus,"* but not so listed].

Astraponotus Holdichi?: Ameghino, 1904b, fig. 223.

Astraponotus (Notamynus)? Holdichi: Ameghino, 1904b, figs. 455, 497.

Astraponotus Holdichi: Ameghino, 1904b, p. 524.

Astraponotus holdichi: Simpson, 1936d, p. 66.

Type: M.L.P. No. 12-1471, two upper molars, the larger of which was said by Ameghino (1904b, p. 102, footnote) to be the type and hence becomes, or is now designated, lectotype. Under the same number are two lower molars, described by Roth at the same time as the types, but not surely associated and explicitly said by Roth to be attributed to the species, hence not part of his original basis for it. Roth Collection.

Hypodigm: Lectotype only.

Horizon and Locality: "Cretáceo superior de Lago Musters"—probably Musters Formation of the Cerro del Humo, Chubut.

Diagnosis: Probably equals *A. assymmetrus.* Lectotype measuring 39 by 46 mm., crista present but weak, protocone well expanded.

Astraponotus dicksoni (Roth, 1903)

Plate 43, figure 2

Notamynus Dicksoni Roth, 1903, p. 135.

Astraponotus dicksoni: Simpson, 1936d, p. 66.

Type: M.L.P. No. 12-2217, isolated right upper molar. Roth Collection.

Hypodigm: Type only.

Horizon and Locality: "Cretáceo superior de Lago Musters"—probably Musters Formation of the Cerro del Humo, Chubut.

Diagnosis: Probably equals *A. assymmetrus.* Well comparable only with *A. holdichi,* from which the type differs in being smaller, with protocone less expanded and crista somewhat stronger. Length of type, 32; width, 40.5 mm.

This might be M^1 of *A. holdichi* or *assymmetrus,* in which case "*Grypolophodon imperfectus*" (see below) is not.

Astraponotus thompsoni (Roth, 1903)

Plate 43, figure 3

Megalophodon Thompsoni Roth, 1903, p. 136; [1927, pl. 5, fig. 8[2]].

Astraponotus thompsoni: Simpson, 1936d, p. 66.

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[1] The intention was to show *Notamynus* as a synonym. not as a subgenus, of *Astraponotus.*

[2] The legend calls this figure "*Blastoconus* sp.; molar," but it is the type of *Megalophodon thompsoni.* Most of the legends for this plate are incorrect. They were evidently written not by Roth but by the editor or an assistant who had become extremely confused. Contrary to the general plate legend, the specimens were not "todas . . . del grupo de los *Astrapotheria,*" since the original of figure 13 is not and was not believed by Roth to be an astrapothere, and they were not, even in Roth's opinion, all "del cretáceo superior de la Patagonia," since the original of figure 12 was labeled by him as from the "terciario inferior" and is of later age than the other specimens. Nor does the implication that the originals of figures 1 through 5 were found under different conditions from any other seem to be correct, for Roth's labels show the originals of figures 1 through 11 and 13 as all from his "cretáceo superior de Lago Musters" deposit. The legends of figures 6 and 8 through 13 are all incorrect or inadequate and should be corrected as follows:

"6, *Notorhinus haroldi*" is 6, *Grypolophodon imperfectus,* type
"8, *Blastoconus* sp." is 8, *Megalophodon thompsoni,* type
"9, *Megalophodon* sp." is 9, *Megalophodon dilatatus,* type
"10, 11, Dos premolares de géneros no determinados (del group *Astrapotheria*)" are 10, *Blastoconus robertsoni,* type; 11, *Blastoconus ?robertsoni*
"12, *Heterolophodon* sp." is not Roth's *Heterolophodon*
"13, *Pehuenia* sp." is 13, *Pehuenia wehrlii,* type

TYPE: M.L.P. No. 12-2181, isolated upper molar. Roth Collection.

HYPODIGM: Type only.

HORIZON AND LOCALITY: "Cretáceo superior de Lago Musters"—probably Musters Formation of the Cerro del Humo, Chubut.

DIAGNOSIS: Probably equals *A. assymmetrus*. With the characters described above as probably of M^3. Inner side slightly angular, protocone vaguely bifid. Length of type, 35; width, 43 mm.

Astraponotus dilatatus (Roth, 1903)

Plate 43, figure 4

Megalophodon dilatatus ROTH, 1903, p. 137; [1927, pl. 5, fig. 9[1]].
Astraponotus dilatatus: SIMPSON, 1936d, p. 66.

TYPE: M.L.P. No. 12-2182, isolated upper molar. Roth Collection.

HYPODIGM: Type only.

HORIZON AND LOCALITY: "Cretáceo superior de Lago Musters"—probably Musters Formation of the Cerro del Humo, Chubut.

DIAGNOSIS: Probably equals *A. assymmetrus*. Well comparable only with *A. thompsoni*, from which the type differs in being slightly smaller, with inner border more rounded and protocone more definitely bifid. Length at top as worn, 31; at base, 26; width, 41.5 mm.

?ASTRAPOTHERIA INCERTAE SEDIS

GRYPOLOPHODON ROTH, 1904, NOMEN DUBIUM

Grypolophodon ROTH, 1904, p. 139; 1927, pp. 195, 210, 213, pl. 5, figs. 1–3. SIMPSON, 1936d, p. 81.

TYPE: *Grypolophodon morenoi*.

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: Uncertain.

The type species of this supposed genus was based on an isolated upper tooth, probably P^4, which could belong to *Astraponotus*, *Albertogaudrya*, or neither. P^4 is not (otherwise?) known in *Astraponotus*. A.M.N.H. No. 28639, tentatively identified as P^4 of *Albertogaudrya*, differs from Roth's type in being probably lower crowned, with more projecting metastylar fold, with shallower trigon basin, with weaker, less continuous internal cingulum, with more lingual hypocone, and smaller in size. Until associated dentitions are found, I see no way to determine to what genus or, indeed, order "*Grypolophodon morenoi*" belongs.

A supposed second species, *G. tuberculosis*, was based on a fragment of upper premolar so uncharacteristic as to be quite meaningless.

The third supposed species, *G. imperfectus*, was based on an odd tooth, perhaps M^1. Its transverse and more or less symmetrical outline suggests the posterior premolars, which was doubtless the reason for its being placed in *Grypolophodon*. It is, however, a molar (conceivably, but improbably, a milk molar), as is shown by the anterior position of the paracone fold, the long and nearly flat labial face of the ectoloph posterior to this, and the distinct development of a metaloph, the inner end of which is free from the protocone. Aside from its quite different proportions and outline and its smaller size, it differs from the type of "*Notamynus*" *holdichi* (M^2?) principally in the less distinct crista, weaker metaloph, and continuity of the internal and posterior cingula around the end of the metaloph. These could be characters of M^1, but are not surely so. There is no evidence that this tooth is congeneric with "*Grypolophodon morenoi.*"

Grypolophodon morenoi Roth, 1903, *nomen vanum*

Plate 43, figure 5

Grypolophodon morenoi ROTH, 1903, p. 139; 1927, pl. 5, figs. 4–5. SIMPSON, 1936d, p. 67.

TYPE: M.L.P. No. 12-1472, an isolated upper premolar. There are included in Roth's description and in this catalogue number another similar premolar and two more anterior premolars, but Roth designated as type "el molar con la corona más complicada," which is the largest tooth in this lot and the original illustration of Roth (1927, pl. 5, fig. 5).

HYPODIGM: Type only.

HORIZON AND LOCALITY: "Cretáceo superior de Lago Musters"—probably Musters Formation of the Cerro del Humo, Chubut.

DIAGNOSIS: Uncertain. Length on ectoloph, 22.5; on inner side, 20; width, 37.5 mm.

Grypolophodon tuberculosis Roth, 1903, *nomen vanum*

Grypolophodon tuberculosis ROTH, 1903, p. 140. SIMPSON, 1936d, p. 67.

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[1] See footnote 2 on page 206.

TYPE: M.L.P. No. 12-2180, part of the inner side of an upper premolar. Roth Collection.

HYPODIGM: Type only.

HORIZON AND LOCALITY: "Cretáceo superior de Lago Musters"—probably Musters Formation of the Cerro del Humo.

DIAGNOSIS: None.

Grypolophodon imperfectus Roth, 1903, *nomen vanum*

Plate 43, figure 6

Grypolophodon imperfectus ROTH, 1903, p. 140; [1927, pl. 5, fig. 6[1]]. SIMPSON, 1936d, p. 67.

TYPE: M.L.P. No. 12-1460, isolated upper tooth, probably a molar. Roth also referred a premolar, which is now catalogued under the same number and was included in the type description but is not a syntype, since Roth said of it "puede pertenecer a la misma especie" and "creo pertenece a esta especie." Roth Collection.

HYPODIGM: Type only.

HORIZON AND LOCALITY: "Cretáceo superior de Lago Musters"—probably Musters Formation of the Cerro del Humo, Chubut.

DIAGNOSIS: Uncertain. Length, 24; width, 38.5 mm.

BLASTOCONUS ROTH, 1903, NOMEN DUBIUM

Blastoconus ROTH, 1903, p. 137; 1927, p. 196, pl. 5, fig. 8. SIMPSON, 1936d, p. 92.

Plastoconus [error]: ROTH, 1927, pp. 211, 214.

TYPE: *Blastoconus robertsoni.*

DISTRIBUTION: Musters Formation, Patagonia.

DIAGNOSIS: Based on anterior premolars with relatively high crowns; wider than long; with swollen outer wall and feeble paracone and metacone swelling; small protocone asymmetrical in position, with weak loph to the parastyle region; a thick extension of the ectoloph in the metaloph region; a small, irregular anterior cingulum and a larger posterior cingulum with a cusplike swelling posterior to the protocone.

A second specimen placed by Roth in the type species differs profoundly from the type, being smaller, more triangular, with a strong and more typical protoloph, more symmetrically placed protocone, no metaloph and no cuspule posterior to the protocone. Roth considered the principal specimen as P^4 or M^1, but it seems almost certain that it is a more anterior premolar, perhaps P^2. In general character, this tooth might belong to an astrapothere, but even this broad assigment is uncertain and its affinities will not be determinable until associated material is found. The size corresponds closely with that of the teeth described above as probably P^2 (or P^3) of *Astraponotus*, but the structure of the inner part of the tooth is quite different. There is more resemblance to the anterior premolar described and figured by Ameghino (1940b, fig. 395) as of *Astraponotus*, but even in this case there are marked differences, Ameghino's specimen being longer than wide, with a stronger anterior cingulum, no cuspule posterior to the protocone, and other differences that make it unlikely that they are homologous teeth of the same genus. There is also some resemblance to *Edvardocopeia*, but only if the probable anterior side of the *Blastoconus* tooth be correlated with what is supposed to be the posterior side in *Edvardocopeia*, and in any case the resemblance is not sufficiently exact to be trustworthy.

Blastoconus robertsoni Roth, 1903, *nomen dubium*

Plate 43, figure 7

Blastoconus Robertsoni ROTH, 1903, p. 137; [1927, pl. 5, figs. 10–11[2]]. SIMPSON, 1936d, pp. 66, 92.

TYPE: M.L.P. No. 12-2207, isolated upper premolar. In the type description Roth also included two other upper premolars, one fragmentary, and a lower premolar or milk molar, but these are not syntypes since he explicitly designated the type and said of the other three only that they might belong, probably belong, or that he believed them to belong to the same species. Roth Collection.

HYPODIGM: Type only.

HORIZON AND LOCALITY: "Cretáceo superior de Lago Musters"—probably Musters Formation of the Cerro del Humo, Chubut.

DIAGNOSIS: Sole species referred to genus. Type measures 17.5 by 23.5 mm.

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[1] See footnote 2 on page 206.

[2] See footnote 2 on page 206. Figure 10 is of the type.

The referred teeth do not merit redescription, since there is no evidence that they really belong to this genus or species.

NOTORHINUS Roth, 1903, nomen vanum

Notorhinus Roth, 1903, p. 136; 1927, p. 214. Simpson, 1936d, p. 93 [as indeterminate]. *Nec Notorhina* Redtenbacher, 1848.

Tonorhinus Ameghino, 1904a, vol. 58, p. 230 [in substitution for *Notorhinus*, wrongly said to be preoccupied].

Tonnorhinus [error]: Ameghino, 1906, p. 470.

Type: *Notorhinus haroldi* Roth, 1903.

Distribution: Musters Formation, Patagonia.

Diagnosis: None. (According to Roth, based on an upper molar similar to upper molars of *Notamynus* [=*Astraponotus*] but with lower crowns, no crista, parastyle more independent, protoloph more prolonged posteriorly, and fossae shallower; these remarks do not suffice for one to recognize the supposed genus.)

The material (two isolated molars) on which this genus was based has not been found and was not figured.[1] From Roth's descriptions, these molars may have been merely slight variants of *Astraponotus*, or may have been quite distinct. They might be identifiable, to some degree, if rediscovered, but in the meantime their affinities are unknown, and the supposed genus has no present meaning.

Notorhinus haroldi Roth, 1903, *nomen vanum*

Notorhinus Haroldi Roth, 1903, p. 136; 1927, pl. 5, fig. 6 [in error, not this genus or species].

Tonorhinus Haroldi: Ameghino, 1904a, vol. 58, p. 230.

Type: Not found. An isolated upper molar.

Hypodigm: None in hand.

Horizon and Locality: "Cretáceo superior de Lago Musters"—probably Musters Formation of the Cerro del Humo, Chubut.

Diagnosis: None. (According to Roth, with anterior and internal cingulum little developed and with [small] denticles, ectoloph length at wear surface, 20; at base, 16 mm.; basal width [whole tooth], 19 mm.)

Notorhinus denticulatus Roth, 1903, *nomen vanum*

Notorhinus denticulatus Roth, 1903, p. 136.

Type: Not found. An isolated upper molar.

Hypodigm: None in hand.

Horizon and Locality: "Cretáceo superior de Lago Musters"—probably Musters Formation of the Cerro del Humo, Chubut.

Diagnosis: None. (According to Roth, anterior and internal cingulum more developed and with pronounced denticles, also extending onto the posterior side of the metaloph; protoloph wider; basal ectoloph length, 33 mm.; basal width [of whole tooth], 30 mm.)

Order **TRIGONOSTYLOPOIDEA,**
NEW RANK

Trigonostylopoidea Simpson, 1934d, pp. 4, 19 (as suborder).

Definition: Extinct South American ungulates of isolated position. Incisors 3-2, small, one-lobed. Large canine tusks, upper and lower, more or less astrapothere-like but rooted and relatively brachydont. P^1_1 becoming reduced and in some cases absent. Cheek teeth brachydont. Upper molars subtriangular; shallow, closed trigon basin; protoloph weak; metaloph short to virtually absent; hypocone (or posterolingual cusp) isolated from trigon and not connected to metaloph; no cristae. Lower molars imperfectly lophodont; anterior wing of trigonid short, ending at midline; no entoconid crest or talonid pillar. Infraorbital foramen multiple. Palate with alate posteromedian process; choanae separated by bony partition. Sagittal crest long and powerful; temporal crests virtually absent. Auditory notch broad, shallow, open; posttympanic process virtually absent. Tympanic nearly horizontal, attached suturally, thick, scalelike, not inflated. Mastoid exposed on occiput. Condylar foramen far from condyle and opening into pit or gap between tympanic and basioccipital.

Trigonostylopids and astrapotheres have canine tusks and simple, brachydont cheek

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[1] The legend says that figure 6 of plate 5 of Roth (1927) is *Notorhinus haroldi*, but it is really *"Grypolophodon" imperfectus*. See footnote 2 on page 206.

teeth with some resemblances as opposed, especially, to those of the notoungulates. It is thus not surprising that they were long considered rather closely related groups. Trigonostylopoids have hitherto always been considered members of the same order, at least, as the astrapotheres, However, as mentioned in the discussion of the Astrapotheria, increased knowledge of both groups has steadily weakened the evidence of relationship, until now reference to the same order can no longer be justified.

The dentition gave the best evidence of possible relationship between astrapotheriids and trigonostylopids, and on this basis alone previous tentative conclusions of affinity were justified. The teeth of *Astrapotherium* differ decidedly from those of *Trigonostylops*, but, if the apparent structural ancestry is followed, certain evolutionary trends are seen in the dentition which suggest that at a still more remote period a dentition somewhat like that of *Trigonostylops* might have occurred in the astrapothere ancestry. The chief points are: 1. The earliest astrapotheres have lower crowns than the latest; and in *Trigonostylops* the crowns are still lower. 2. The earlier astrapotheres have rooted canines, and these are smaller and with shorter crowns than in the later; in *Trigonostylops* the canines are rooted, still smaller, with still shorter crowns. 3. The latest astrapotheres have a premolar formula of $\genfrac{}{}{0pt}{}{2}{1}$, presumably reduced from $\genfrac{}{}{0pt}{}{4}{4}$. In *Trigonostylops* the formula is $\genfrac{}{}{0pt}{}{4}{4}$, becoming reduced to $\genfrac{}{}{0pt}{}{3}{3}$. 4. In the latest astrapothers the entoconid is not distinguishable, there is an accessory pillar in the anterior part of the talonid basin, whereas in the early forms there is a separate posterolingual entoconid and the pillar is absent or very feebly developed. In *Trigonostylops* the talonid is somewhat more cuspidate than in early true astrapotheres but otherwise similar. 5. The upper molar pattern is fully lophodont in later astrapotheres, with a strong crista (or crista plus crochet) cutting off an external fossette, a posterior cingulum fossette, a short but strong metaloph with which the hypocone is fully merged, and a deep central valley open between the protocone and hypocone, whereas in the earliest forms the metaloph is shorter, the posterior cingulum narrow, the crista absent, the median valley shallower. In *Trigonostylops* the metaloph is barely developed, the posterior cingulum is smaller, there is no crista, and the median valley is broad, shallow, and closed.

Trigonostylops thus has a dentition that is a conceivable early structural stage in the evolution of the astrapothere dentition, but all that is established by these facts is that a relationship *might* exist. The fact remains that there is a marked difference between the teeth of any definitely classified astrapothere and *Trigonostylops*. About the most that can be said is that they are rather more like each other than either is like any of a number of extraneous groups, such as the Notoungulata, and that the molar patterns are not incompatible with a theory of distant relationship between them. At the same time the teeth provide no impelling evidence of such relationship, and their resemblances could equally well be explained by remote common ancestry, such as within the Condylarthra, perhaps with a limited degree of convergence.

The skulls of *Astrapotherium* and *Trigonostylops* are on the whole so different that they go far to oppose any possibility of close relationship. Aside from the differences of size, proportion, and various other points which are probably not important as indication of affinities, which cannot in any event be really intimate, there are the outstanding differences in apparently more deep-seated and important structures that are listed in table 73.

Some further comparisons in the ear region are noted in the previous comparison of that region in notoungulates, astrapotheres, and trigonostylopids (table 72).

The skull is very inadequately known in *Scaglia*, the only astrapothere known to be contemporaneous with *Trigonostylops*, but what is known of the skull does not suggest that the two groups had much more in common at that time. The skull is entirely unknown in *Astraponotus*, and *Astrapotherium* itself is a highly advanced astrapothere much later in age than *Trigonostylops*. Nevertheless, the differences are so pronounced as to preclude anything like an ancestral relationship and to minimize special relationships of any kind within the broad category of archaic ungulates.

TABLE 73

DIFFERENCES BETWEEN *Astrapotherium* AND *Trigonostylops*

Astrapotherium	*Trigonostylops*
Infraorbital foramen single, immediately anterior to orbit, beneath orbital rim	Infraorbital foramen multiple, far from orbit
Orbital rim prominent, crested	Orbital rim low and rounded
Lacrimal foramen, apparently also whole lacrimal, intraorbital	Lacrimal foramen and lacrimal on orbital rim
Palate normal	Peculiar median, bilaterally alate process on palatines
Choanae tubular, undivided	Choanae completely divided by bony median partition
Interorbital foramen entirely in palatine, posterior to maxilla	Interorbital foramen at junction of palatine, orbitosphenoid, and maxilla
Sagittal crest very short	Sagittal crest very long
Great overhanging temporal crests	Temporal crests virtually absent
Strong posttympanic process of squamosal, closely applied to paroccipital process	Posttympanic process very short, almost absent, far removed from paroccipital process
Postglenoid and paroccipital processes strong, converging distally, enclosing a very deep, narrow auditory notch	Postglenoid and paroccipital processes weak, enclosing a broad, shallow, open auditory notch
Occiput deeply emarginate on both sides	Occiput not distinctly emarginate
No occipital exposure of mastoid	Occipital vacuity with good exposure of mastoid
Basisphenoid-presphenoid exposures very short	Basisphenoid-presphenoid exposures very long
Condylar foramen large, separate, at posterointernal end of paroccipital process	Condylar foramen small, opening into a large pit into which posterior lacerate foramen also opens, internal to and some distance from paroccipital process
Whole ventral aspect of auditory region exposed only in roof of a small, deep, constricted pit	Auditory region well exposed ventrally, periotic nearly on a level with surrounding external elements
Tympanic (not known itself) evidently small and loosely attached	Tympanic large but not inflated, suturally united to surrounding bones
Hyoid attachment crowded into a groove at junction of posttympanic and paroccipital processes	Hyoid attachment at posterior edge of tympanic, far from posttympanic or paroccipital processes

As against these impressive differences, and others not listed either because they are are of minor importance or because the condition in *Astrapotherium* is not known beyond any doubt, there are a few special resemblances:

The frontals are domed and contain large sinuses in both (but the shape is different and so far as can be seen their relationship to surrounding bones are also different).

Both have a possible homologue of the ethmoid foramen in the orbit between the lacrimal foramen and posterior end of the infraorbital canal.

The arrangement of foramina in and around the orbitosphenoid is somewhat distinctive, although not unique, and is much the same in both.

In both, the alisphenoid is unpierced externally, the foramen rotundum confluent with the foramen lacerum anterius, and the foramen ovale nearly or quite confluent externally with the foramen lacerum medium.

What may correspond to the epitympanic recess in both communicates with a small sinus in or near the zygomatic root of the squamosal, anterior to the ear region.[1]

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[1] It has generally been said of astrapotheres and litopterns, and would also have been said of *Trigonostylops* on the same basis, that these groups, in contrast to the notoungulates proper, have no bulla and no epitympanic sinus. The expanded, platelike tympanic of at

It is quite possible that these features, with the equally sparse and inconclusive dental resemblances, do indicate some special relationship, but that this can only be rather remote is fully shown by the more numerous and more marked differences. Furthermore, these resemblances are also shared, in greater or less degree, with the Litopterna and hence do not definitely unite trigonostylopids and astrapotheres to the exclusion of the litopterns, which yet are almost always placed in a different order.

Resemblance of *Astrapotherium* to litopterns hardly goes beyond this point. *Trigonostylops*, however, does have other points of resemblance to the Litopterna. Its dentition is on the whole more astrapothere- than litoptern-like, although the lower cheek teeth, particularly, are very similar to those of some early Litopterna, e.g., *Xesmodon*. The trigonostylopid dentition does not exclude a distinct possibility of litoptern relationships, but shows that these cannot be close. In litopterns the frontals are also domed, although less so than in *Trigonostylops*, and their relationships are somewhat more as in the latter than are those of the frontals of *Astrapotherium*. The foramen rotundum is also confluent with the foramen lacerum anterius in litopterns. The foramen ovale is not fully confluent externally with the foramen lacerum medium, but they are separated only by a thin plate of bone. Litopterns also have an epitympanic sinus, although small, in the zygomatic base of the squamosal. Sagittal, temporal, and lambdoid crests of *Trigonostylops* are rather more litoptern- than astrapothere-like. The posttympanic process, auditory notch, exposure of periotic region, paroccipital and hyoid processes in litopterns are generally more or less intermediate between the conditions in *Astrapotherium* and those in *Trigonostylops*.

Such special resemblance as exists between *Trigonostylops* and the Litopterna seems to be largely in primitive or adaptive characters. It is probable that if we had more primitive astrapothere skulls, these also would make a closer approach to the Litopterna in these respects than does *Astrapotherium*.

Much of the crucial evidence is still lacking. From what is available it is a reasonable theory that trigonostylopids, astrapotheriids, and litopterns are three groups which have diverged from a more remote common ancestry, the early litopterns having retained more ancestral features than had the other two groups. Extrapolation of evolutionary trends in each of the three groups backward in time suggests intersection in a common ancestry within very primitive Condylarthra.

At present only two clearly definable genera are referred to this order: *Trigonostylops* and *Albertogaudrya*. As noted above in the discussion of the Astrapotheria, until 1957 everyone referred *Albertogaudrya* to the Astrapotheria without question, some in a separate family, Albertogaudryidae, and some as a subfamily of Astrapotheriidae. It is amusing and of some psychological interest that students of these animals, including me, pointed to the many resemblances between *Albertogaudrya* and *Trigonostylops* as evidence of relationship between the latter and the Astrapotheria. Only when *Scaglia* was described (Simpson, 1957) did it dawn on anyone that the resemblances of *Albertogaudrya* and *Trigonostylops* indicate special relationship between *them*, not between the latter and a third group. Even though *Albertogaudrya* is still very poorly known, I think it highly probable that it is a trigonostylopoid. Its differences from *Trigonostylops* are considerable, but I see no reason to retain a second monotypic family in this order.

Aside from *Trigonostylops* and *Albertogaudrya*, the following genera referred by Ameghino to the Trigonostylopidae or Albertogaudryidae may be mentioned here: *Pleurostylops* (referred to the Trigonostylopidae), *Rutimeyeria*, *Amilnedwardsia*, and *Scabellia* (all referred to the Albertogaudryidae) from the Casamayoran; *Edvardocopeia* and *Pseudostylops* (referred to the Trigonostylopidae) from the Mustersan. *Pleurystylops* was based on a single milk molar with no particular resemblance to this group. *Rutimeyeria*, based on an upper molar, is a small animal rather unlike the groups here considered,

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least *Trigonostylops* and some litopterns is morphologically a bulla, although not inflated, and the small sinus in all three groups which communicates with the ear region by a canal directed downward and backward seems to be an epitympanic sinus, although not apparent externally and probably not strictly homologous with the notoungulate epitympanic sinus.

incertae sedis but possibly a litoptern. *Amilnedwardsia* is similar to *Rutimeyeria*. *Scabellia* is a synonym of *Albertogaudrya*. *Edvardocopeia* is known chiefly from an upper premolar, indeterminate but probably notoungulate. *Pseudostylops* was based on an upper premolar quite unlike that of *Trigonostylops*, now known to belong to a notohippid. Thus none of these genera shows any real approach to *Trigonostylops*.

Shecenia Simpson, an inadequately known form, may be a Riochican trigonostylopid. (Unquestionable trigonostylopids are abundant in the Riochican of Itaborai.) *Hedralophus* Ameghino, referred by its author to the Leontiniidae, may be a trigonostylopid.

FAMILY TRIGONOSTYLOPIDAE AMEGHINO, 1901

DIAGNOSIS: Sole known family of the order as defined above.

TRIGONOSTYLOPS AMEGHINO, 1897

Trigonostylops AMEGHINO, 1897a, p. 492; 1906, p. 467. GAUDRY, 1904, pp. 13, 19, 23; 1906, pp. 33–34, figs. 3, 7, 9, 16. SCOTT, 1913, p. 509; 1937a, p. 543. ROTH, 1927, pp. 228, 240, 246, pl. 9, fig. 6, pl. 12, fig. 9. SIMPSON, 1933c, pp. 1, 15.

Trigonostilops [misprint]: ROTH, 1927, p. 247.

Staurodon ROTH, 1899, p. 386, *nec Staurodon* Lowe, 1854. SIMPSON, 1933c, p. 1; 1936d, p. 92 [as synonym of *Trigonostylops*].

Chiodon BERG, 1899, p. 79 [to replace *Staurodon*, preoccupied].

Staurodon = Pleurocoelodon: AMEGHINO, 1899, p. 12 [in error].

Staurodon = Chiodon = Trigonostylops: AMEGHINO, 1904a, vol. 58, p. 225.

TYPE: *Trigonostylops wortmani.*

TYPE OF *Staurodon = Chiodon*: *Staurodon* or *Chiodon gegenbauri* Roth.

DISTRIBUTION: Casamayoran, and perhaps also Riochican and Mustersan, South America.

DIAGNOSIS: Upper molars with broadly transverse trigon basin, almost equilaterally triangular, rimmed by metaloph-like crested metaconule posteriorly, posterolingual cusp (in position of hypocone) fully lingual, terminus of posterior cingulum.

There are 22 specimens of this genus in the Ameghino Collection, consisting of single teeth or parts of dentitions, none very complete. Tournouër found some better material, from which Gaudry (1904, figs. 14, 24, 36) figured upper and lower dentitions. Roth found three specimens (Roth, 1899, p. 386; 1927, pl. 9, fig. 6, pl. 12, fig. 9) including a good lower jaw, which, however, was not figured and was described only in a cursory way. The collection of the Field Museum of Natural History contains a good lower jaw, included in this study. We found more than 20 specimens surely referable to *Trigonostylops*, mostly isolated teeth but including a nearly complete skull, the only one known of this genus, family, or order. With this skull and the several lower jaws now known, the essential structure of the genus can be rather fully described.

Ameghino named 14 species of *Trigonostylops*. Ten are based primarily on single upper molars, in several cases with other fragments very doubtfully or incorrectly associated. All these types were supposed by him to be M^1, but there can be no doubt that some are M^2 or M^3. One species is based on M^{1-3}, the most nearly adequate type. One is based on P^{3-4} and P_{2-4} of different and not demonstrably conspecific individuals, neither specimen being comparable with any other of Ameghino's types. One is based on two M_2's of different individuals, likewise not comparable with any other type. One is based on a toothless symphysis, also not comparable. From the very nature of the types a real revision of species is impossible.

Ameghino had in his collection 16 identified specimens from one locality, south of Lago Colhué-Huapí, and he distributed these in all 14 of his supposed species. Even were one to suppose (against probability) that these are from several distinctive horizons, it is virtually impossible that 14 species of about the same size should represent a single genus at a single locality, and, even if so, the probabilities are enormously against 16 identifiable specimens representing 14 different species. The fact is that in this genus (as in some others) Ameghino placed almost every recognizable specimen in a species different from any other.

In an effort to sort these teeth out, I have made a detailed analysis of all the specimens available to me. Apart from size, discussed below, various morphological characters were given as characterizing the species. In many cases these were merely given descriptively, not explicitly as diagnostic, and in fact most of them are not distinctive from other comparable species. Checking over the types and other specimens to determine the validity of these characters and to seek for others possibly distinctive, I believe the following to be those features of the upper molars that vary most distinctly and hence might give true materials for taxonomic definition: parastyle in some cases small, in others salient; metaconule smaller or larger; hypocone weaker or stronger; ectoloph face more or less concave; and external cingulum tubercles present or absent.

The few more complete specimens show, however, that nearly or quite as much variation may be shown by adjacent or opposite teeth of a single individual as between the extremes in supposedly different species. The species, then, cannot be distinguished on this basis. The only possible exception to this statement is the last character, the cingulum cusps supposedly typifying *T. germinalis*. I think, however, that it cannot be seriously maintained that the appearance of two tiny cusps, of a sort that may appear in almost any species of mammals as an occasional variation or aberration, in a single specimen otherwise virtually identical with the genotype in structure is adequate evidence of the presence of a distinct species.

Concentrating on upper molars, since the majority of types are or include an upper molar and since the other types and specimens are almost impossible to compare with each other anyway, I studied their proportions and size. Numerical studies not necessary to publish *in extenso* show that the length-to-width ratio is nearly constant, all the points of a scatter diagram being clustered about a rectilinear regression line quite as closely as in most single, pure species. The most deviant tooth, measuring 11.8 by 15.5 mm., happens to belong to the same individual as two teeth that are in the main series. No specific separations are possible on this basis. The ectoloph lengths, which are on the whole more accurate than other linear dimensions, are about equally variable, and are involved in most of the type descriptions, are summarized in the following statistical constants:

N, 24
OR, 9.5–17.0
$\bar{X}$, 13.1 ± 0.3
s, 1.55 ± 0.22
V, 11.9 ± 1.7

For the size of the sample, the frequency distribution approximates a single normal curve remarkably closely. There is no basis for splitting this curve. The standard deviation, or, more clearly, the coefficient of variation, is large for a single species, although equally large figures have been found for analogous variates of pure races. Even this, however (in any case merely suggestive of heterogeneity and providing no means for separating the elements involved), has no value in the present case, for it is certain that the sample is heterogeneous even if of a single species. It includes M^1, M^2, and M^3, and the differences among these provide an adequate explanation for the broad dispersion of the figures, making any hypothesis of specific differentiation unnecessary to explain the facts. For instance, the difference in length between M^2 and M^3 of one individual (type of *T. subtrigonus*) is 2.5 mm., which is more than one and a half times the standard deviation of the heterogeneous distribution.

In short, there is no objective evidence that any of Ameghino's species, except the first one, are valid. On the basis of the evidence at hand, the types of all 14 (or, making an exception of the remarkably large but practically indeterminate *?T. duplex*, perhaps not of this genus, 13) supposed species could well belong to only one real species. This is not to say that they necessarily do. On more theoretical considerations, which perhaps should be inadmissable in formal taxonomy, it is possible that more than one species is present, if only because the geographic and geologic ranges are considerable.

The reviser's duty in such a case is a moot problem. It is a fact that none of Ameghino's definitions is diagnostic and that none of his species, beyond the genotype, can surely be recognized. On that basis it would seem fair and convenient simply to list *T. wortmani*, with 12 synonyms of Ameghino. On the other hand, it is possible that more than one species is present, although indistinguishable now, and in such a case, given the plethora of names available, it is virtually certain that Ameghino has applied other names to such specimens as do not belong to *T. wortmani.* If such could ever be shown to be the case, presumably it would be necessary to resurrect one or more of his names and to define them again and correctly. In this unsatisfactory sense, some of them (no one can now say which ones) are quite possibly "valid," so in principle should not be reduced to synonymy. Having pointed out the facts, as I understand them, I place 13 of the "species" below as synonymous but give the dimensions and peculiarities of each type so that any given name can readily be recovered if (as I fear is highly improbable) any but the first can eventually be given a biological diagnosis.

If species in this genus ever are to be sorted out and distinguished, it seems virtually certain that it can be done only by comparing lots of specimens each from one exact horizon and locality. Association of characters or values of variates with the provenience of the specimens might then reveal real taxonomic distinctions. At present this cannot be done; the highest available number of possibly homologous teeth known to be from one limited horizon is four, data entirely inadequate to approach the problem from this side. Present data do not even hint that there will prove to be a significant difference between samples of different origin. The four teeth of exactly known provenience, one horizon in Cañadón Vaca, for instance, average 13.4 mm. in length, a wholly insignificant deviation from the average (13.1) for the whole group, and the 12 molars from south of Colhué-Huapí (possibly from several horizons) average 13.2 in this dimension, obviously not significantly different either from the mean of the whole or from that of the Cañadón Vaca specimens. The frequency distributions of such samples as can thus be sorted by locality do not show any significant discontinuities and are all unimodal in form. All the data are thoroughly consistent with the presence of one, and only one, species.

Staurodon Roth *nec* Lowe, *Chiodon* Berg, was compared by Roth (1899, p. 386) with *Astrapotherium* and *Notostylops*, but not with *Trigonostylops* (which had at that time been described only incorrectly and from a few isolated teeth). Ameghino at first (1899) erroneously considered Roth's genus synonymous with *Pleurocoelodon*, but later (1904a) placed it as a synonym of *Trigonostylops*. The cheek teeth are quite indistinguishable from those of *Trigonostylops*, and the only definite distinctions observable are that P_1 is absent and the symphysis and horizontal ramus are more slender than in some specimens of *Trigonostylops*. In spite of the possibility that "*Staurodon*" is of later age, there seems no good basis for separating it generically, and little for separating it specifically.

Price and Paula Couto (1950; see also Paula Couto, 1952b) have described a species *Trigonostylops apthomasi*, abundant in the Riochican of Itaborai, Brazil. That is indeed a distinctive and clearly valid species, to such a point that I consider its reference to this genus questionable although it is obviously a true trigonostylopid.

MORPHOLOGY

Aside from their necessity for taxonomy, the types and various isolated teeth have little importance. The structure of the genus is described chiefly on the basis of the following specimens:

M.L.P. No. 12-1736, symphysis and left ramus; collected by Roth near Lago Musters; possibly of post-Casamayor age, but of this genus; type of *Staurodon gegenbauri.*

C.N.H.M. No. P13323, lower jaw with left C, P_1, P_{3-4}, and M_1; and right P_2-M_3; Casamayor Beds near Punta Casamayor, Santa Cruz.

A.M.N.H. No 28700, skull, with rostrum and face injured but cheek teeth and nearly perfect cranium preserved; collected by Justino Hernández in Casamayor Beds south of Lago Colhué-Huapí, Chubut,

M.H.N. No. 32 (Tournouër Collection), right maxilla with P^2-M^3 and alveoli of P^1 and C; the original of Gaudry (1904, fig. 14).

M.H.N. No. 33 (Tournouër Collection), nearly complete lower jaw; the original of Gaudry (1904, fig. 24).

DENTITION: The premaxillae are unknown, and no isolated teeth can be recognized as upper incisors of this genus. The upper incisors may have been absent. There are isolated tusklike teeth in the collections which undoubtedly belong in the upper jaw of *Trigonostylops*. These are relatively large, moderately curved teeth with long, closed roots. The crown doubtless was enamel-covered, but the known specimens are all worn to the dentine, and the actual crown pattern is unknown. There are two wear facets, both strongly oblique to the tooth axis and probably nearly vertical in life, the larger on the anterior, more convex, side, and the other contiguous but at an angle of about 225 degrees to this, on the anterointernal side of the tooth. From the relationship of these wear surfaces to the lower tusks, it appears that these teeth probably pointed well forward, were widely separated at the alveoli, but converged slightly at the tips.

It has been assumed that the tusks are canines in *Trigonostylops*. The evidence, all inconclusive, is chiefly that they are morphologically more like some canine tusks than like most incisive tusks, that the opposite upper tusks were apparently widely separated at the alveoli, and that they somewhat resemble astrapothere tusks. The last, probably the real reason why they have been so identified, is the least conclusive reason of all, as the resemblance is not an identity and as the reasoning seems to have been that these were canines because they were like astrapothere canines and that the animal is related to the astrapotheres because its canines are similar. Opposed to their being canines are the facts that they are extremely anterior, at least in the lower jaw, and that there are only two pairs of lower incisors between them. Yet it does seem probable that they are really canines.

M.H.N. Tournouër Collection No. 32 has a single alveolus for P^1 near the middle of the diastema. Our specimen stops just where this alveolus should be and does not show it, although it may have been present immediately anterior to the parts preserved. There is no known upper jaw of the same provenience as Roth's lower jaw, which has no P_1. Probably P^1 also was absent from some individuals.

P^{2-4} are apparently invariably present and are contiguous. P^2 is a small tooth, longer than wide, with a single main cusp, keeled anteroposteriorly. On our skull and some isolated specimens it has an internal basal swelling, not cuspidate, but this is absent from M.H.N. Tournouër Collection No. 32. P^{3-4} have about the same structure and proportions, but P^4 is larger. The ectoloph has distinct paracone, metacone, and metastyle, united nearly to the apices but distinguished by individual convex vertical folds on the outer surface. The paracone and metacone are nearly equal, the parastyle is considerably smaller but prominent and separated by a sharp deep fold from the paracone, and the metastyle is still smaller and much less sharply distinguished, in some cases hardly visible, especially on worn teeth. The whole inner side of the tooth is formed by the crescentic protocone, which is lower than the ectoloph. A low but sharp ridge runs from it to the junction of the parastyle and paracone, and another, rounded and even less prominent but in some cases bearing a very feeble metaconule, runs to the base of the metacone. There are anterior and posterior cingula, the posterior usually slightly wider but not cuspidate. These are in some cases continuous across the inner face. A weak external cingulum may also be present.

The molars are not very different from the premolars but differ in their considerably greater length, anteroposteriorly, in proportion to the width, and in a number of structural details. The ectoloph is more prolonged posterior to the paracone fold, and the region between this and the metacone fold is not a vertical groove but a rather broad flattened surface. The metacone fold is less prominent. Paracone and metacone are of about equal height on M^1, but the metacone is somewhat smaller on M^2 and definitely smaller on M^3. The crest from the protocone to the parastyle-paracone junction has no protoconule and is sharp and definite, although low, but the crest from protocone to metacone is very feeble or hardly present as such, although a small metaconule of varying prominence is invariably present. The anterior cingulum is well developed. In some cases it crosses the inner face of the protocone, but in none does it run directly into the posterior cingulum, but at most abuts against the base of the elevated internal end of the latter. The posterior cingulum is wider than the anterior, and its inner end, directly posterior to the protocone, rises to form a small ridged or cingulum-like hypocone, of varying development but in every instance much smaller and lower than the primary cusps and excluded from the trigon basin. This basin is shallow and broad, with a rounded, featureless bottom. An external cingulum is generally present, at least between paracone and metacone folds, and may give rise to basal cuspules (as in Ameghino's *T. germinalis*).

M^3 is not reduced in size, and it is difficult or impossible surely to distinguish the position of isolated upper molars. Tooth replacement in this genus seems to be normal, rather than much delayed as it commonly is in notoungulates. In our specimen M^3 is fully formed but not erupted, M^2 in place but little worn, M^1 more worn, and all the permament premolars in place and normally worn—premolar replacement followed the eruption of M^1 but is complete before the eruption of M^3.

The enamel is finely wrinkled on all the cheek teeth, upper and lower.

The lower incisors are known only in M.H.N. Tournouër Collection No. 33, and those have been damaged since Gaudry's study. Gaudry's figure shows two pairs of incisors of equal size, each with the crown consisting of a simple rounded lobe.

The lower tusks, presumably canines, have long but closed roots. Upon emerging from the alveolus, the tooth curves sharply outward and upward. The crown is enameled and more or less caniniform, a curved cone modified by an anterior keel. Roth's specimen preserves both canines. The roots are strongly appressed in the symphysis but are about 45 mm. apart at the tips, which point outward, upward, and backward. On this specimen each canine has a groove, the bottom enamel-coated and hence not due to wear, in the anteroexternal face. This is not visible in the other specimens seen by me, but may have been removed by wear in them. In these teeth there are generally two wear facets, a small one truncating the tip nearly at right angles, and a much larger facet on the posterior side nearly parallel to the long axis of the tooth. It is interesting that on Roth's specimen the right canine is much more worn than the left.

Ameghino (1901, p. 391) wrote that "la première molaire [i.e., P^1_1] d'en haut et d'en bas, toujours très petite, varie d'emplacement selon les espèces; elle se trouve placée tantôt contre la canine et separée de la suivante par une barre; et tantôt contre la deuxième, la barre se trouvant alors entre la canine et la première molaire [P^1_1]." Unless it was based on specimens unknown to me and not now in the Ameghino or other collections examined, this statement rests on no objective evidence and is probably not true. In Roth's specimen P^1_1 is lacking altogether, which may have been true of some of Ameghino's own specimens, although they are too imperfect for certainty on this point. In Gaudry's figures and on the specimen in the Field Museum of Natural History, P_1 is a vestigial tooth in the middle of the diastema. On the latter, and apparently also the former, it is one-rooted and has one low, blunt cusp with an anteroposterior keel, followed by an incipient heel.

P_2 is in some cases smaller than the following teeth, but is two-rooted. The crown is highly variable in structure, and I doubt whether this variation has any taxonomic significance. The tooth may consist of one low, heavy cusp followed by a very small heel. In other cases there is a small anterior basal cusp. The heel is in some cases larger, with a single cusp, or with a larger external and smaller internal cusp. In the Field Museum specimen a metaconid is tending to bud from the tip of the protoconid.

P_3 has an elongate triangular trigonid, with the anterior crest descending rapidly, anterointernally, and not cuspidate. The metaconid is immediately posterointernal to the protoconid, nearly as high, and connate with it nearly to the apex. The heel has a distinct, small, posterointernal cusp (not distinctly shown in Gaudry's figure, but present in all the other specimens examined) and a slightly curved external crest. P_4 has the protoconid and metaconid farther apart, joined by a sharp crest which is notched in the middle. The heel is larger, and the external crest is fully marginal and more distinctly crescentic.

The molar trigonid consists of a sharp oblique crest, anteroexternal-posterointernal with a cusp at each end, the anterior face excavated between them, without median or internal cusps (which occur in most contemporary notoungulates). From the external cusp, protoconid, a small sharp crest falls away rapidly anteriorly and anterointernally, ending at the midline where in some, but rare, cases it terminates in a small, vague cuspule (paraconid?). The talonid, considerably larger than the trigonid, has an external crescent departing from the posterior side of the protoconid base, more external than in most contemporary notoungulates, and ending on the posterior margin near the internal side. It is clearly composed of two cusps, a heavy crescentic hypoconid, and a more conical terminal hypoconulid. The entoconid is nearly conical, not transversely crested, and is close to the hypoconulid, separated by a sharp notch when unworn but merging into it when worn. The talonid basin is broad, excavated, simple, and closed except for the deep notch between the metaconid and entoconid. On M_3 the heel is larger, the hypoconulid projecting farther posteriorly and crescentic, and the entoconid more independent. Lower molar cingula are often present but of very variable strength and character.

SKULL: The nasals and the premaxillae are not preserved. Judged from the presence, position, and character of the tusks, the reduction and position of the lower incisors, the shape of the preserved part of the maxilla, and analogy with the functionally similar astrapotheres, it may be reasonably inferred that it had reduced premaxillae and retracted nasals.

The facial part of the maxilla has two large, well-marked hollows, one immediately anterior to the zygomatic root, the other higher, anterior to the upper part of the orbit. They are separated by a nearly horizontal, rounded ridge running anteriorly from the lacrimal region. On this ridge some distance from the orbit are four small foramina, and there is another, of about the same size, below and slightly posterior to them. There is no infraorbital foramen in the normal position, and I believe these small foramina, jointly, to represent the anterior end of the infraorbital canal.

The whole base of the zygoma and the whole border of the orbit are preserved. As no suture is visible and as the break does appear suggestively as if it had in part followed a suture, it is probable, although not certain, that the jugal did not extend anterior to the postorbital process of the zygoma. The zygoma arises opposite M^{1-2} in this young individual. Probably it would be opposite M^{2-3} in an adult.

The palate is wide, its sides are nearly parallel, and, as seen from below, it resembles a wide shallow channel with raised edges and a nearly flat floor. The broad palatal processes of the palatines extend forward to the level of the posterior parts of P^4. Near the anterolateral corners, on the suture, there is a pair of posterior palatine foramina, and there appear to have been other very small vascular foramina in the palatines themselves.

The posterior border of the palate and the choanae likewise present very striking features which appear to be quite unique. Near the posterior end of the surface of the palate, the palatines form a prominent median process, with an anterior median crest and a broad, shallow, irregular, posterior groove running obliquely up into the choanae. On each side this process is produced into a pointed, winglike process, between which and the general surface there is a large open groove. Within the choanae the palatines send upward a stout median process, fully united to the presphenoid or vomer, so that the choanae are divided into two wholly separated orifices.

Continuing into the pterygoid crests, in which the pterygoids themselves cannot be distinguished on the specimen, the palatines are at first thick and somewhat recurved below the passage. In the median and posterior parts, however, the crests are vertical and simple, with the edge only slightly thickened and no pterygoid fossae or hamular process.

The supraorbital process and the median part of the zygoma are broken, so that it is not known whether the orbit was enclosed. Its anterosuperior and anterior border is rounded, without development of a distinct crest or tubercle. The lacrimal is a small, simple, rounded element squarely on the orbital rim, with a large foramen a little below the middle. It appears to be in contact only with the frontal and the maxilla.

Within the orbit, between the lacrimal foramen and the posterior end of the infraorbital canal, nearer the latter, there is a foramen on the maxillo-frontal suture. The interorbital foramen lies at the posterointernal corner of the floor of the orbit, at the junction of the palatine, orbitosphenoid, and maxilla. The palatine does not extend above the pterygoid crests and plays a very minor part in this region of the skull, containing no foramina here. The orbitosphenoid was apparently well developed, but its upper limit is one of the very few sutures that careful scrutiny did not reveal. In the orbitosphenoid or along its edges there are four foramina. The most posterior is a large fissure between alisphenoid and orbitosphenoid, clearly the foramen lacerum anterius. The foramen rotundum must be merged with this also, as it is not present in the alisphenoid itself. Immediately anterior to the upper edge of this, and in part covered by this edge, is a much smaller foramen directed forward. This may be the optic foramen, but this function belongs with greater probability to another larger and more independent foramen above and anterior to this. The fourth foramen, also directed anteriorly, is the smallest of all and is near the lower edge of the groove running forward from the supposed optic foramen.

The alisphenoid, apparently fused to the basisphenoid and perhaps also to the pterygoid, which cannot be distinguished, is long anteroposteriorly, its course nearly horizontal, and shallow vertically. It extends for a short distance above the foramen lacerum anterius, but does not reach the parietal here. The frontal region is domed, the frontals themselves being markedly convex and inflated by large sinuses in at least their posterior part, which is all that is preserved of them on the skull roof. The frontals here form an angle, directed backward, clasped between the divergent anterior ends of the parietals. The frontals are also extensively developed in the orbital wall.

The parietals are large, long elements, but their great development is due to the large muscular origins on them rather than to their taking any unusual part in the roofing of the braincase. They form a tremendous sagittal crest, very high and long. The extreme posterior end is formed by the supraoccipital (or interparietal), the anterior end of which, in the crest, is wedged between thin plates of the parietal, but far the greater part of the crest is on the parietals only. At about the postorbital constriction the crest ends, as such, dividing into two divergent angulations formed by the parietals, which here clasp between them the sharply domed frontals. In the posterior parts of the parietals and along the parietosquamosal sutures there are a number of large vascular foramina. The parietals do not form any significant part of the lambdoid crests.

The squamosal forms a moderate part of the lateral cranial wall. This part is triangular, much elongate anteroposteriorly, its only marked irregularity a projection near the posterior angle, between the parietal and the lambdoid crest. The squamosal projects posterior to the auditory meatus, but the projection is very slight and is above, rather than behind, the tympanic and does not form a posttympanic process. The postglenoid process is heavy, but low and blunt, and is moderately expanded transversely. The postglenoid foramen is at the internal end of the postglenoid process, in the squamosal, but very near its suture with the tympanic. The glenoid surface is nearly flat and approximately horizontal, slightly tilted so as to face a little backward and outward. It is nearly equidimensional. From this point the squamosal extends forward in the cranial wall, becoming a featureless and nearly vertical plate which reaches the frontal in the region of the postorbital constriction.

The occiput, which is nearly vertical, is of equal height and width and is very strongly sculptured. Its elements appear to be fused. The supraoccipital region is marked by a broad concavity, divided by a small median vertical ridge, the upper margin of which is very rough. Lateral to the rounded ridges bounding this concavity on each side is a smaller, roughly triangular concavity facing more outward and downward. On the lateral edge of this is a narrow notch leading into a vacuity through which the mastoid is seen. From the mastoid a posterosuperior, styliform process extends backward and upward to appear on the surface of the occiput where it is clasped between sutures with the exoccipital. The paroccipital processes are moderately developed, extending to about the same level as the postglenoid processes, and elon-

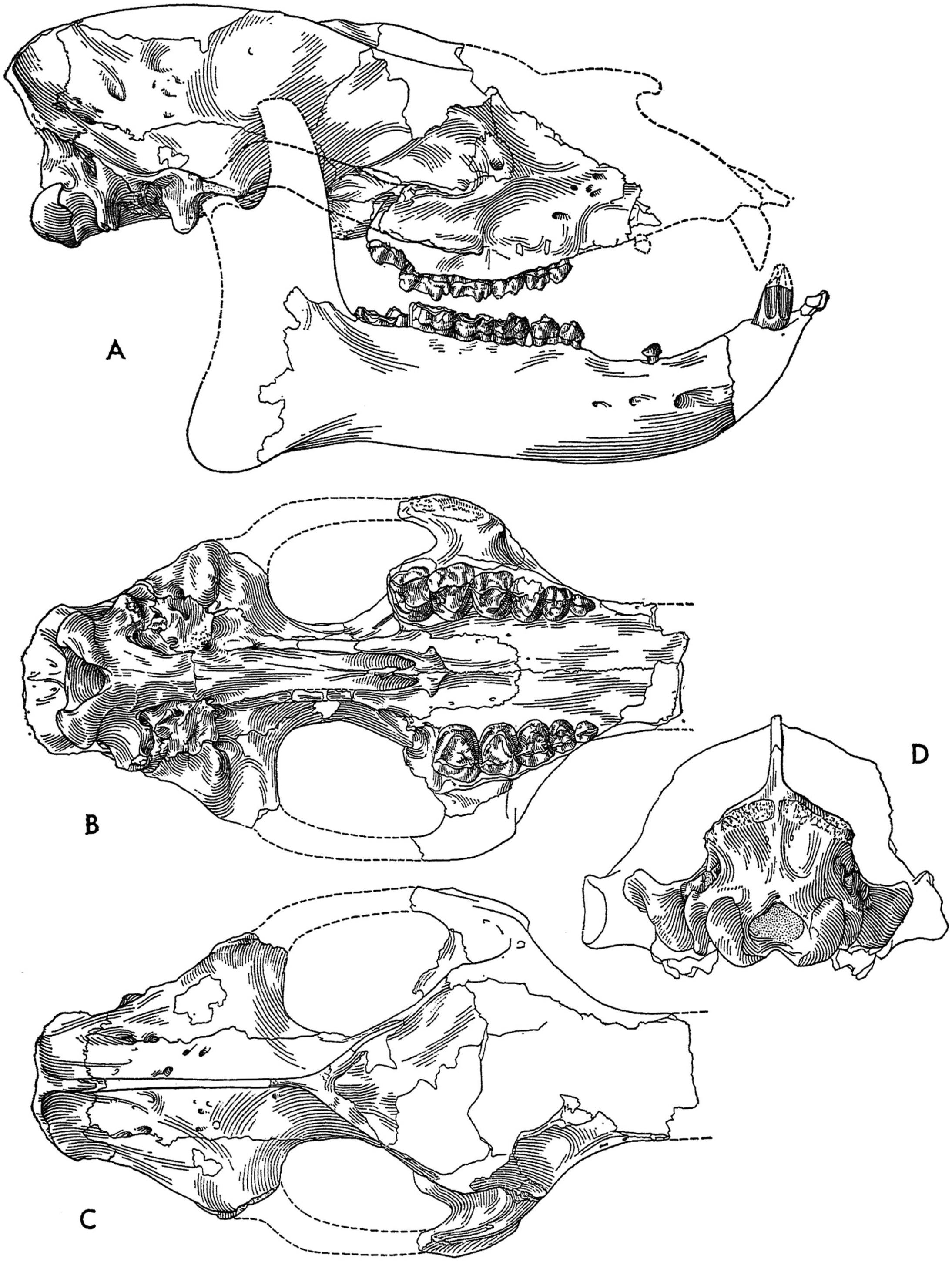

FIG. 42. *Trigonostylops wortmani* Ameghino, A.M.N.H. No. 28700, skull. A. Right lateral view, with C.N.H.M. No. P13323, lower jaw. B. Ventral view. C. Dorsal view. D. Occipital view. All ×0.55.

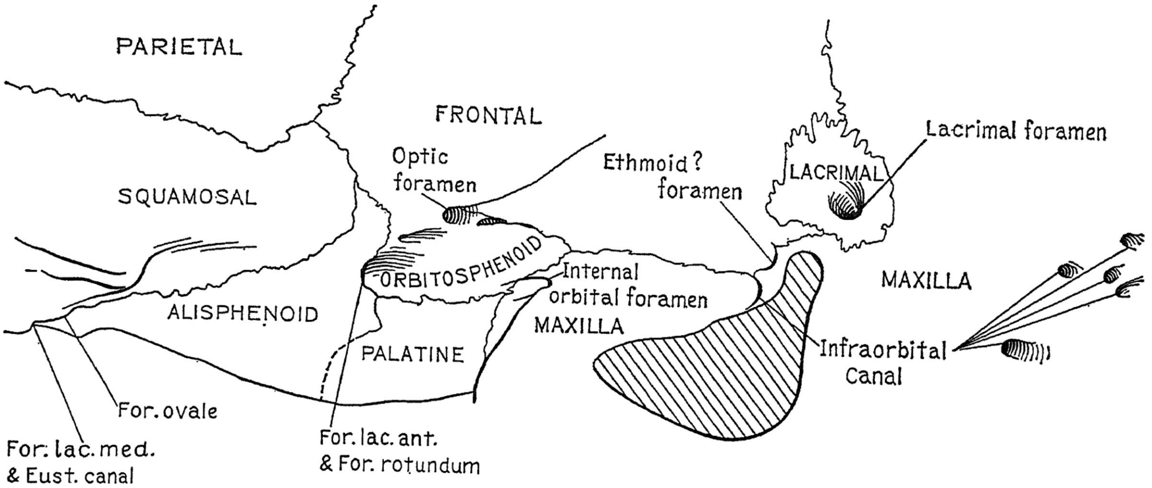

FIG. 43. *Trigonostylops wortmani* Ameghino, A.M.N.H. No. 28700, skull, diagram of right lateral view of posterior facial and anterior cranial regions, with anterior root of zygoma (cross hatched) shown as sectioned.

Abbreviations: Eust. canal, Eustachian canal; For. lac. ant., foramen lacerum anterius; For. lac. med., foramen lacerum medium; For. ovale, foramen ovale.

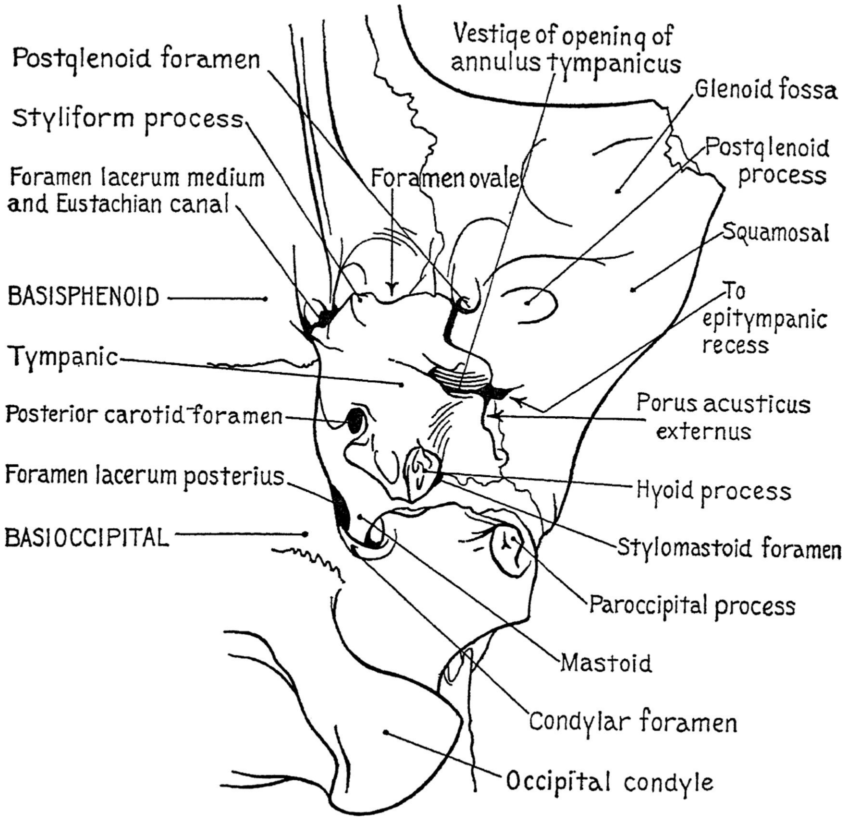

FIG. 44. *Trigonostylops wortmani* Ameghino, A.M.N.H. No. 28700, skull, diagram of ventral view of left side of basicranium.

gate anterointernal-posteroexternally. The occipital condyles are well rounded, separated basally, and directed almost straight posteriorly. The foramen magnum is slightly transverse. Nearly 2 cm. of the sagittal crest and almost all of the very strong lambdoid crest are formed by the supraoccipital. The lambdoid crests are not very distinctly emarginate, but become much less prominent about 2 cm. before reaching the upper rim of the meatus, and here the superior surface is formed by the squamosal, and the inferior by the exoccipital. The extensive dorsal exposure of the upper part of the fused occipital elements may cause suspicion that a distinct interparietal has also been merged with this complex, but, as the exposure is due rather to the great development of muscular crests than to any part in the dorsal roofing of the actual braincase, it may not really involve an interparietal.

The basioccipital, basisphenoid, and presphenoid are all relatively long and narrow, giving the cranium proper a very elongate aspect, more noticeable in this ventral view than dorsally. These elements lie in a straight line, not significantly inclined with respect to one another, and are also nearly parallel to the palatal surface, the face being only very slightly depressed relative to the basicranium. The basioccipital-basisphenoid junction is slightly swollen, and the presphenoid bears two narrow converging grooves, but these bones are otherwise nearly featureless.

The auditory region is highly distinctive, fundamentally unlike that of any true notoungulate, with some distant and doubtful resemblance to that of the astrapotheres, and unique in general, although with some minor details suggestive of diverse groups of mammals manifestly quite unrelated to *Trigonostylops*. The tympanic appears to be a single element, although the possibility of complete fusion of two or three elements is not absolutely excluded. It is a thick, heavy bone but is not at all inflated, and the lower surface is flattened and nearly horizontal. Apparently the original tympanic ring was horizontal, or gently inclined, certainly not near verticality. It lies with a loose suture, perhaps even an open contact, against the junction of the basioccipital and basisphenoid but has strong sutures against the squamosal anteroexternally and against the exoccipital posteriorly and also has ascending processes, transversely expanded, on each side of the porus acusticus, which are in tight sutural contact with the squamosal. The flattened ventral exposure of the bone is of very irregular shape. The outer part probably formed the floor of the internal end of the external auditory meatus, although an ossified meatus can hardly be said to be present in the ordinary usage of the term. Along the anterior part of this portion of the tympanic there is a deep narrow notch.[1] The anterointernal end of the tympanic is produced into a short styliform process which underhangs a very large deep transverse pit, extending upward and backward and roofed by the alisphenoid. This pit is double, and its outer part rather clearly served for the exit of the mandibular nerve, thus being homologous with the foramen ovale, whereas the inner part probably combined the functions of the foramen lacerum medius and the Eustachian canal. Slightly posterior to the middle side of the tympanic is a prominent, nearly circular notch which I take to represent the posterior carotid foramen. On the posterior margin of the tympanic there is a roughly hemispherical swelling, which may not belong to the bone itself but may be a descending process from the periotic or may be an independent element. In any event, this seems to be the place of attachment of the hyoid arch, and the margin of the tympanic around it is probably homologous with the vagina hyoidei, although it does not form a true and prominent vagina, strictly speaking, as in the notoungulates, for instance. The stylomastoid foramen is immediately external to this, and is definitely anterior and not very close to the anterointernal end of the paroccipital process.

Posterointernal to the tympanic there is a large oval vacuity, in the roof of which the mastoid is extensively exposed. Along the medial and posterior edges of this is the foramen lacerum posterius, and in the same pit, although with a distinct opening, is the

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[1] Apparently a remnant of the original circular opening of the nearly horizontal ring, not completely closed by ossification, extending inward from it—a normal condition in a few mammals and an occasional abnormality in others, including man. Here it is symmetrical on the two sides and was probably normal.

condylar foramen, which is thus far in advance of the condyle and directly internal to the anterior end of the paroccipital process.

There is not, as in notoungulates, an epitympanic sinus extending backward and upward into the posterior part of the squamosal, near or along the lambdoid crest. But in the anteroexternal part of the roof of the auditory cavity there is a large circular opening which runs forward and upward into a sinus of moderate size, not particularly noticeable externally, in the part of the squamosal forming the posterior root of the zygoma, chiefly above, internal, and also somewhat posterior to the glenoid surface.

For convenient reference to their important characters, what can be determined regarding the cranial foramina may be gathered together as follows:

Optic foramen: Apparently independent and some distance above and anterior to the foramen lacerum anterius, presumably in the upper part of the orbitosphenoid.

Foramen lacerum anterius: Large and with its usual relations.

Foramen rotundum: Not present in the alisphenoid and hence presumably confluent with the foramen lacerum anterius.

Foramen ovale: Not surrounded by the alisphenoid externally, but relatively posterior and ventral in position, between the alisphenoid and the tympanic, and in a common large pit with the foramen lacerum medium.

Stylomastoid foramen: At the posterior edge of the tympanic, external to the hyoid attachment and anterior to the paroccipital process.

Foramen lacerum posterius: Large and in its normal position between periotic and basioccipital and opening into a large pit or gap left between the latter and the tympanic.

Condylar foramen: Opening into the pit just mentioned, internal to the paroccipital process and some distance anterior to the condyle.

Infraorbital foramina: Multiple, relatively high on the face, and far anterior to the orbit.

Internal orbital foramen: Small, at the posterointernal corner of the orbital floor at the junction of the maxilla, palatine, and orbitosphenoid.

Ethmoid foramen: Although unusual in position, the foramen on the maxillo-frontal suture in the anterointernal wall of the orbit may fulfill this function.

Posterior palatine foramen: On the maxillopalatine suture near the anteroexternal angle of the palatine, with subsidiary foramina in the palatine.

Foramen lacerum medium: A large opening at the anterointernal corner of the tympanic and confluent externally with the foramen ovale.

Posterior carotid foramen: In a large notch on the posterointernal border of the tympanic.

Postglenoid foramen: Immediately medial to the postglenoid process.

Choanae: Immediately posterior to M^3, considerably narrower than the palate, and completely divided into two by a median ascending process from the palatines.

Lacrimal foramen: Large, simple, without a spine, on the rounded orbital rim.

Eustachian canal: Apparently confluent externally with the foramen lacerum medium.

External auditory aperture: Roofed by the squamosal, and with the tympanic forming a short partial meatus by anterior, posterior, and incomplete inferior plates.

Foramen magnum: Large and very slightly transverse.

Miscellaneous, vascular or unidentified: A small foramen anterior to the supposed optic foramen. Several large vascular foramina in the parietal. Vacuity in the occipital exposure of the exoccipital, through which the mastoid projects.

MANDIBLE: The most striking feature of the lower jaw is the long, cylindrical symphysis. Its width and depth are nearly equal, and the lateral and inferior surfaces are continuous and rather evenly rounded. The upper surface is marked by a groove, limited by crests continuing the dental borders. The interior is occupied almost entirely by the closely appressed, triangular to semicircular canine roots. The symphysis extends to the anterior border of P_2. There are two mental foramina, one beneath each half of the diastema. The horizontal ramus beneath the cheek teeth is of normal proportions, its lower border nearly straight and parallel to the dental border. The angular region is large and flat, expanding abruptly below the lower border of the horizontal ramus. The condyle is well above the molar level, and the coronoid is high and slender.

Trigonostylops wortmani Ameghino, 1897

Plate 43, figures 8–20; plate 44, figures 2, 3;
text figures 41D, 42–46

Trigonostylops wortmani AMEGHINO, 1897a, p. 492, fig. 72 [but fig. 72g is not this genus or species]; 1898, p. 175; 1904b, p. 100, fig. 111. GAUDRY, 1904, pp. 15, 20, 24, figs. 14, 24, 36. SCHLOSSER, 1923, p. 617, fig. 763. SIMPSON, 1933c, p. 6, figs. 1–6. CABRERA, 1935, p. 14.

Trigonostylops wortmanni [error]: Ameghino, 1901, p. 391.

Trigonostylops secondarius Ameghino, 1901, p. 391; 1904b, p. 100, figs. 112, 511.

Trigonostylops integer Ameghino, 1901, p. 391; 1904b, p. 99, figs. 110, 263, 331.

Trigonostylops minimus Ameghino, 1901, p. 392.

Trigonostylops trigonus Ameghino, 1901, p. 392.

Trigonostylops subtrigonus Ameghino, 1901, p. 392; 1904b, p. 383, fig. 501. Simpson, 1933c, p. 16.

Trigonostylops insumptus Ameghino, 1901, p. 392; 1904b, p. 389, fig. 510.

Trigonostylops eximius Ameghino, 1901, p. 393; 1904b, p. 387, fig. 508.

Trigonostylops scabellum Ameghino, 1901, p. 393.

Trigonostylops hemicyclus Ameghino, 1901, p. 394.

Trigonostylops columnifer Ameghino, 1904a, vol. 58, p. 225.

Trigonostylops coryphodontoides Ameghino, 1904a, vol. 58, p. 226; 1904b, p. 369, fig. 483; 1906, p. 321, fig. 141.

Trigonostylops germinalis Ameghino, 1904a, vol. 58, p. 226; 1904b, p. 84, figs. 86, 171, 484, 509.

Type: M.A.C.N. No. 10651, right upper molar, probably M^2, lectotype; left upper premolar, probably P^4; talonid of right M_3; canine. These isolated teeth evidently were not associated, and the canine does not belong to this genus or species. No locality data.

Types of Synonyms: Of *Trigonostylops secondarius:* M.A.C.N. No. 10645, left upper molar, lectotype; right upper molar; left upper premolar. The three teeth are probably not associated. Colhué-Huapí.

Of *Trigonostylops integer:* M.A.C.N. No. 10643, complete left upper molar, lectotype; broken left upper molar; associated left P^{2-3}. Certainly two and probably three individuals are represented. North of Colhué-Huapí.

Of *Trigonostylops minimus:* M.A.C.N. No. 10660, left upper molar, probably M^3. Colhué-Huapí.

Of *Trigonostylops trigonus:* M.A.C.N. No. 10656, broken and deeply worn right upper molar. Colhué-Huapí.

Of *Trigonostylops subtrigonus:* M.A.C.N. No. 10642, fragment of left maxilla with M^{1-3}. Río Chico.

Of *Trigonostylops insumptus:* M.A.C.N. No. 10654, left upper molar, perhaps M^2, lectotype; talonid of M_3, probably not associated. Colhué-Huapí.

Of *Trigonostylops eximius:* M.A.C.N. No. 10650, right upper molar, lectotype; two left M_3's; talonid of right M_3; left ?M_2; left ?M_1; upper canine. At least three individuals are represented. Colhué-Huapí.

Of *Trigonostylops scabellum:* M.A.C.N. No. 10657, fragment of right maxilla with P^{3-4}, lectotype. M.A.C.N. No. 10629, fragment of right lower jaw with P_{2-4}, may have been a syntype. Lectotype from west of the Río Chico. Other specimen from Colhué-Huapí.

Of *Trigonostylops hemicyclus:* M.A.C.N. No. 10659, right M_2, lectotype; left M_2 of a different individual. Colhué-Huapí.

Of *Trigonostylops columnifer:* M.A.C.N. No. 10638, two isolated left upper molars; the one measuring 11.6 by 12.6 mm. is taken as lectotype. Colhué-Huapí.

Of *Trigonostylops coryphodontoides:* M.A.C.N. No. 10641, right upper molar. Colhué-Huapí.

Of *Trigonostylops germinalis:* M.A.C.N. No. 10639, left upper molar. Colhué-Huapí.

Hypodigm: Indefinite, as the character of the biological species remains indefinite. Essentially all the types listed above plus, at least, C.N.H.M. No. P13323, A.M.N.H. No. 28700, M.N.H. Tournouër Collection No. 32, described under the genus, and M.A.C.N. No. 10627, left lower jaw with P_2–M_3.

Horizon and Locality: Casamayoran, Patagonia. As far as available, more specific localities for the included types are given above.

Diagnosis: The only certainly valid species of the genus, as defined above.[1] Measurements of teeth are given in tables 74 and 75.

Characteristics of the individual type (or lectotype) specimens are as follows. These are not diagnoses of taxa. In my opinion all these characters are or may be individual variations within the single taxon *T. wortmani.*

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[1] "*Trigonostylops*" *apthomasi*, certainly a valid species, is excluded by the generic diagnosis here adopted.

TABLE 74

MEASUREMENTS OF UPPER TEETH OF *Trigonostylops wortmani* AND PROBABLE SYNONYMS

	P^2		P^3		P^4		M^1		M^2		M^3		$M?^a$	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
T. wortmani[b]	—	—	—	—	—	—	—	—	—	—	—	—	13.9	15.2
T. secundarius[b]	—	—	—	—	—	—	—	—	—	—	—	—	13.0	13.2
T. integer[b]	—	—	—	—	—	—	—	—	—	—	—	—	10.8	12.4
T. minimus[b]	—	—	—	—	—	—	—	—	—	—	—	—	9.5	9.8
T. trigonus[b]	—	—	—	—	—	—	—	—	—	—	—	—	12.7	*ca.* 14
T. insumptus[b]	—	—	—	—	—	—	—	—	—	—	—	—	*ca.* 17	*ca.* 18
T. eximius[b]	—	—	—	—	—	—	—	—	—	—	—	—	15.5	17.5
T. columnifer[b]	—	—	—	—	—	—	—	—	—	—	—	—	11.6	12.6
T. coryphodontoides[b]	—	—	—	—	—	—	—	—	—	—	—	—	*ca.* 14	15.9
T. germinalis[b]	—	—	—	—	—	—	—	—	—	—	—	—	13.8	15.2
T. scabellum[b]	—	—	*ca.* 7½	9.8	*ca.* 8½	12.4	—	—	—	—	—	—	—	—
T. subtrigonus[b]	—	—	—	—	—	—	*ca.* 12	13.7	14.3	15.4	11.8	*ca.* 15½	—	—
T. integer[c]	8.0	6.3	8.8	9.8	—	—	—	—	—	—	—	—	—	—
A.M.N.H. No. 28700	7.2	5.8	8.5	10.3	10.0	13.4	13.4	14.4	14.3	16.4	—	*ca.* 16½	—	—
M.H.N. Tournouër No. 32	6.2	5.7	7.9	9.0	9.4	11.7	10.8	13.4	13.0	16.1	12.7	15.1	—	—

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[a] In this genus M^{1-3} are so much alike that isolated teeth cannot be certainly placed in the sequence. These are upper molars of uncertain homology. Ameghino considered them all to be M^1, which is extremely unlikely.

[b] Type.

[c] Syntype, not lectotype.

TABLE 75

MEASUREMENTS OF LOWER TEETH OF *Trigonostylops wortmani* AND *T. gegenbauri*

	P_2		P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W	L	W
T. wortmani												
T. "scabellum"[a]	6.2	4.4	8.6	6.3	9.6	6.7	—	—	—	—	—	—
T. "hemicyclus"[b]	—	—	—	—	—	—	—	—	13.5	8.9	—	—
C.N.H.M. No. P13323	7.3	5.2	8.7	6.1	9.5	7.1	10.7	7.5	—	8.9	17.5	9.6
T. gegenbauri[b]	—	—	—	—	10.7	7.8	12.7	8.0	14.7	9.6	16.8	9.7

[a] Syntype, not lectotype.
[b] Type.

Trigonostylops wortmani: Upper molar parastyle relatively small; metaconule well developed.

Trigonostylops secondarius: Upper molar smaller than in type of *T. wortmani.*

Trigonostylops integer: Upper molar slightly smaller than in type of *T. secondarius*; metaconule rudimentary; hypocone relatively strong.

Trigonostylops minimus: Upper molar smaller than in any other of Ameghino's types.

Trigonostylops trigonus: Slightly smaller than in type of *T. wortmani.* Ameghino said that the metaconule was replaced by a transverse crest, but the metaconule in *Trigonostylops* is normally somewhat crested, and as far as this specimen seems distinctive that is only an effect of wear.

Trigonostylops subtrigonus: Not different from type of *T. wortmani.* Ameghino described this species as larger than *T. wortmani,* with two transverse crests, the posterior with a rudiment of the metaconule, the posterior cingulum forming an incipient posterointernal lobe. I see no differences from typical *T. wortmani* not due to wear or not within the range of the slightest individual variation. The valueless character of the "species" of *Trigonostylops* is well shown by these three associated teeth which would certainly have been placed in three different species if found separated.

Trigonostylops insumptus: Upper molar larger than average; hypocone relatively strong. The external cingulum has probably been corroded away.

Trigonostylops eximius: Upper molar like that of type of *T. insumptus* but slightly shorter.

Trigonostylops scabellum: Not comparable with any other type. Not distinguishable from referred upper dentitions with molars as in *T. wortmani.*

Trigonostylops hemicyclus: Not comparable with any other Casamayoran type. Not distinguishable from lower dentitions referred to *T. wortmani.*

Trigonostylops columnifer: Upper molar with wall between paracone and metacone less concave than usual.

Trigonostylops coryphodontoides: Upper molar like that of type of *T. subtrigonus,* but proportionately longer and with more salient parastyle.

Trigonostylops germinalis: Upper molar with two labial cingular tubercles.

Trigonostylops gegenbauri (Roth, 1899), *nomen dubium*

Plate 44, figure 1

Staurodon gegenbauri ROTH, 1899, p. 386.

=*Pleurocoelodon Wingei:* AMEGHINO, 1899, p. 12 [in error].

Trigonostylops gegenbauri: SIMPSON, 1933c, p. 16; 1936d, p. 66.

TYPE: M.L.P. No. 12-1736, symphysis and left ramus of jaw, with both canines and left P_4-M_3.

HYPODIGM: Type only.

HORIZON AND LOCALITY: "Cretáceo superior de Lago Musters" (Roth), that is, Lower Tertiary, west of the Cerro del Humo, Chubut. As far as definitely determined, Roth's specimens from this locality are Mustersan, but Casamayoran beds do also occur there, and it is possible that this was derived from them.

DIAGNOSIS: Comparable only with the inadequately known and later-named *T. "hemicyclus"* among Ameghino's types. No real diagnosis possible. P_1 absent and dimensions (see table 75) not in exact agreement with those of any of the better lower jaws from other localities. Symphysis and horizontal ramus slender.

The species may be valid, although no useful comparisons can be made. If the type is really from the Mustersan, specific distinction (at least) is extremely probable.

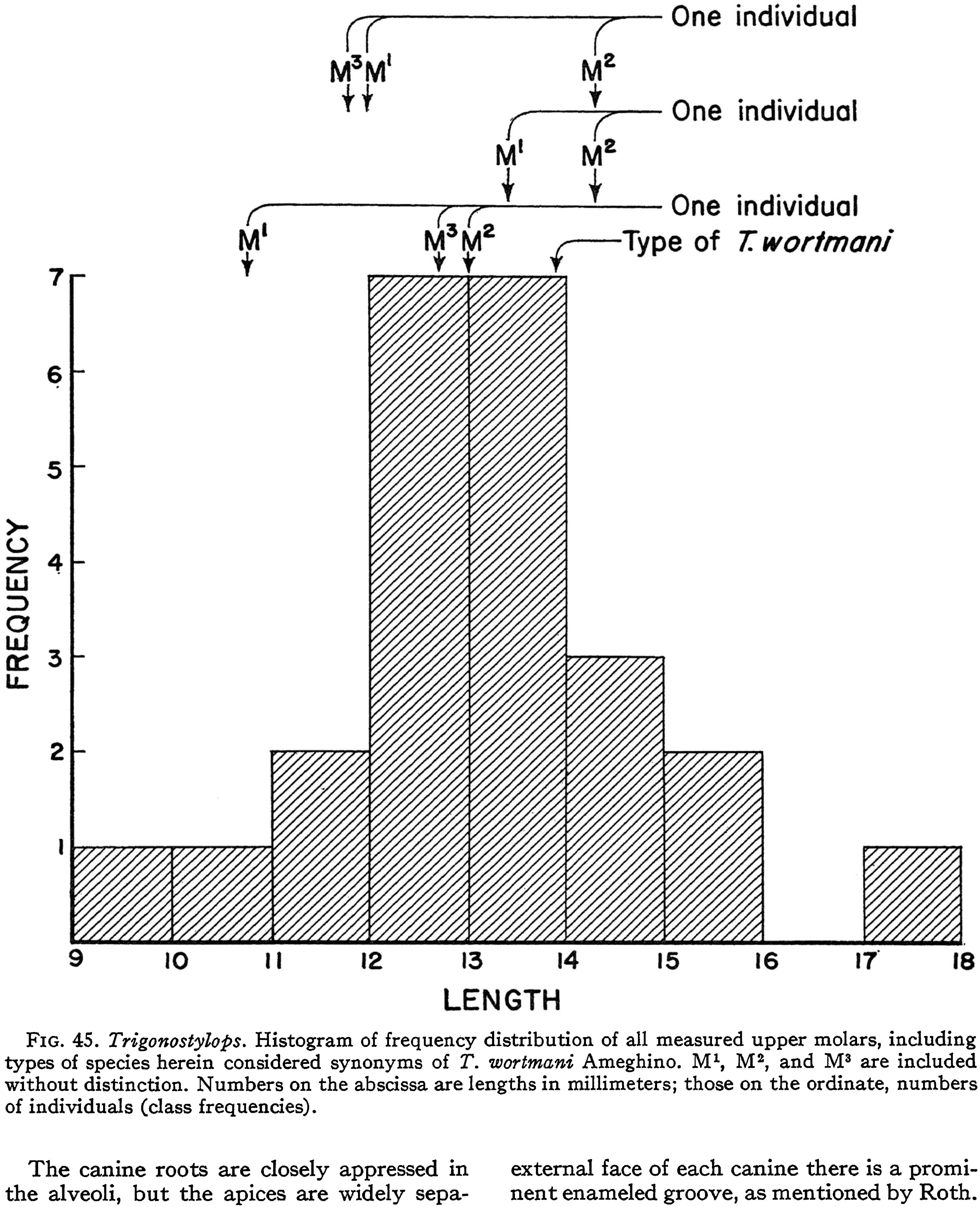

FIG. 45. *Trigonostylops*. Histogram of frequency distribution of all measured upper molars, including types of species herein considered synonyms of *T. wortmani* Ameghino. M^1, M^2, and M^3 are included without distinction. Numbers on the abscissa are lengths in millimeters; those on the ordinate, numbers of individuals (class frequencies).

The canine roots are closely appressed in the alveoli, but the apices are widely separate, about 45 mm., and point outward, upward, and backward. The right canine is much more worn than the left. In the antero-external face of each canine there is a prominent enameled groove, as mentioned by Roth. The incisive region is broken. The long, completely fused symphysis is characteristic of the genus, considerably wider than deep,

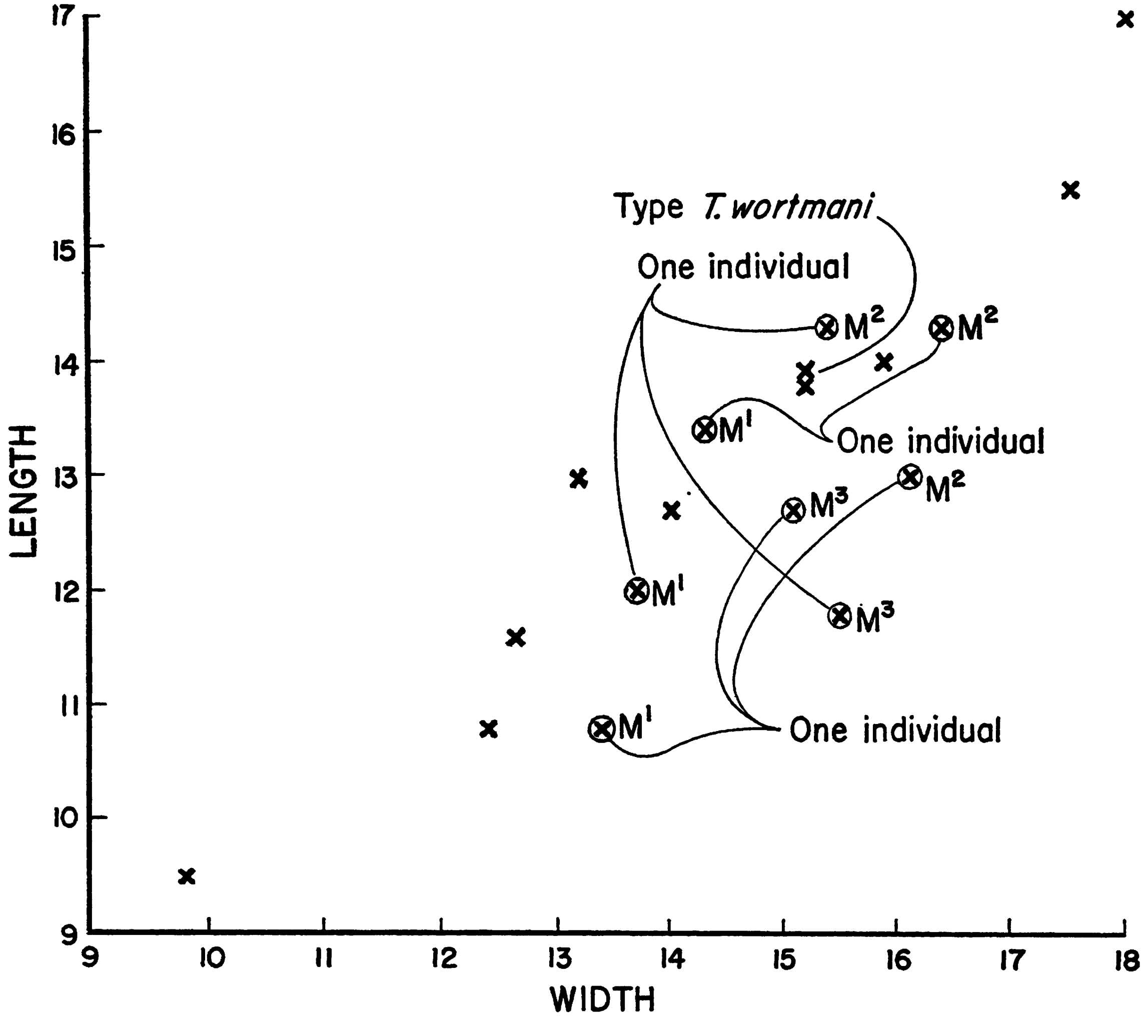

FIG. 46. *Trigonostylops*. Regression of length (ordinate) on width (abscissa) in all measured upper molars of the genus.

rounded below and grooved longitudinally above, ending at the anterior end of P_2. The angular region is long and flat, extending to an angulation well below the lower border of the horizontal ramus. The condyle is far above the molar level, and the coronoid is high and slender.

ALBERTOGAUDRYA AMEGHINO, 1901

Albertogaudrya AMEGHINO, 1901, p. 399; 1902a, p. 21; 1904a, vol. 58, p. 229; 1904b, p. 101; 1906, pp. 467, 470, 472. SCHLOSSER, 1923, p. 618. SCOTT, 1913, pp. 509, 512; 1928a, p. 335; 1937a, pp. 530, 543. SIMPSON, 1933c, p. 19.

Scabellia AMEGHINO, 1901, p. 400; 1904a, vol. 58, p. 227; 1906, p. 467. SCHLOSSER, 1923, p. 618. SIMPSON, 1933c, p. 15; SCOTT, 1937a,p. 543.

TYPE: *Albertogaudrya unica*.

TYPE OF SYNONYM: *Scabellia laticincta* Ameghino.

DISTRIBUTION: Casamayoran.
Ameghino also reported the genus in the Mustersan and doubtfully in the Deseadan, but no species were named for these formations, the evidence is inadequate, and the identifications are probably incorrect.

DIAGNOSIS: Trigonostylopids individually much larger than species of *Trigonostylops*. Upper molars with transversely narrowed basin; very short, buccal metaloph or crested metaconule, large posteromedian hypocone.

Scabellia, with its two or three supposed species, was based on three broken, isolated teeth and some other scraps of doubtful pertinence. Not even one complete tooth was known. As isolated teeth, these are distinctive, and they are morphologically somewhat intermediate between molars of *Albertogaudrya* and those of *Trigonostylops,* as Ameghino pointed out. As far as the poor fragments show, the chief differences from *Albertogaudrya* molars are that the hypocone is relatively smaller, more internal in position, and nearer to the protocone, and that the inner border is nearly a simple curve without the emargination seen in the *Albertogaudrya* molars. I believe that these are, with great probability, anterior cheek teeth of *Albertogaudrya,* on the following grounds: 1. The fragments are more suggestive of premolars than of molars, and are more or less what would be expected, *a priori,* in *Albertogaudrya.* 2. In M.A.C.N. No. 12000, type of *Albertogaudrya unica,* there is a probably associated upper premolar, probably P^2, which is smaller than the *Scabellia* fragments (probably P^3 and P^4) but of the same general character. 3. A.M.N.H. Nos. 28639 and 28947 have P^4 of *Scabellia* type in positive association with a M^1 congruent with known M^2 and M^3 of *Albertogaudrya.*

Ameghino named five supposed species of *Albertogaudrya* and two of *Scabellia.*[1] I am not able to distinguish any of these as true biological species, and I think it probable that all seven names are synonymous. I so list them below, but treated in such a way that any can be readily recovered if further discoveries warrant.

Upper incisors of *Albertogaudrya* may have existed but are unknown. The upper canine is a large, long tooth, compressed laterally, and oval to triangular in section. The crown is enameled except near the alveolus on the anterior face and the adjacent part of one side. The long axis is gently curved, convex forward, and wear is on the anterior side at about 45 degrees to this axis. There is much variation in the teeth provisionally considered as upper canines of *Albertogaudrya.* In addition to the typical condition described, there are teeth with more limited and differently distributed enamel and some with the lateral compression almost lacking. As these teeth have never been found in association with any others, they may not all belong in this genus, although it seems likely that some of them do.

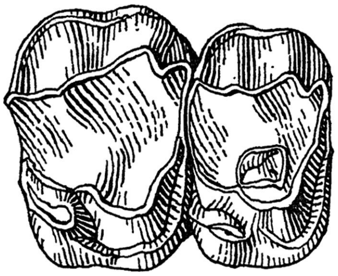

FIG. 47. *Albertoguadrya ?unica* Ameghino, A.M.N.H. No. 28639, right P^4–M^1, crown view. ×1.

The upper premolars, as seen in "*Scabellia*" and P^4 of A.M.N.H. No. 28639, are rounded-quadrate, much wider than long. The ectoloph wall has a strong parastylar fold and distinct, subequal, evenly spaced paracone and metacone folds. The protoloph is similar to that of the molars, and a notch between protocone and metaconule enters the shallow median valley. The metaconule is nearly or fully attached to the ectoloph. The anterior, internal, and posterior sides are surrounded by a cingulum which swells into a small distinct hypocone posterointernal to the protocone. This is purely cingular, quite distinct from the protocone, and still more so from the metaconule. On the molars it is more external relative to the protocone, more sharply divided from the latter, and more nearly confluent, basally, with the metaconule.

A toothless symphysis in our collection, A.M.N.H. No. 28641, may be referred to this genus with little doubt. The symphysis itself is very long and narrow, about 110 mm. long and about 50 mm. wide behind the canines. Opposite rami are indistinguishably fused. There were three pairs of lower incisors, I_2 having the largest alveolus, as in

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[1] Another species, "*Trigonostylops*" *duplex,* was transferred to *Scabellia.* It is listed on a following page under ?Trigonostylopidae *incertae sedis.*

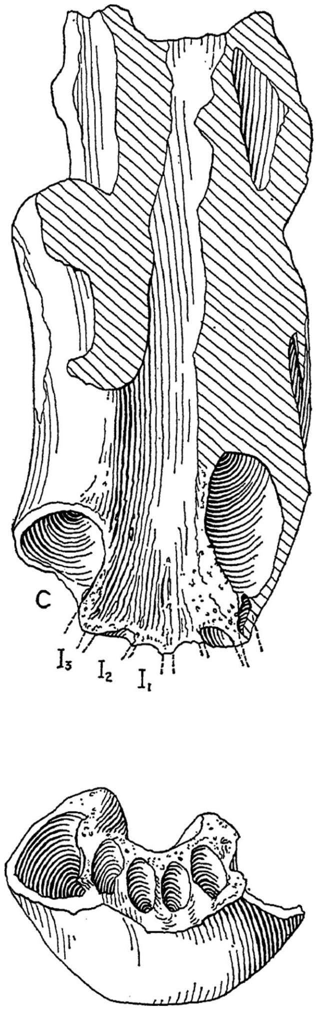

FIG. 48. *Albertogaudrya ?unica* Ameghino, A.M.N.H. No. 28641, symphysis without teeth, dorsal and anterior views. ×1.5.

Astrapotherium, and I_3 crowded closely against the canine.

The great canine alveolus of our toothless symphysis tapers to a blunt-pointed end harmonious with the closed canine roots and is curved and points forward, outward, and upward. The lower canines themselves, known from several isolated specimens, have oval roots, only slightly compressed, and trihedral crowns flattened on one side. The sides have heavy enamel, stopping at or near the alveolar mouth, but these bands do not meet on the proximal part of the front face. The large wear facet is on the posterior and more concave face, but there is a much smaller and more transverse facet at the extreme tip on the anterior face.

A specimen in the Tournouër Collection, M.H.N. No. 10, includes much of the symphysis except its anterior end, with alveoli for right P_{2-3}, and the crown of right P_4. This confirms the reference of A.M.N.H. No. 28641 to this genus and adds some further information. The long symphysis is seen to end beneath P_3. The diastema, not fully preserved, was about 75 mm. long in this specimen and has a sharply elevated border throughout. Between these crests on the two sides, a deep, narrow lingual gutter occurs above the symphysis. By comparison, particularly, with M.A.C.N. No. 12001, it is established beyond serious doubt that the preserved tooth in this Tournouër specimen is P_4. Anterior to it are two pairs of alveoli for P_{2-3}, and, although the dental border anterior to P_2 is perfectly preserved, there is no trace of an alveolus for P_1. There were, then, three premolars only, contrary to Ameghino's suggestion that four were probably present. It is, of course, possible that P_1 was variable in occurrence, as in *Trigonostylops*, but no known specimen has it. The various known materials thus combine to give the lower dental formula 3 1 3 3.

All the lower cheek teeth are known in M.A.C.N. No. 12001, and various of them in other specimens. P_2 is a simple but two-rooted tooth with a high main cusp and low heel. P_3 is molariform except that the anterior wing of the trigonid crescent is very slight, almost lacking. P_4 is molariform, but the talonid is relatively smaller than in the true molars. M_{1-3} are almost identical in structure with those of *Trigonostylops*.

Albertogaudrya unica Ameghino, 1901

Plate 44, figure 4; text figures 41E, 47, 48

Albertogaudrya unica AMEGHINO, 1901, p. 399; 1904b, p. 101, figs. 113, 221, 456, 473, 475, 477, 479, 493; 1906, p. 321, figs. 142, 144. SCOTT, 1928a, pl. 35, figs. 3, 3a; 1937a, p. 542, fig. 339.

Scabellia laticincta AMEGHINO, 1901, p. 400; 1904b, p. 378, fig. 495.

Albertogaudrya regia AMEGHINO, 1902a, p. 21; 1904a, vol. 58, p. 228.

Albertogaudrya tersa AMEGHINO, 1902a, p. 21.

Scabellia cyclogona AMEGHINO, 1904a, vol. 58, p. 227; 1904b, p. 378, fig. 494.

Albertogaudrya separata AMEGHINO, 1904a, vol. 58, p. 229; 1904b, p. 101, figs. 114, 188, 222, 314, 480, 497; 1904e, p. 60, fig. 44.

Albertogaudrya oxygona AMEGHINO, 1904a, vol. 58, p. 229; 1904b, p. 377, fig. 492.

TYPE: M.A.C.N. No. 12000, a right upper molar (lectotype); broken left upper molar; right upper premolar; three tusk fragments. These may be associated. In the same lot, however, are two other tooth fragments and an astragalus, probably not associated. Ameghino mentioned M^{1-3} in his description, but, as in many other cases, he probably based that description, ostensibly of the whole molar series, on a single upper molar, which he considered M^1 but which is probably M^2 (the lectotype). No locality data.

M.A.C.N. No. 12001, lower jaw with right P_2–M_3, left P_4–M_3 (M_{1-2} shattered), and canine fragments. Ameghino's description of lower teeth was based on this specimen, but he definitely labeled M.A.C.N. No. 12000 as the type. The two are not associated but probably are of the same species. No locality data.

TYPES OF SYNOMYNS: Of *Scabellia laticincta:* M.A.C.N. No. 12008, posterointernal part of a left upper cheek tooth. Colhué-Huapí.

Of *Albertogaudrya regia:* M.A.C.N. No. 12014, broken right M_3 (lectotype); right ?P_1; left ?P_2; part of inner side of a right upper molar. Probably from several individuals. North of Colhué-Huapí.

Of *Albertogaudrya tersa:* Probably a single upper molar, not found in the collection. The following were referred by Ameghino: M.A.-C.N. No. 10633, isolated upper canine; a syntype. M.A.C.N. No. 12012, isolated lower incisor; possibly also a syntype, as Ameghino mentioned lower incisors, but pertinence to species or genus highly doubtful. Colhué-Huapí.

Of *Scabellia cyclogona:* M.A.C.N. No. 12005, two dissociated but similar fragments of lingual parts of upper cheek teeth. Colhué-Huapí.

Of *Albertogaudrya separata:* M.A.C.N. No. 12004, isolated right upper molar. Colhué-Huapí.

Of *Albertogaudrya oxygona:* M.A.C.N. No. 12007, posterolingual part of upper molar. Colhué-Huapí.

HYPODIGM: The types, as above, and A.M.N.H. No. 28639, associated right P^4–M^1, Colhué-Huapí; A.M.N.H. No. 28947, associated P^4 (broken) and M^1, Riconada de Lopez; A.M.N.H. No. 28641, symphysis, Cerro Blanco; A.M.N.H. No. 28640, jaw fragment with left M_3, Cerro Blanco; M.H.N. Tournouër Collection No. 10, symphysis and right P_4, "Cerro Negro."

HORIZON AND LOCALITY: Casamayoran, Patagonia. More precise localities given above.

DIAGNOSIS: Only surely established species of the genus. Measurements are given in tables 76 and 77.

Since most of the types of the supposed species here brought together are inadequate, not comparable, or both, comparisons are limited and of little value.

The types of the two "species" of "*Scabellia*" permit no useful measurements, but they are from animals of about the size of *A. unica* and morphologically connected by the association of P^4–M^1 in two of the speci-

TABLE 76

MEASUREMENTS OF UPPER TEETH OF *Albertogaudrya unica*

	P^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W
M.A.C.N. No. 12000[a]	—	—	—	—	29	37	—	—
M.A.C.N. No. 12004[b]	—	—	—	—	—	—	30.3	38.2
A.M.N.H. No. 289639	18.5	32.4	24.8	35.4	—	—	—	—
A.M.N.H. No. 28947	18.3	—	23.4	35.2	—	—	—	—

[a] Lectotype.

[b] Type of *A.* "*separata*."

TABLE 77

MEASUREMENTS OF LOWER TEETH OF *Albertogaudrya*

	P_2		P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W	L	W
A. unica												
M.A.C.N. No. 12001	16.3	12.5	19.9	15.4	20.6	15.9	22.0	16.4	25.5	19.0	35.1	18.7
M.A.C.N. No. 12014[a]	—	—	—	—	—	—	—	—	—	—	36.6	—
A.M.N.H. No. 28640	—	—	—	—	—	—	—	—	—	—	34.0	17.5
M.H.N. Tournouër No. 10	—	—	—	—	20.4	19.0	—	—	—	—	—	—
A. sp.												
M.A.C.N. No. 12002	—	—	17.3	13.3	20.1	15.3	22.1	15.7	—	—	—	—

[a] Type of *Albertogaudrya regia.*

mens in the American Museum of Natural History. The type of "*Scabellia cyclogona*" differs from that of "*S. laticincta*" by having a somewhat smaller, more conical hypocone, a metaconule slightly larger, also more conical, and more separate from the ectoloph. It is highly unlikely that these slight variations have taxonomic value.

The type of *A. regia* cannot be compared with any other type, but it is clearly a specimen of *Albertogaudrya* of about the same size as *A. unica.*

The lectotype upper molar of *A. tersa* has not been found in the collection. According to Ameghino, it was smaller than that of *A. unica* and was excavated medially on the buccal face of the ectoloph above a very strong basal cingulum. Perhaps this should have been listed separately as a *nomen vanum,* but if it was indeed a specimen of *Albertogaudrya* it was more likely than not *A. unica.* Ameghino's description dwelt extensively on the syntype canine and incisor, but the association of these is doubtful, and if either were taken as lectotype no comparisons at all with other types would be possible.

The type upper molar of *A. separata* is larger than that of *A. unica,* but the difference is insignificant. Other slight differences suggest strongly that *A.* "*separata*" is based on M^3 and *A. unica* on M^2 of the same species.

I do not detect any difference at all between the types of *A. oxygona* and *A. unica.* The supposed distinctions arose from the less worn state of the former type and from its poor restoration (Ameghino, 1904b, fig. 492).

Albertogaudrya sp.

M.A.C.N. No. 12002, part of a right lower jaw with P_3–M_1 and various other fragments, from "Colhué-Huapí Norte," was referred by Ameghino to *A. regia.* P_4 and M_1 are as in No. 12001 (referred to *A. unica*) except for being more lightly built, but P_3 is considerably smaller, has the trigonid more excavated anterointernally, and the paraconid crest curving around internally. The dimensions of the teeth are given in table 77.

?TRIGONOSTYLOPIDAE INCERTAE SEDIS

"Staurodon" supernus Roth, 1899, *nomen dubium*

Staurodon supernus ROTH, 1899, p. 387.

=*Pleurocoelodon cingulatus* [in error]: AMEGHINO, 1899, p. 12.

Trigonostylops supernus: SIMPSON, 1933e, p. 16; 1936d, p. 66.

TYPE: Roth's description was based on M_3 and a lower canine. The M_3 must be presumed to be more distinctive and is taken as lectotype, but it was not found in the collection. The only lot labeled with this name is M.L.P. No. 12-2223, which includes the probable syntype, a right lower canine, three broken teeth not of this genus (or *Trigonostylops*), and a wholly unidentifiable bone fragment.

HYPODIGM: None in hand.

HORIZON AND LOCALITY: Mustersan, "Lago Musters" (Cerro del Humo).

DIAGNOSIS: Uncertain. Roth stated that M_3 measures 20 by 12 mm., which would make it the largest known for *Trigonostylops* (or *Staurodon*).

In the absence of the lectotype or of a figure of it, the status of this supposed species is entirely dubious. The presumably syntype canine has the peculiar anteroexternal groove seen in *Trigonostylops gegenbauri* and may belong to that species, although somewhat larger than the type. Its maximum basal diameter is 11.5 mm.

"Trigonostylops" duplex Ameghino, 1901

(?) *Trigonostylops duplex* AMEGHINO, 1901, p. 394.

Scabellia duplex: AMEGHINO, 1904a, vol. 58, p. 228; 1904b, p. 379, fig. 496, but this figure probably is not of this species.

TYPE: M.A.C.N. No. 12010, broken, toothless mandibular symphysis.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayoran, Colhué-Huapí.

DIAGNOSIS: Considerably larger than any other known specimens of *Trigonostylops,* but smaller than any known specimens surely of *Albertogaudrya.*

The affinities of this fragment are uncertain. It might represent a valid species, but if so that is not now definable. The presence of P_1, given as a distinction by Ameghino, does not necessarily exclude it from *Trigo-*

nostylops. The upper teeth later referred to this species are probably anterior premolars of *Albertogaudrya*, and there is no evidence that they belong to *duplex*.

HEDRALOPHUS AMEGHINO, 1901, NOMEN DUBIUM

Hedralophus AMEGHINO, 1901, p. 406; 1906, p. 468.

TYPE: *Hedralophus bicostatus*.

DISTRIBUTION: Casamayoran, Patagonia.

DIAGNOSIS: None. Based on a mixture of two or more different genera (families, orders). As limited by type selection (below) may be a synonym of *Albertogaudrya*.

Hedralophus bicostatus Ameghino, 1901, *nomen dubium*

Plate 45, figure 1

Hedralophus bicostatus AMEGHINO, 1901, p. 406; 1904b, p. 141, fig. 172.

TYPE: M.A.C.N. No. 10938, isolated left P^3 or P^4, lectotype. M.A.C.N. No. 10535, right P_4; two broken tusks; two ungual phalanges. Ameghino's label with this lot is "*Hedralophus irregularis*," but as far as I can determine that name was never published.[1] The published description of *H. bicostatus* included lower premolars, almost certainly referring to the P_4 in this lot of specimens, which therefore is a syntype of that specific name. As noted below, it does not belong to the same species (or probably order) as the lectotype.

HYPODIGM: Lectotype only.

HORIZON AND LOCALITY: Casamayoran, Patagonia. No other data for lectotype. Syntype (not this genus or species) from Casamayoran "parte supérieure," Colhué-Huapí.

DIAGNOSIS: Uncertain. The lectotype P^3 or P^4 measures 20 by 32½ mm. Perhaps synonymous with some name under "*Scabellia*" = *Albertogaudrya*.

The lectotype differs from specimens of "*Scabellia*," that is, upper premolars of *Albertogaudrya*, only in having the hypocone a little more separate and an incipient metaloph visible. The specimen probably, but not surely, belongs to *Albertogaudrya*. The specific taxonomy of that genus is already chaotic, and the possible status in it of the present nominal species is altogether uncertain.

It was apparently the syntype P_4 that led Ameghino to compare this "genus" with *Leontinia* and refer it to the Leontiniidae. In fact the specimen is indistinguishable from P_4 of the isotemnid *Thomashuxleya rostrata*.

Genus and species indeterminate

Text figure 49

A.M.N.H. No. 28450 is an isolated left upper molar found by C. S. Williams in the Casamayoran at Cañadón Vaca. It resembles *Trigonostylops* but is distinctly outside the already considerable established range of variation for that genus or for *T. wortmani*. It probably represents a new taxon, but I do not want to add another name based on an inadequate type to this confused group.

In 24 measured upper molars referred to *T. wortmani*, the ratio of length to width has a range of 0.76 to 0.99 and a mean of 0.91. The present tooth measures 12.5 by 18.0 mm., ratio 0.69, different from *T. wortmani* with high significance. The tooth is more massive than that of *T. wortmani;* metaconule distinct, conical; cingula strong on all sides of lingual half of tooth; hypocone on cingulum posterolingual to protocone, conical, attached to protocone at base.

SHECENIA SIMPSON, 1935

Shecenia SIMPSON, 1935a, p. 19.

TYPE: *Shecenia ctirneru*.

DISTRIBUTION: Río Chico Formation, Cañadón Hondo, Chubut, Argentina.

DIAGNOSIS: Symphysis very long, fused, channeled above, lower surface plane transversely and gently curved longitudinally, meeting the lateral surfaces at a sharp angle. Median teeth small, followed by an also median, but more posterior, larger pair. Lateral to these two pairs of teeth is a greatly enlarged, long-rooted, strongly curved, procumbent pair. These are followed by a long, crested diastema, and then (at about the middle of the symphysis) by a somewhat smaller, short-rooted, semi-procumbent pair of teeth.

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[1] Its mention here in this way does not make it an available name under the Code.

FIG. 49. Trigonostylopoid *incertae sedis*, A.M.N.H. No. 28450, left upper molar, crown view. ×1.5.

This cannot be an animal represented by cheek teeth from the same level or locality, for the only cheek teeth of comparable size are fairly orthodox isotemnids.

The only genus with which comparison is possible is *Trigonostylops*. They agree in the long, fused symphysis, the presence of two pairs of small incisors enclosed by a pair of greatly enlarged, curving, procumbent teeth posterior to which is a diastema, and (in some species of *Trigonostylops*) the presence of a tooth in the middle of this diastema and (longitudinally) of the symphysis. A tentative suggestion of relationship is warranted. But the peculiar flattening of the lower surface of the symphysis in *Shecenia* is not seen in *Trigonostylops*, and the tooth ($P_{?1}$) in the diastema of *Shecenia* is large and semi-procumbent, but in *Trigonostylops*, if present at all, it is small and vertical. *Shecenia ctirneru* is much smaller than any known species of *Trigonostylops*.

Shecenia ctirneru Simpson, 1935

Text figure 50

Shecenia ctirneru SIMPSON, 1935a, p. 20, fig. 20.

TYPE: A.M.N.H. No. 28531, mandibular symphysis with various alveoli and roots or worn bases of one pair of teeth.

HYPODIGM: Type only.

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

DIAGNOSIS: Sole known species of genus. Width of flat lower surface of symphysis, 13.5 mm. Length of anterior diastema, 10 mm. Maximum diameter of bases of largest pair of teeth, 6.2 mm.

ORDER **PYROTHERIA** AMEGHINO, 1895

DEFINITION: South American Eogene ungulates or subungulates. One pair of lower and two pairs of upper incisors enlarged to form tusks, retaining enamel bands. Other incisors, canines, and first premolars small or absent. P^3–M^3 and P_4–M_3 developing into nearly square grinding teeth with two strong feebly cuspidate or denticulate transverse or slightly oblique lophs on each, arched forward on the upper teeth and backward on the lower, remaining brachydont and without cement. Rostrum and symphysis elongate and fused. Nares and nasals retreating. Cranium cancellous. Basicranium short, without inflated bullae, flexed upward relative to the palate. Neck short and skeletal habitus graviportal. Limbs short and stout, distal segments relatively shortened.

Few groups of animals are more striking and more mysterious than the pyrotheres. In spite of the fact that the skull, jaws, complete dentition, and most of the skeleton are now known in the terminal genus, *Pyrotherium* itself, no theory of relationship has really been well established. Discussion has been and must be based chiefly on *Pyrotherium*, beyond the scope of this memoir, and the definition above is based on that genus and does not necessarily apply precisely to other possible members of the order.

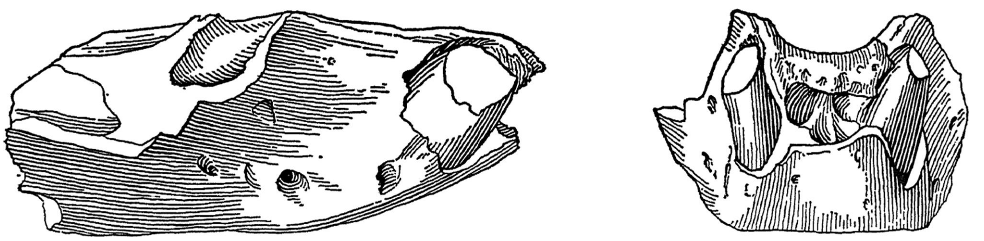

FIG. 50. *Shecenia ctirneru* Simpson, A.M.N.H. No. 28531, type, mandibular symphysis, right lateral and anterior views. ×2.

Most of our knowledge of the pyrotheres has so far been in old studies by Ameghino (especially 1902b), Gaudry (1909), and Loomis (1914). Ameghino believed them to be derived from condylarths and to be ancestral to the Proboscidea, to which order he referred them in his later works (e.g., 1906). Loomis agreed that they were proboscideans,[1] but considered them an aberrant side line not ancestral to any other proboscideans. Gaudry (1909, p. 28) concluded that: "En réalité, *Pyrotherium* est très different de tous les grands animaux décrits jusqu'à ce jour. Il ne rentre dans aucun ordre connu." Misled by a preliminary note by Loomis, Scott (1913) at first believed *Pyrotherium* to be a notoungulate. On acquiring better first-hand knowledge of the genus, he observed that pertinence to the Notoungulata (or Toxodonta) is impossible and adopted Gaudry's opinion that this "strangest of known mammals" belongs to no order but its own (Scott, 1937a). As far as I know, no one with any knowledge of the evidence has since questioned that conclusion. Scott also noted that the Pyrotheria presumably originated from some condylarth group but that the ancestry and connections are quite unknown.

Supposed genera that have been considered pyrotheres at one time or another include Riochican *Carodnia* and *Ctalecarodnia*, Casamayoran *Paulogervaisia* and *Carolozittelia*, Mustersan *Propyrotherium* and *Promoeritherium*, Deseadan *Rodiotherium*, *Parapyrotherium*, *Pyrotherium*, *Ricardowenia*, and *Archaeolophus*, and *Griphodon* of unknown age. *Carodnia* and *Ctalecarodnia* are synonyms now placed in a distinct order Xenungulata, treated on a page below of this work. *Paulogervaisia* is a condylarth, as previously discussed (Simpson, 1948, p. 105). *Carolozittelia* is *incertae sedis*, probably a pyrothere, but perhaps a xenungulate or neither (see below). *Promoeritherium* is also *incertae sedis*, perhaps a synonym of *Propyrotherium*. *Griphodon* is, again, *incertae sedis*, perhaps a pyrothere but possibly a xenungulate (as also mentioned below). The various supposed Deseadan forms are outside the scope of this study, but I may cite Bryan Patterson (personal communication) to the effect that only one valid genus and species is at present known from the Deseadan. Thus *Propyrotherium* is the only definitely valid pyrothere genus in the field of this present work.

FAMILY **PYROTHERIIDAE** AMEGHINO, 1895

DISTRIBUTION: Casamayoran to Deseadan, South America.

DEFINITION: With the characters of the order, of which this is the only family now recognized.

PROPYROTHERIUM AMEGHINO, 1901

Propyrotherium AMEGHINO, 1901, p. 387; 1902b, p. 27; 1906, p. 470. GAUDRY, 1909, p. 24. SCOTT, 1913, pp. 462, 487; 1937a, p. 544. SCHLOSSER, 1923, p. 601.

TYPE: *Propyrotherium saxeum.*

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: Upper cheek teeth (probably P^3–M^3) quadratic; lophs nearly straight, directly transverse, completely separated at labial (as well as lingual) ends. Lower cheek teeth (probably P_2–M_3) longer than wide; M_3 with heel or third lobe. Lophs and lophids with more distinct terminal cusps and fewer intermediate denticles than in *Pyrotherium.*

The Ameghino Collection contains four isolated specimens referred to this genus: two cheek teeth and two tusks (one a mere fragment). The only other specimens known to me are approximately 30 isolated teeth, mostly broken, in the American Museum of Natural History collection from the Mustersan of Cerro Talquino.[2] In spite of this relatively rich material, I have not found it possible to reconstruct the dentition, especially as most of the teeth are broken, upper and lower teeth apparently (as also in *Pyrotherium*) were more similar than in most mamals, and the specimens differ greatly in degree of wear and also in proportions. However, these specimens have provided the preceding diagnosis, more clearly differential than was

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[1] He later retracted this opinion in conversation, but as far as I know never published this change of view.

[2] These are part of the collection, mentioned several times on previous pages, that is, a mixture of Casamayoran, Mustersan, and Deseadan specimens from Sierra Cuadrada and Cerro Talquino. Although most of those specimens are of uncertain age and locality, the specimens of *Propyrotherium* are almost certainly Mustersan and from Cerro Talquino.

previously possible. The genus is sharply distinct from either Casamayoran *Carolozittelia* or Deseadan *Pyrotherium* but closer to the latter.

Propyrotherium saxeum Ameghino, 1901

Plate 45, figures 2–6

Propyrotherium saxeum Ameghino, 1901, p. 387; 1902b, p. 27, figs. 18–20; 1904b, p. 159, fig. 198; 1906, p. 330, fig. 156. Gaudry, 1909, p. 24, fig. 10.

Type: M.A.C.N. No. 10929, upper cheek tooth, probably left P^4 (lectotype); much worn lower cheek tooth, perhaps P_4 or M_1; lower tusk; and a fragment perhaps of an upper tusk. Specimens probably not associated.

Hypodigm: Essentially the lectotype. Some 30 specimens in the American Museum of Natural History are almost surely of this genus and quite likely of this species, but accurate specific identification is not possible at present.

Horizon and Locality: Mustersan, Patagonia. No other data for Ameghino's specimens. Cerro Talquino for doubtfully referred specimens in the American Museum of Natural History.

Diagnosis: Only species now definitely referred to the genus. Some measurements are given in table 78.

TABLE 78

Measurements of Teeth of *Propyrotherium*

	L	W
M.A.C.N. No. 10929, upper cheek tooth, lectotype of *P. saxeum*	29	30
M.A.C.N. 10929, lower cheek tooth, syntype (not lectotype) of *P. saxeum*	28	25
A.M.N.H. No. 29391, upper cheek tooth	20	28½
A.M.N.H. No. 29394, lower cheek tooth	35	29
A.M.N.H. No. 29392, last cheek tooth	42½	36
A.M.N.H. No. 29393, last cheek tooth	35½	30

As shown in table 78, two morphologically similar, apparently posterior teeth, probably M_3 but one or both conceivably M^3, differ so markedly in size that they are unlikely to belong to the same species if homologous.

PROMOERITHERIUM Ameghino, 1906, NOMEN DUBIUM

Promoeritherium Ameghino, 1906, pp. 333, 336, 470.[1]

Type: *Promoeritherium australe.*

Distribution: Mustersan, Patagonia.

Diagnosis: Doubtful. Perhaps synonymous with *Propyrotherium.*

Ameghino's entire description and discussion of this supposed genus were as follows: "*Promoeritherium* ([Ameghino, 1906] fig. 160), un peu plus grand que *Paulogervaisia* et d'une époque un peu plus récente, par l'intermédiaire de *Rodiotherium* du pyrothéreen [Deseadan] est sans doute l'ancêtre de *Moeritherium;* dans la denture, la ressemblance est si grande qu'elle fait croire à une identité générique." In fact only a single tooth, identified as P^2, was or is known, and this does not at all resemble any tooth of *Moeritherium* either in Andrews' figures (to which Ameghino doubtless referred) or in specimens known to me. "*Rodiotherium,*" a supposed genus of wholly unknown affinities, was based on a symphyseal fragment without teeth (never figured), with no basis for comparison with *Promoeritherium* and likewise apparently without any special resemblance to *Moeritherium.* The tooth called *Promoeritherium* does somewhat resemble P^2 of *Pyrotherium,* but is smaller, has two more cusps, and does not have quite the same arrangement of cusps. If it belongs to a pyrothere at all, it may be P^2 of *Propyrotherium.* It is not otherwise identifiable at present.

Promoeritherium australe Ameghino, 1906, *nomen dubium*

Plate 45, figure 9

Promoeritherium australe Ameghino, 1906, p. 333, fig. 160.

Type: M.A.C.N. No. 10903, isolated tooth. The box containing this specimen was labeled by Ameghino "Molares de Propyrotherium, Capas del Astraponotus, Colhuapi" and in

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[1] This work does not state that the genus or species is new, but the names were never published elsewhere. They were not accompanied by a diagnosis or description, but were accompanied by an illustration and are therefore available in nomenclature under the Code [Article 12; Article 16 (a) (vii)].

keeping with the plural it contains three teeth. One is that figured in Ameghino (1906, fig. 160) and unquestionably is the basis for *Promoeritherium*. The other two are the originals of Ameghino (1902b, fig. 27) where they are labeled as milk teeth of *Pyrotherium romeroi*, a Deseado species. Probably these were put in this box for comparison only. Nothing was found that might have been considered as more material of *Promoeritherium*.

Hypodigm: Type only.

Horizon and Locality: Mustersan, south of Lake Colhué-Huapí.

Diagnosis: Sole species referred to genus. Maximum diameter of type, 26½ mm.; minimum, 19½.

?PYROTHERIA incertae sedis

CAROLOZITTELIA Ameghino, 1901

Carolozittelia Ameghino, 1901, p. 388; 1902b, p. 26; 1906, pp. 467, 472. Loomis, 1914, p. 162. Schlosser, 1923, p. 601. Scott, 1913, pp. 462, 488; 1937a, p. 544.

Type: *Carolozittelia tapiroides*.

Distribution: Casamayoran, Patagonia. Ameghino also recorded the genus as from the Deseadan, but probably in error (see below).

Diagnosis: M_2^{2-3} bilophodont. M^{2-3} with strongly oblique, curving lophs; intermediate valley not fully open on external side; ends of lophs cuspidate; protocone and hypocone (lingual ends of lophs) completely separate on M^3 as well as M^2. M_{2-3} much longer than broad; narrower than upper molars. M_3 with strong, separate second lophid; distinct vestige of crista obliqua; smaller but well-developed third lobe.

This is an extremely rare genus. In the Ameghino Collection there are remains of probably three individuals, and no one else has reported any specimens. The known specimens definitely indicate the presence of a distinct genus, but do not suffice for its classification. Until recognition of the separate status of the Xenungulata (see below), the only definitely recognized old native South American mammals with simple transverse lophs (and lophids) on the cheek teeth were pyrotheres. Moreover, the known differences between *Carolozittelia* and *Pyrotherium* (involving only M_{2-3}^{2-3}) could all be interpreted as primitive characters of the earlier genus. It was therefore logical and even (by Ockam's razor) requisite for Ameghino to interpret *Carolozittelia* as an ancestral pyrothere, and until 1952 no one questioned that opinion. At that time, however, Paula Couto (1952b) pointed out (in somewhat different words) that M_2^2 of *Carolozittelia* resemble those of *Carodnia* more than those of *Pyrotherium*, and that *Carodnia* is definitely not a pyrothere. However, as Paula Couto also noted, M_3^3 of *Carolozittelia* are markedly different from those of *Carodnia*. It may be added that M_3^3 of *Carolozittelia* are much more like those of *Pyrotherium* than like those of *Carodnia*, although also different from those of *Pyrotherium*, M^3 in having the lophs more curved and oblique, M_3 in being much longer than wide and having a well-developed third lobe. In the latter, but not (as far as known) the former, respect, *Propyrotherium* is about intermediate between *Carolozittelia* and *Pyrotherium* and hence tends to link the two. It is, however, highly improbable that *Carolozittelia* is the direct ancestor of *Propyrotherium*, even if both are indeed pyrotheres. The difference between them is definitely greater than between most reasonably established ancestral-descendent Casamayoran and Mustersan genera (or species), and *Propyrotherium* is distinctly closer to Deseadan *Pyrotherium* than to Casamayoran *Carolozittelia*.

The affinities of *Carolozittelia* must remain uncertain until something is known of its antemolar dentition. It might be a xenungulate, but it still seems somewhat more probable that it is either a pyrothere or a representative of still another group of bilophodont ungulates. In any case, I think it probable that the Casamayoran ancestor of *Pyrotherium* is as yet unknown.

Carolozittelia tapiroides Ameghino, 1901

Plate 45, figures 10–13; plate 46, figures 1–4

Carolozittelia tapiroides Ameghino, 1901, p. 388; 1902b, p. 26, figs. 14–17; 1904b, p. 160, fig. 200; 1906, p. 329, fig. 155.

Type: M.A.C.N. No. 10666, fragment of right upper jaw with M^{2-3} and roots of M^1 (lectotype); fragment of left lower jaw with imperfect M_3 and roots of M_2; fragment of left lower jaw with one molar, probably M_2. Considered associated by Ameghino, but probably two individuals.

M.A.C.N. No. 10663, a caniniform tooth and five phalanges. Essentially syntypes, but doubtfully conspecific with M.A.C.N. No. 10666. Tooth and phalanges considered associated by Ameghino, but such an association is highly unreliable.

HYPODIGM: The lectotype, as above, and M.A.C.N. No. 10665 (see below).

HORIZON AND LOCALITY: Both the above lots of materials are from the Casamayoran, west of the Río Chico, Chubut, Argentina.

DIAGNOSIS: Conules distinct on little-worn M^2. This tooth in lectotype about 25 mm. in length and 23½ in width.

Ameghino was of the opinion that the three fragments now included under M.A.C.N. No. 10666 were of one individual, and his figure of the lower teeth (e.g., 1906, fig. 155c) shows M_{2-3} together as if they were associated, but such cannot be the case. This M_2 cannot be of the same individual as the M_3 because large parts of the roots are duplicated. It can hardly be M_1 of that individual because it does not make contact, which it should do in that case, some of the bone may be duplicated, and the tooth is not enough worn. Nor can it be P_4 from the shape of the jaw fragment. Improbable as it seems, this must belong to another individual and is probably M_2. The upper jaw may be of a third individual but is probably associated with one or the other of the lower fragments. As a precaution, I designate the upper jaw fragment as lectotype. The measurements of the teeth of M.A.C.N. No. 10666 are: M^2, length, *ca.* 25, width, *ca.* 23½; M^3, length, *ca.* 26, width, *ca.* 26; $M_{?2}$, length, 23.6, width, 18.3; M_3, 29.8, width, *ca.* 20.

Ameghino referred to the type species, and in fact included in his type description, a caniniform or tusklike tooth, with rather short, completely enameled crown, and long root. The identification is not impossible, but, as the specimen was isolated, there is no good evidence that it does belong here. The same is true of five phalanges placed with this tooth by Ameghino. Another interesting specimen, M.A.C.N. No. 10662, was referred but not published by Ameghino. It is a broken symphysis with an incisor just erupted and root fragments of others. There were two strongly procumbent pairs of incisors, the central pair somewhat larger, followed by a long diastema. These further specimens could belong to *Carolozittelia*, but that reference is so doubtful that it cannot now be considered as adding to knowledge of the genus.

All that is really known are M^{2-3}_{2-3} and the immediately adjacent parts of bones. The latter show that the zygoma arose opposite and perhaps also anterior to M^{1-2}, that the rim of the choanae extended forward to about the middle of M^3, and that the palatines extended forward along the alveolar border to the posterior end of M^1. The zygoma was thus more posterior and the choanae and palatines more anterior than in *Pyrotherium*. The palate was also relatively wider. The lower jaw was stout, and the coronoid arose posterior and external to M_3, much as in *Pyrotherium*. The essential characters of the known teeth are given above.

There is one undescribed specimen in the collection, M.A.C.N. No. 10665, fragments of right and left lower jaws, apparently of one individual, left with one root of M_2 and roots of M_3, right with poorly preserved crown of M_3, without data as to origin. M_3 is larger than in the figured specimen and longer relative to its width, with larger third lobe and cingulum passing almost completely around it, and the jaw is of equal depth but thicker. Some variation in the species, or diversity in the genus, is indicated. This M_3 measures about 34 mm. by 22.

Carolozittelia eluta Ameghino, 1901, *nomen dubium*

Carolozittelia eluta AMEGHINO, 1901, p. 388.

TYPE: M.A.C.N. No. 10973, isolated, imperfect M^1.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Said to be Deseadan from "Oeste de Río Chico cerca Chubut," but see below.

DIAGNOSIS: Uncertain. If this genus, probably a synonym of *C. tapiroides*.

This tooth resembles M^2 of *C. tapiroides*, but it is slightly smaller, and the lophs are slightly less oblique. Both characteristics might be expected in M^1 of the same species. It is, however, incredible that *Carolozittelia* should have survived from Casamayoran to Deseadan; no other genera in the two faunas are even closely similar or could be confused on the basis of single molar teeth. It is therefore probable either that *C. eluta* is Casamayoran, not Deseadan, and in that case a probable synonym of *C. tapiroides*, or that it is not *Carolozittelia* but decidedly *incertae sedis*. The former alternative seems more likely.

Order **XENUNGULATA** Paula Couto, 1952

Diagnosis: "Extinct, large, digitigrade South American primitive ungulates with relatively short and somewhat slender limbs, pentadactyl extremities, broad and flat ungual phalanges. Carpal bones alternating. Mandible strong, high, but relatively slender and short. Dentition complete. Incisors strong, chisel-shaped. Canines strong and sharp pointed. Cheek teeth brachydont. Upper and lower first and second premolars simple, compressed laterally, with a main mesial cusp. Upper third and fourth premolars with V-shaped protocone and strong meso-external paracone. Upper molars bilophodont, but the third one with protoloph and metaloph converging inwardly, and low, basal hypocone. Last lower premolar somewhat molariform, with low and short talonid, slightly crested. First and second lower molars bilophodont; third molar with strong protolophid and more or less isolated hypoconid and entoconid, followed by strong hypoconulid" (Paula Couto, 1952b, p. 370).

The genus *Carodnia* (with its synonym *Ctalecarodnia*) was originally based on a few isolated and, in part, broken teeth, somewhat comparable to those of pyrotheres but unique in detail and of uncertain affinities. Later discoveries at Itaborai in Brazil included the whole dentition and much of the skull, jaws, and skeleton. As described and discussed by Paula Couto (1952b), these specimens show that except for bilophodont M^{1-2}_{1-2} *Carodnia* is quite unlike the Pyrotheria and cannot possibly be referred to that order. Closest resemblance is to the Holarctic Dinocerata, but a common ancestor could hardly have been more advanced than a rather primitive condylarth. The resemblance suggests more or less parallel evolution of stocks with similar evolutionary potentials rather than a common ancestry with homologous specializations. Paula Couto therefore placed the genus in a separate order of ungulates, and his arrangement is accepted here. Repetition of his diagnosis, descriptions, and discussion is unnecessary.

Family **CARODNIIDAE** Paula Couto, 1952

Diagnosis: Only recognized family of the order as defined above.

The possibility that *Carolozittelia* is a xenungulate was mentioned by Paula Couto and is referred to on preceding pages of the present monograph. If that should prove to be correct, it would be necessary either to recognize two families of xenungulates or to give the single family the prior name Carolozitteliidae Ameghino, 1901. That conclusion is, however, uncertain and improbable.

There is a further possibility that the enigmatic genus *Griphodon* Anthony, 1924, belongs to this order and, if so, probably also to this family. It was based on a jaw fragment with dm_4 and P_3–M_1 from beds of unknown age on the Río Huallaga in Peru. It is certainly not a perissodactyl as Anthony thought, and later students have agreed that it is probably a pyrothere. (The definitive review and description are by Patterson, 1942.) However, that view (as well as similar opinions about *Carolozittelia* and *Carodnia*) was influenced or induced by the belief that pyrotheres were the only strictly bilophodont native ungulates in South America. Now it is certain that *Carodnia* is not a pyrothere, and it is seen that P_4–M_1 of *Griphodon* are more like those of *Carodnia* than of any certainly classified pyrothere. M_1 is virtually identical in structure in the two genera, and P_4 differs essentially only in that the second lophid is somewhat better developed in *Griphodon*. P_3 of *Griphodon* is decidedly unlike that of any certainly classified pyrothere and differs rather less, although still distinctly, from P_3 of *Carodnia*, a somewhat simpler, more bulbous tooth.

CARODNIA Simpson, 1935

Carodnia Simpson, 1935a, p. 20.
Ctalecarodnia Simpson, 1935a, p. 22.

Type: *Carodnia feruglioi.*

Type of Synonym: *Ctalecarodnia cabrerai.*

Distribution: Riochican, South America (Río Chico formation, Argentina, and Itaborai formation, Brazil).

Diagnosis: Only known genus surely referable to the order as defined above. Differs from known parts of *Carolozittelia* most notably in structure of M$^3_3$ as summarized in the ordinal definition, and from known parts of *Griphodon* in simpler P$_3$ and less molariform P$_4$.

Carodnia was based on M$_3$ and *Ctalecarodnia* on incomplete P$_4$ and M$_1$. Direct comparison was impossible, and indirect comparisons suggested that *Carodnia feruglioi* was a much larger animal than "*Ctalecarodnia cabrerai*" and had a different molar structure. Discovery of complete lower dentitions of *Carodnia vieirai* showed, however, that just these incongruities of size and structure characterize this peculiar genus. As first reviser, Paula Couto (1952b) gave priority to *Carodnia.*

Carodnia feruglioi Simpson, 1935

Text figures 51–53

Carodnia feruglioi Simpson, 1935a, p. 22, fig. 21.
Ctalecarodnia cabrerai Simpson, 1935a, p. 24, fig. 22.

Type: In the University of Padua, Italy (cast, A.M.N.H. No. 27886), isolated left M$_3$.

Type of *Ctalecarodnia cabrerai:* In the University of Padua, Italy; casts, A.M.N.H. No. 27897. Probably associated left P$_4$, slightly broken; talonid of left M$_1$; talonid and posterior part of trigonid of right M$_1$.

Hypodigm: The types only.

Horizon and Locality: Riochican, Patagonia. Lower beds of the Río Chico formation in the Bajo de la Palangana, Chubut, Argentina (see Simpson, 1935b).

Diagnosis: Much smaller than *C. vieirai.* Comparative measurements are given in table 79.

Paulo Couto (1952b) suggested that my two supposed species, shown by him to be congeneric, might be synonymous but considered that "the difference in size between the type lower teeth . . . is so great that it is possible that they belong in two different species, as I have left them, or at least that the specimens are from two or more individuals of a single species (*C. feruglioi*), but of different ages." The difference in size cannot be due to different ages of the individual animals, since brachydont teeth do not grow after eruption, and the given dimensions of these teeth have not been reduced by wear. There is no difference in geological age, the specimens being from the same horizon and locality. As can be seen in table 79, the discrepancy in measurable dimensions of the types of *C. feruglioi* and *C. "cabrerai"* is distinctly *less* than in single individuals of *C. vieirai.* My two supposed species are certainly synonymous. Because Paula Couto did not flatly state that the two names are synonymous, his preference for the name *C. feruglioi* does not establish priority under the current Code. As technically the first reviser, I hereby assign priority to that name.

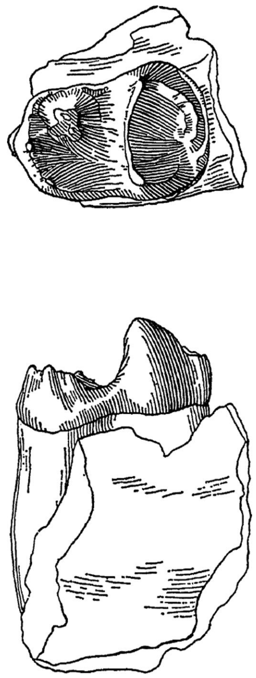

Fig. 51. *Carodnia feruglioi* Simpson, Feruglio Collection, University of Padua, type, left M$_3$, crown and lingual views. ×1.

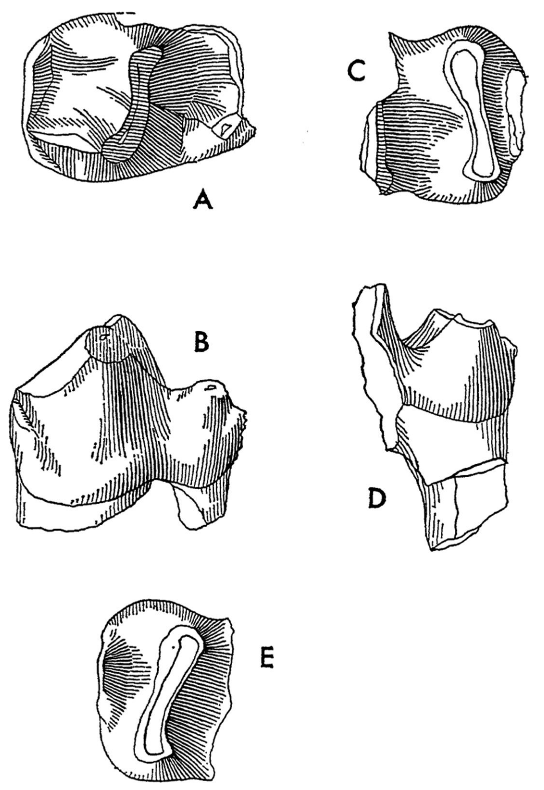

FIG. 52. *Carodnia feruglioi* Simpson, Feruglio Collection, University of Padua, type of *Ctalecarodnia cabrerai* (= *Carodnia feruglioi*), probably associated broken lower cheek teeth. A, B. Left P_4. A. Crown view. B. Buccal view. C, D. Posterior part of right M_1. C. Crown view. D. Lingual view. E. Posterior part of left M_1, crown view. All ×2.

MAMMALIA INCERTAE SEDIS

Some of the names here considered may, or even in one or two cases clearly do, represent valid taxa, but most of them will probably prove either to be synonyms of better-defined names or permanently unrecognizable. They have in common the fact that I am at present unable to classify them even as to order. Some are probably notoungulates and might have been listed in the previous section, Notoungulata *incertae sedis*. (It is also possible that some of the names there given should be here.)

FLORENTINOAMEGHINIA SIMPSON, 1932

Florentinoameghinia SIMPSON, 1932c, p. 18.

TYPE: *Florentinoameghinia mystica.*

DISTRIBUTION: Casamayoran, Patagonia.

DIAGNOSIS: Upper molariform teeth with subequal, well-separated paracone and metacone. Protocone and hypocone about equal; partly connate on more anterior but well separate on more posterior tooth. Protoconule and metaconule almost as large as protocone and hypocone and tending to form incipient lophs with the latter and the paracone and metacone. Metaconule partly connate with hypocone and not at all with protocone. No mesostyle. Anterior and posterior but no lingual cingula. No true ectoloph, crista, or crochet.

No other teeth remotely like these have been described from South America, and there can hardly be a doubt that the genus is valid as diagnosed. By the same token, however, it cannot now be assigned to any known supergeneric taxon up to the subclass level. A dagger-like tooth, possibly reptilian but possibly a mammalian canine, was buried next to the unique type specimen and may belong to this genus, but that is quite uncertain. The possible association and the characteristics of the various fragments are more fully discussed in the original publication.

Florentinoameghinia mystica Simpson, 1932

Text figure 54

Florentinoameghinia mystica SIMPSON, 1932c, p. 18, fig. 7.

TYPE: A.M.N.H. No. 28402, three somewhat imperfect upper cheek teeth and skull fragments, all of one individual.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayoran, Cañadón Vaca, Patagonia.

DIAGNOSIS: Only known species of the genus. ?M^1 measuring 10 by 10 mm.

ANAGONIA AMEGHINO, 1904, NOMEN DUBIUM

Anagonia AMEGHINO, 1904a, vol. 58, p. 185; 1906, p. 467.

TYPE: *Anagonia insulata.*

DISTRIBUTION: Casamayoran, Patagonia.

DIAGNOSIS: Uncertain.

The type species is based on a broken lower premolar with an elevated trigonid, moderrately oblique metalophid, simple metaconid,

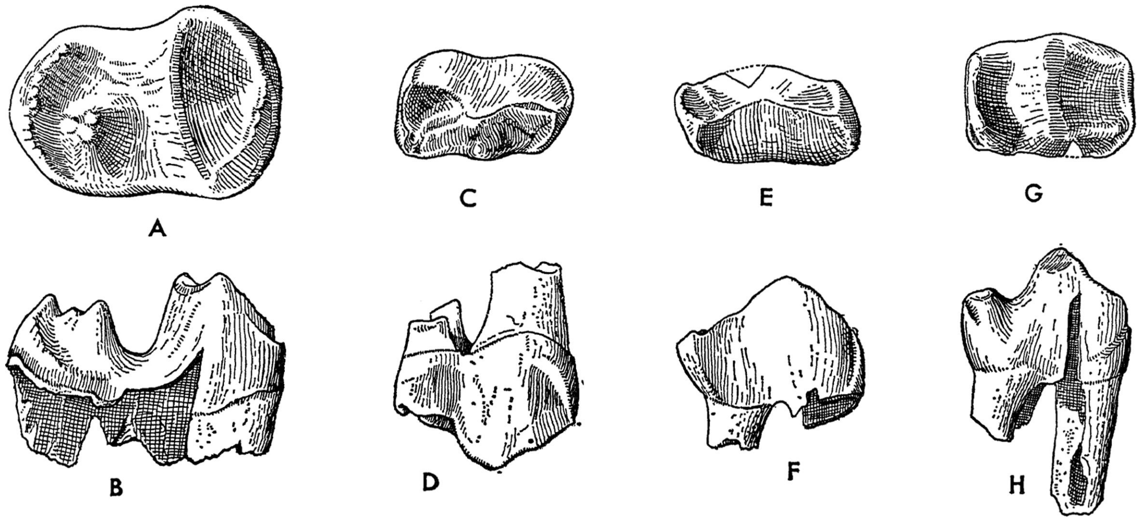

FIG. 53. *Carodnia feruglioi* Simpson, various isolated teeth in the Museo de La Plata, not numbered. A, B. Right M_3. A. Crown view. B. Buccal view. C, D. Left P_3 (incorrectly identified by Cabrera as right P^2). C. Crown view. D. Buccal view (upside down). E, F. Right P_2. E. Crown view. F. Buccal view. After Cabrera. All ×1.5.

and simple talonid crescent incorporating the entoconid. These characters exclude some known taxa, but do not positively diagnose one.

Anagonia insulata Ameghino, 1904

Plate 46, figure 8

Anagonia insulata AMEGHINO, 1904a, vol. 58, p. 185; 1906, p. 327, fig. 151 [in error].

TYPE: M.A.C.N. No. 10635, broken, isolated left lower premolar, perhaps P_4.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Casamayoran, Patagonia. No other data.

DIAGNOSIS: Essentially none. Talonid of type, about 13 mm. in width.

Although the type is essentially indeterminate, it does suffice to show that the specimen figured as of this species (Ameghino, 1906, fig. 151) cannot be either conspecific or congeneric. The figured specimen, not found in the collection, was apparently an otherwise unidentified isotemnid notoungulate.

TABLE 79

MEASUREMENTS OF LOWER TEETH OF *Carodnia*

	P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W
C. feruglioi								
A.M.N.H. No. 27886[a]	—	—	—	—	—	—	24.3	17.5
A.M.N.H. No. 27897[b]	—	*ca.* 12.2	—	11.4	—	—	—	—
C. vieirai								
Type[c]	19.5	17.8	22.4	19.2	28.8	27.2	34	30.5
Referred[c]	22.2	18	25	20.2	33.5	28.2	39	32.5

[a] Cast of the type of *C. feruglioi;* measurements were made on the original specimen in the University of Padua, Italy.

[b] Cast of the type of "*C. cabrerai*"; measurements were made on the original specimen in the University of Padua, Italy.

[c] Measurements from Paula Couto (1952b, table 7).

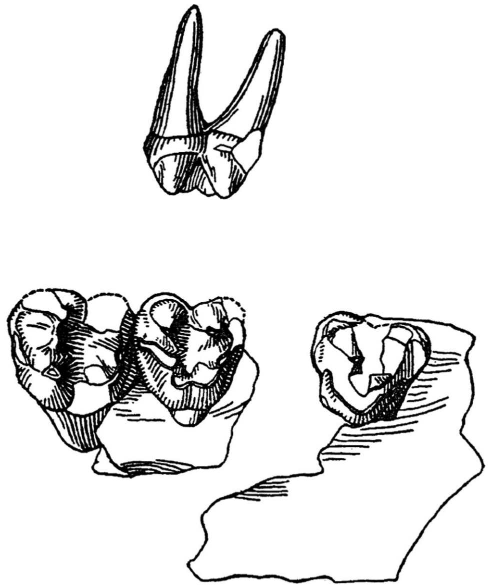

FIG. 54. *Florentinoameghinia mystica* Simpson, A.M.N.H. No. 28402, type, fragments of right maxilla with three broken cheek teeth, crown view and buccal view of the most complete teeth. ×1.5.

ANISORHIZUS Ameghino, 1902

Anisorhizus Ameghino, 1902a, p. 27.
Anissorhizus [lapsus?]: Ameghino, 1906, p. 468.

Type: *Anisorhizus atriarius.*

Distribution: Casamayoran, Patagonia.

Diagnosis: Based on a tooth pointed at both ends, with two infolds or valleys on one side, one on the other, and two fossettes at the blunter end.

This taxon should prove identifiable if a homologous tooth is found associated with others. No other tooth at all like this is known to me. Ameghino's reference of it to the Isotemnidae is almost certainly wrong.

Anisorhizus atriarius Ameghino, 1902

Plate 46, figure 9

Anisorhizus atriarius Ameghino, 1902a, p. 27.

Type: M.A.C.N. No. 10620, an isolated cheek tooth of undetermined position.

Hypodigm: Type only.

Horizon and Locality: Casamayoran ("partie supérieure"), Patagonia. No other data.

Diagnosis: Only species of the genus. Type measuring about 10 by 8½ mm.

DIPLODONOPS Ameghino, 1902, nomen vanum

Diplodon Roth, 1902, p. 252, *nec* Spix, 1827.
Diplodonops Ameghino, 1902a, p. 28 [to replace *Diplodon*, preoccupied]. Simpson, 1936d, p. 93.

Type: *Diplodon ampliatus.*

Distribution: Probably Mustersan, Patagonia.

Diagnosis: None.

The only known specimen was never figured and has not been located in the Roth Collection, and Roth's description is far from diagnostic.

Diplodonops ampliatus (Roth, 1902), *nomen vanum*

Diplodon ampliatus Roth, 1902, p. 252.
Diplodonops ampliatus: Ameghino, 1902a, p. 28.

Type: An isolated tooth, not found in the collection.

Hypodigm: None in hand.

Horizon and Locality: Probably Mustersan; no data.

Diagnosis: None.

EUTROCHODON Roth, 1904

Eutrochodon Roth, 1904, p. 157. Simpson, 1936d, p. 93,

Type: *Eutrochodon inceptus.*

Distribution: Mustersan, Patagonia.

Diagnosis: Based on a tooth with root and crown both slightly curved but otherwise nearly perfect, subequal cones.

This tooth is absolutely unique to the best of my knowledge, and, as Roth also wisely concluded, nothing can be said as to its homology or affinities. It is doubtless a vertebrate, but otherwise unclassifiable until someone finds a jaw with a similar tooth and other teeth in it.

Eutrochodon inceptus Roth, 1904

Eutrochodon inceptus Roth, 1904, p. 157.
Eutrochodon inaeptus [misprint]: Simpson, 1936d, p. 93.

Type: An isolated tooth in the Museo de La Plata.

Hypodigm: Type only.

HORIZON AND LOCALITY: Mustersan, Roth's "Lago Musters" locality.

DIAGNOSIS: Only species referred to the genus. Maximum diameter of type (at junction of crown and root cones), 22.6 mm.

HETEROLOPHODON ROTH, 1904

Heterolophodon ROTH, 1904, p. 147; 1927, p. 236. SIMPSON, 1936d, p. 89.

TYPE: *Heterolophodon ampliatus.*

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: Upper molar longer than wide; buccal face almost flat, only slightly undulant; protoloph and protocone enormous, sharply separated from hypocone or metaloph.

The tooth on which this genus was based is unusual and probably does not belong to any otherwise named taxon in which upper molars are known. It may therefore prove to represent a valid genus, but one of undetermined affinities. Roth referred other upper teeth to the genus, but probably in error. He also mentioned but did not describe a lower jaw with imperfect teeth, but this was not found in the collection, and its relevance is dubious at best. Figure 12 on plate 5 in Roth (1927) is labeled as of this genus, but in error. The specimen there shown has nothing to do with *Heterolophodon* and is, furthermore, from a different horizon and locality.

Heterolophodon ampliatus Roth, 1904

Plate 46, figure 6

Heterolophodon ampliatus ROTH, 1904, p. 147. SIMPSON, 1936d, pp. 67, 89.

TYPE: M.L.P. No. 12-2194, isolated upper molar.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Mustersan, Patagonia. Roth's "Lago Musters."

DIAGNOSIS: Only species referred to the genus as defined above. Upper molar measuring about 40 mm. in length by 36 in width.

"Isolophodon" aplanatus Roth, 1904, *nomen vanum*

Isolophodon aplanatus ROTH, 1904, p. 144.

"Isolophodon" aplanatus: SIMPSON, 1936d, p. 90.

TYPE: M.L.P. No. 12-2193, isolated broken left lower molar.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Mustersan, Patagonia. Roth's "Lago Musters."

DIAGNOSIS: Indeterminate.

The type tooth does not belong to *Isolophodon*, an archaeohyracid of uncertain but probably Deseadan age.

LAMBDACONUS AMEGHINO, 1897, NOMEN VANUM

Lambdaconus AMEGHINO, 1897a, p. 439; 1906, pp. 467, 470, 471. SCOTT, 1913, p. 489; 1937a, p. 490. SCHLOSSER, 1923, p. 525. SIMPSON, 1948, p. 104.

TYPE: *Lambdaconus suinus.*

DISTRIBUTION: Probably Casamayoran,[1] Patagonia. (Also reported, probably in error, from Mustersan and Deseadan.)

DIAGNOSIS: Indeterminate.

The unfortunate history of this name was discussed in Part 1 of this monograph (Simpson, 1948, p. 106). The type of the type species is essentially indeterminate but does suffice to show that it cannot belong to the same genus or family as subsequently referred specimens. It was the latter, under the names *"Lambdaconus inusta"* and *"Lambdaconus mamma,"* and not the real type, on which Ameghino's subsequent understanding of the supposed genus and that of others following him were based. Those later referred specimens belong to the condylarth genus *Paulogervaisia; Lambdaconus suinus* does not.

Lambdaconus suinus Ameghino, 1897, *nomen vanum*

Lambdaconus suinus AMEGHINO, 1897a, p. 439, fig. 23; 1898, p. 160.

TYPE: M.A.C.N. No. 10718, fragment of

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[1] In Ameghino's great pioneering paper of 1897 the faunas we now call Casamayoran, Mustersan, and Deseadan had not yet been sorted out. They were thereafter well differentiated (on Carlos Ameghino's field work), and the full generic faunal lists of 1906 have remarkably few errors as to age. However, then-indicated Casamayoran *"Lambdaconus"* was in fact *Paulogervaisia,* and listing of *Lambdaconus* also in the Mustersan and Deseadan, for which no other basis is known, might even indicate that the specimen of 1897 was later considered post-Casamayoran. Since true *Lambdaconus* seems at present to be indeterminate, the question is not of prime importance.

lower jaw with one tooth, labeled as P_4 in Ameghino's figure, called M_1 in his text, probably M_2; badly preserved, most of enamel broken off.

Hypodigm: Type only.

Horizon and Locality: Probably Casamayoran, Patagonia. No other data.

Diagnosis: Indeterminate.

PACHYPITHECUS Ameghino, 1897, nomen dubium

Pachypithecus Ameghino, 1897a, p. 423; 1906, p. 466.

Type: *Pachypithecus macrognathus.*

Distribution: Casamayoran, Patagonia.

Diagnosis: Probably synonymous with some name based on tooth crowns. Antemolar teeth in continuous series except for short diastema after ?C; lower C relatively small.

This supposed genus was based on alveoli and roots (no crowns) of lower incisors, canine, and premolars. The arrangement and relative sizes of these alveoli and roots are not exactly as in any species in which the whole anterior dentition is known, but there are many possible synonyms in which it is not known. There is no real basis for reference to the Archaeopithecidae.

Pachypithecus macrognathus Ameghino, 1897, *nomen dubium*

Plate 46, figure 10

Pachypithecus macrognathus Ameghino, 1897a, p. 423; 1898, p. 150.

Type: M.A.C.N. No. 10817, fragment of anterior part of left ramus of mandible, without tooth crowns.

Hypodigm: Type only.

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

Diagnosis: Uncertain.

PICUNIA Roth, 1902, nomen vanum

Picunia Roth, 1902, p. 254. Simpson, 1936d, p. 93.

Type: *Picunia nitida.*

Distribution: Mustersan, Patagonia.

Diagnosis: Possibly synonymous with *Rhyphodon* but essentially indeterminate on present evidence.

Roth said that this supposed genus is intermediate between *Pehuenia* and *Rhyphodon.* Since those names are synonymous, *Picunia* would presumably be another synonym for the same genus if Roth was right. However, the now actually available data (consisting only of Roth's brief and not characteristic description) do not warrant any definite placing of *Picunia.*

Picunia nitida Roth, 1902, *nomen vanum*

Picunia nitida Roth, 1902, p. 254.

Type: Probably an isolated upper molar; not fond in collection.

Hypodigm: None in hand.

Horizon and Locality: Probably Mustersan. No other data.

Diagnosis: Uncertain.

PROPLANODUS Ameghino, 1902, nomen dubium

Proplanodus Ameghino, 1902a, p. 22; 1906, p. 467. Schlosser, 1923, p. 619.

Type: *Proplanodus adnepos.*

Distribution: Casamayoran, Patagonia.

Diagnosis: Indeterminate.

This supposed genus was based on virtually nondescript and entirely non-diagnostic incisors. They were at first (1902) referred to the Astrapotheriidae and later (1906) to the Lophiodontidae. I see no basis for either reference.

Proplanodus adnepos Ameghino, 1902, *nomen dubium*

Proplanodus adnepos Ameghino, 1902a, p. 22.

Type: M.A.C.N. No. 12015, four incomplete, one-rooted, simple-crowned teeth, presumably incisors, probably not associated.

Hypodigm: Type only.

Horizon and Locality: Casamayoran, Colhué-Huapí.

Diagnosis: None.

Ameghino also referred to this species but did not describe M.A.C.N. No. 12014, fragments of two upper molars and of a tusk. It is not likely that these belong to a single species, or that any belong to *P. adnepos.*

PROSTYLOPHORUS Roth, 1902, nomen dubium

Prostylophorus Roth, 1902, p. 252. Simpson, 1936d, p. 88.

Type: *Prostylophorus margeriei.*

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: Essentially indeterminate; based on a bilobate incisor.

As noted by Roth, the incisor that is alone known of this "genus" is like that of "*Stylophorus*" (*Distylophorus*) but has a lower crown. This tooth probably belongs to some genus known from cheek teeth.

Prostylophorus margeriei Roth, 1902

Plate 46, figure 11

Prostylophorus margeriei Roth, 1902, p. 252.

Prostylophorus margariei [misprint]: SIMPSON, 1936d, p. 88.

TYPE: M.L.P. No. 12-2211, isolated incisor.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Mustersan, Patagonia. Roth's "Lago Musters."

DIAGNOSIS: Bilobate incisors of unknown affinities.

"Stenogenium" aenigmaticum Ameghino, 1901

Plate 46, figure 5

Stenogenium aenigmaticum AMEGHINO, 1901, p. 407.

TYPE: M.A.C.N. No. 10899, symphysis without teeth.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Mustersan, Patagonia. No other data.

DIAGNOSIS: Symphysis very long; two pairs of small anterior teeth followed immediately by a pair of much larger teeth, then by a long diastema.

This species will be recognizable and perhaps valid if a specimen including symphysis and cheek teeth is found. The known specimen is somewhat suggestive of the Trigonostylopoidea, but it is not *Trigonostylops* (or *Staurodon*). It certainly does not belong to the genus *Stenogenium*, and Ameghino's reference of it to the Leontiniidae, a family characterized by *lack* of the only characteristic features of this specimen, is one of his most baffling eccentricities.

TRILOBODON ROTH, 1902

Trilobodon ROTH, 1902, p. 253; 1927, pp. 191, 209. SIMPSON, 1936d, p. 89.

TYPE: *Trilobodon brancoi.*

DISTRIBUTION: Mustersan, Patagonia.

DIAGNOSIS: Trilobate incisors of unknown affinities.

These incisors are highly unusual and remarkably attractive. In appearance each resembles three plump little fingers, slightly bent and pressed together. They probably belong to some genus known from cheek teeth, but the association is unknown, and the incisors in themselves are unclassifiable.

Trilobodon brancoi Roth, 1902

Plate 46, figure 7

Trilobodon Brancoi ROTH, 1902, p. 253; 1927, pl. 3, fig. 13.

Trilobodon brancoi: SIMPSON, 1936d, p. 69.

TYPE: M.L.P. No. 12-1465, isolated incisor.

HYPODIGM: Type and A.M.N.H. No. 29431, isolated incisor.

HORIZON AND LOCALITY: Mustersan, Patagonia. Roth's "Lago Musters" and our Cerro del Humo.

DIAGNOSIS: As for the genus.

FAUNAL LISTS

The following lists are substantive and not exhaustive. They include all names of taxa (species and higher) for which there is positive evidence of biological validity. They exclude not only names here considered synonyms but also those of supposed taxa here considered of strongly questionable or unknown validity. Riochican taxa entered by the symbol "I" are from Itaborai as treated by Paula Couto (1950, 1952a, 1952b, 1952c, 1952d, 1954, 1958, 1961, 1962) and not elsewhere included in the present work. The others are from Patagonia and are included in Part 1 (Simpson, 1948) or Part 2 of this study.

The columns are as follows:

1. Riochican
2. Casamayoran
3. Mustersan

MARSUPIALIA

	1	2	3
Didelphoidea			
Didelphidae			
Eobrasilia coutoi	I		
Ischyrodidelphis castellanosi	I		
Protodidelphis vanzolinii	I		
Didelphopsis cabrerai	I		
Mirandatherium alipioi	I		
Derorhynchus singularis	I		
Guggenheimia brasiliensis	I		
Schaefferia fluminensis	I		
Gaylordia macrocynodonta	I		
Monodelphopsis travassosi	I		
Marmosopsis juradoi	I		
Xenodelphis doelloi	I		
Minusculodelphis minimus	I		
Coona pattersoni		x	
?Coona gaudryi		x	
Caroloameghiniidae			
Caroloameghinia mater		x	
C. tenuis		x	
Borhyaenidae			
Arminiheringia auceta		x	
A. cultrata		x	
Patene coluapiensis		x	
P. simpsoni	I		
Procladosictis anomala		x	
Argyrolestes peralestinus		x	
?Pharsophorus cretaceus			x
Caenolestoidea			
Polydolopidae			
Epidolops ameghinoi	I		
E. gracilis	I		
Seumadia yapa	x		
Polydolops thomasi		x	
P. serra		x	
P. clavulus		x	
P. princeps		x	
P. primulus		x	
P. bocurhor		x	
P. rothi	x		
P. winecage	x		
?P. kamektsen	x		
Amphidolops serrula		x	
Eudolops tetragonus		x	
E. acuminatus		x	
E. caroliameghinoi		x	
?Marsupialia *incertae sedis*			
Gashternia ctalehor	x		

EDENTATA

	1	2	3
?Megalonychidae			
Proplatyarthrus longipes			x
Dasypodidae			
Machlydotherium asperum			x
M. ater			x
?Meteutatus attonsus			x
?M. percarinatus		?	
Utaetus buccatus		x	
U. lenis		x	
U. deustus		x	
?U. laevus		x	
"Pseudostegotherium" chubutanum[1]		x	
Coelutaetus cribellatus		x	
Astegotherium dichotomum		x	
Prostegotherium notostylopianum		x	
Pseudeutatus clypeus			x
P. depictus			x
P. circundatus			x
P. cuneiformis			x
Dasypodidae *incertae sedis*	x		
Glyptodontidae			
"Glyptatelus" fractus		x	
"Palaeopeltis" tesseratus		x	

CONDYLARTHRA

	1	2	3
Didolodontidae			
Lamegoia conodonta	I		
Didolodus multicuspis		x	
D. latigonus		x	
D. minor		x	
Argyrolambda conidens		x	

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[1] A generic name in quotation marks indicates the opinion that the named species does not belong to the named genus but is of unestablished generic pertinence. A question mark before a generic name indicates possible but doubtful pertinence of the named species to the named genus.

	1	2	3
Paulogervaisia inusta		x	
P. porca		x	
Proectocion argentinus		x	
P. precisus		x	
Enneoconus parvidens		x	
Asmithwoodwardia subtrigona		x	
A. scotti	I		
Ernestokokenia nitida		x	
E. patagonica		x	
E. yirunhor	x		
E. protocenica	I		
E. parayirunhor	I		
E. chaishoer	x		
LITOPTERNA			
Macraucheniidae			
Victorlemoinea labyrinthica		x	
V. emarginata		x	
V. prototypica	I		
?V. sp.	x		
Ernestohaeckelia aculeata		x	
E. acutidens		x	
Proterotheriidae			
Wainka tshotshe	x		
Josepholeidya adunca		x	
J. sp.	x		
Ricardolydekkeria praerupta		x	
?R. sp.	x		
Guilielmofloweria plicata		x	
Anisolambda fissidens		x	
A. amel		x	
A. prodromus	I		
Polymorphis lechei			x
P. alius			x
Polyacrodon ligatus			x
Xesmodon langi			x
?X. prolixus			x
Heteroglyphis dewoletzky			x
NOTOUNGULATA			
Henricosborniidae			
Henricosbornia lophodonta		x	
H. ampla		x	
H. waitehor	x		
H. minuta	x		
Othnielmarshia lacunifera		x	
?O. sp.	x		
Peripantostylops minutus		x	
?P. orehor	x		
Notostylopidae			
Notostylops murinus		x	
N. pendens		x	
N. appressus		x	
N. pigafettai		x	
Homalostylops parvus		x	
?H. atavus	I		
Edvardotrouessartia sola		x	
Otronia muhlbergi			x

	1	2	3
?Notostylopidae *incertae sedis*			
Seudenius cteronc	x		
Oldfieldthomasiidae			
Kibenikhoria get	x		
Colbertia magellanica	I		
Maxschlosseria praeterita		x	
M. minima		x	
M. rusticula		x	
M. consumata		x	
Oldfieldthomasia debilitata		x	
O. parvidens		x	
Ultrapithecus rutilans		x	
Tsmanichoria cabrerai			x
Acoelodus oppositus		x	
"Acoelodus" proclivus		x	
Paginula parca		x	
Archaeopithecidae			
Archaeopithecus rogeri		x	
Acropithecus rigidus		x	
Interatheriidae			
Notopithecus adapinus		x	
?N. amplidens		x	
?N. sp.	x		?
Antepithecus brachystephanus		x	
Transpithecus obtentus		x	
?T. sp.	x		
Guilielmoscottia plicifera			x
Archaeohyracidae			
Eohyrax rusticus		x	
E. praerusticus		x	
?E. platyodus			?
Pseudhyrax eutrachytheroides			x
P. strangulatus			x
Bryanpattersonia nesodontoides			x
B. sulcidens			x
?Archaeohyracidae *incertae sedis*			
Eohegetotherium priscum			x
Isotemnidae			
Pleurostylodon modicus		x	
P. similis		x	
P. complanatus		x	
?P. recticrista		x	
Anisotemnus distentus		x	
Acoelohyrax coronatus		x	
A. complicatissimus		x	
?A. coalitus			x
?A. coarctatus			x
Isotemnus primitivus		x	
I. latidens		x	
I. haugi	x		
?I. ctalego	x		
Thomashuxleya rostrata		x	
T. externa		x	
Periphragnis harmeri			x
?P. circunflexus			x
Rhyphodon lankesteri			x
Distylophorus alouatinus			x
Notohippidae			

	1	2	3
Eomorphippus obscurus			x
Interhippus deflexus			?
ASTRAPOTHERIA			
Astrapotheriidae			
Scaglia kraglievichorum		x	
Astraponotus assymmetrus			x
TRIGONOSTYLOPOIDEA			
Trigonostylopidae			
Trigonostylops wortmani		x	
Trigonostylops gegenbauri			?
"*Trigonostylops*" *apthomasi*	I		
Albertogaudrya unica		x	
?Trigonostylopidae *incertae sedis*			
Shecenia ctirneru	x		
PYROTHERIA			
Pyrotheriidae			
Propyrotherium saxeum			x
?Pyrotheriidae *incertae sedis*			
Carolozittelia tapiroides		x	
XENUNGULATA			
Carodniidae			
Carodnia feruglioi	x		
C. vieirai	I		
MAMMALIA INCERTAE SEDIS			
Florentinoameghinia mystica		x	

Each of the three designated ages includes an appreciable span in time, and fossil-bearing rocks of the corresponding stages have an appreciable extent in space. It is therefore not to be assumed that all the species listed as of a given age were synchronous and sympatric. On the contrary it is already evident that different local faunas and different horizons may have different species or subspecies within a single nominal age. Preceding pages give evidence of the fact, mostly for our 1930–1931 and 1933–1934 collections, virtually the only ones so far with precise records of horizon and locality. More extended and exhaustive analysis will require much more collecting with similar precision.

The latest Riochican faunules, notably the faunule from the uppermost Riochican of the Bajo de la Palangana near Comodoro Rivadavia in Chubut, differ little and for the most part only up to the specific level from almost immediately overlying Casamayoran faunules. There is thus little hiatus between late Riochican and early Casamayoran as now known. The situation as regards Casamayoran and Mustersan requires further study, but here, too, scattered and small faunules suggest that even known occurrences involve a transition with a smaller hiatus than has commonly been supposed hitherto. There are several possible but no absolutely established cases of the occurrence of the same species in both stages, and there are probable occurrences of the same genus. Some other generic distinctions, although tentatively accepted, are more nominal than real. For example, as noted on previous pages, there would be little reason to distinguish *Thomashuxleya* from *Periphragnis* or *Anisotemnus* from *Rhyphodon* if they were not known to be from different stages. However, as far as adequately identified and published faunas go, there is still a very definite hiatus between the Mustersan and Deseadan. That will doubtless be filled by further discoveries, as it is known that there are rich and inadequately or not exploited fossil deposits of those and probably intermediate ages. Whether intermediate faunas should be assigned to later Mustersan, early Deseadan, both, or a separate intervening age must of course wait on better data.

It is also clear, but also cannot be properly and fully analyzed without more and better data, that various faunules differ ecologically. The most obvious example at present is the contrast between the Itaborai fauna and Patagonian faunules of approximately the same and also of later age. At Itaborai didelphid marsupials are extraordinarily varied and abundant, but notoungulates are so far represented by only two species, only one of which is common. In the Riochican of Patagonia and indeed in all the known Tertiary faunas of Patagonia didelphids are extremely rare or quite unknown, and notoungulates are the dominant faunal element both in species and in individuals.

The present study is far from being definitive in any respect. It may, however, have pulled current knowledge and inference together in such a way as to provide a basis and stimulus for better future studies.

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1923–1924. Pattedyr-Slaegter. Copenhagen, H. Hagerups Forlag, vol. 1 (1923), Monotremata, Marsupialia, Insectivora, Chiroptera, Edentata, viii+360 pp.; vol. 2 (1924), Rodentia, Carnivora, Primates, 321 pp.; vol. 3 (1924), Ungulata, Cetacea, 270 pp.

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PLATES 1–46

PLATE 1

1–3. "*Odontomysops spiniferus*" Ameghino, syntypes belonging to different individuals and taxa. 1. M.A.C.N. No. A55-2a, an anterior tooth. Lateral view. *Ca.* ×3. 2. M.A.C.N. No. A55-2b, fragment of the left lower jaw with traces of three or more cheek teeth. Dorsal view. *Ca.* ×3.5. 3. M.A.C.N. No. A55-2c, fragment of right lower jaw with a partly erupted tooth. Dorsal view. *Ca.* ×3.5.

4. *Protobradys harmonicus* Ameghino, type, M.A.C.N. No. A10330, fragment of left maxilla with alveoli. Ventral view. ×3.3.

5. "*Protobradys harmonicus*" Ameghino, M.A.C.N. No. A10331, abraded fragment of root of a tooth. An unidentifiable scrap probably not of this genus or species, but referred here by Ameghino. Lateral view. ×5.

6. *Didolodus ?multicuspis* Ameghino, M.H.N. Tournouër Collection No. 4, P_{2-4}. Crown view. ×2.2.

7. *Didolodus* cf. *minor* Simpson, M.H.N. Tournouër Collection No. 5, P_{2-3}. Crown view. ×2.2.

8–10. *Ernestokokenia* sp. 8. M.H.N. Tournouër Collection No. 7, dissociated M_1 and M_3. Crown views. ×2.23. 9. M.H.N. Tournouër Collection No. 8, possibly associated P_4 and M_1. Crown views. ×2.3. 10. M.H.N. Tournouër Collection No. 6, two dissociated M^1's. Crown views. ×2.3.

11. *Josepholeidya* sp., M.H.N. Tournouër Collection No. 9, three dissociated M^1's. Crown views. ×2.3.

12. *?Ricardolydekkeria* sp., M.H.N. Tournouër Collection No. 9 (catalogued with but distinct from the specimen shown in figure 11), upper molar. Crown view. ×2.3.

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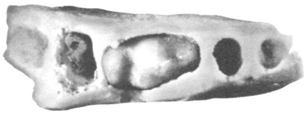

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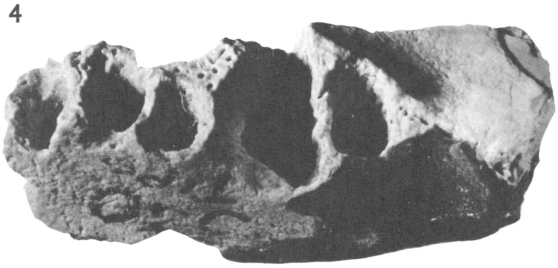

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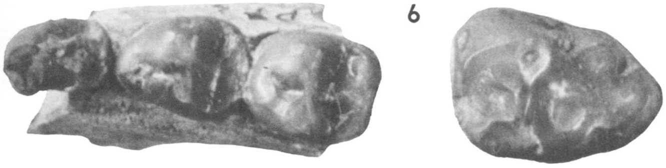

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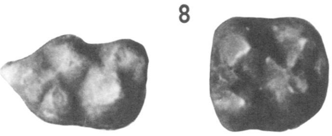

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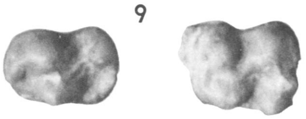

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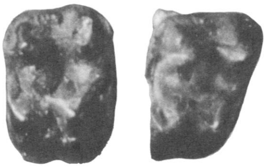

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PLATE 2

1–3. *Oldfieldthomasia debilitata* Ameghino, type, M.A.C.N. No. 10376, skull. 1. Right lateral view. 2. Ventral view. 3. Dorsal view.

All *ca.* ×1.

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PLATE 3

Oldfieldthomasia debilitata AMEGHINO

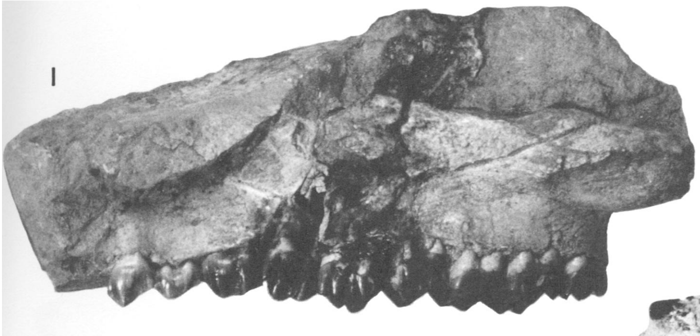
1, 2. M.A.C.N. No. 10748, left P^1–M^3 (type of the synonym *Oldfieldthomasia furcata* Ameghino). 1. Buccal view. 2. Crown view. Both ×1.25.

3. M.A.C.N. No. 10764, isolated right dm^4 and left M$^{1-3}$ (type of the synonym *Oldfieldthomasia plicata* Ameghino). Crown view. ×1.25.

4, 5. M.A.C.N. No. 10762, right P^1–M^3 (type of the synonym *Oldfieldthomasia cuneata* Ameghino). 4. Buccal view. 5. Crown view. Both ×1.25.

6. M.A.C.N. No. 10772, palate with right P^2–M^3 and left P^4–M^3 (type of the synonym *Oldfieldthomasia cingulata* Ameghino). Palatal view. ×1.55.

7. M.A.C.N. No. 10757, left P^4–M^3 (type of the synonym *Oldfieldthomasia conifera* Ameghino). Crown view. ×1.25.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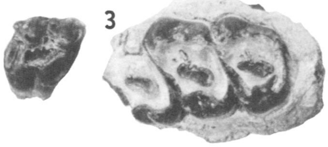
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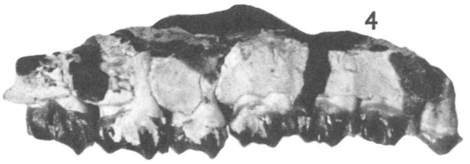
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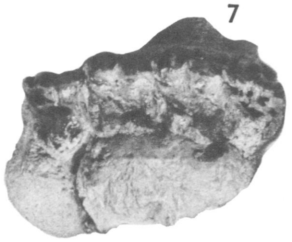
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PLATE 4

Oldfieldthomasia debilitata AMEGHINO

1, 2. M.A.C.N. No. 10400, palate with right and left P^1–M^3. 1. Left lateral view. 2. Crown view. Both ×1.25.

3. M.A.C.N. No. 10765, palate with right P^2–P^4 and left P^3–M^3. Palatal view. ×1.25.

4. M.A.C.N. No. 10761, right P^4–M^3. Crown view. ×1.5.

5. M.A.C.N. No. 10750, left P_2–M_1. Crown view. ×2.

6, 7. M.A.C.N. No. 10749, right P_2–M_3. 6. Crown view. 7. Buccal view. Both ×1.5.

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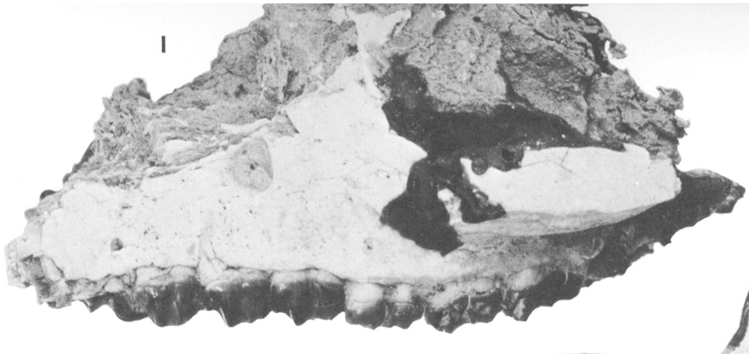

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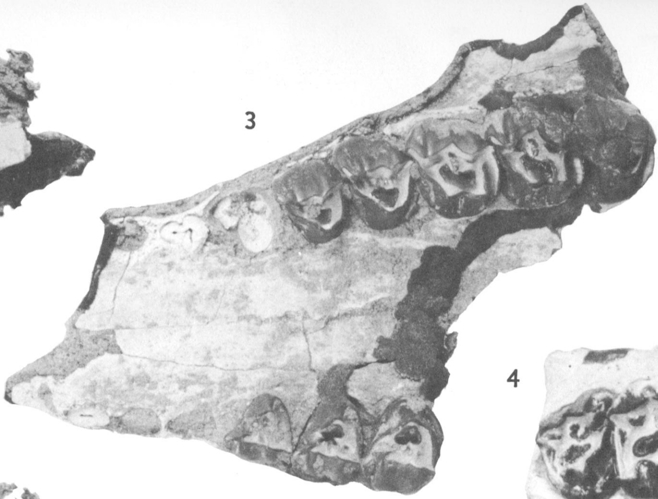

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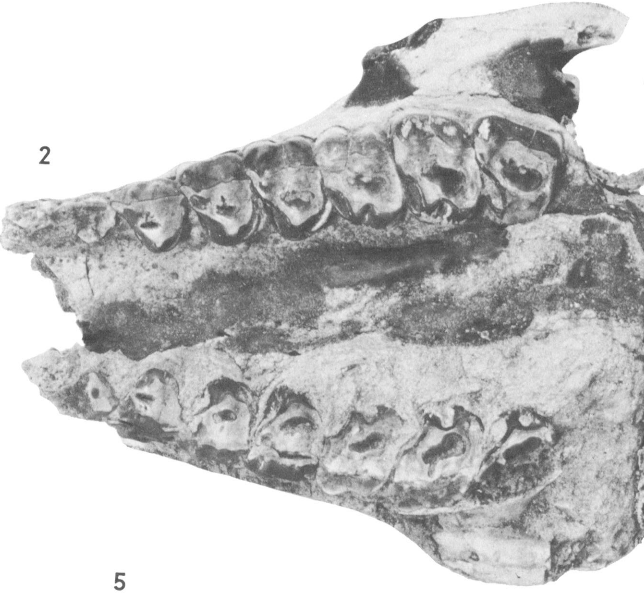

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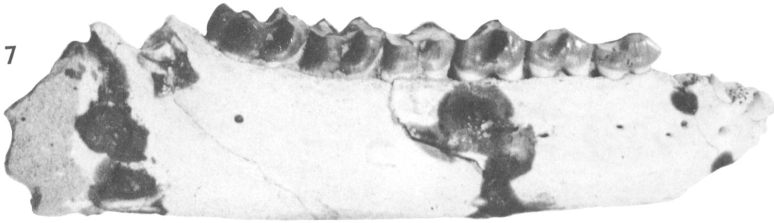

PLATE 5

Oldfieldthomasia debilitata AMEGHINO

1, 2. A.M.N.H. No. 28730, partial lower jaw with left P_1–M_2 and right I_1–C. 1. Composite left lateral view, with I_1–C reversed from the other side. 2. Crown view.

3, 4. A.M.N.H. No. 28780, part of palate with left I^2–P^3. 3. Crown view. 4. Left lateral view.

All ×2.2.

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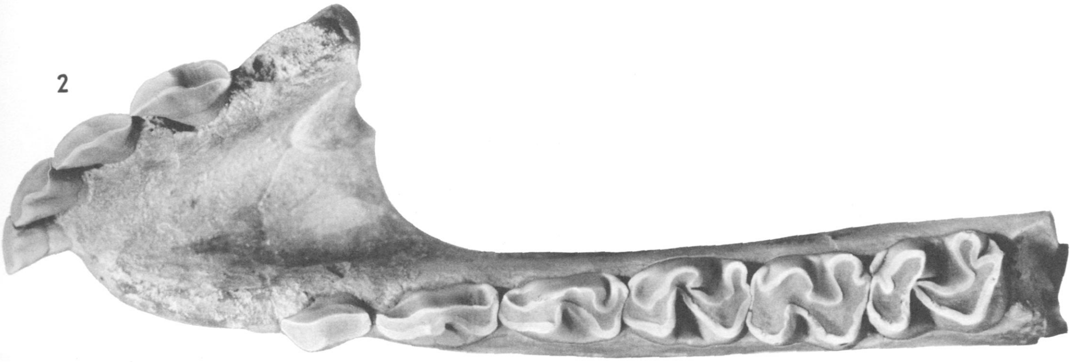

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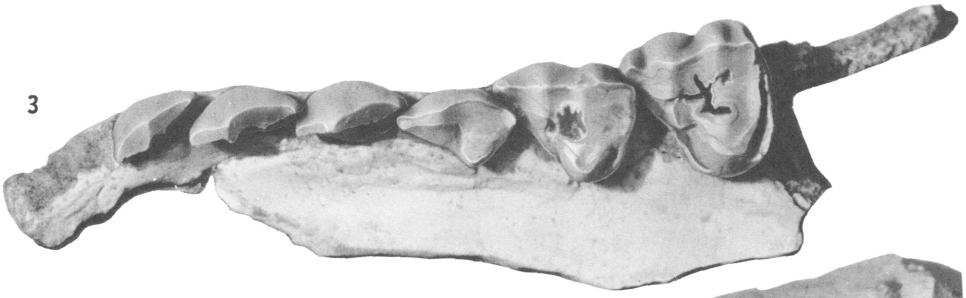

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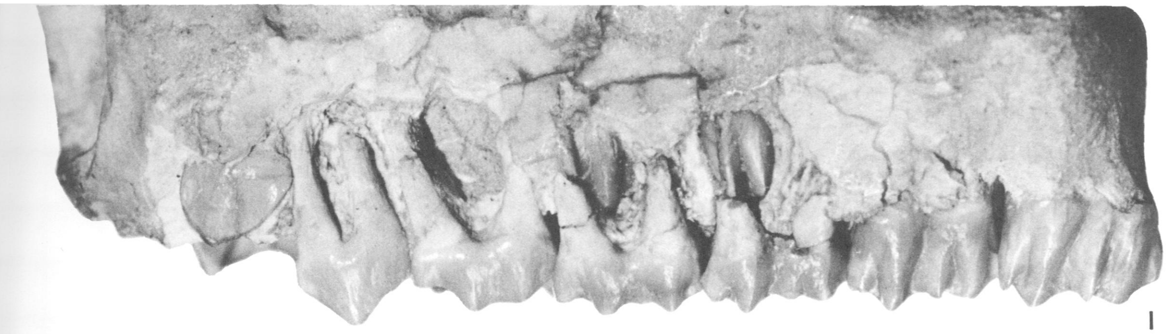
PLATE 6

Oldfieldthomasia debilitata Ameghino

1, 2. A.M.N.H. No. 28691, left C, dm^{1-4}, M^{1-2}. 1. Buccal view. 2. Crown view of left tooth series, with dm^4 and M^1 reversed from the right side (drawing by Chester Tarka). Both ×3.2.

3. A.M.N.H. No. 28780, partial endocranial cast, associated with teeth shown in plate 5, figures 3 and 4. Dorsal view. *Ca.* ×1.9.

4, 5. C.N.H.M. No. 191c, left lower jaw with P_4–M_3. 4. Crown view. ×3.2. 5. Buccal view. *Ca.* ×1.9.



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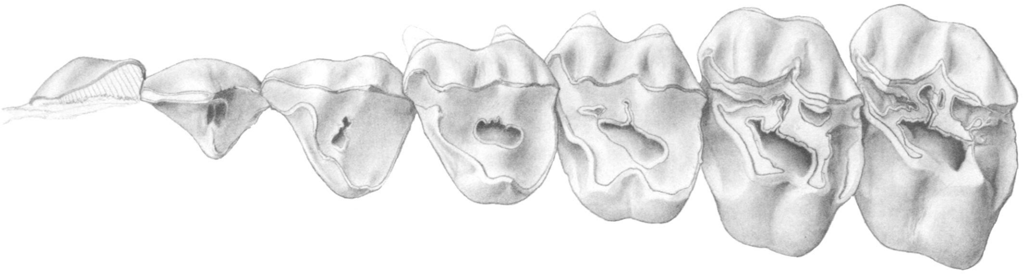

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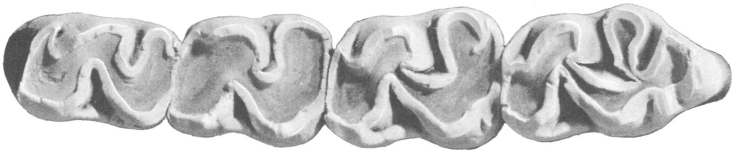

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PLATE 7

OLDFIELDTHOMASIIDAE

1, 2. *Oldfieldthomasia parvidens* Ameghino. 1. Type, M.A.C.N. No. 10763, right P^4–M^2. Crown view. ×1.7. 2. M.H.N. Tournouër Collection No. 21, palate with right P^3–M^3 and left P^1–M^3. Crown view. *Ca.* ×2.

3. *Oldfieldthomasia anfractuosa* Ameghino, type, M.A.C.N. No. 10746, right dm^3–M^2. Crown view. ×1.7.

4. *Oldfieldthomasia transversa* Ameghino, type, M.A.C.N. No. 10754, left dm^4–M^1 or, less probably, M^{1-2}. Crown view. ×1.7.

5–7. *Ultrapithecus rutilans* Ameghino. 5, 6. Type, M.A.C.N. No. 10818, right P^1–M^2. 5. Crown view. 6. Buccal view. Both ×1.7. 7. M.H.N. Tournouër Collection No. 24, palate with P^2–M^3 of both sides. Palatal view. ×1.9.

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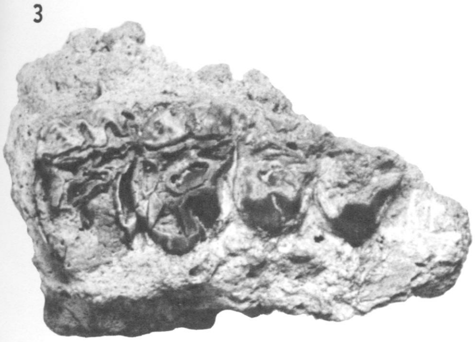

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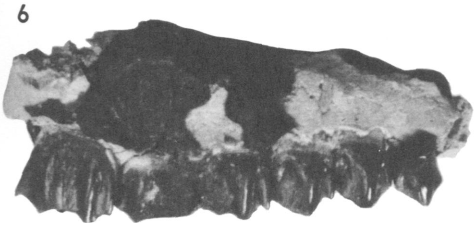

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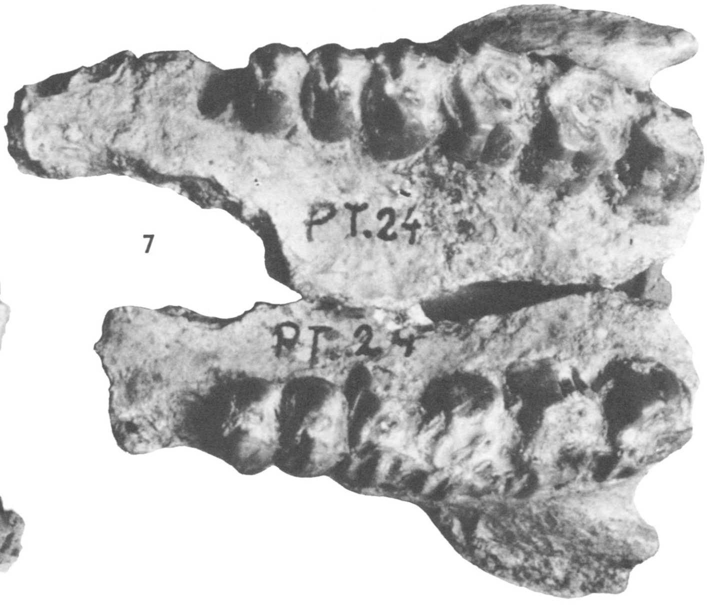

PLATE 8

Ultrapithecus rutilans AMEGHINO

1, 2. A.M.N.H. No. 28583, left di^3–M^1. 1. Buccal view. 2. Crown view.

3, 4. A.M.N.H. No. 28583, right dm^1–M^2, reversed so as to appear left, for comparison with figures 1 and 2. 3. Crown view. 4. Buccal view.

All × 4.

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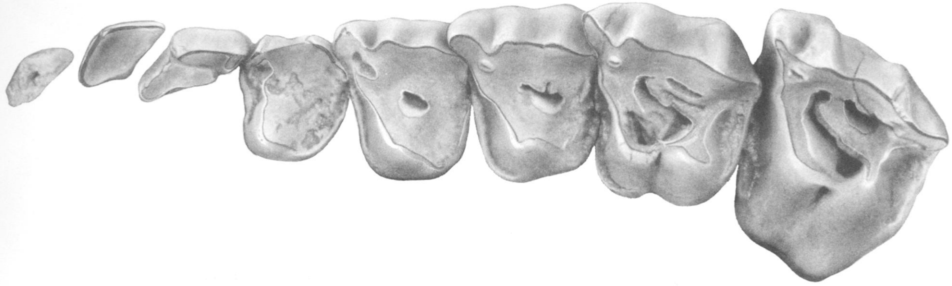

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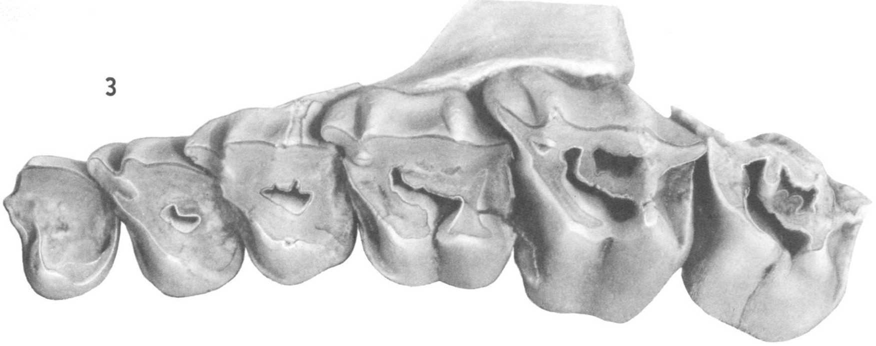

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PLATE 9

Maxschlosseria

1, 2. *Maxschlosseria praeterita* Ameghino, type, M.A.C.N. No. 10624, left P^4–M^3. 1. Buccal view. 2. Crown view. Both ×2.

3–5. *Maxschlosseria minima* (Ameghino). 3. Lectotype, M.A.C.N. No. 10572, isolated left M^2. Crown view. ×2. 4. M.A.C.N. No. 10617, right P^4–M^3 (type of the synonym *Maxschlosseria anatona* Ameghino). Buccal view. ×2. 5. M.A.C.N. No. 10840, isolated, incomplete right ?M^2 (type of the synonym *Antepithecus plexostephanos* Ameghino). Crown view. ×2.

6. *Maxschlosseria septa* (Ameghino), type, M.A.C.N. No. 10758, fragment of left maxilla with three incomplete teeth. Crown view. ×2.

7. *Maxschlosseria consumata* (Ameghino), M.A.C.N. No. 10482, fragment of right maxilla with M^2 (type of the synonym *Eostylops obliquatus* Ameghino). Crown view. ×2.

8, 9. *Maxschlosseria rusticula* Ameghino, M.A.C.N. No. 10578, part of right maxilla with incomplete P^4–M^3 (type of the synonym *Isotemnus emundatus* Ameghino). 8. Buccal view. 9. Crown view. Both ×2.

10, 11. *Maxschlosseria consumata* (Ameghino), type, M.A.C.N. No. 10580, fragment of left maxilla with imperfect P^4–M^3. 10. Buccal view. 11. Crown view. Both ×2.

12. *Maxschlosseria minuta* (Ameghino), type, M.A.C.N. No. 10595, right M_{1-2}. Crown view. ×6.

13. ?*Maxschlosseria expansa* (Ameghino), type, M.A.C.N. No. 10856, right P_{2-4}. Crown view. ×2.5.

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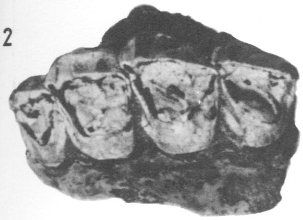

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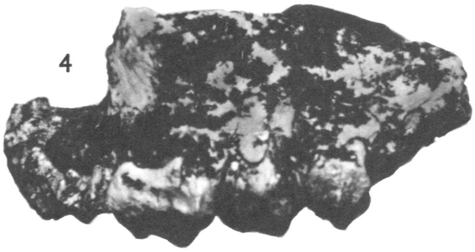

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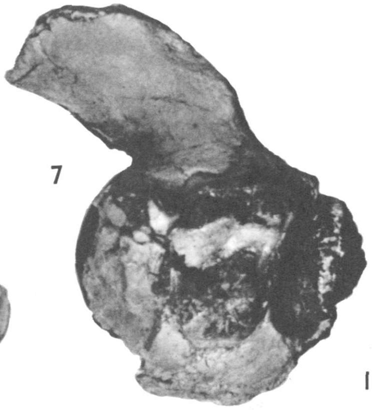

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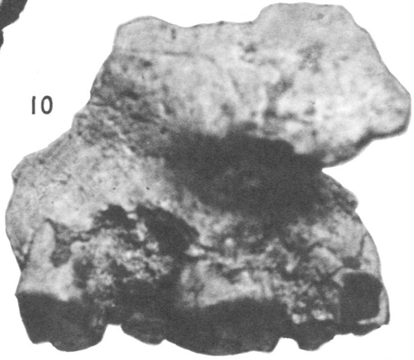

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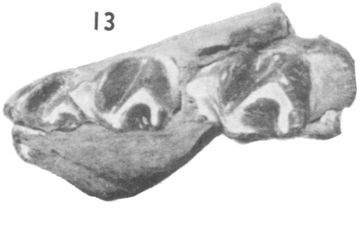

PLATE 10

Maxschlosseria

1–4. *Maxschlosseria consumata* (Ameghino). 1, 2. A.M.N.H. No. 28753, right I^3, P^1–M^3. 1. Buccal view. 2. Crown view. Both ×2.1. 3, 4. A.M.N.H. No. 28753, right C–M_3 (associated with the teeth shown in figures 1 and 2). 3. Crown view. 4. Buccal view. Both ×2.1.

5, 6. *Maxschlosseria minuta* (Ameghino), A.M.N.H. No. 28660, left M_{1-3}. 5. Buccal view. 6. Crown view. Both ×3.

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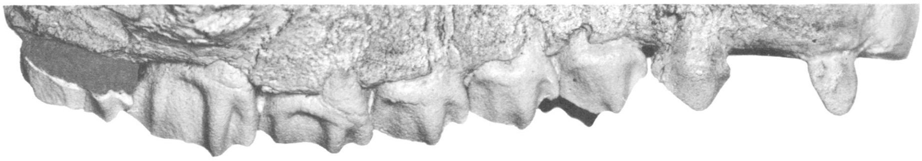

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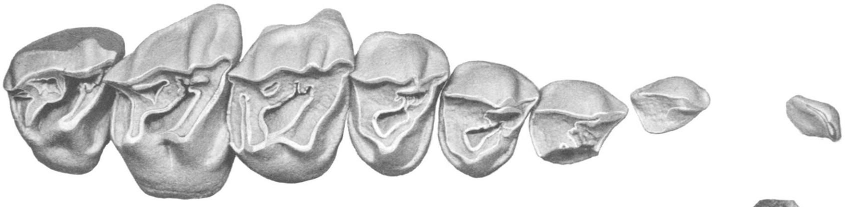

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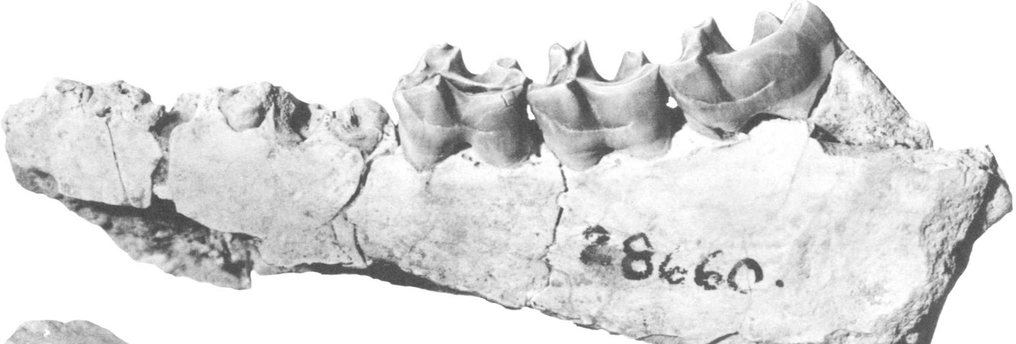

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PLATE 11

OLDFIELDTHOMASIIDAE

1–3. *Acoelodus oppositus* Ameghino. 1. Neotype, M.A.C.N. No. 10753, incomplete skull with left I^1–C, P^2–M^3, and right C, P^2–M^3. Palatal view. ×1.25. 2, 3. Type, M.A.C.N. No. 10770, fragment of left lower jaw with P_{2-3} and part of P_4. 2. Lingual view. 3. Crown view. Both ×2.

4. "*Acoelodus*" *terminalus* Ameghino, type, M.A.C.N. No. 10755, isolated right upper molar. Crown view. ×2.

5–11. *Paginula parca* Ameghino. 5, 6. Type, M.A.C.N. No. 10596, fragment of right lower jaw with M_3 and part of M_2. 5. Lingual view. 6. Crown view. Both ×2. 7, 8. M.A.C.N. No. 10747, fragment of left lower jaw with M_{1-3} (type of the synonym *Acoelodus connectus* Ameghino). 7. Lingual view. 8. Crown view. Both ×2. 9. M.H.N. Tournouër Collection No. 29, fragment of right lower jaw with P_{3-4}. Crown view. *Ca.* ×2. 10. M.A.C.N. No. 10698, fragment of left lower jaw with P_{2-4} (type of the synonym *Acoelodus microdon* Ameghino). Crown view. ×2. 11. M.H.N. Tournouër Collection No. 22, fragment of right lower jaw with P_3–M_3. Crown view. *Ca.* ×2.

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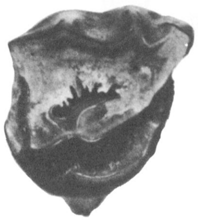

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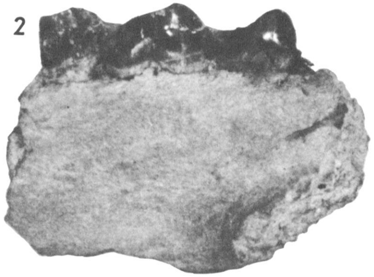

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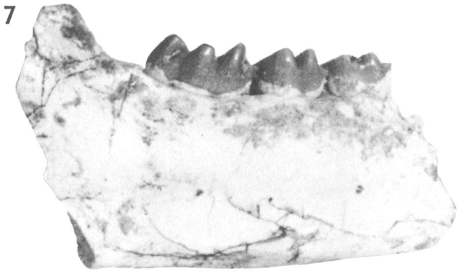

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PLATE 12

ARCHAEOPITHECIDAE AND INTERATHERIIDAE

1, 2. *Archaeopithecus rogeri* Ameghino. 1. Type, M.A.C.N. No. 10816, part of right maxilla with P^1–M^2. Crown view. *Ca.* ×2.1. 2. M.A.C.N. No. 10851, fragment of left maxilla with M^2 and part of M^1 (type of the synonym *Adpithecus plenus* Ameghino). Crown view. *Ca.* ×1.9.

3, 4. ?*Archaeopithecus fossulatus* (Ameghino), lectotype, M.A.C.N. No. 10824, fragment of left lower jaw with P_{3-4}. 3. Lingual view. 4. Crown view. Both *ca.* ×1.9.

5–7. *Acropithecus rigidus* Ameghino. 5. Lectotype, M.A.C.N. No. 10813, fragment of left maxilla with P^4–M^2. Crown view. *Ca.* ×2.1. 6. M.A.C.N. No. 10850, right M^3 (lectotype of the synonym *Acropithecus tersus* Ameghino). Crown view. *Ca.* ×1.9. 7. M.A.C.N. No. 10815, fragment of right maxilla with M^{1-3} (type of the synonym *Archaeopithecus alternans* Ameghino). Crown view. *Ca.* ×1.9.

8–12. *Notopithecus adapinus* Ameghino. 8. Type, M.A.C.N. No. 10822, right maxilla with C–M^2. Lingual view. ×1.6. 9, 10. M.A.C.N. No. 10790, skull (type of the synonym *Adpithecus secans* Ameghino). 9. Left lateral view. 10. Ventral view. Both ×1.6. 11, 12. M.A.C.N. No. 10790, left lower jaw, lacking anterior end; the same individual as is shown in figures 9 and 10. 11. Left lateral view. 12. Dorsal view. Both ×1.6.


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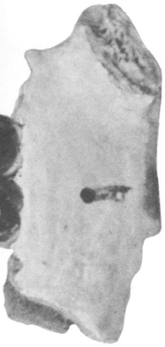
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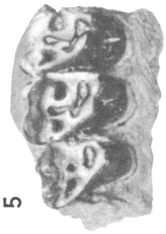
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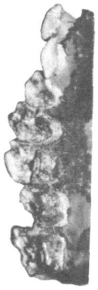
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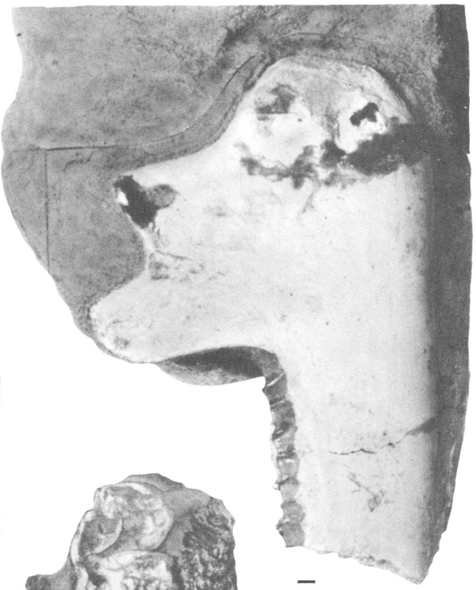
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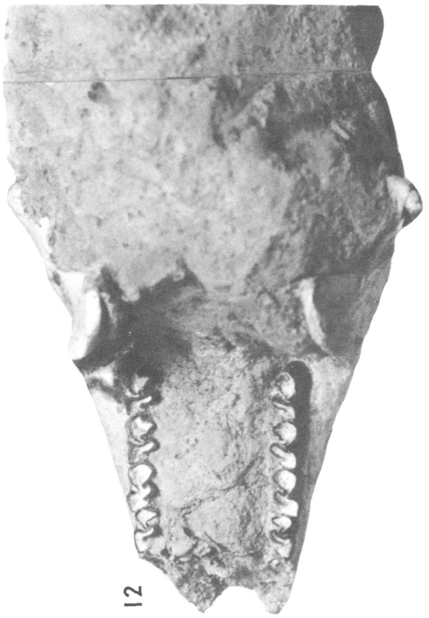
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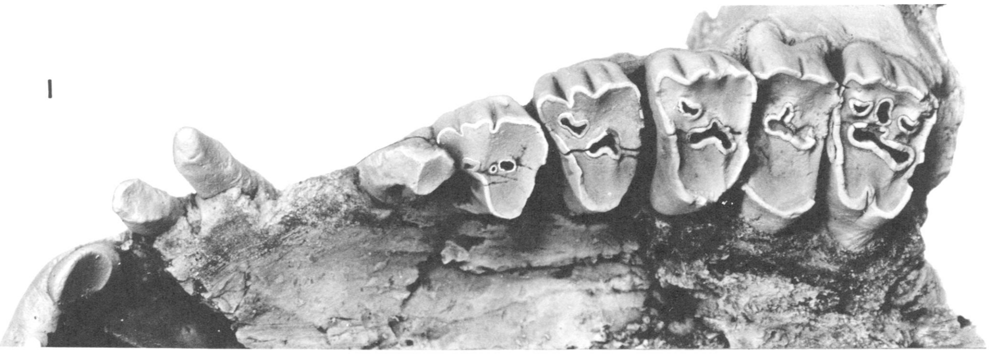
PLATE 13

1–6. *Acropithecus rigidus* Ameghino, A.M.N.H. No. 28782, partial skull and jaws. 1, 2. Left I^{1-3}, P^1–M^2. 1. Palatal view. 2. Buccal view. 3. P_{2-4}, shown as left side, but composite with left P_2 and reversed right P_{3-4}. Crown view. 4. Part of left lower jaw with P_3–M_3. Crown view. 5. P_{2-3}, shown as left, but P_2 reversed from right side. Buccal view. 6. Part of left lower jaw with P_3–M_3. Buccal view.

All ×3.

1



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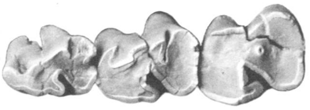

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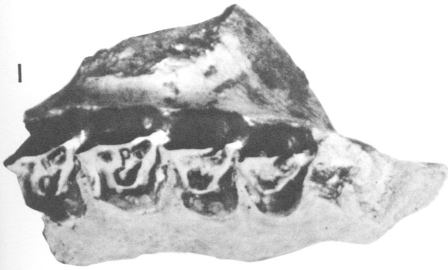
PLATE 14

INTERATHERIIDAE

1–7. *Notopithecus adapinus* Ameghino. 1. M.A.C.N. No. 10834, fragment of right maxilla with P^3–M^2 (lectotype of the synonym *Adpithecus subtenuis* Ameghino). Crown view. *Ca.* ×3. 2. M.A.C.N. No. 10858, fragment of right lower jaw with M_{2-3} (lectotype of the synonym *Adpithecus reduncus* Ameghino). Crown view. *Ca.* ×3.2. 3. M.A.C.N. No. 10838, fragment of left lower jaw with P_{2-4} (type of the synonym *Infrapithecus diversus* Ameghino). Crown view. *Ca.* ×3.2. 4. M.A.C.N. No. 10862, fragment of right maxilla with P^4–M^2 (type of the synonym *Epipithecus confluens* Ameghino). Crown view. *Ca.* ×3. 5. M.A.C.N. No. 10828, fragment of left maxilla with M^{1-2} (type of the synonym *Antepithecus gradatus* Ameghino). Crown view. *Ca.* ×3.2. 6. M.A.C.N. No. 10827, three isolated right upper molars and an isolated right upper premolar (including type or syntypes of the synonym *Gonopithecus trigonodontoides* Ameghino). Crown views. *Ca.* ×3. 7. A.M.N.H. No. 28718, lower jaw with P_1–M_3. Left lateral view. Compare with figure 8. ×2.8.

8. *Antepithecus brachystephanus* Ameghino, A.M.N.H. No. 28687, lower jaw with P_2–M_3. Left lateral view. Compare with figure 7. ×2.8.

1



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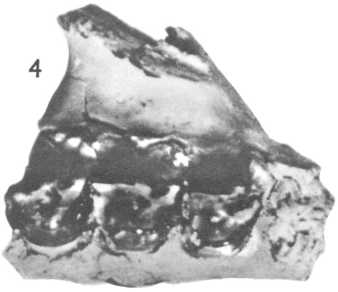

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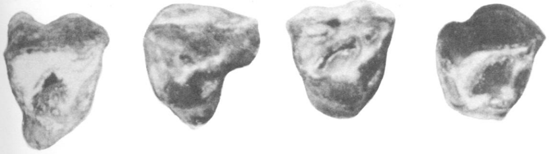

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PLATE 15

1–3. *Notopithecus adapinus* Ameghino, A.M.N.H. No. 28949, skull. 1. Dorsal view. 2. Left lateral view. 3. Ventral view.

All ×2.

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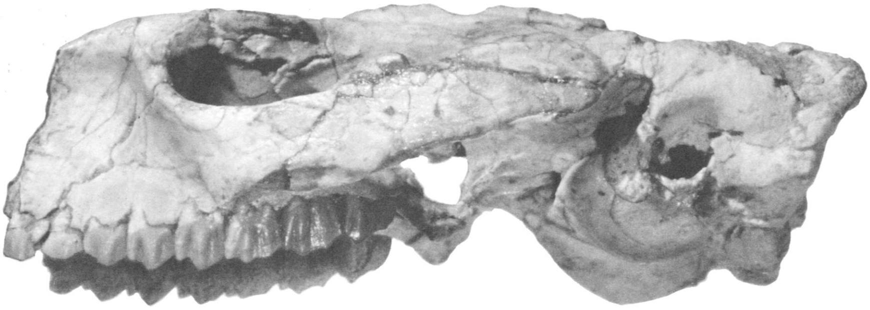

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PLATE 16

INTERATHERIIDAE

1–7. *Antepithecus brachystephanus* Ameghino. 1, 2. M.A.C.N. No. 10826, part of left lower jaw with P_2–M_3 (type of the synonym *Infrapithecus cinctus* Ameghino). 1. Crown view. 2. Buccal view. Both *ca.* ×2.5. 3. Lectotype, M.A.C.N. No. 10841, right M^2. Crown view. *Ca.* ×2.5. 4. M.A.C.N. No. 10669(a), right lower jaw fragment with P_{2-3} (type of the synonym *Pseudadiantus secans* Ameghino). Crown view. *Ca.* ×2.5. 5. M.A.C.N. No. 10669(b), left lower jaw fragment with P_{1-2} (type of the synonym *Pseudadiantus imperfectus* Ameghino). Crown view. *Ca.* ×2.5. 6. M.A.C.N. No. 10859, fragment of right maxilla with incomplete P^2–M^2 (type of the synonym *Antepithecus interrasus* Ameghino). Crown view. *Ca.* ×2.6. 7. M.A.C.N. No. 10691, fragment of left maxilla with M^{1-2} (lectotype of the synonym *Patriarchippus annectens* Ameghino). Crown view. *Ca.* ×2.6.

8. *?Antepithecus innexus* Ameghino, type, M.A.C.N. No. 10839, isolated upper molar. Crown view. *Ca.* ×2.5.

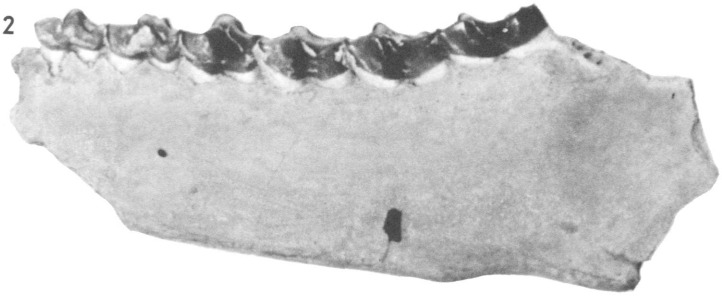
9, 10. *Guilielmoscottia plicifera* Ameghino. 9. Type, M.A.C.N. No. 10898, partial left maxilla with P^1–M^3. Crown view. ×2. 10. M.L.P. No. 12-2280, right upper molar. Crown view. *Ca.* ×3.

11. *Transpithecus obtentus* Ameghino, type, M.A.C.N. No. 10833, fragment of left maxilla with M^{1-3}. Crown view. *Ca.* ×2.6.

12. *Guilielmoscottia plicifera* or *?Notopithecus amplidens*, M.A.C.N. No. 10786, right lower jaw with P_1–M_3. Crown view. ×2.

1

2



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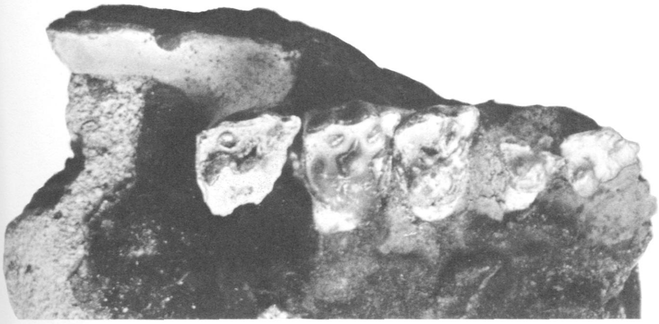

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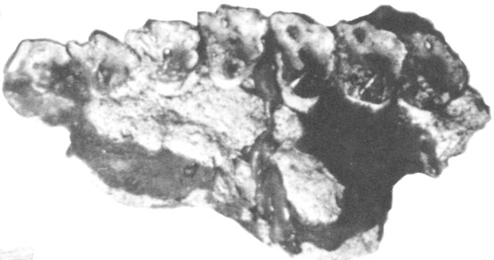

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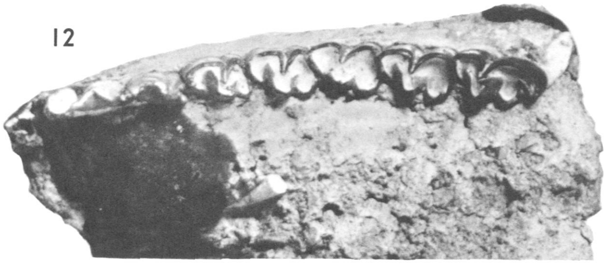

PLATE 17

Eohyrax

1. *Eohyrax rusticus* Ameghino, lectotype, M.A.C.N. No. 10775, part of left lower jaw with P_4–M_2. Crown view. ×2.

2, 3. *Eohyrax isotemnoides* Ameghino. 2. M.A.C.N. No. 10778, right M_3. Crown view. *Ca.* ×1.8. 3. Type, M.A.C.N. No. 10776, part of left lower jaw with P_4–M_3. Crown view. *Ca.* ×1.8.

4. *Eohyrax* cf. *rusticus* Ameghino, M.A.C.N. No. 10777, right upper molar. Crown view. ×2.

5. *Eohyrax isotemnoides* Ameghino, M.A.C.N. No. 10778, left upper molar (not the same individual as is shown in figure 2). Crown view. ×1.8.

6. *Eohyrax praerusticus* Ameghino, lectotype, M.A.C.N. No. 10780, right M_1. Crown view. ×1.9.

7–11. *Eohyrax isotemnoides* Ameghino. 7. M.H.N. Tournouër Collection No. 31, three dissociated upper molars. Crown view. ×2.24. 8. M.A.C.N. No. 10778, right M_3 and heel of M_2 (not associated with the individuals that are shown in figures 2 and 5). Crown view. ×1.8. 9–11. A.M.N.H. No. 28665, fragment of right lower jaw with P_1–M_3. 9. Buccal view. ×2.4. 10. Crown view (drawing by Chester Tarka). ×2.4. 11. Lingual view. ×2.4.

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2

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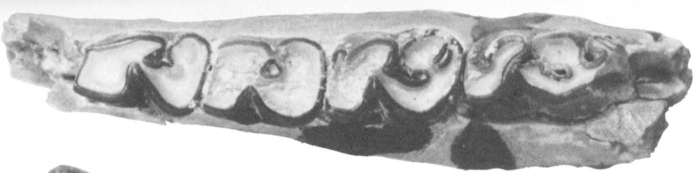

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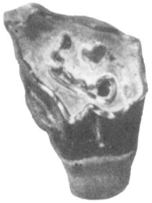

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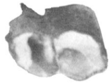

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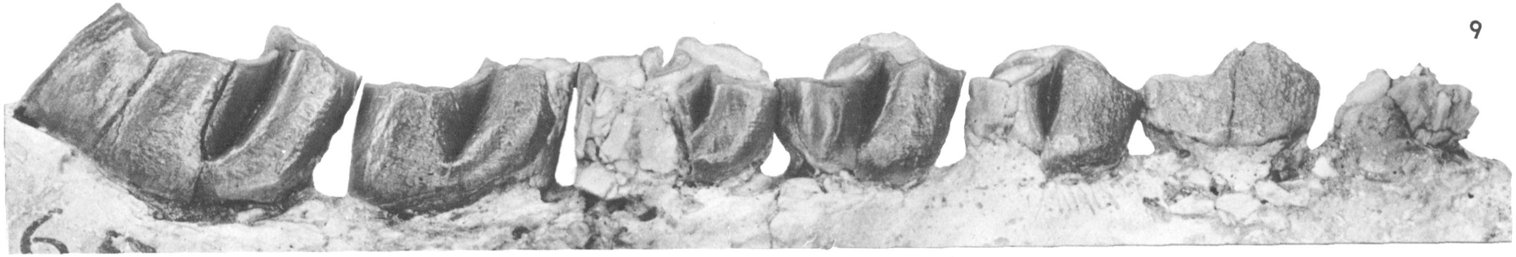

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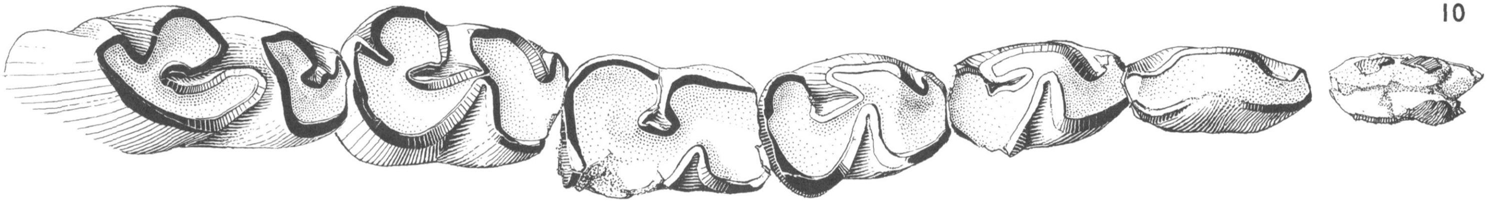

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PLATE 18

Eohyrax isotemnoides Ameghino

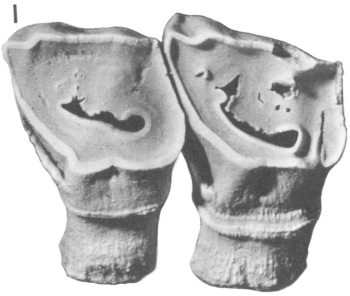
1, 2. A.M.N.H. No. 28844, Left M^{1-2}. 1. Crown view. 2. Buccal view.

3–5. A.M.N.H. No. 28628, left P_3–M_2. 3. Buccal view. 4. Lingual view. 5. Crown view.

6–8. A.M.N.H. No. 28628, right P_1–M_3, the same individual as is shown in figures 3–5. 6. Crown view. 7. Buccal view. 8. Lingual view.

All ×2.6.

1



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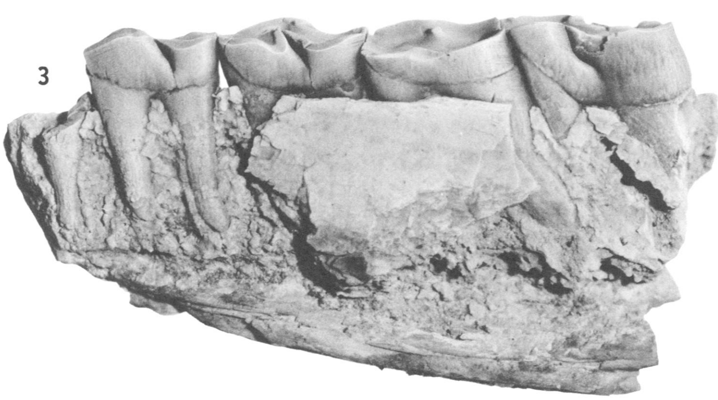

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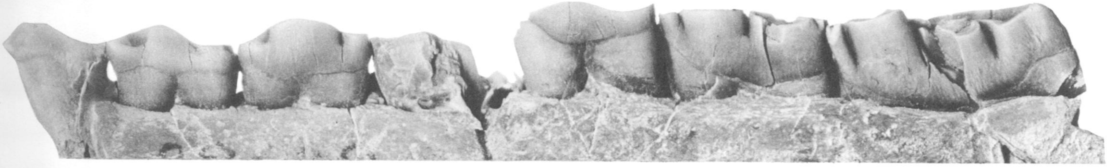


PLATE 19

Pseudhyrax eutrachytheroides Ameghino

1. M.L.P. No. 12-2200, right dm^{2-4} (type of the synonym *Pseudopithecus modestus* Roth). Crown view. ×1.5.

2. M.L.P. No. 12-2199, three right upper molars, possibly associated M^{1-3} (type or syntypes of the synonym *Degonia kollmanni* Roth). Crown views. *Ca.* ×1.5.

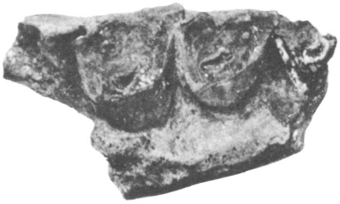
3. M.L.P. No. 12-2286, right upper molar (type of the synonym *Rankelia elegans* Roth). Crown view. ×1.5.

4. M.L.P. No. 12-1740, part of right lower jaw with P_2–M_3. Crown view. ×1.5.

5–7. A.M.N.H. No. 29406, right M_{1-3}. 5. Crown view. ×1.92. 6. Buccal view. ×1.92. 7. Lingual view. ×1.92.

8–10. A.M.N.H. No. 29410, right M_{1-3}. 8. Crown view. ×1.92. 9. Buccal view. ×1.92. 10. Lingual view. ×1.92.

1



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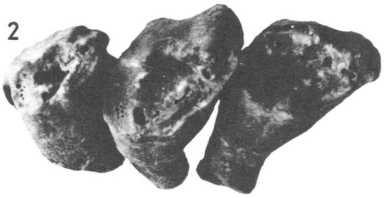

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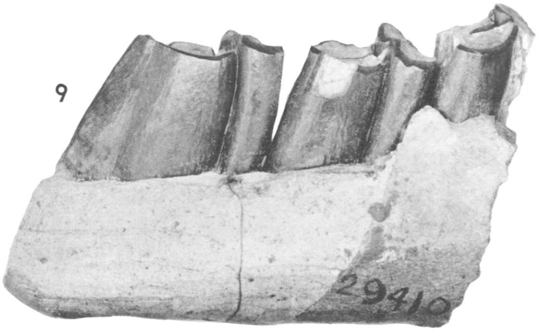

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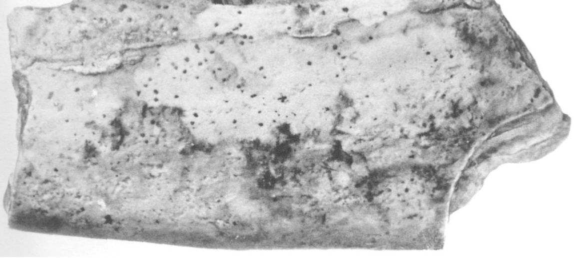

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PLATE 20

Pseudhyrax

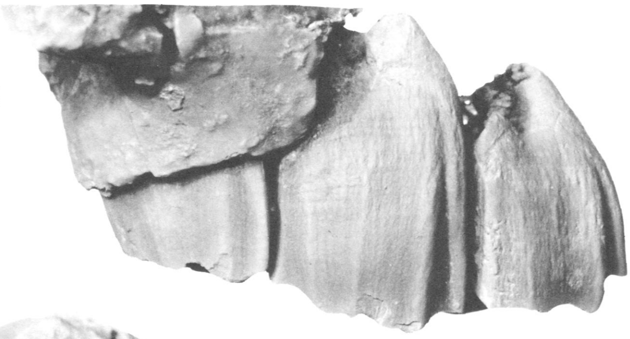
1, 2. ***Pseudhyrax eutrachytheroides*** Ameghino, A.M.N.H. No. 28883, right M^{1-3}. 1. Buccal view. 2. Crown view.

3, 4. ***?Pseudhyrax*** sp., A.M.N.H. No. 29458, fragment of right maxilla with P^{3-4} and part of M^1. 3. Buccal view. 4. Crown view.

5–7. ***Pseudhyrax eutrachytheroides*** Ameghino, A.M.N.H. No. 29469, right M_{1-2}. 5. Lingual view. 6. Crown view. 7. Buccal view.

All ×2.52.

1



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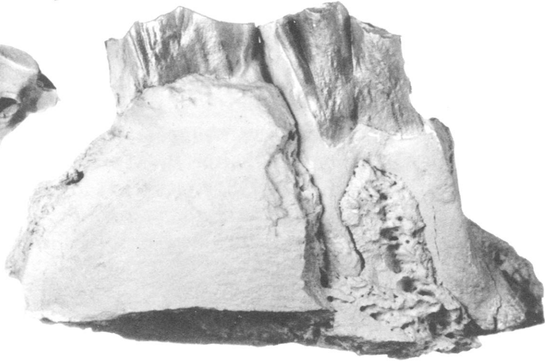

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PLATE 21

ARCHAEOHYRACIDAE

1–3. *Pseudhyrax strangulatus* (Ameghino). 1, 2. Type, M.A.C.N. No. 10774, part of right lower jaw with P_4–M_2. 1. Crown view. ×1.72. 2. Lingual view. ×1.74. 3. M.L.P. No. 12-2198, part of left lower jaw with P_4–M_3. Crown view. ×2.

4, 5. *Bryanpattersonia nesodontoides* (Ameghino), M.A.C.N. No. 10915, right upper molar (type of the synonym *Eomorphippus rutilatus* Ameghino). 4. Crown view. 5. Lingual view. Both ×1.8.

6–9. *?Bryanpattersonia* sp. 6, 7. A.M.N.H. No. 28943, left ?M^3. 6. Crown view. 7. Lingual view. Both ×2. 8, 9. A.M.N.H. No. 28955, left P^2–M^3. 8. Crown view. 9. Buccal view. Both ×2.

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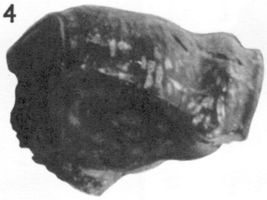

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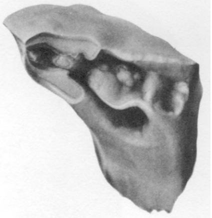

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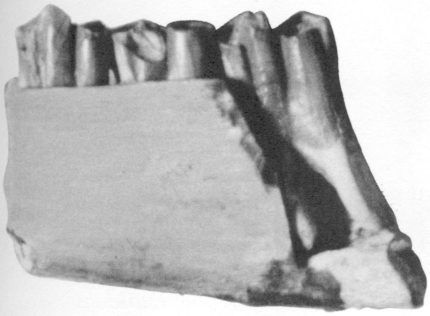

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PLATE 22

Pleurostylodon

1, 2. *Pleurostylodon* sp., A.M.N.H. No. 28878, right basal part of skull, mainly ear region. 1. Ventral view. 2. Medial view.

Abbreviations: c. m., crista meatus; c. pg., postglenoid canal; c. ty., tympanic cavity; cr. ty., crista tympanica; f. c. p., foramen caroticum posterius; f. h., hypoglossal foramen; f. l. p., foramen lacerum posterius; f. pg., postglenoid foramen; f. pn., foramen pneumaticum of epitympanic sinus; m. a. e., external auditory meatus; oc. c., occipital condyle; p. a. e., porus acusticus externus; p. et., pars epitympanica of squamosal; p. pg., postglenoid process; p. po., paroccipital process; r. et., epitympanic recess; s. et., epitympanic sinus; s. g., glenoid surface; s. v. pl., posterolateral venous sinus; v. p. h., vagina processus hyoidei.

3–14. *Pleurostylodon modicus* Ameghino. 3–5. Type, M.A.C.N. No. 10566, right M^{1-3}. 3. Crown view. 4. Lingual view. 5. Buccal view. 6. M.A.C.N. No. 10618, left M^3 (lectotype of the synonym *Parastylops coelodus* Ameghino). Crown view. 7. M.A.C.N. No. 10625, left M^3 (type of the synonym *Tychostylops marculus* Ameghino). Crown view. 8, 9. M.A.C.N. No. 10767, left dm^{2-4}, M^1 (type of the synonym *Anchistrum sulcosum* Ameghino). 8. Crown view. 9. Buccal view. 10. M.A.C.N. No. 10567, broken left ?M^2 (type of the synonym *Pleurostylodon divisus* Ameghino). Crown view. 11. M.A.C.N. No. 10570, left M^1 (lectotype of the synonym *Pleurostylodon plexus* Ameghino). Crown view. 12. M.A.C.N. No. 10571, broken left M^1 (type of the synonym *Pleurostylodon sinuosus* Ameghino). Crown view. 13. M.A.C.N. No. 10573, left M^3 (type of the synonym *Pleurostylodon limpidus* Ameghino). Crown view. 14. M.A.C.N. No. 10574, left M^3 (type of the synonym *Pleurostylodon obscurus* Ameghino). Crown view.

All ×1.

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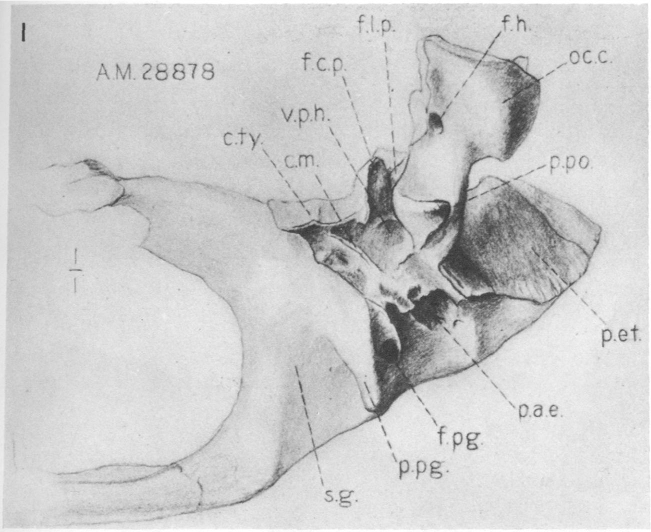

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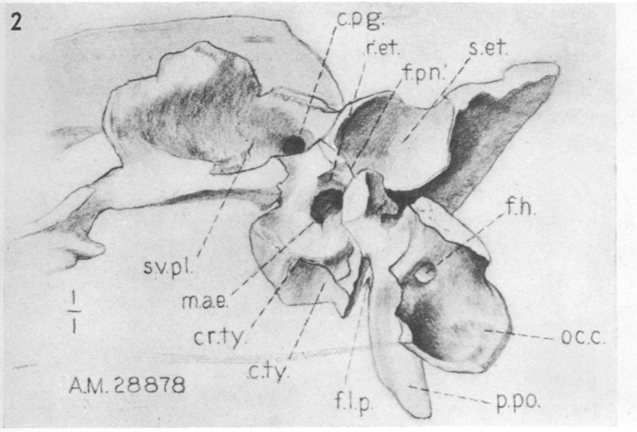

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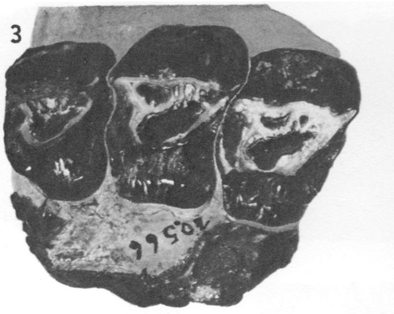

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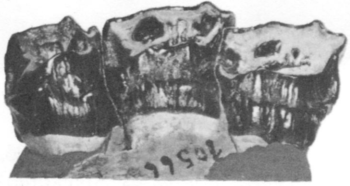

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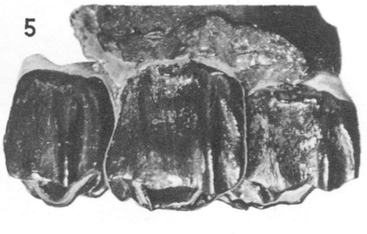

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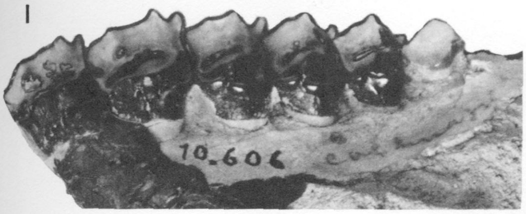
PLATE 23

Pleurostylodon modicus Ameghino

1–3. M.A.C.N. No. 10606, part of right maxilla with P^1–M^2 (type of the synonym *Paratemnus geminatus* Ameghino). 1. Lingual view. ×1. 2. Crown view. ×1. 3. Buccal view. ×1.

4, 5. M.A.C.N. No. 10554, lower jaw with all teeth except right I_3. 4. Crown view. 5. Right lateral view. Both ×1.33.

1



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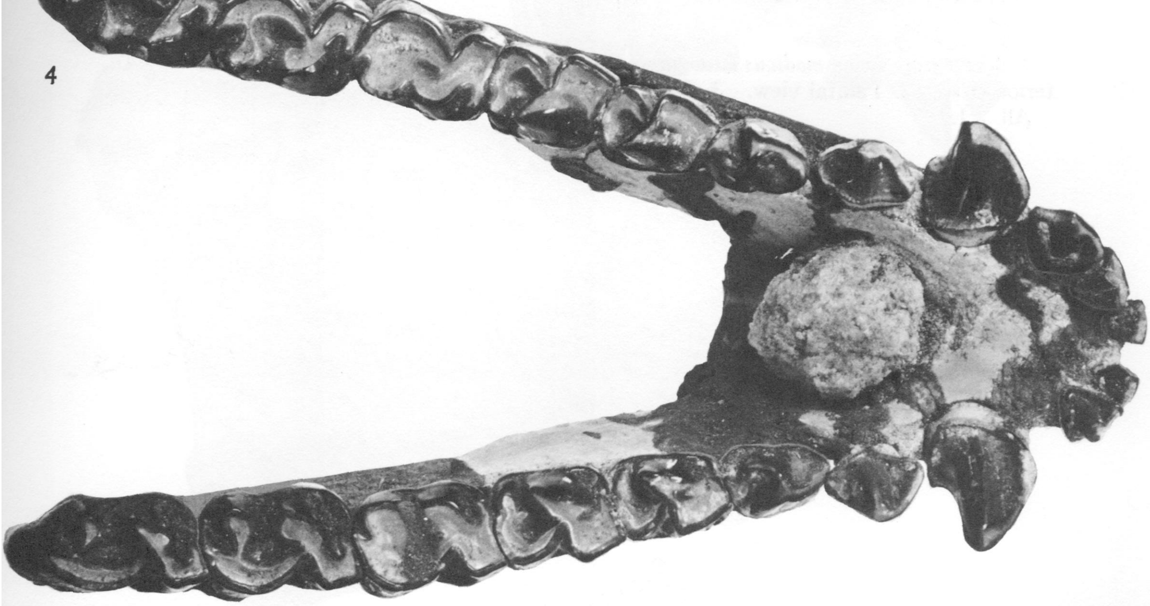

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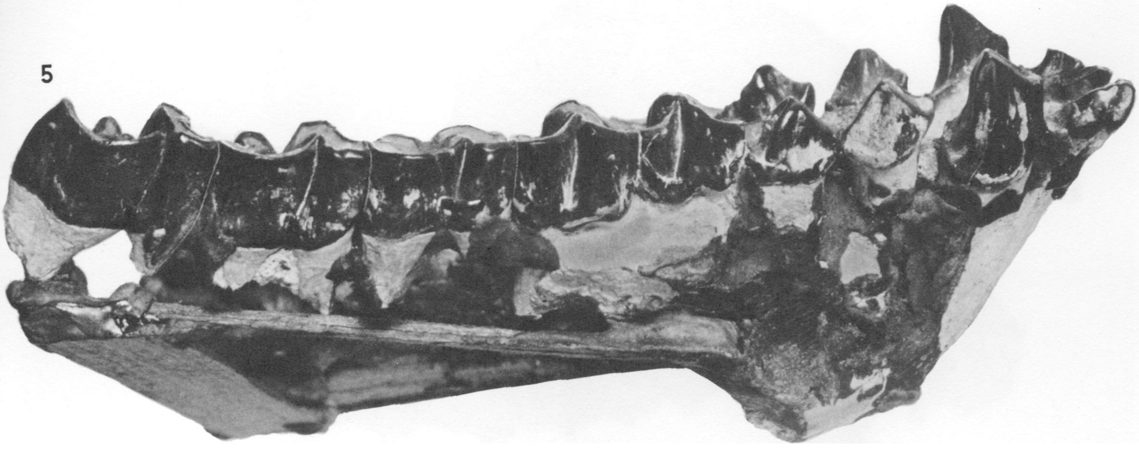


PLATE 24

1–3. *Pleurostylodon modicus* Ameghino, A.M.N.H. No. 28646, facial part of skull. 1. Anterior view. 2. Palatal view. 3. Right lateral view.

All ×1.

1

2

3

PLATE 25

ISOTEMNIDAE

1–4. *Pleurostylodon similis* Ameghino. 1–3. Type, M.A.C.N. No. 10549, fragment of left maxilla with P^4–M^3. 1. Lingual view. ×1.12. 2. Buccal view. ×1.12. 3. Crown view. ×1.12. 4. M.A.C.N. No. 10607, right P^4, M^{2-3}, and left P^4, M^1, and M^3 of one individual (type of the synonym *Tychostylops simus* Ameghino). Crown view. ×1.5.

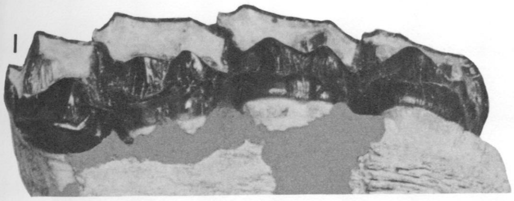
5, 6. *?Pleurostylodon crassiramis* Ameghino, type, M.A.C.N. No. 10610, fragment of left lower jaw with P_4. 5. Buccal view. 6. Crown view. Both ×1.5.

7, 8. *Pleurostylodon complanatus* Ameghino. 7. Type, M.A.C.N. No. 10564, right M^3. Crown view. ×1.5. 8. M.A.C.N. No. 10568, left M^3 (type of the synonym *Pleurostylodon neglectus* Ameghino). Crown view. ×1.5.

9. *?Pleurostylodon recticrista* (Ameghino), type, M.A.C.N. No. 10590, fragment of right lower jaw with dm_4 and M_1. Crown view. ×1.5.

10. *Acoelohyrax coronatus* Ameghino, type or lectotype, M.A.C.N. No. 10781, left P^4. Crown view. ×1.35.

1



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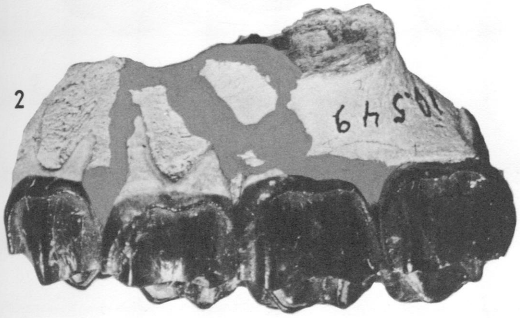

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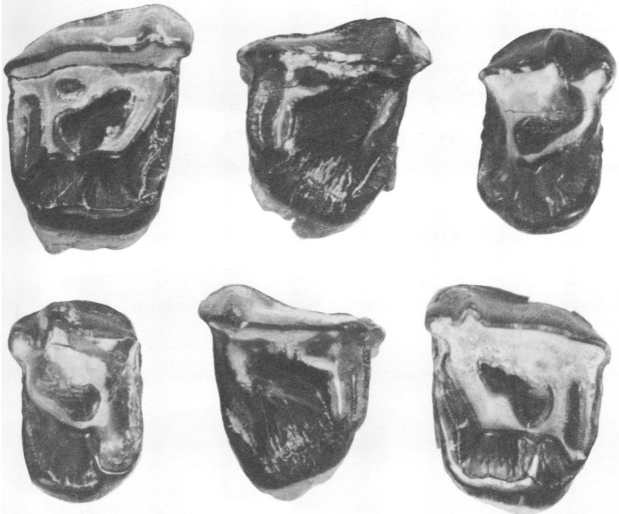

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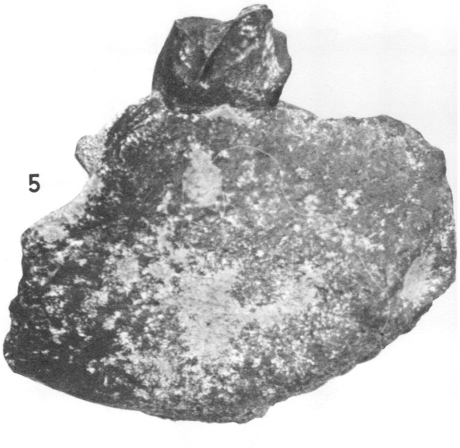

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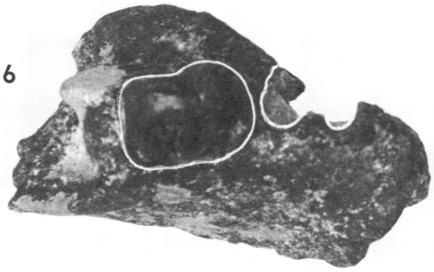

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PLATE 26

ISOTEMNIDAE

1,2. *Anisotemnus distentus* (Ameghino), type or lectotype, M.A.C.N. No. 10588, right P^2–M^2. 1. Crown view. 2. Buccal view. Both ×1.

3, 4. *Acoelohyrax complicatissimus* (Ameghino), lectotype or syntype, M.A.C.N. No. A55-1. 3. Right P^4–M^3. Crown view. *Ca.* ×1. 4. Left M^{2-3}. Crown view. *Ca.* ×1.

5–7. *Anisotemnus distentus* (Ameghino). 5, 6. Type or syntype, M.A.C.N. No. 10588. right P_2–M_3, probably same individual as is shown in figures 1 and 2. 5. Crown view, 6. Buccal view. Both ×1. 7. M.A.C.N. No. 10615, broken right M^2 (type of the synonym *Isotemnus lophiodontoides* Ameghino). Crown view. ×1.

8. *?Acoelohyrax coarctatus* (Ameghino), M.A.C.N. No. 10966B, left ?M^2. Crown view. ×1.

9. *Acoelohyrax complicatissimus* (Ameghino), type or syntype, M.A.C.N. No. A55-1, left M_3, probably same individual as is shown in figures 3, 4, and 11. Crown view. *Ca.* ×1.

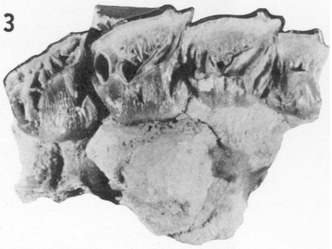
10. *?Acoelohyrax coarctatus* (Ameghino), syntype (not lectotype), M.A.C.N. No. 10966A, fragment of left lower jaw with P_{1-4}. Crown view. ×1.

11. *Acoelohyrax complicatissimus* (Ameghino), type or syntype, M.A.C.N. No. A55-1, right P_4–M_2, probably the same individual as is shown in figures 3, 4, and 9. Crown view. *Ca.* ×1.

12. *?Acoelohyrax coalitus* (Ameghino), type, M.A.C.N. No. 10964, fragment of right lower jaw with P_4–M_1. Crown view. ×1.

13. *?Acoelohyrax coarctatus* (Ameghino), lectotype, M.A.C.N. No. 10965A, fragment of left lower jaw with P_4–M_3. Crown view. ×1.

1



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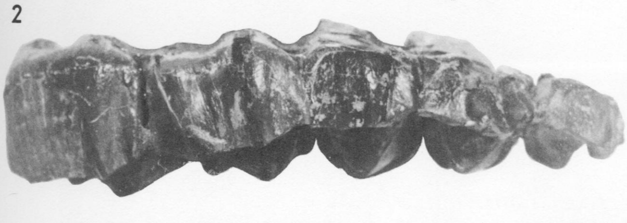

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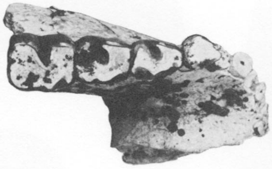

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PLATE 27

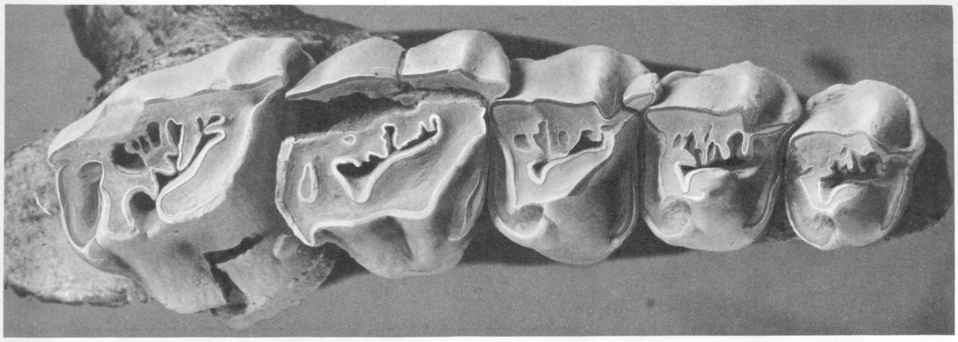
ISOTEMNIDAE

1, 2. *?Acoelohyrax* sp., A.M.N.H. No. 29487, part of right maxilla with P^2–M^2. 1. Crown view. 2. Buccal view. Both ×2.75.

3, 4. *?Acoelohyrax sigma* (Ameghino), type, M.A.C.N. No. 10967, part of left lower jaw with M_{1-3}. 3. Crown view. 4. Buccal view. Both ×1.33.

5–8. *Isotemnus primitivus* Ameghino. 5–7. Type, M.A.C.N. No. 10556, part of right maxilla with P^2–M^2. 5. Crown view. ×1. 6. Buccal view. ×1. 7. Lingual view. ×1. 8. M.A.C.N. No. 10583, right M^{1-2} (type of the synonym *Isotemnus conspiquus* Ameghino). Crown view. ×1.33.

1



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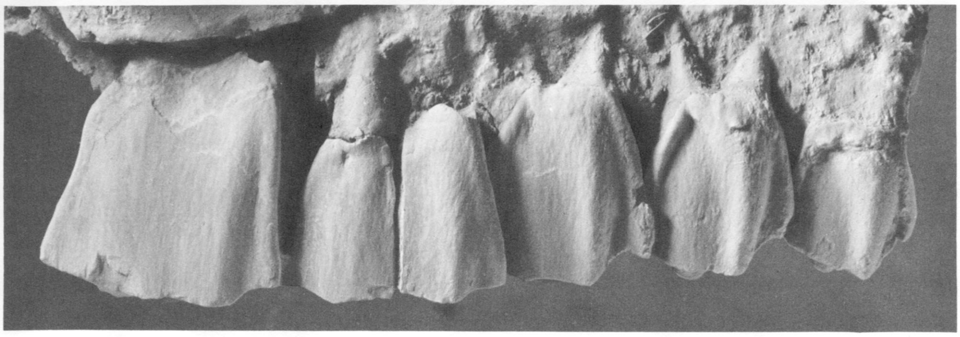

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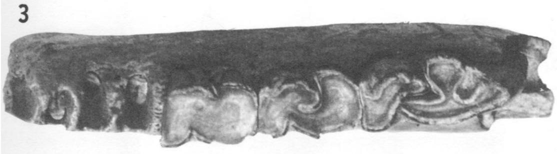

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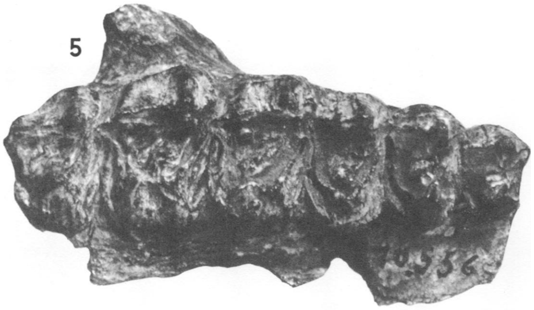

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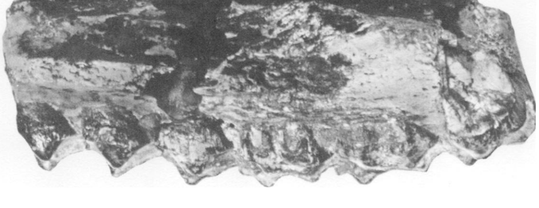

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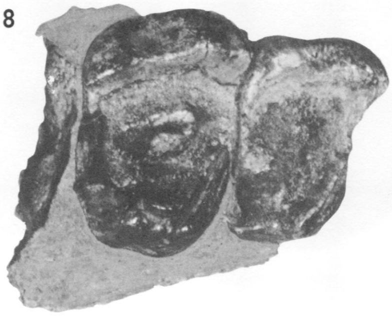

PLATE 28

Isotemnus primitivus Ameghino

1–3. A.M.N.H. No. 28666, right M_{1-3}. 1. Crown view. 2. Buccal view. 3. Lingual view.

4–6. A.M.N.H. No. 28940, right P_3–M_2. 4. Crown view. 5. Buccal view. 6. Lingual view.

All ×1.5.

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PLATE 29

1–3. *Isotemnus primitivus* Ameghino, C.N.H.M. No. P13441, left P_4–M_2. 1. Crown view. 2. Buccal view. 3. Lingual view.

All ×1.9.

1

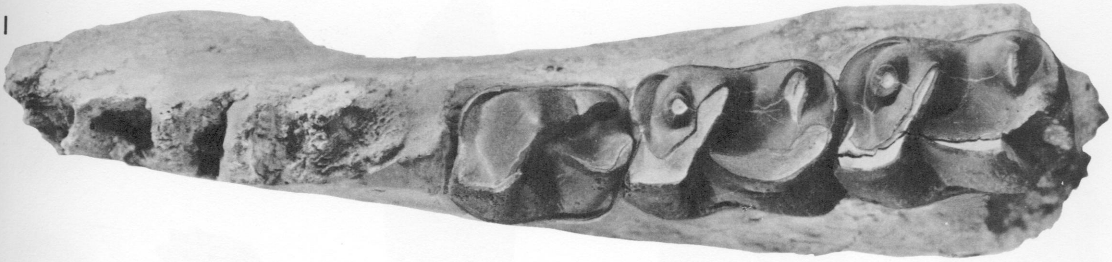

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PLATE 30

Isotemnus

1–4. *Isotemnus primitivus* Ameghino. 1, 2. M.A.C.N. No. 10593, part of left lower jaw with P_2–M_2 (type of the synonym *Trimerostephanos angustus* Ameghino). 1. Crown view. 2. Buccal view. 3, 4. M.A.C.N. No. 10623, associated M_{2-3} (type of the synonym *Amphitemnus transitorius* Ameghino). 3. Crown view. 4. Lingual view.

5–7. *Isotemnus latidens* Ameghino. 5. Type, M.A.C.N. No. 10667, fragment of left lower jaw with M_{1-2}. Crown view. 6. M.A.C.N. No. 10587, fragment of right maxilla with incomplete P^4–M^3 (type of the synonym *Isotemnus enecatus* Ameghino). Crown view. 7. M.A.C.N. No. 10594, fragment of left lower jaw with M_1 (lectotype of the synonym *Eochalicotherium robustum* Ameghino). Crown view.

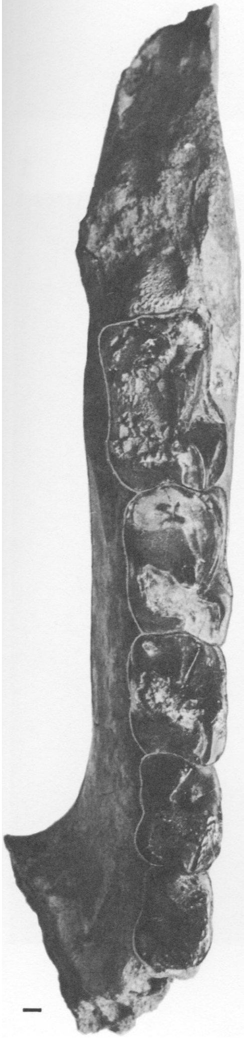
8. *Isotemnus primitivus* Ameghino, M.A.C.N. No. 10619, broken left M^3 (type of the synonym *Amphitemnus nucleatus* Ameghino). Crown view.

9. *Isotemnus latidens* (Ameghino), M.A.C.N. No. 10601, fragment of right lower jaw with M_2 and part of M_1 (type of the synonym *Eochalicotherium crassidens* Ameghino). Crown view.

10. *?Isotemnus colhuehuapiensis* (Ameghino), type, M.A.C.N. No. 10604, part of left lower jaw with P_4–M_3. Crown view.

11, 12. *Isotemnus latidens* (Ameghino), M.A.C.N. No. 10614, part of right maxilla with P^3–M^2 (type of the synonym *Isotemnus apicatus* Ameghino). 11. Crown view. 12. Buccal view.

All ×1.25.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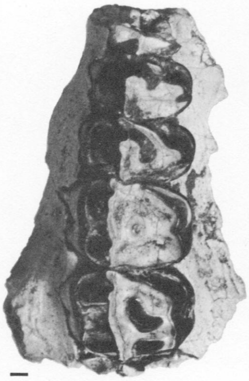
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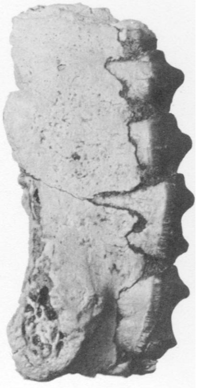
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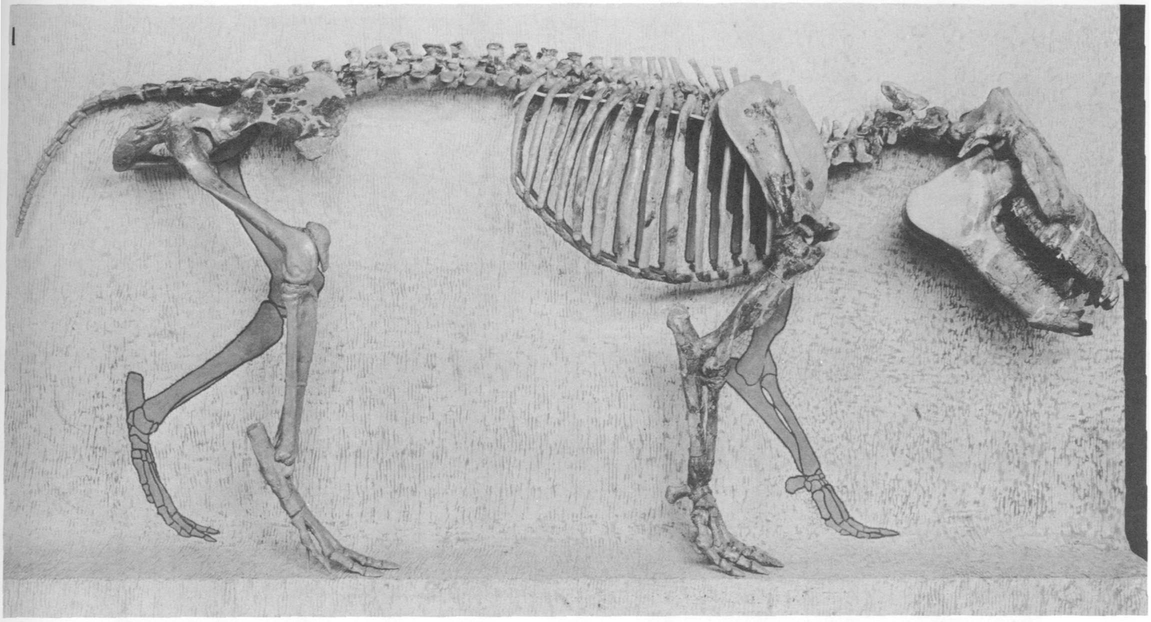
PLATE 31

1, 2. *Thomashuxleya externa* Ameghino, A.M.N.H. Nos. 28447 (skull) and 28905 (postcranial skeleton), mounted skeleton, partly restored. 1. Right lateral view. 2. Oblique right anterior view.

Not to scale.

1



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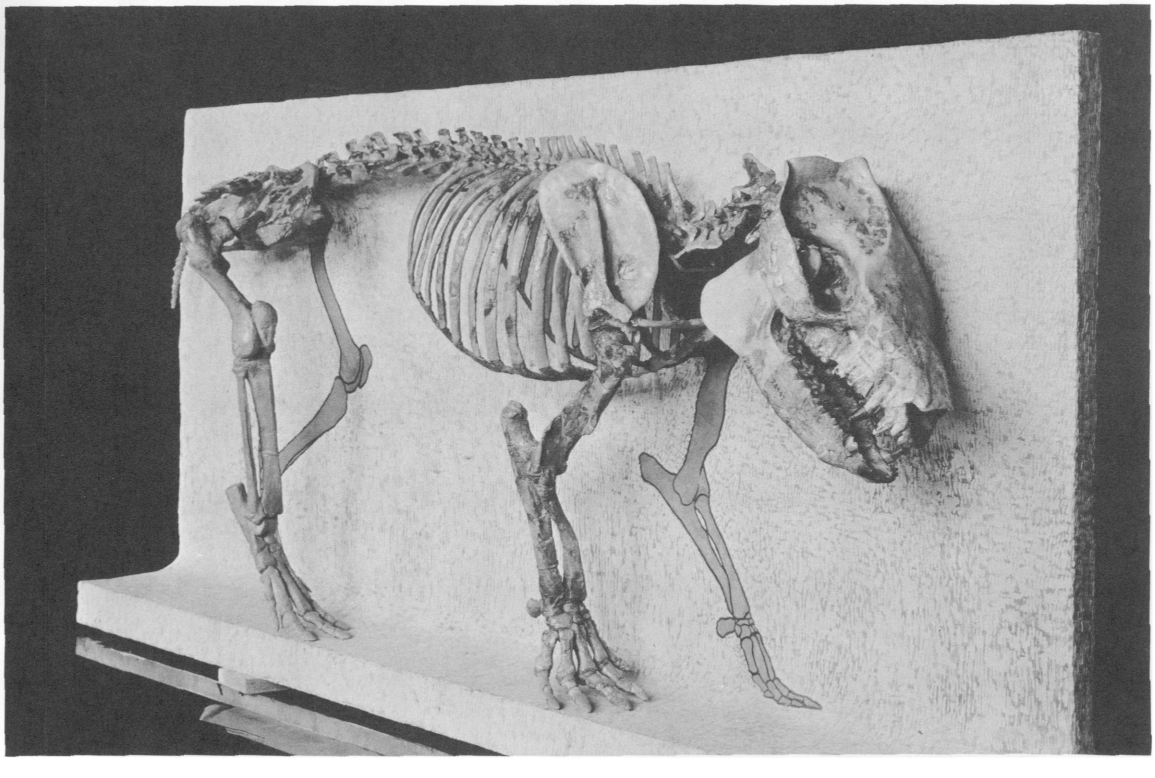
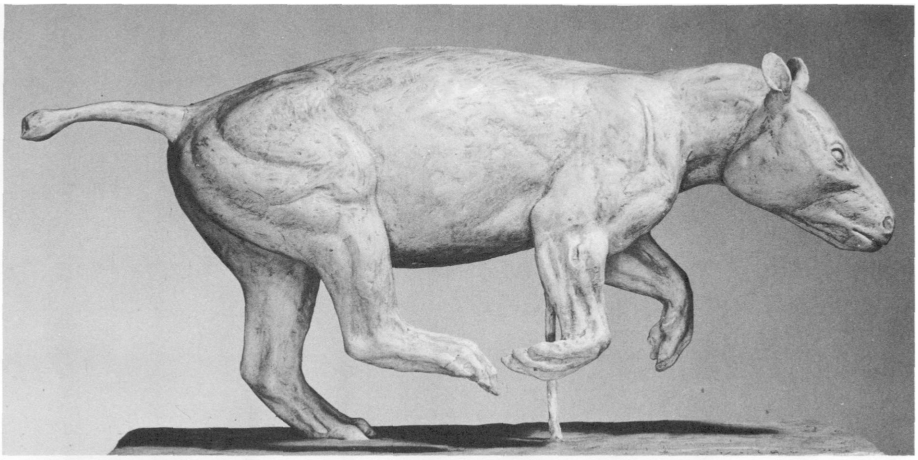


PLATE 32

1–3. *Thomashuxleya externa* Ameghino, restoration by France Baker under the author's direction, based on the mount shown in plate 31. 1. Right lateral view. 2. Left lateral view. 3. Oblique right anterior view.

Not to scale.

1



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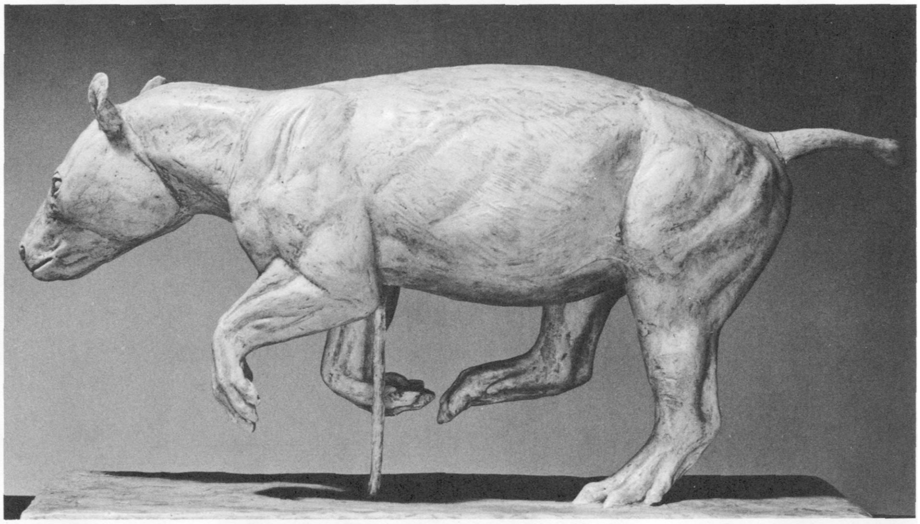

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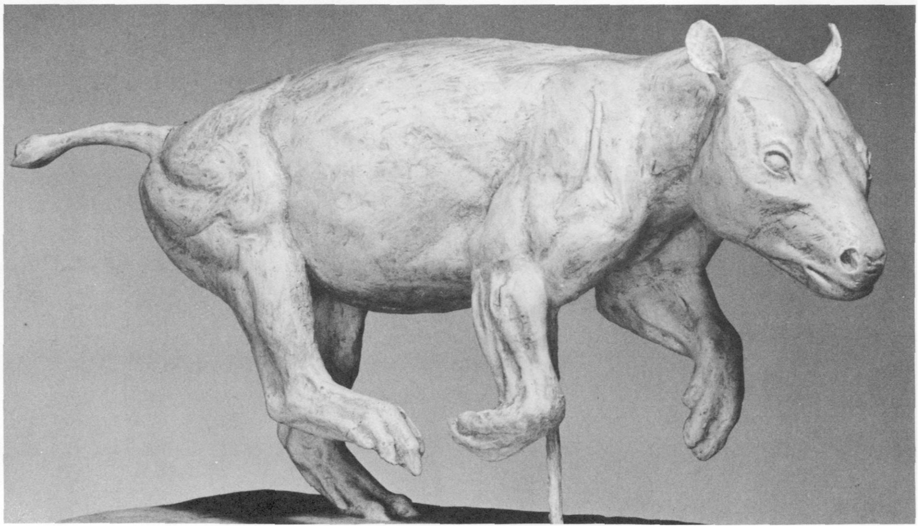

PLATE 33

Thomashuxleya rostrata AMEGHINO

1, 2. Type or lectotype, M.A.C.N. No. 10370, part of left lower jaw with I_2–P_4. 1. Crown view. 2. Buccal view. Both ×0.75.

3, 4. Type or syntype, M.A.C.N. No. 10370, part of left upper jaw with I^1–P^4, possibly the same individual that is shown in figures 1 and 2. 3. Crown view. 4. Buccal view. Both ×0.75.

5, 6. M.A.C.N. No. 10542, left M^{1-3}. 5. Crown view. 6. Buccal view. Both ×1.


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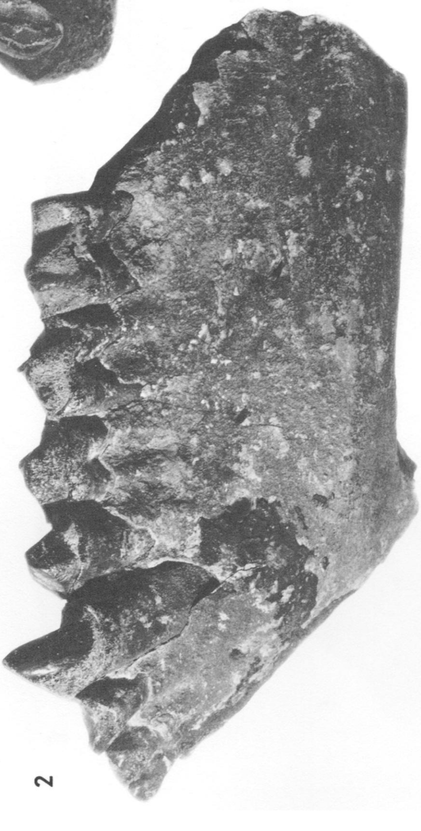
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PLATE 34

ISOTEMNIDAE

1. *Thomashuxleya externa* Ameghino, M.A.C.N. No. 10540, part of left lower jaw with broken P_3–M_3 (type of the synonym *Thomashuxleya artuata* Ameghino). Crown view. ×1.

2. *Thomashuxleya rostrata* Ameghino, M.A.C.N. No. 10539, part of right lower jaw with P_4–M_3. Crown view. ×0.75.

3. *Thomashuxleya externa* Ameghino, type, M.A.C.N. No. 10537, part of left lower jaw with P_4–M_2. Crown view. ×1.

4. *Periphragnis harmeri* Roth, M.L.P. No. 12-2197, probably associated right P^3–M^2 (type of the synonym *Calodontotherium varietatum* Roth). Crown view. *Ca.* ×1.

5. *Periphragnis* sp., M.L.P. No. 12-1711, forefoot. Dorsal view. ×0.64.

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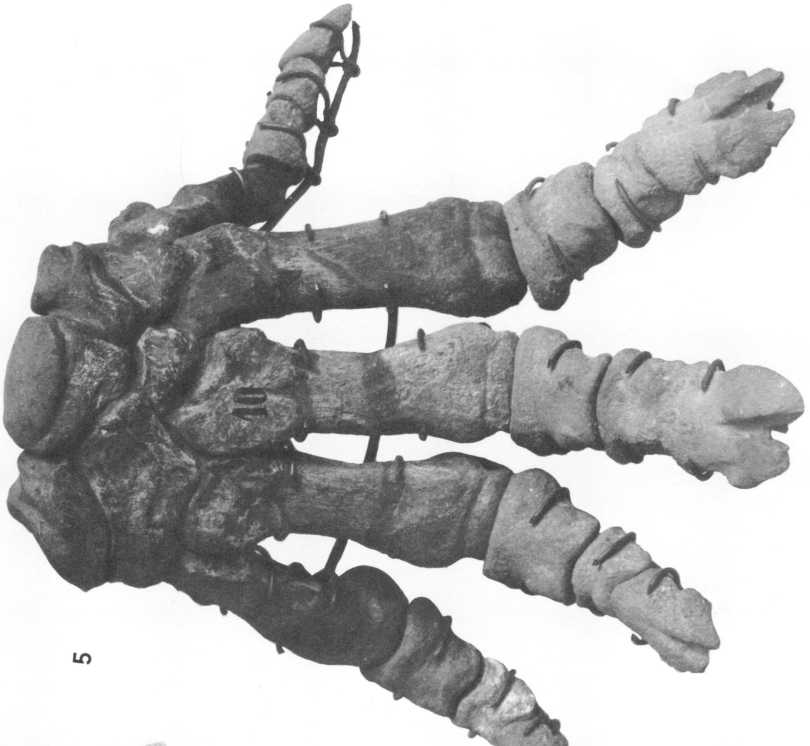

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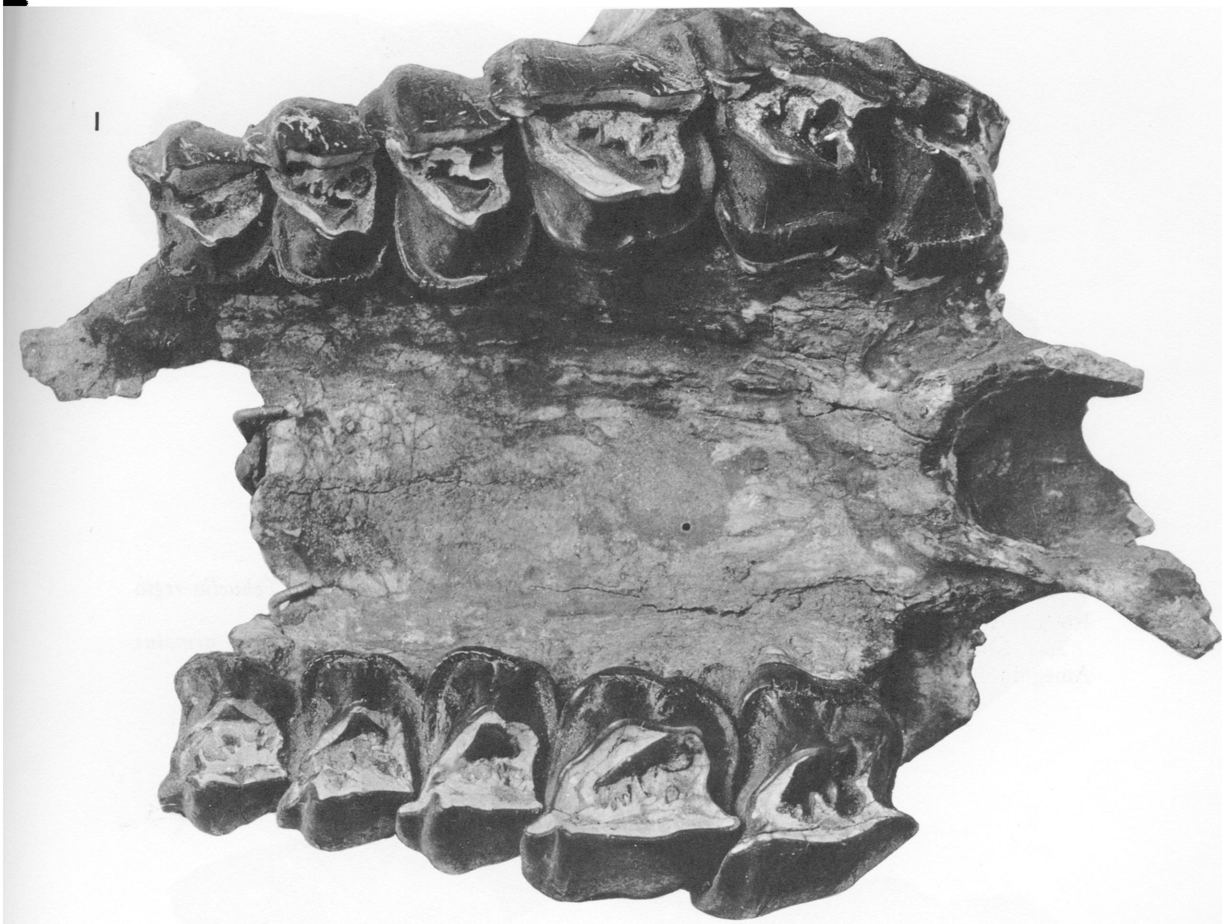
PLATE 35

1, 2. *Periphragnis harmeri* Roth, type, M.L.P. No. 12-1769. 1. Palate with left P^2–M^3 and right P^2–M^2. Palatal view. ×1. 2. Left P^2–M^3 only. Crown view. Slightly more than ×1.

1



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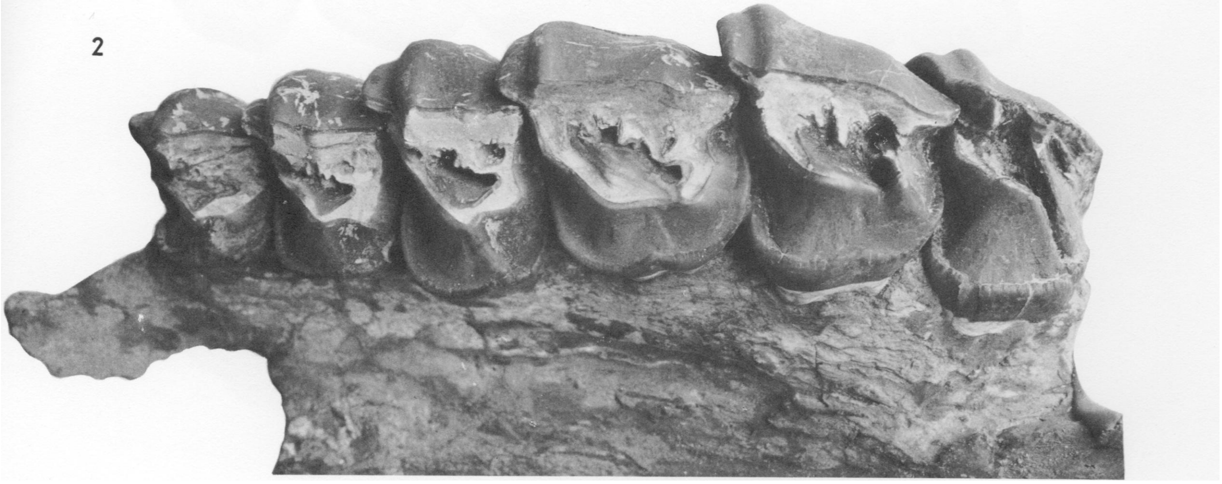


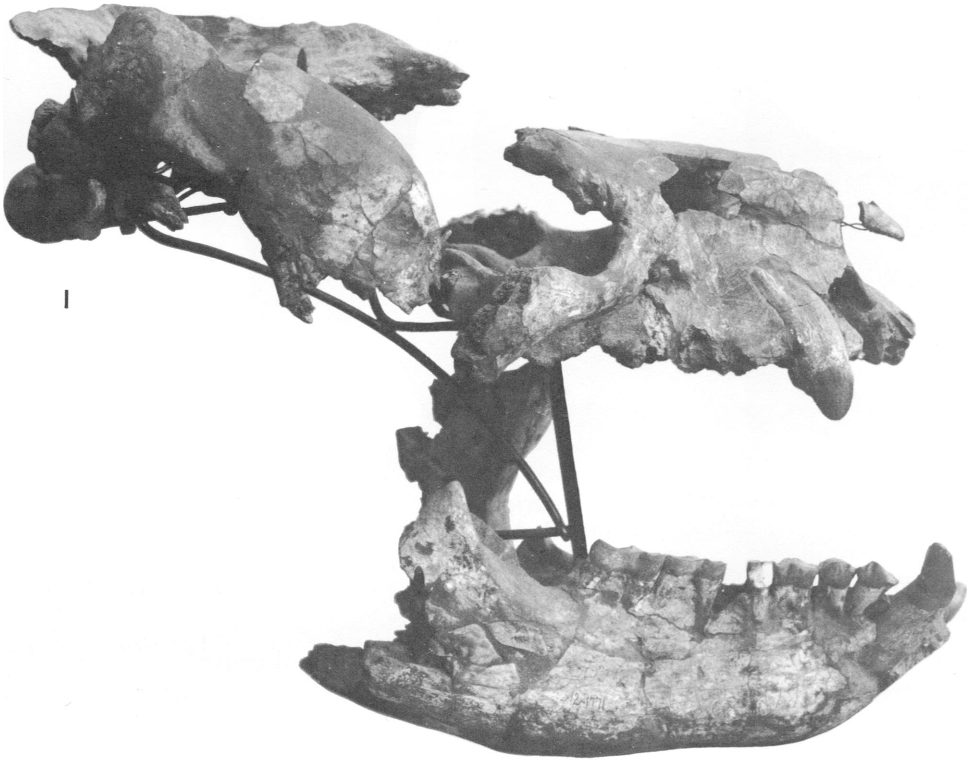
PLATE 36

Periphragnis harmeri Roth

1. M.L.P. No. 12-1771, partial skull and mandible (type of the synonym *Tehuelia regia* Roth). Right lateral view. *Ca.* ×0.33.

2, 3. M.A.C.N. No. 10925, right P^2–M^3 (lectotype of the synonym *Asmodeus armatus* Ameghino). 2. Crown view. 3. Buccal view. Both ×1.

1



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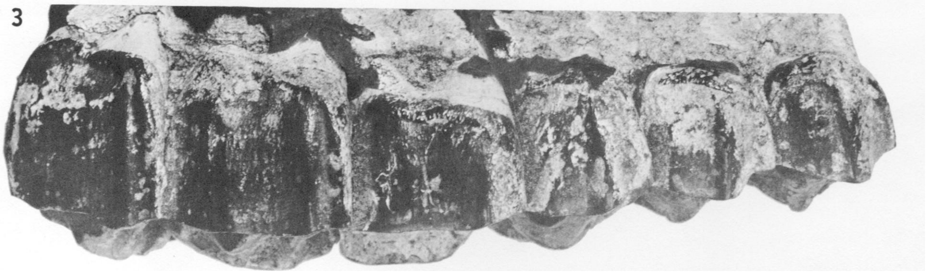

PLATE 37

Periphragnis

1. *Periphragnis harmeri* Roth, M.L.P. No. 12-1714, partial skull. Ventral view. *Ca.* ×0.5.

2. *Periphragnis exauctus* (Ameghino), type, M.A.C.N. No. 10926, part of left lower jaw with P_2–M_3. Crown view. *Ca.* ×0.75.

3, 4. *Periphragnis harmeri* Roth. 3. M.L.P. No. 12-1708, right P_3–M_3. Crown view. ×1. 4. M.L.P. No. 12-1705, part of left lower jaw with P_3–M_3 (lectotype of the synonym *Periphragnis cristatus* Roth). Crown view. *Ca.* ×0.8.

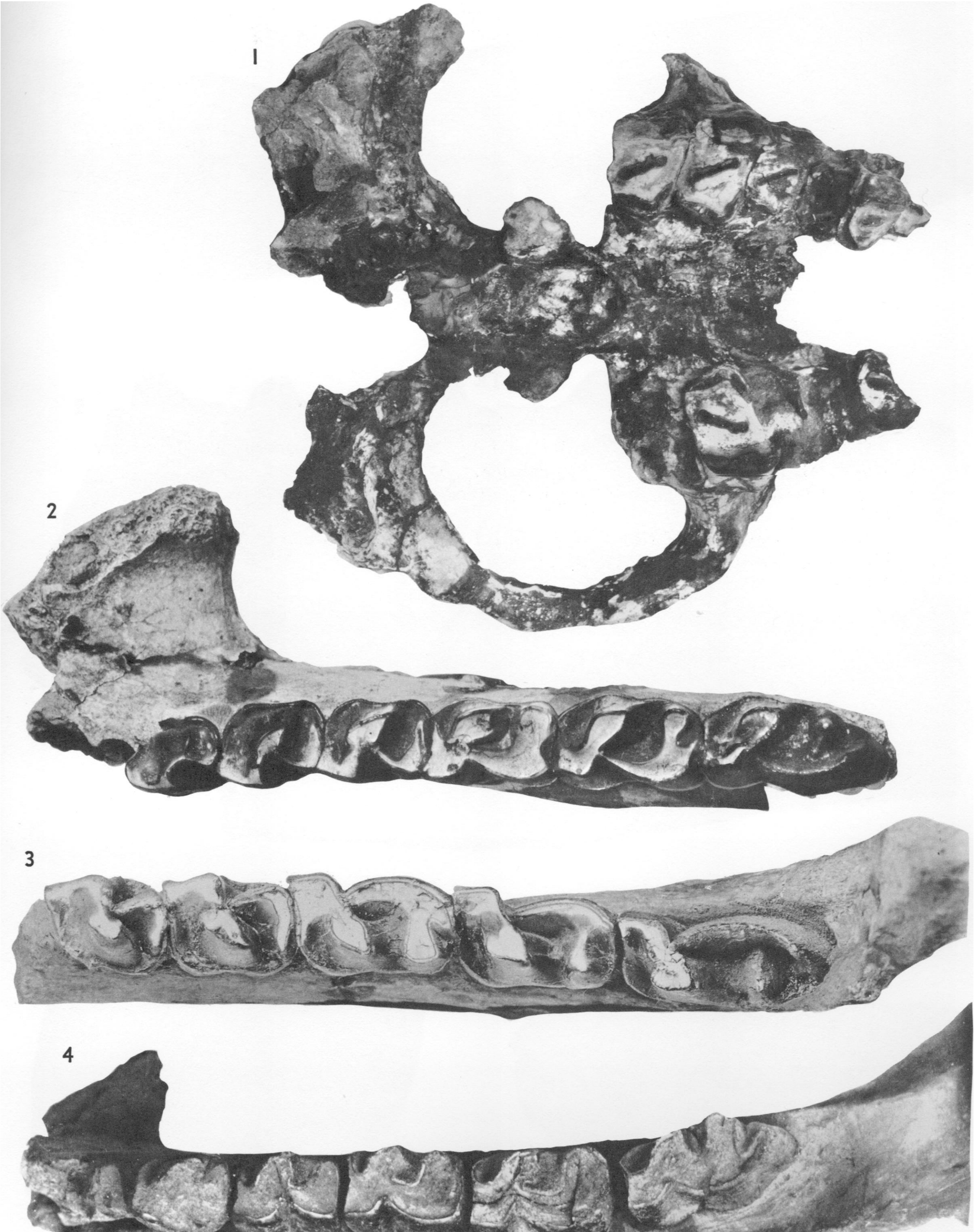
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PLATE 38

Periphragnis

1, 2. ***Periphragnis exauctus*** (Ameghino), M.A.C.N. No. 10928, part of right lower jaw with P_4–M_3. 1. Crown view. 2. Lingual view. Both *ca.* ×0.9.

3. ***?Periphragnis circunflexus*** (Ameghino), type, M.A.C.N. No. 10896, right P_4–M_1. Buccal view. ×1.

4. ***Periphragnis palmeri*** (Roth), type, M.L.P. No. 12-1737, fragment of right maxilla with M^{1-2}. Crown view. *Ca.* ×1.

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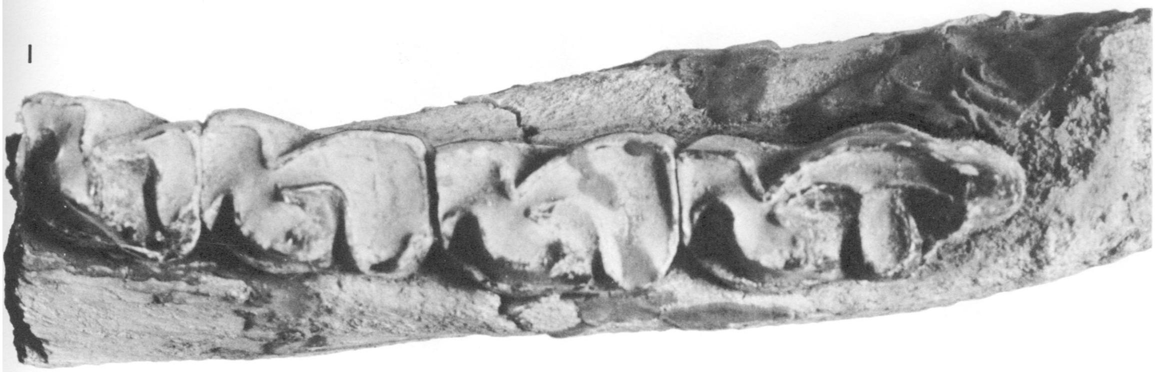

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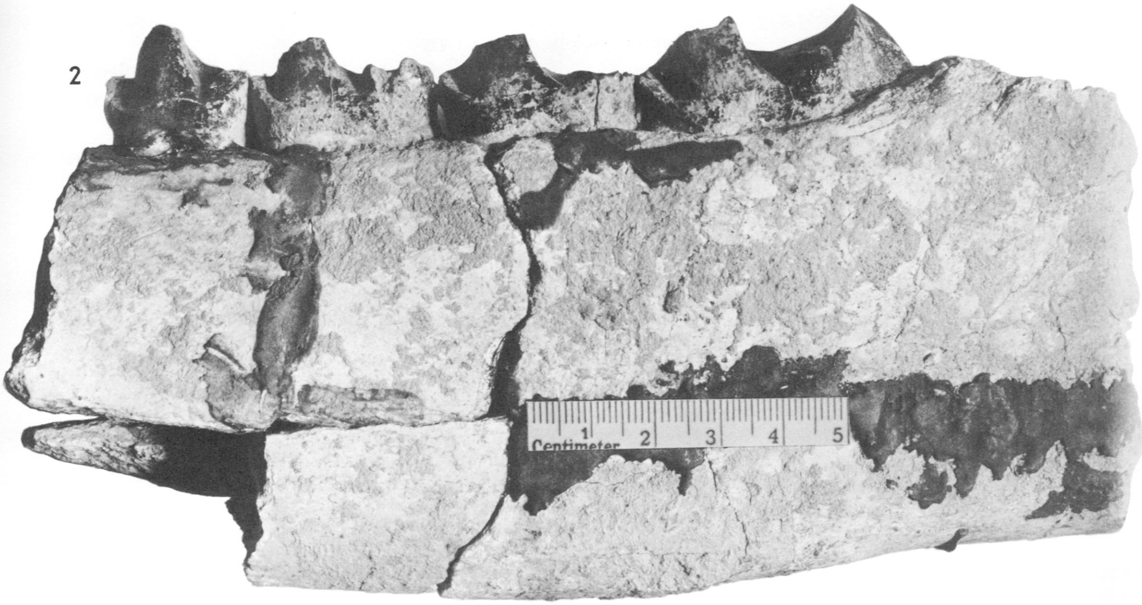

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PLATE 39

Rhyphodon lankesteri ROTH

1, 2. Type, M.L.P. No. 12-1717, partial skull. 1. Left lateral view. 2. Dorsal view.

3. M.L.P. No. 12-1744, partial skull (type of the synonym *Setebos terribilis* Roth). Dorsal view.

All ×0.5.

1

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PLATE 40

ISOTEMNIDAE

1. *Rhyphodon lankesteri* Roth, M.L.P. No. 12-2186, palate with right P^2–M^1 and left P^2–M^2 (type of the synonym *Pehuenia wehrlii* Roth). Palatal view. ×0.9.

2–4. *Distylophorus alouatinus* (Roth). 2. Unnumbered specimen in the Museo de La Plata, right ?I^3–M^2. Crown view. Scale not known but probably *ca.* ×1. 3, 4. Type, M.L.P. No. 12-2210, right I_1–M_3. 3. Crown view. 4. Buccal view. Both *ca.* ×1.

1

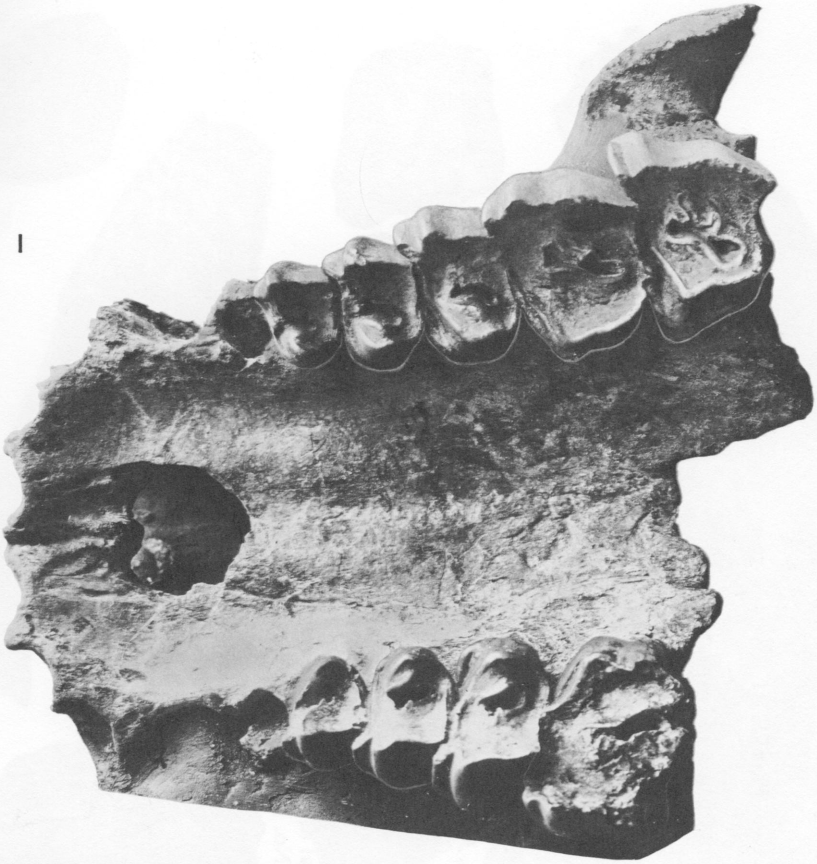

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PLATE 41

?ISOTEMNIDAE AND NOTOHIPPIDAE

1. *Lafkenia sulcifera* Roth, type, M.L.P. No. 12-1461, right upper molar. Crown view. ×1.

2. *Colhuelia fruhi* Roth, lectotype, M.L.P. No. 12-2216, left upper deciduous molar. Crown view. *Ca.* ×1.

3. "*Trigonolophodon*" *modicus* Roth, type, M.L.P. No. 12-2190, left upper molar. Crown view. *Ca.* ×1.

4. "*Pehuenia*" *magna* Roth, type, M.L.P. No. 12-2189, left upper molar. Crown view. *Ca.* ×1.

5. *Lafkenia schmidti* Roth, type, M.L.P. No. 12-2188, fragment of right maxilla with two deciduous molars. Crown view. *Ca.* ×1.

6. *Colhuapia rosei* Roth, type, M.L.P. No. 12-2221, right upper deciduous molar. Crown view. *Ca.* ×1.

7–12. *Eomorphippus obscurus* Ameghino. 7. Syntype (not lectotype), M.A.C.N. No. 10917, left M^1 or M^2. Crown view. ×0.86. 8. Syntype (not lectotype), M.A.C.N. No. 10917 (not the same individual as is shown in figure 7), right M^1 or M^2. Crown view. ×0.86. 9. Lectotype, M.A.C.N. No. 10917 (not the same individual as is shown in figure 7 or that shown in figure 8), left M^3. Crown view. ×0.86. 10. M.A.C.N. No. 10904, right upper premolar (type of the synonym *Pseudostylops subquadratus* Ameghino). Crown view. *Ca.* ×1. 11. M.A.C.N. No. 10914, right M_3. Lingual view. ×0.9. 12. A.M.N.H. No. 29462, fragment of right maxilla with M^{2-3}. Crown view. *Ca.* ×1.5.

13–15. ?*Eomorphippus pascuali*, new species. 13. Type, A.M.N.H. No. 29405, left P^2–M^2. Crown view. ×1.6. 14, 15. A.M.N.H. No. 29474, right lower jaw with I_3–M_3. 14. Buccal view. 15. Crown view. Both ×1.4.

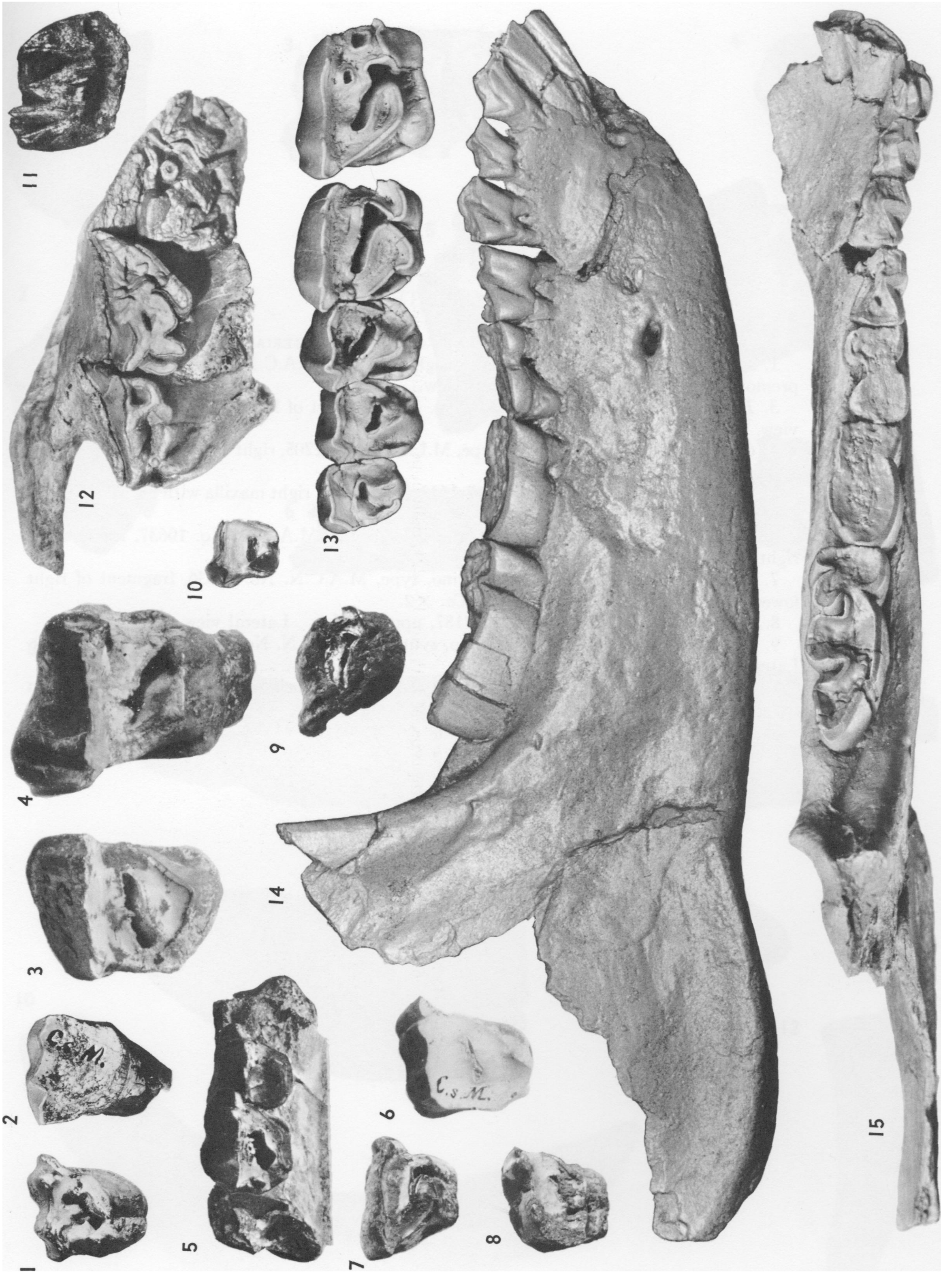
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PLATE 42

NOTOUNGULATA AND ASTRAPOTHERIA

1, 2. *Carolodarwinia pyramidentata* Ameghino, type, M.A.C.N. No. 10900, right upper premolar. 1. Crown view. 2. Buccal view. Both ×1.

3. *Puelia plicata* Roth, type, M.L.P. No. 12-1536, part of left maxilla with P^{2-3}. Crown view. *Ca.* ×2.

4. *Ortholophodon prolongus* Roth, type, M.L.P. No. 12-2205, right lower premolar. Crown view. *Ca.* ×2.

5. *Puelia plicata* Roth, M.L.P. No. 12-1533, fragment of right maxilla with P^2–M^1. Crown view. *Ca.* ×2.

6. *Lophiodonticulus patagonicus* Ameghino, lectotype, M.A.C.N. No. 10637, fragment of right lower jaw with M_{1-2}. Crown view. *Ca.* ×2.

7. *Lophiodonticulus retroversus* Ameghino, type, M.A.C.N. No. 10636, fragment of right lower jaw with M_{1-2}. Lingual view. *Ca.* ×2.

8. *Astraponotus* sp., M.L.P. No. 12-2187, upper canine. Lateral view. *Ca.* ×0.71.

9. *Astraponotus assymmetrus* Ameghino, syntype, M.A.C.N. No. 10971, fragment of tusk. Lateral view. *Ca.* ×1.

10. *Astraponotus* sp., M.L.P. No. 12-2187 (not surely associated with the specimen shown in figure 8), lower canine. Lateral view. *Ca.* ×0.71.

11, 12. *Astraponotus assymmetrus* Ameghino, syntype, M.A.C.N. No. 10971, incisor. 11. Crown view. 12. Lingual view. Both *ca.* ×1.

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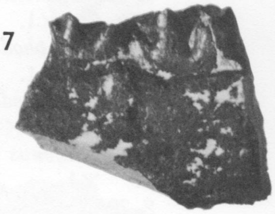

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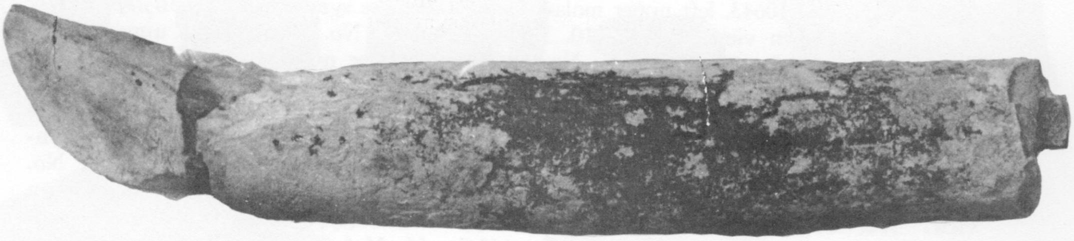

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PLATE 43

ASTRAPOTHERIA AND TRIGONOSTYLOPOIDEA

1. *Astraponotus holdichi* (Roth), type, M.L.P. No. 12-1471, right upper molar. Crown view. ×1.

2. *Astraponotus dicksoni* (Roth), type, M.L.P. No. 12-2217, right upper molar. Crown view. ×1.

3. *Astraponotus thompsoni* (Roth), type, M.L.P. No. 12-2181, right upper molar. Crown view. *Ca.* ×0.8.

4. *Astraponotus dilatatus* (Roth), type, M.L.P. No. 12-2182, left upper molar. Crown view. *Ca.* ×1.

5. *Grypolophodon morenoi* Roth, type, M.L.P. No. 12-1472, right upper premolar. Crown view. *Ca.* ×1.

6. *Grypolophodon imperfectus* Roth, type, M.L.P. No. 12-1460, right upper ?molar. Crown view. ×1.

7. *Blastoconus robertsoni* Roth, type, M.L.P. No. 12-2207, left upper premolar. Crown view. ×1.

8–20. *Trigonostylops wortmani* Ameghino. 8. M.A.C.N. No. 10645, left upper molar (lectotype of the synonym *Trigonostylops secondarius* Ameghino). Crown view. ×1.8. 9. M.A.C.N. No. 10643, left upper molar (lectotype of the synonym *Trigonostylops integer* Ameghino). Crown view. ×1.8. 10. Type, M.A.C.N. No. 10651, right upper molar. Crown view. ×1.9. 11. M.A.C.N. No. 10660, left upper molar (type of the synonym *Trigonostylops minimus* Ameghino). Crown view. ×1.9. 12. M.A.C.N. No. 10647, fragment of right maxilla with P^{3-4} (lectotype of the synonym *Trigonostylops scabellum* Ameghino). Crown view. ×1.8. 13. M.A.C.N. No. 10642, left M^{1-3} (type of the synonym *Trigonostylops subtrigonus* Ameghino). Crown view. ×1.9. 14. M.A.C.N. No. 10654, left upper molar (type of the synonym *Trigonostylops insumptus* Ameghino). Crown view. ×2. 15. M.A.C.N. No. 10656, right upper molar (type of the synonym *Trigonostylops trigonus* Ameghino). Crown view. ×1.8. 16. M.A.C.N. No. 10650, right upper molar (type of the synonym *Trigonostylops eximius* Ameghino). Crown view. ×1.9. 17. M.A.C.N. No. 10659, right M_2 (lectotype of the synonym *Trigonostylops hemicyclus* Ameghino). Crown view. ×1.9. 18. M.A.C.N. No. 10638, left upper molar (lectotype of the synonym *Trigonostylops columnifer* Ameghino). Crown view. ×1.9. 19. M.A.C.N. No. 10641, right upper molar (type of the synonym *Trigonostylops coryphodontoides* Ameghino). Crown view. ×2. 20. M.A.C.N. No. 10639, left upper molar (type of the synonym *Trigonostylops germinalis* Ameghino). Crown view. ×2.

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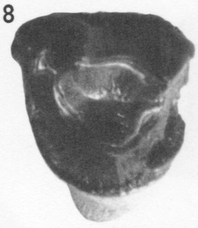

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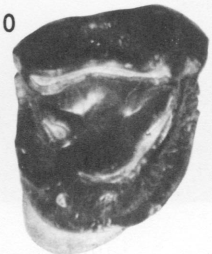

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PLATE 44

TRIGONOSTYLOPIDAE

1. *Trigonostylops gegenbauri* (Roth), type, M.L.P. No. 12-1736, symphysis and left ramus of lower jaw. Crown view. ×0.87.

2, 3. *Trigonostylops wortmani* Ameghino, M.A.C.N. No. 10627, left lower jaw with P_2–M_3. 2. Crown view. 3. Buccal view. Both ×1.

4. *Albertogaudrya unica* Ameghino, M.A.C.N. No. 12001, right lower jaw with P_2–M_3. Buccal view. Photograph by W. B. Scott. *Ca.* ×1.

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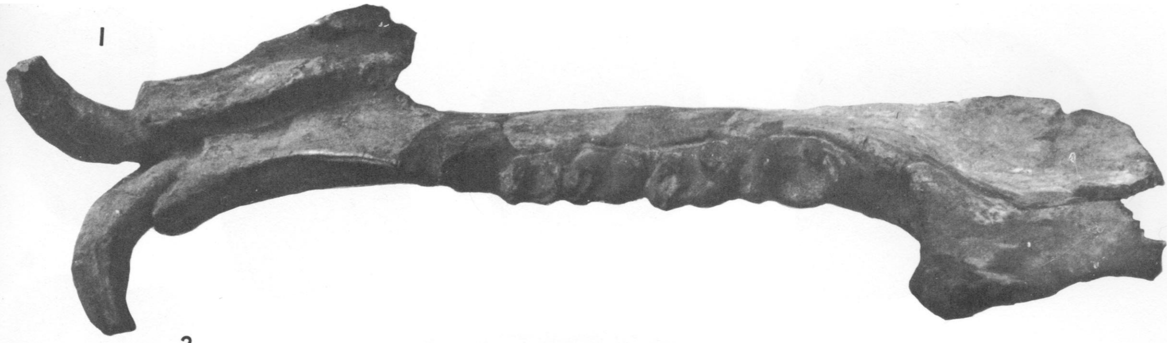

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PLATE 45

ASTRAPOTHERIA AND PYROTHERIA

1. *Hedralophus bicostatus* Ameghino, lectotype, M.A.C.N. No. 10938, left upper premolar. Crown view. ×1.

2–6. *Propyrotherium saxeum* Ameghino. 2. Lectotype, M.A.C.N. No. 10929, upper cheek tooth. Crown view. ×1. 3. Syntype (not lectotype), M.A.C.N. No. 10929, tusk. Lateral view. ×1. 4, 5. A.M.N.H. No. 29392, M^3 or M_3. 4. Crown view. 5. Lateral view. Both ×1. 6. Syntype (not lectotype), M.A.C.N. No. 10929, lower cheek tooth. Crown view. ×1.

7, 8. *Propyrotherium ?saxeum* Ameghino. 7. A.M.N.H. No. 29391, ?upper molar. Crown view. ×1. 8. A.M.N.H. No. 29394, ?lower molar. Crown view. ×1.

9. *Promoeritherium australe* Ameghino, type, M.A.C.N. No. 10903, tooth (position uncertain). Crown view. ×1.

10–13. *Carolozittelia tapiroides* Ameghino. 10, 11. Lectotype, M.A.C.N. No. 10666, part of right maxilla with M^{2-3}. 10. Crown view. *Ca.* ×1. 11. Lingual view. *Ca.* ×0.8. 12, 13. Syntype (not lectotype), M.A.C.N. No. 10666, fragment of left lower jaw with M_3. 12. Crown view. *Ca.* ×1. 13. Lingual view. *Ca.* ×0.8.

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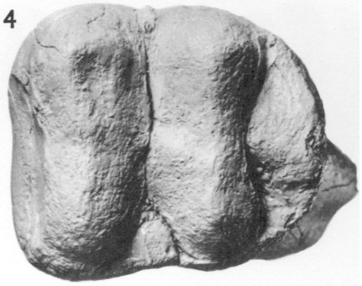

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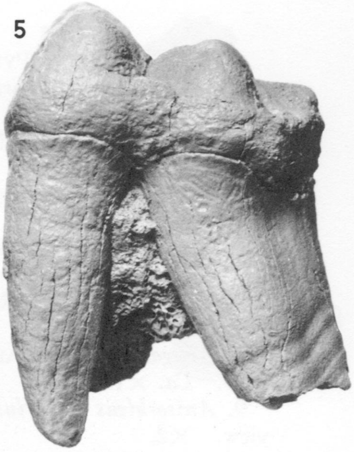

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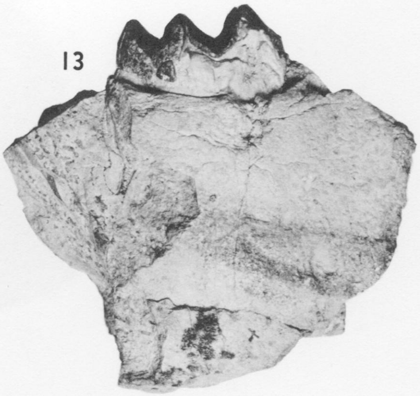

PLATE 46

PYROTHERIA, AND MAMMALIA INCERTAE SEDIS

1–4. *Carolozittelia tapiroides* Ameghino. 1, 2. Syntype (not lectotype), M.A.C.N. No. 10666, fragment of left lower jaw with M_2. 1. Crown view. *Ca.* ×1. 2. Buccal view. *Ca.* ×0.8. 3, 4. M.A.C.N. No. 10665, fragment of right lower jaw with M_3. 3. Crown view. 4. Lingual view. Both *ca.* ×1.

5. "*Stenogenium*" *aenigmaticum* Ameghino, type, M.A.C.N. No. 10899, fragment of symphysis without teeth. Dorsal view. ×1.

6. *Heterolophodon ampliatus* Roth, type, M.L.P. No. 12-2194, left upper molar. Crown view. *Ca.* ×1.

7. *Trilobodon brancoi* Roth, syntypes, M.L.P. No. 12-1465, two isolated teeth. Buccal views. ×1.5.

8. *Anagonia insulata* Ameghino, type, M.A.C.N. No. 10635, left lower premolar. Buccal view. *Ca.* ×1.35.

9. *Anisorhizus atriarius* Ameghino, type, M.A.C.N. No. 10620, cheek tooth. Crown view. ×2.

10. *Pachypithecus macrognathus* Ameghino, type, M.A.C.N. No. 10817, fragment of left lower jaw without teeth. Dorsal view. ×1.87.

11. *Prostylophorus margeriei* Roth, type, M.L.P. No. 12-2211, incisor. Lingual view. ×1.5.

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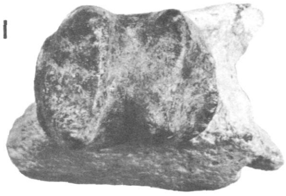

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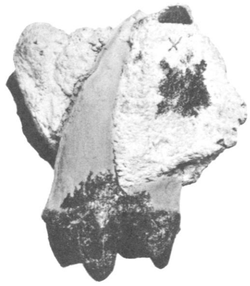

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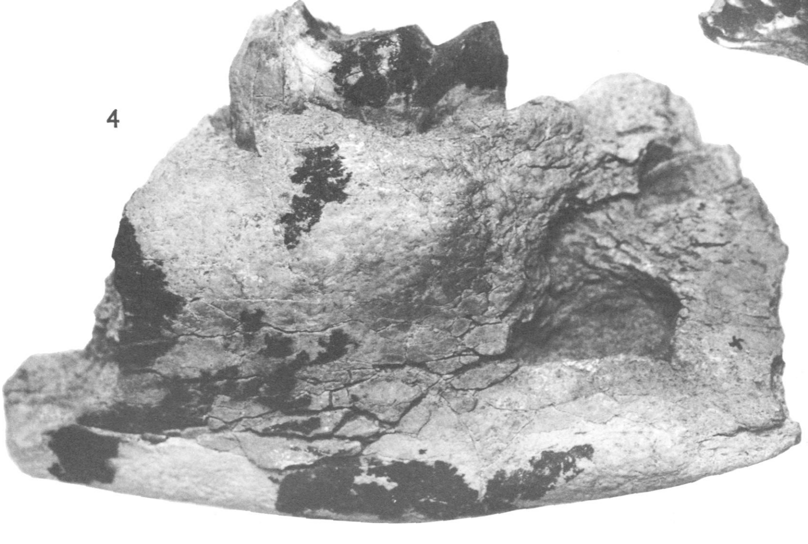

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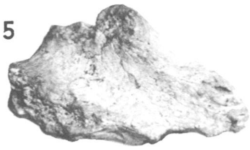

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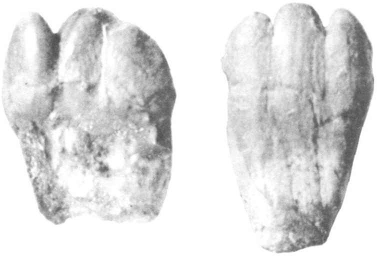

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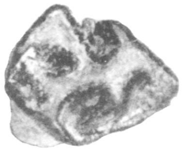

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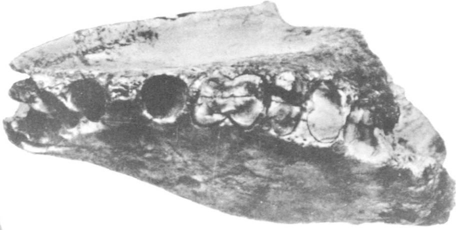

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