THE MAMMALIAN FAUNA OF THE DIVISADERO LARGO FORMATION, MENDOZA, ARGENTINA

By George Gaylord Simpson,
José Luis Minoprio, and
Bryan Patterson

With Seven Plates

No. 4 — *The Mammalian Fauna of the Divisadero Largo Formation, Mendoza, Argentina*

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INTRODUCTION

The presence of thick series of sedimentary rocks in the Andine precordillera of Mendoza has been known since the earliest days of geological exploration. In a general way, it was noted by Darwin, who visited the area in 1835 and published on its geology in 1846. It was early recognized that some of these sediments are Triassic, and studies concentrating on that part of the sequence have been numerous (see Minoprio, 1958, also review and extensive references in Romer, 1960). Demonstration that part of the post-Triassic sequence belongs somewhere in the Eogene was, however, comparatively tardy. The first definite proof of that fact was probably the discovery of a hegetothere (named *Ethegotherium* on a later page of this paper) in the region of Cerro Divisadero Largo some eight kilometers west of the city of Mendoza. In June, 1936, while on a botanical excursion, Adrián Ruiz Leal found a rock fragment that contained that specimen and took it to his home, where it remained until Minoprio became cognizant of it and asked Ruiz Leal for the fossil and for permission to study the occurrence (Minoprio, 1947).

From 1943 to 1946 Olivo Chiotti made a geological map and stratigraphic study of the region. His thesis has not been published, but the manuscript has been available to those interested and data from it have been included in several publications (especially Minoprio, 1947; Simpson and Minoprio, 1949). First recognition and definition of a Divisadero Largo formation were based on Chiotti's work. Chiotti found further vertebrate fossils, which were sent to the Museo de La Plata and tentatively identified, but not published upon, by Ángel Cabrera, who recognized their early Tertiary character and considered them possibly Eocene. Minoprio began his study of and collecting in the Divisadero Largo in connection with his identification of the first find

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and with Chiotti's field project. In 1946 Minoprio showed the fossil localities to Carlos Rusconi, who with M. Tellechea made further collections from the Divisadero Largo formation.

The first publications on the fauna were made independently and based on different collections by Minoprio (1947) and by Rusconi (1946a, b, c). Other specimens found by Minoprio have been described by Simpson and Minoprio (1949, 1950 [1]), and in extension of that work Minoprio (1951) published a preliminary stratigraphic note. Since then Minoprio has continued to collect in the Divisadero Largo as opportunity presented, and he discovered the important extension of the fossil-bearing beds to Papagallos, all earlier collections being from the type locality only. A number of other paleontologists and geologists, both Argentine and foreign, have visited the area through the years and most of them have picked up some specimens, but further publication has been only that by Patterson (1952) on one of the specimens found by Federico García Romeu and Osvaldo A. Reig in 1951. Patterson and Simpson visited the Divisadero Largo under Minoprio's guidance in 1952 and 1955 respectively, and in 1958 a joint expedition of the Museum of Comparative Zoology (Harvard University) and the Museo Argentino de Ciencias Naturales (Buenos Aires), including A. S. Romer and Patterson, made a collection there.

For the past ten years the present three authors have been accumulating further materials and observations with the hope of producing a more nearly definitive study of this important and peculiar fauna. Publication has been repeatedly deferred as new specimens required emendation or new problems called for better evidence. It is still quite impossible to produce anything like a definitive study or to solve all major problems, but we have decided that a halt must be called at this point and that what is now available should be published. We have been able to study most, although not quite all, of the mammalian fossils known to have been collected from the Divisadero Largo. So many people have picked up odd specimens that there are doubtless some of whose existence we are unaware. The most extensive collections by Minoprio have been studied not only by him but also, at first hand, by Simpson, and most of them also by Patterson. Other collections in Mendoza, Buenos Aires, and La Plata have been

[1] This is an abbreviated Spanish version of Simpson and Minoprio (1949). Through an editorial oversight, a genus and two species were said to be new in the Spanish version. They were in fact new in the English version published in the previous year.

studied especially by Patterson, among the present authors. Materials in New York and Cambridge have been studied by Simpson and Patterson. In this connection we are much indebted to the Museo de La Plata and Dr. Rosendo Pascual, the Museo Argentino de Ciencias Naturales and Dr. Noemí Cattoi, and the Museo de Historia Natural de Mendoza and Sr. Carlos Rusconi. The late Dr. Ángel Cabrera kindly provided Minoprio with extensive notes on the Chiotti collection in the Museo de La Plata, and his courtesy is gratefully recorded even though our treatment of that collection is based on first-hand study mainly by Patterson.

Some of the work included in this paper was done by Simpson while on the staff of the American Museum of Natural History and some manuscript drafted there was released for publication here. Copy for the new Figures 5-6 and 8-9 (drawn by John Le Grand) and for Plates 1-4 was provided by that museum, and the original copy for Figures 2-3, 16, and 21 and Plate 6 (photograph), previously published in Simpson and Minoprio (1949), was also furnished for reproduction here. We are glad to acknowledge this cooperation from what is now the Department of Vertebrate Paleontology of that institution and from Dr. E. H. Colbert, its present chairman.

Figures 4, 7, 10-15, 17, and 19-20 and Plate 6 (section) are new and have been drawn for the Museum of Comparative Zoology by Mrs. Dorothy H. Marsh, in some instances from sketches by Patterson, as indicated in the captions, and in others from the specimens. It is to be understood that Patterson's sketches were necessarily made rather rapidly and free-handedly. They are believed to represent structures adequately, but may not be exactly in scale as to details.

Simpson's visit to Mendoza in 1955 was a side trip made possible by his presence in southern Brazil under the auspices of the Conselho Nacional de Pesquisas of the United States of Brazil.

Patterson's studies of Divisadero Largo specimens in Argentina and his visit to the locality during 1952 were carried out during tenure of a John Simon Guggenheim Memorial Foundation Fellowship. The joint Museum of Comparative Zoology-Museo Argentino de Ciencias Naturales expedition was supported in part by grants from *Life* magazine and the National Science Foundation. To these organizations we express our sincere thanks.

In order to expedite this publication, we have confined it to the mammals. Rusconi (1946b, c) has described a bird, *Cunampaia simplex,* and a crocodilian, *Ilchunia parca,* from the Divisadero Largo, and Minoprio (1947) figured but did not name or identify a turtle carapace. Considerably more unpublished material of chelonians, crocodilians, and snakes is known to us. Some of those specimens are of great interest, but they evidently will not add significantly to the evidence of the mammals on the main problems presented by the fauna. Adequate treatment of the nonmammals will require considerable further study, preferably by specialists in the respective groups. At present we remark only that the bird *Cunampaia,* although its relationships have not been determined, definitely does not belong to the ''Stereornithes'' (Phororhacoidea), to which it was originally referred by Rusconi (see Patterson and Kraglievich, 1960).

The following designations are used for the various collections:

A.M.N.H. American Museum of Natural History, New York. In general these catalogue numbers are those of casts, not the originals, of specimens collected by Minoprio and now deposited in Argentine museums, but they thus precisely designate the originals.

M.A.C.N. Museo Argentino de Ciencias Naturales, Buenos Aires. These include the first discovery made by Ruiz Leal, other specimens collected by Minoprio, and still others by the joint M.C.Z.--M.A.C.N. expedition.

M.C.Z. Museum of Comparative Zoology at Harvard College, Cambridge. Collected by Patterson and others on the joint M.C.Z.–M.A.C.N. expedition.

M.H.N.M. Museo de Historia Natural de Mendoza, Mendoza. Specimens collected by Rusconi and Tellechea and by Minoprio.

M.L.P. Museo de La Plata, La Plata. Specimens collected by Chiotti and by Castro.

M.M.M.P. Museo Municipal de Ciencias Naturales y Tradicionales de Mar del Plata, Mar del Plata. Reference is to a single specimen (*Groeberia*), of which a description has already been published, collected by García Romeu and Reig. Other specimens in that collection were kindly made available to us for a time, but they apparently represent no species not otherwise known and it was eventually decided not to include them in this publication.

TAXONOMY

Order MARSUPIALIA Illiger, 1811

Superfamily CAENOLESTOIDEA Osborn, 1910

Family GROEBERIIDAE Patterson, 1952

Groeberiidae, Patterson, 1952, p. 39.

Known Distribution: Divisadero Largo Formation, Mendoza, Argentina.

Definition: Dental formula $\overline{1\cdot0\cdot0\cdot4}$ or possibly $\overline{1\cdot0\cdot1\cdot3}$. Incisor hypselodont, very long, with axis parallel to and near the midline of the symphysis, moderately large, laterally compressed, with enamel limited to the anterior face. A diastema between the incisor and the cheek teeth. Anterior cheek tooth (M_1 or perhaps P_3) not enlarged. Cheek teeth subequal in size, rooted, not multicuspidate, without cingula, with anteroexternal paraconid. Mandible extremely short and deep with rami divergent posteriorly. Symphysis fused, steeply sloping, extending posteriorly to behind the penultimate cheek tooth, with a median posterior projection beyond the level of the last cheek tooth. Fossa for the lingual muscles prominent on the labial side of the symphysis. Coronoid process strong, projecting, arising opposite the middle part of the cheek tooth series. Masseteric fossa large, without masseteric crest. Ventral border of the horizontal ramus inflected lingually.

GROEBERIA Patterson, 1952

Groeberia, Patterson, 1952, p. 39.
Type: G. minoprioi Patterson, 1952.
Known Distribution: As for the family.
Diagnosis: Sole known member of the family Groeberiidae.

GROEBERIA MINOPRIOI Patterson, 1952

Figure 1

G. minoprioi, Patterson, 1952, p. 39.
Type: M.M.M.P. No. 738 (Coll. Scaglia), symphysis and left ramus of the mandible with right and left incisors lacking their apices, and the four left cheek teeth, the first broken and the last represented only by the roots.
Hypodigm: Type, only.

Horizon and Locality: Divisadero Largo formation, probably from level F of the section by Minoprio (1951, p. 66), about one-half kilometer east of the Cerro Divisadero Largo, Mendoza, Argentina.
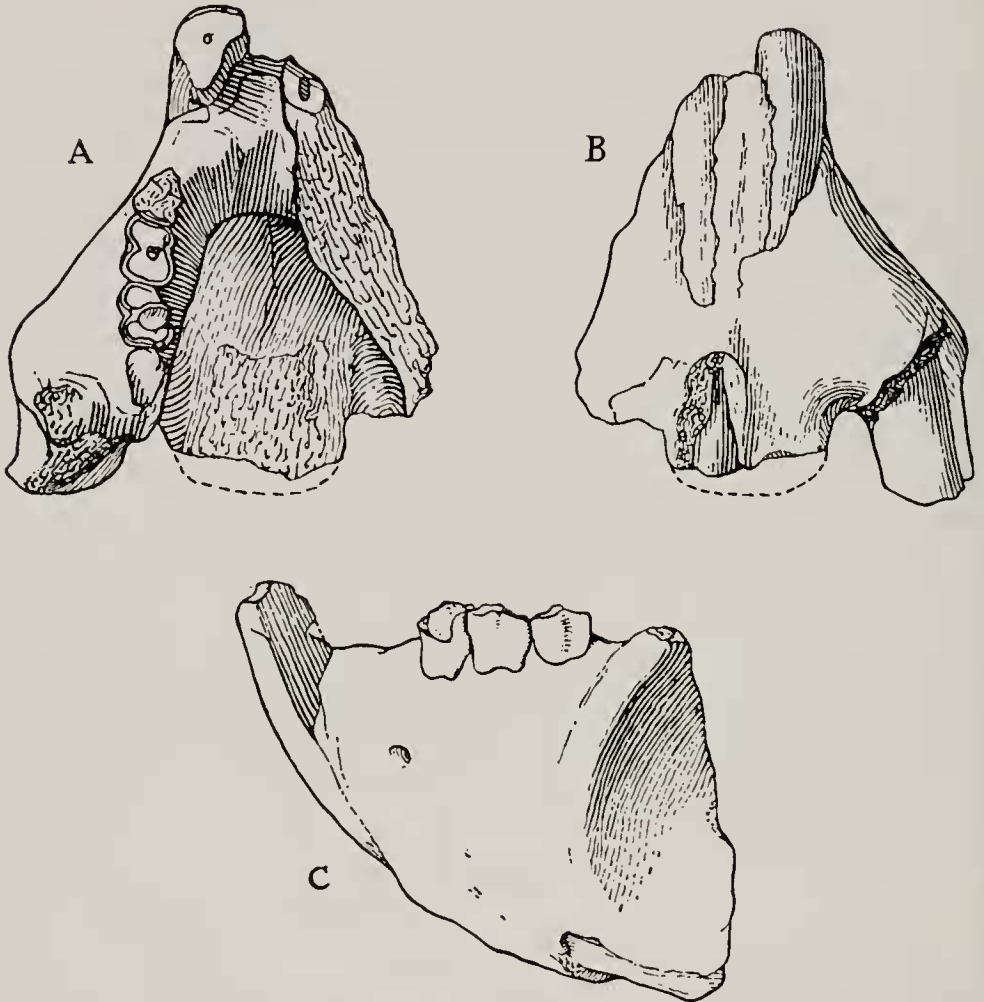

Fig. 1.   *Groeberia minoprioi.* M.M.M.P. No. 738 (Coll. Scaglia), type. A, dorsal view. B, ventral view. C, lateral view. X5. (After Patterson.)

Diagnosis: Only known species of *Groeberia.*

Affinities: This extraordinary little animal is so markedly unlike anything else known that its reference to monotypic genus and family can hardly be questioned. Broader affinities are somewhat uncertain, but Patterson (1952) pointed out resemblances to various caenolestoids that justify placing it in that superfamily, especially: probably inflected angular process, enlarged procumbent lower incisor with limited enamel band, strong and salient coronoid process, simple molars suggestive of some

caenolestids and excluding close comparison with, for example, rodents or notoungulates. No new specimens are available to us, and we can add nothing to the original description and discussion by Patterson (1952).

Order LITOPTERNA Ameghino, 1889

Family ADIANTHIDAE Ameghino, 1891

Simpson and Minoprio (1949) followed Patterson (1940) and what was then a consensus in considering Ameghino's Adianthidae as a subfamily, Adianthinae, of the Macraucheniidae. We now are in agreement that family separation is justified and we therefore return the group to the rank originally given it by Ameghino. It has considerable known diversity. Four generic groups, although somewhat confused in nomenclature and definition, have been rather clearly recognized and they belong to three or more different lines of descent. The now positively recorded time range is Deseadan to Santacrucian. The resemblances to macraucheniids are real but not detailed and seem to be convergent specializations, precocious in the adianthids, rather than indications of close affinity. Any phylogenetic connection between the two groups would almost have to be pre-Casamayoran and to date from the very beginning of litoptern differentiation.

There is doubt as to the proper spelling of the name now usually applied to the type genus and consequently also as to the name of the family. The spellings are *Adianthus* and Adianthidae in the original publication, where no derivation is given. Ameghino subsequently wrote *Adiantus* and Adiantidae, with no explanation of the emendation. Palmer (1904) quoted Ameghino (evidently from a personal letter) as saying that *Adianthus* was, "Par erreur, écrire *Adiantus*, ἀδίαντος, sec." That is puzzling as the appropriateness is far from apparent and Ameghino was not ordinarily given to such a solecism as using a Greek adjective as if it were a noun. In any case, it does seem probable that the original spelling, whether correctly derived or not, was intentional and we therefore retain it — as, in fact, did Palmer in the face of Ameghino's objection. It will be noted below that neither Adianthidae nor Adiantidae may after all be an available name for this family.

ADIANTOIDES Simpson and Minoprio, 1949

Adiantoides, Simpson and Minoprio, 1949, p. 6; 1950, p. 247.
Type: A. *leali* Simpson and Minoprio, 1949.
Known Distribution: Divisadero Largo formation, Mendoza, Argentina.
Diagnosis: A fully brachydont adianthid litoptern with dentition somewhat similar to that of *Proadiantus* but probably closer to *Adianthus.* P^2 obliquely triangular, smaller and less transverse than P^3. P^{3-4} similar but progressively larger, strongly transverse, with persistent median internal fossette, very large and prominent parastyle, and labial face of ectoloph posterior to the parastyle excavated, with basal cingulum. Postero-internal cingulum of P^4 barely larger than antero-internal cingulum and not cuspidate or projecting to form a hypocone. Upper
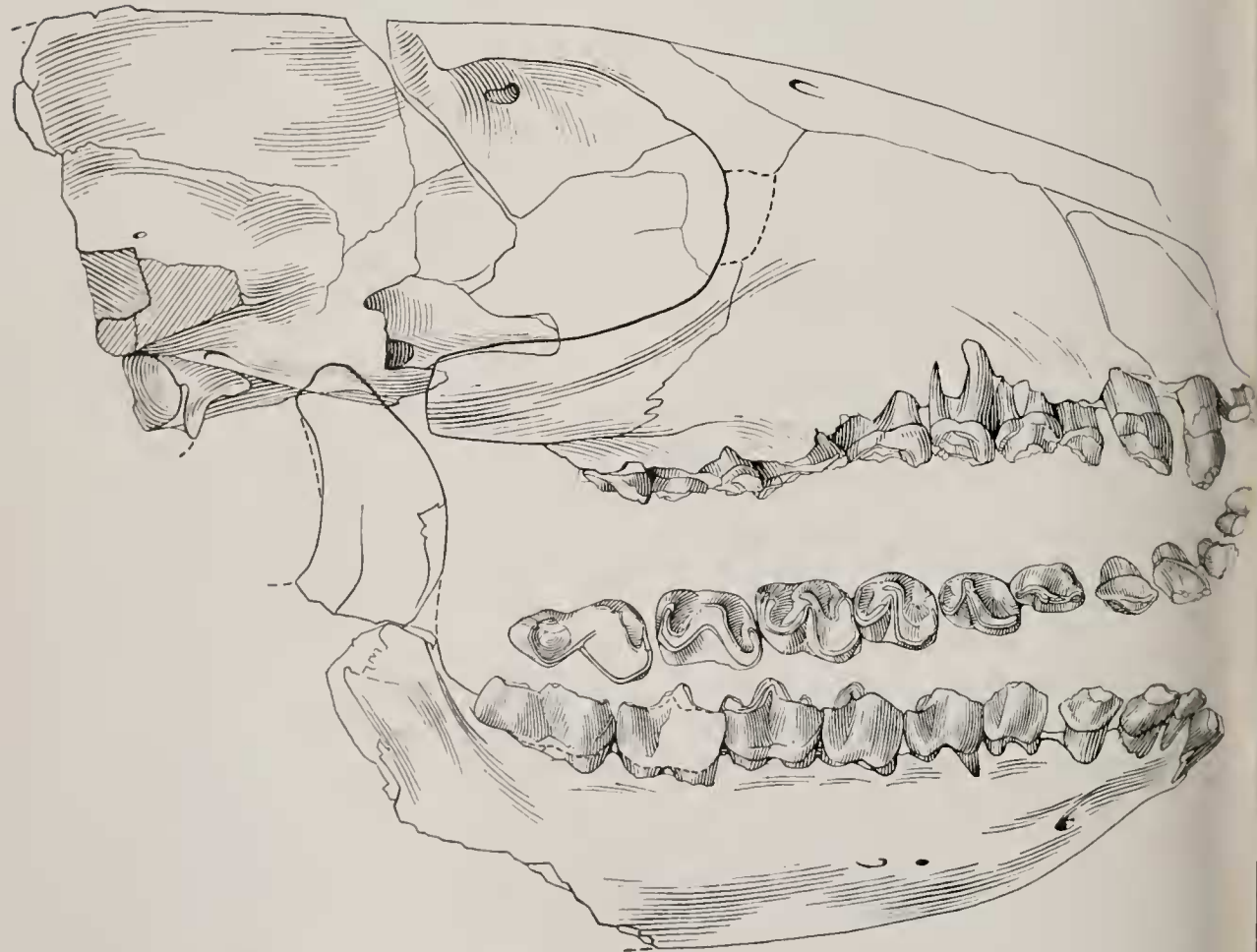

Fig. 2. *Adiantoides leali.* M.H.N.M. No. 3004 P.V., type, associated skull and lower jaw. Right lateral views and crown view of lower teeth. X2. (After Simpson and Minoprio.)

molars relatively transverse, with projecting parastyles and ecto-
lophs probably relatively simple posterior to parastyles. M^{1-2}
with median internal and weak postero-internal fossettes, an-
terior cingulum apparently small and forming no, or only a very
transitory, antero-internal fossette. M^2 short anteroposteriorly,
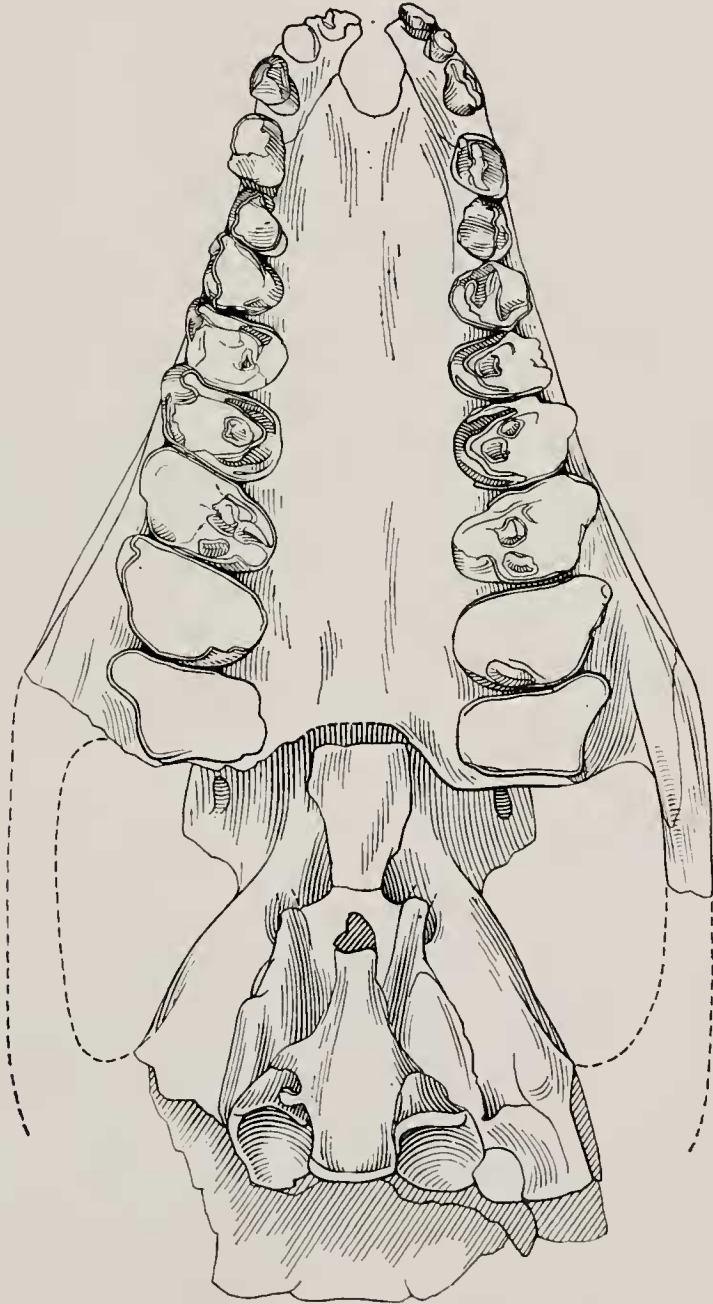obliquely triangular. Lower cheek teeth generally more as in

Fig. 3. *Adiantoides leali.* M.H.N.M. No. 3004 P.V.,
type skull. Palatal view. X2. (After Simpson and
Minoprio.)

Proadiantus, but talonids on M_{1-2} shorter and narrower than trigonids and M_3 strongly distinctive in having the talonid only slightly greater than the trigonid in length and much narrower, with entoconid continuing hypoconulid crest and barely differentiated, not forming a transverse crest.

Affinities: Further (unpublished) study by Patterson since publication of Patterson (1940) and Simpson and Minoprio (1949) has revealed that the taxonomy of the Adianthidae is even more confused than previously realized and has raised several serious problems. We cannot attempt to solve or even to state those problems here, and indeed their solution probably must await discovery of better post-Deseadan specimens and perhaps also arbitrary designation of neotypes or of *nomina conservanda.* In the meantime the following conclusions, although uncertain at various points, form the basis for our present understanding of the family and of the position of *Adiantoides* in it:

Proadiantus Ameghino, 1897, Deseadan, is a valid genus and the conception of it in Patterson (1940) is essentially correct. It is on about the same level of specialization as *Adiantoides* but the two are quite distinct and represent different generic lineages.

Proheptaconus Bordas, 1936, Colhuehuapian, is based on a specimen belonging to *Adianthus patagonicus* Ameghino but it is nevertheless probably a valid genus and not a synonym of *Adianthus.* In either case it represents a third generic lineage probably not directly derivable from either *Proadiantus* or *Adiantoides.*

In the Santacrucian and perhaps but not certainly in the Colhuehuapian there is another member of this general group probably distinct from *Proheptaconus* and more nearly allied to, perhaps even derived from, *Adiantoides.* This is what we (Patterson, 1940; Simpson and Minoprio, 1949) have been calling *Adianthus* although the circumscription, exact character, and nomenclature are not as clear as we previously supposed. It is quite uncertain whether the type specimen of the type species, *Adianthus bucatus* Ameghino, 1891, really belongs to the same genus, or indeed family or order, as the subsequently referred specimens on which the concept of the genus and family have really been based. For the time being, however, we continue to call the more *Adiantoides*-like later forms *Adianthus* and the family Adianthidae.

In any case *Adiantoides* is certainly a valid genus and its affinities are clearly with forms hitherto referred to the Adianthidae whatever their correct nomenclature and definitions may prove to be. We have no additional material of *Adiantoides* and cannot otherwise add to the description and discussion in Simpson and Minoprio (1949). As there noted, *Pseudadiantus* Ameghino, 1901, certainly has nothing to do with this group and *Tricoelodus* Ameghino, 1897, is very different from *Adiantoides* and its established allies even if it might prove to have some special but considerably more remote connection.

ADIANTOIDES LEALI Simpson and Minoprio, 1949

Figures 2-3

Adiantoides leali, Simpson and Minoprio, 1949, p. 10; 1950, p. 247.

Type: M.H.N.M. No. 3004 P.V. Associated skull and jaws, incomplete posteriorly.

Hypodigm: Type only.

Horizon and Locality: Divisadero Largo formation at its type locality, Mendoza, Argentina.

Diagnosis: Only known species of *Adiantoides*.

Family PROTEROTHERIIDAE? Ameghino, 1887

PHORADIADIUS,[1] new genus

Type: *P. divortiensis* (below).

Known Distribution: Divisadero Largo formation, Mendoza, Argentina.

Diagnosis: Upper molars with W-shaped ectoloph; anterior cingulum with cuspidate lingual ending anterior to protocone: protoconule, protocone, and hypocone basally united by ridge, separated by shallow notches; a pronounced fossa posterolabial to the hypocone; metaconule produced anteriorly, crista-like. Lower molars with W-shaped lophids; labial separation of trigonid and talonid V's deep, extending to lingual side of tooth: paraconid fully lingual; metaconid flattened on lingual face, with a posterior crest descending from its apex; entoconid poorly

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1 Anagram of *Diadiaphorus*. We adopt one of Ameghino's devices for coining names unlikely to be preoccupied and for suggesting relationships. In this case the suggested relationship is only that the animals are litopterns and not that these two particular genera necessarily have a special connection.

or not distinguished; no talonid pillar; M_3 with simple but somewhat elongate, narrow talonid, no third lobe.

PHORADIADIUS DIVORTIENSIS,[1] new species
Figure 4; Plate 1; Plate 2, figures *A-B*

Type: M.A.C.N. No. 18.061, part of right maxilla with imperfect M^{2-3}.

Hypodigm: Type and:

M.C.Z. No. 7407, part of right maxilla with imperfect M^3 and fragment of M^2.

M.C.Z. No. 7416, part of left lower jaw with incomplete M_2, base of M_1.

M.H.N.M. No. 3005 P.V., part of right lower jaw with unerupted M_3 (posterior end broken) and roots of M_2.

A.M.N.H. No. 45932, parts of both rami and symphysis, badly broken, left ramus through P_2 but without teeth, right ramus with part of I_3, P_{2-4} and partial alveoli or roots for M_{1-2}. Juvenile, permanent teeth just erupting.

A.M.N.H. No. 45933, part of right ramus, with M_3 (somewhat broken) erupting and roots of M_{1-2}.

A.M.N.H. No. 45931, part of left upper jaw with probable dm^{3-4} and M^1, all very poorly preserved.

A.M.N.H. No. 45930, part of left upper jaw with parts of P^3-M^3, all very poorly preserved.

Horizon and Locality: All specimens of the hypodigm are from the type area of the Divisadero Largo formation, Mendoza, Argentina.

Diagnosis: Sole known species of *Phoradiadius*.

Description: It is not absolutely certain that all specimens of the hypodigm belong to a single species, but that is sufficiently probable. All belong to litopterns of nearly the same size and suggestive of the same apparent relationships and there is no indication of more than one such litoptern in the collections. Minoprio (1947) figured a litoptern lower jaw, without tooth crowns, perhaps of this species. Simpson and Minoprio (1949) mentioned other fragmentary specimens possibly of the same form. The additional specimens now available are all poorly preserved, but on the reasonable assumption that they are conspecific they suffice to describe essential features of the dentition and to distinguish it from all genera previously adequately defined.

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1 *Divortium,* "separation," for Divisadero (Largo), *-ensis,* locative suffix.

The upper premolars, P$^{3-4}$, of A.M.N.H. No. 45930 are too poorly preserved for useful description except to note that their squared lingual contours suggest the presence of well developed hypocones, perhaps as in *Diadiaphorus*. The presumed deciduous upper molars and the permanent molars have strongly W-shaped ectolophs. Details of structure are reasonably well shown only on M^2 of the type, but as far as preserved in the hypodigm M^1 and M^3 seem to be essentially similar except for expectable differences of proportions. On M^2 a strong anterior cingulum runs posterolingually from the ectoloph, ending in a cusplike projection anterior to the protocone. There is a sulcus between this cingulum, the protoconule, and the protocone, but no closed fossa.
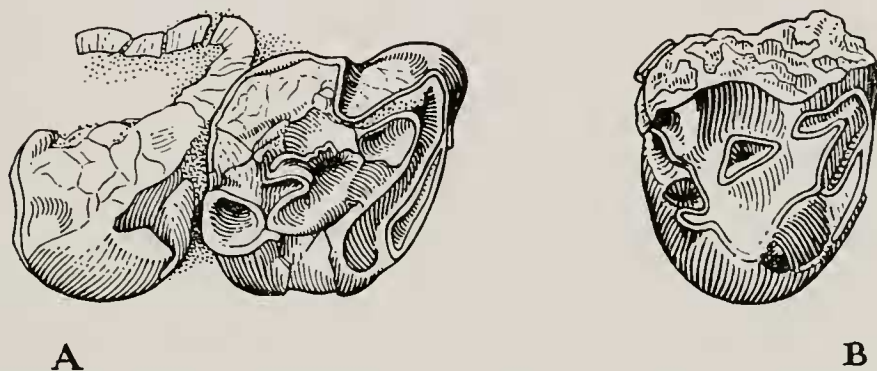

Fig. 4. *Phoradiadius divortiensis. A,* M.A.C.N. No. 18.061, type, right M$^{2-3}$. *B,* M.C.Z. No. 7407, right M^3. X2.

The slightly crescentic protocone is connected by a basal ridge to the protoconule but separated by a shallow apical notch. There is a deeper separation between the protoconule and the paracone. There is a simple and shallow central fossa between the protocone and the ectoloph. The prominent metaconule projects forward into this fossa, resembling a small crista. Protocone and hypocone are united basally and slightly separated apically as are protocone and protoconule. The hypocone also seems to be united, at least basally, with the metaconule. On the posterolingual part of the tooth there is a small but deep and prominent fossa bounded anterolingually by the hypocone. anterolabially by the metaconule, and posteriorly by a strong crest curving first posteriorly from the hypocone apex and then turning labially along the posterior margin of the tooth.

M^3 is as large as M^2, not reduced, but with the lingual contour more rounded and the hypocone considerably smaller, relatively, than on M^2.

A.M.N.H. No. 45932 has a large anterolateral tooth, the crown broken, assumed to be I3 by comparison with proterotheres. The tooth is as large, relatively, as in any Santacrucian form and is a striking distinction from *Thoatherium*. A canine was probably present and, if so, there was virtually no diastema. P1 was small; its crown is not preserved. P2 is large, with a long, simple anterior blade, convex labially and excavated lingually, probably with a small anterolingual cuspule. The talonid, sharply differentiated by a labial groove, is shorter and wider. Its coronal structure is obscure. P3 has a simple, sharp-crested, crescentic trigonid. The talonid is apparently shorter and wider, but it is badly preserved. P4 consists of two rather simple and subequal crescents. The inner face of the metaconid is flattened and a ridge descends posteriorly from the apex. The posterior end of the tooth is somewhat broken, but it appears that the entoconid was a slight swelling at the posterolingual end of the crescent and not a distinctly separate column. It is just possible that the teeth described are P3-4 and M1, but interpretation as P2-4 seems much more likely, on the evidence of their congruent stages of eruption (M1 is usually fully in place when P4 erupts) and the position of the, or the main, mental foramen beneath the anterior end of P2.

M3 is preserved in A.M.N.H. No. 45933 and M.H.N.M. No. 3005 P.V. Its structure is essentially like that ascribed above to P4 except that M3 is larger and has a somewhat more elongate, relatively narrow talonid. The paraconid is fully lingual, the posterior crest from the tip of the metaconid is again evident, and although the entoconid region is imperfect in both specimens it is clear that the entoconid did not block the lingual opening of the talonid crescent.

All teeth are fully brachydont on both labial and lingual sides.

No precise standard measurements are possible on the imperfect specimens but the median anteroposterior length of the type M^2 is about 11 mm.

Affinities: This animal is clearly a litoptern, but its affinities within that order are not entirely clear. It has many of the basic features of the Proterotheriidae and its general aspect is somewhat like *Diadiaphorus* among the well-known Santacrucian proterotheriids. When, however, details are taken into consideration the differences are so striking that they may preclude any close or special relationship. Neither *Diadiaphorus* nor any other

positively referred proterotheriid has a crista-like metaconule, a posterolingual fossa on upper molars, or so distinctly a lingually flattened and posteriorly crested metaconid. Other details in the description are also distinctive to at least a generic degree. Known pre-Santacrucian litopterns are even less similar to *Phoradiadius*, so far as comparable parts are known,[1] to such a degree that explicit comparisons would be pointless.

There is some faint possibility that *Phoradiadius* may be more nearly related to the Adianthidae, Macraucheniidae, or both, than to the Proterotheriidae. Simply bicrescentic lower cheek teeth and a tendency to form a posterior fossa on upper cheek teeth occur in some adianthids and macraucheniids. The known genera of those families are, however, all so unlike *Phoradiadius* that special relationship is improbable.

Order NOTOUNGULATA Roth, 1903

Family OLDFIELDTHOMASIIDAE? Simpson, 1945

The most abundant fossils in the collections are small, brachydont, and generally very primitive notoungulates. All resemble each other quite closely and they seem to represent a fairly compact taxonomic unit. Most of the specimens, however, fall rather clearly into three different groups and on the basis of the best materials, dentitions and skulls, these are distinctive enough that they must be placed not only in three species but also in three genera: *Allalmeia* Rusconi and two others defined as new below, *Brachystephanus* and *Xenostephanus*. All three are highly variable, and less complete specimens are often of dubious specific or generic reference. We cannot be quite certain that all the specimens listed below in the specific hypodigms are correctly placed, but the presence and distinction of the three genera are beyond serious doubt. It is possible that more than three species, or even more than three genera, are represented.

Each of the three genera now recognized has some special features, such as the enormous bullae of *Brachystephanus* and *Xenostephanus* or the peculiar upper premolars of the latter, but those peculiarities are matters of detail and all three genera come close to a picture of an entirely primitive or generalized

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1 The Deseadan litopterns *Coniopternium andinum* Ameghino, 1895, *Caliphrium simplex* Ameghino, 1895, and *Notodiaphorus crassus* Loomis, 1914, appear to have been based on remains of one species close to if not in the direct ancestry of *Theosodon*. It can safely be concluded that these forms have nothing to do with *Phoradiadius*.

notoungulate. They have the characters common to all notoungulates, and they lack any of the specializations by which most of the established notoungulate suborders and families are readily recognized, even as early as the Casamayoran for some of them. Reference to the Oldfieldthomasiidae is really *faute de mieux,* based more on the absence of special characters of other defined families than on the presence of special resemblances to *Oldfieldthomasia* and other known, more surely allied early forms. Affinities are further discussed under *Brachystephanus,* below.

Although *Allalmeia* was described first, *Brachystephanus* is now best known. It will be considered first here, as more or less typifying the group, and *Allalmeia* and *Xenostephanus* will then be compared with it.

BRACHYSTEPHANUS,[1] new genus

Type: Brachystephanus postremus, see below.

Known Distribution: Divisadero Largo formation, Mendoza, Argentina.

Definition: Small notoungulates of primitive aspect. Dental formula $\frac{3 \cdot 1 \cdot 4 \cdot 3}{3 \cdot 1 \cdot 4 \cdot 3}$. All teeth brachydont. Incisors not or little procumbent, none particularly enlarged. Canines vertical, slightly differentiated from adjacent teeth. P^1 small, longer than wide. P^2 moderately, P^{3-4} progressively more strongly transverse. Anterior cingulum slight on P^2, stronger on P^3, and nearly equal to posterior cingulum on P^4, without cuspule on any of these teeth. Inner faces of P^{2-4} simply rounded, not quadrate or divided. Paracone and metacone barely or not distinguishable, at least when slightly worn. Strong paracone-metacone (or amphicone) fold on external face; distinct but less prominent parastyle and metastyle folds. Coronal ridges from protocone to parastyle and metastyles enclosing a single, strong, central fossette. M^{1-2} with subequal protocone and hypocone, confluent at the base, well separated by apical notch and sharp groove on lingual face. Single deep central fossa, elongate anterolabially-posterolingually; no other coronal depressions on moderately worn teeth. Crochet and cristae, if present, confluent with ectoloph after slight wear. Labial face of ectoloph with strong

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1 From Greek βραχύς, short, στέφανος, crown, in allusion to the brachydont condition of the teeth, and also in parallel with *Trimerostephanos* Ameghino, another survivor of a primitive group.

paracone and metacone folds, excavated between these; parastyle moderate, metastyle slight or not distinguished, no mesostyle. Well developed, simple anterior and posterior cingula. M^3 similar but much smaller and with hypocone and metacone strongly reduced.

Lower cheek teeth as far as preserved much like a miniature *Maxschlosseria*. Possible faint twinning of metaconid on M_{1-2}, not M_3.

Bullae enormous, occupying virtually whole ventral aspect of basicranium and leaving only very narrow basioccipital-basisphenoid exposure. Porus acusticus externus comparatively large, meatus very short, crista meatus [1] not distinguishable. Occiput comparatively broad, distance between mastoid foramina equal to or greater than total depth of occiput.

Affinities: This highly distinctive genus does not particularly resemble anything previously know from Descadan or later beds. Among earlier forms (Riochican to Mustersan), it resembles primitive members of a number of different but, at these ages, rather closely similar notoungulate families. In most cases the resemblance is just to the extent to which they and *Brachystephanus* share primitive features. Among families as recognized in Simpson (1945), the Henricosborniidae, Oldfieldthomasiidae, Archaeopithecidae, and Isotemnidae come into question, but *Brachystephanus* seems to lack the more distinct special characters of any of these families.

The extreme simplicity of the dentition, except for basic notoungulate characters, is like the Henricosborniidae, but the upper premolars are more transverse, more isotemnid-like. The strong basal fusion of protocone and hypocone, the deep, simple fossa, and the early obliteration of the crochet (if, indeed, one occurred, which is most probable as this element is virtually universal in Notoungulata) are not like the henricosborniids. On the whole, close affinities with this family are improbable. Closer comparison with the Archaeopithecidae also seems to exclude reference to that family. The molar patterns of *Brachystephanus* are much simpler in comparable stages of wear, and the archaeopithecids in Casamayoran time were already more hypsodont than the present genus.

Closest resemblance seems to be with the Oldfieldthomasiidae, on one hand, and the Isotemnidae, on the other, two families

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1 We take this opportunity to correct the ungrammatical form "crista meati" previously used by Patterson and by Simpson.

quite distinct in their type genera but more or less intergrading in the known parts of some other Casamayoran representatives. Resemblances of *Brachystephanus* to either family are mostly in characters shared by both. It is, however, sharply distinct
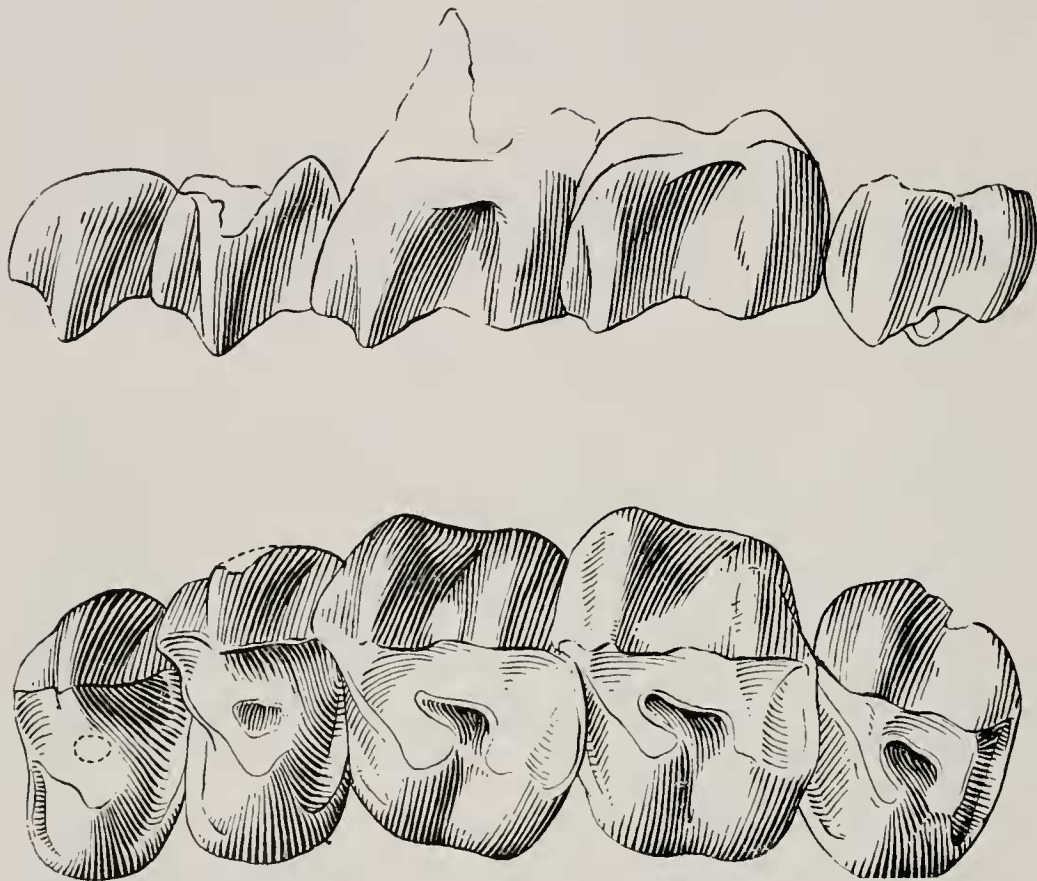
Fig. 5. *Brachystephanus postremus.* Drawn from original of A.M.N.H. No. 45946, cast of type. Left P³-M³, external and crown views. X about 5.

from the well-defined genera currently referred to the Iso-temnidae (as listed in Simpson, 1945), and seems somewhat closer to some referred to the Oldfieldthomasiidae, particularly *Maxschlosseria.* *Brachystephanus* differs from *Maxschlosseria* in the less procumbent incisors and more differentiated canine, stronger metacone fold and weaker anterolabial fossette on the molars, and other minor particulars. The dental resemblance is, however, closer than to any other genus known to us, and in default of other evidence it is accepted tentatively as possibly indicative of relationship. Resemblance to other oldfieldthoma-siids is distinctly less. The family position of *Maxschlosseria* is,

indeed, uncertain. It was referred to the Isotemnidae by Ameghino and may belong there, but reference to the Oldfieldthomasiidae seems somewhat more probable on the basis of
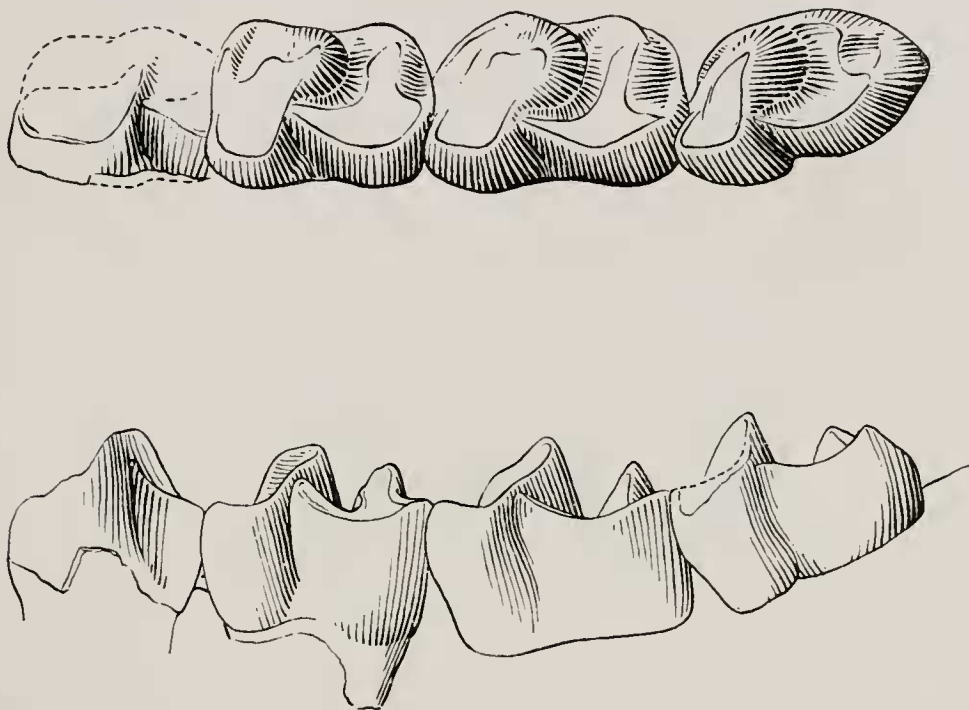restudy of Ameghino's specimens and of others even better
(Simpson, in manuscript).

Fig. 6. *Brachystephanus postremus.* Drawn from original of A.M.N.H.
No. 45946, cast of type. Left P$_4$-M$_3$, crown and external views. X about 5.

Among earlier oldfieldthomasiids, the skull is adequately
known only in *Oldfieldthomasia* itself (see especially Simpson,
1936a). As far as the characters are known in both genera, the
Brachystephanus skull is in general quite like that of *Oldfieldthomasia* and differences are almost entirely rather trivial matters
of sizes or proportions of various features. That resemblance
is, however, again a matter of both genera having extremely
primitive, almost generalized notoungulate characters. They do
differ in special details, e.g. the enormous bullae and short
meatus of *Brachystephanus* or the prominent, grooved crista
meatus of *Oldfieldthomasia*. There is, then, no adequate positive
evidence for a special phyletic relationship between the genera.
Reference of *Brachystephanus* to the Oldfieldthomasiidae is
based more on negative than on positive considerations and
must be accompanied by a large question mark.

Regardless of its family reference, *Brachystephanus* seems to be as primitive as any notoungulate known from the Riochican or Casamayoran but (as will be shown on a later page) its age is much later, Deseadan or immediately pre-Descadan. With its allies *Allalmeia* and *Xenostephanus*, described below, it evidently represents a late survival of a group little changed from late Paleocene or early Eocene times, but its source at those earlier times is unknown or at least not surely identified. Perhaps these late genera merit group designation at a subfamily or family level, but definition of such a group would have to be largely negative and could not, at present, clearly differentiate it from all the Casamayoran groups.
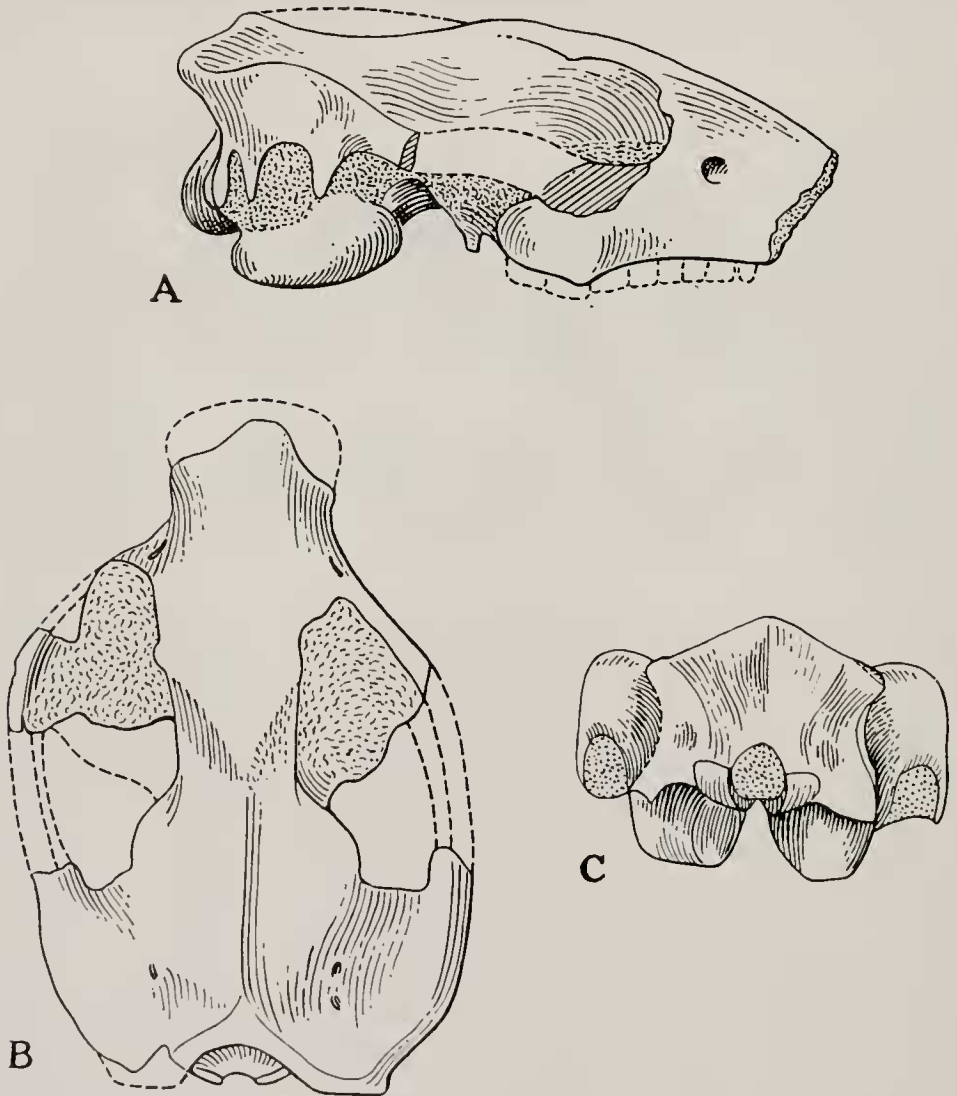

Fig. 7. *Brachystephanus postremus*. M.L.P. No. 49-XI-21-16, skull. *A*, right lateral view. *B*, dorsal view. *C*, occipital view. From sketches by Patterson. About natural size.

Table 1

Measurements in millimeters of lengths (L) and widths (W) of teeth of *Brachystephanus postremus* (*B.p.*), *Xenostephanus chiottii* (*X.c.*), and *Allalmeia atalaensis* (*A.a.*).

	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
B.p. Type			3.4	ca. 4	3.4	6.1	3.8	6.4	5.3	6.9	5.6	7.3	4.4	6.2
AMNH 45945	...	...	2.9	3.3	2.9	4.3	3.4	5.2	4.4	6.1	ca. 5	ca. 6	...	...
MLP 45-VII-10-12	...	...	3.7	...	...	...	4.1	...	4.4	...	6.0	...	...	...
X.c. Type	3.1	2.5	5.0	6.1	5.6	7.4	5.5	ca. 8	6.8	8.3	ca. 6.5	...	6.1	7.8
A.a. Type	...	...	4.0	...	3.7	6.2	4.1	7.0	5.0	7.9	5.5	9.7	5.7	ca. 9
MLP 45-VII-10-16	...	...	3.5	4.9	3.7	5.9	3.9	6.8	4.9	...	5.7	9.0	...	...
MLP 49-XI-21-21	...	...	...	...	...	...	...	...	...	...	...	...	4.9	8.6

	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
B.p. Type	...	...	...	...	...	...	3.9	2.8	4.7	3.5	5.3	3.8	5.6	3.5
AMNH 45945	...	...	...	...	3.4	1.6	3.7	2.2	4.2	3.3	4.8	3.6	ca. 5.5	ca. 3
X.c. Type	3.6	2.0	4.4	2.8	5.7	3.3	5.7	3.8	6.9	4.3	...	4.9	7.6	4.3
AMNH 45948	...	...	...	...	...	...	...	...	5.9	4.9	6.6	4.9	7.5	4.4
A.a. MLP 45-VII-10-9	...	...	...	...	3.4	...	3.9	3.2	4.9	3.3	6.4	3.8	...	...

Brachystephanus postremus,[1] new species

Figures 5-7; Plate 2, figures C-D; Plates 3-4

Type: A.M.N.H. No. 45946, associated partial skull and jaws with right I^{2-3}, P^{2-4}, M^{1-3}, left P^{1-4}, M^{1-3}, right lower canine, P_{3-4}, M_{1-3}, left P_{3-4}, M_{1-3} (some of these teeth incomplete), and other alveoli or roots.

Hypodigm: The type and:

A.M.N.H. No. 45945, associated partial skull and jaws with right P^{1-4}, M^{1-2}, left P^{2-4}, M^{1-2}, right P_{3-4}, M_{1-3}, left P_{1-4}, M_{1-3} (some of these teeth incomplete), and other alveoli or roots.

A.M.N.H. No. 45940, right P^3-M^3, in jaw, all badly broken.

A.M.N.H. No. 45941, left P^2-M^2, in jaw, all badly broken.

A.M.N.H. No. 45942, right P^3-M^2, in jaw, all but P^4 badly broken.

A.M.N.H. No. 45943, right P^3-M^3, in jaw, mostly broken.

A.M.N.H. No. 45944, left P^3-M^2, in jaw, all broken.

M.C.Z. No. 7408, parts of both mandibular rami with left P_4-M_2.

M.C.Z. No. 7406, badly preserved lower jaw, both rami, with broken left M_{1-3} and fragments of other teeth.

M.C.Z. No. 7409, part of left maxilla with poorly preserved P^2-M^3.

M.C.Z. No. 7410, fragment of left maxilla with incomplete M^{1-2}.

M.C.Z. No. 7411, part of right lower jaw with M_{2-3} and part of M_1.

M.C.Z. No. 7413, associated lower jaw fragments, one with right M_1 and part of M_2.

M.L.P. No. 49-XI-21-16, nearly complete skull but end of rostrum and parts of zygomatic arches missing and teeth badly broken.

M.L.P. No. 49-XI-21-22, part of right maxilla with P^2-M^3, all somewhat broken.

M.L.P. No. 45-VII-10-12, considerable part of skull, poorly preserved, with imperfect right P^2 and P^4-M^3, with associated fragments of lower jaw.

M.H.N.M. No. 3006 P.V., part of right maxilla with somewhat broken P^3-M^2.

M.H.N.M. No. 3007 P.V., fragment of left maxilla with broken M^2 and complete M^3.

Horizon and Locality: Divisadero Largo formation, 8 kilometers west of the city of Mendoza, Argentina.

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[1] Latin, *postremus*, latest, in reference to the late occurrence of so primitive a notoungulate.

Diagnosis: Sole named species of the genus as defined above. Measurements in Table I.

Description: The dentition is adequately characterized in the generic diagnosis and the figures, so that tooth-by-tooth description is unnecessary.

Considerable parts of the skull are present in A.M.N.H. No. 45946 (a cast of the type, collected by Minoprio), A.M.N.H. No. 45945 (also collected by Minoprio), M.L.P. No. 45-VII-10-12 (collected by Chiotti), and M.L.P. No. 49-XI-21-16 (collected by Antonio Castro). In detail these specimens are disappointing, because parts grossly present are nevertheless badly distorted and fragmented. It seems to be a characteristic of the Divisadero Largo that its fossils are often preserved rather as a mosaic of fragments than in the original state, and that enamel, especially, but also often dentine and bone tend to pulverize and spall off in almost explosive fashion on exposure. Nevertheless, comparison of the four specimens reveals much of the essential skull structure.

No specimen has the tip of the rostrum complete, but the face was clearly rather short, with the anterior border of the orbit, which is above P^4, well anterior to the midpoint of skull length. The rostrum narrows markedly in the premolar region, expands again slightly at the canines, and is truncate across the arcuate but largely transverse incisor series. The narrow nasals were not retracted. The infraorbital foramen is above P^{2-3} and the anterior root of the zygomatic arch is above M^{1-2}. The orbit, of moderate size, has a broad floor but is completely open posteriorly. There is no distinct postorbital constriction and, as shown in a partial natural endocranial cast in A.M.N.H. No. 45945, the olfactory bulbs are large, fully exposed dorsally, and as wide as the anterior parts of the cerebrum. The cerebrum widens posteriorly and is followed by a slightly narrower, broadly exposed cerebellum of almost equal length. The single sagittal crest became rather high and sharp in adults. The zygoma, although not complete in any specimen, seems to have been normal (lacking, e.g., the characteristic interatheriid specialization of the jugal).

Reference has been made in the generic diagnosis to the enormous pear-shaped bullae, which occupy virtually the whole ventral aspect of the basicranium. The porus acusticus externus, at the posterolateral end of the bulla, is comparatively very large and is extraordinarily posterior and ventral in position,

only a little anterior to the level of the condyles and quite as low in its lower part. The meatus is so short as to be virtually nonexistent, in sharp contrast to the transversely elongate, anteroposteriorly pinched meatus of most specialized notoungulates. The porus faces posterolaterally. The anterior edge of the porus is elevated and liplike, running into and hardly distinct from the postglenoid process. No distinct crista meatus is present, an absence also peculiar but not unique and possibly primitive for a notoungulate. The usual notoungulate epitympanic inflation of the squamosal is present and strongly marked, but the epitympanic sinuses are here surpassed in size by the large bullae.

The occiput consists of a central portion or occiput proper and of the more lateral, large posterior faces of the epitympanic inflations. Between the two is a groove which seems to have contained a mastoid foramen, mastoid exposure, and "posterior adventitious bone" much as in *Oldfieldthomasia* (Simpson, 1936a, and see also Patterson, 1936). The occiput proper, relatively broad as noted in the generic diagnosis, is convex just above the large, almost circular foramen magnum, but is excavated medially above that and also laterally on each side.

XENOSTEPHANUS,[1] new genus

Type: Xenostephanus chiottii, see below.

Known Distribution: Divisadero Largo formation, Mendoza, Argentina.

Diagnosis: Small notoungulates of generally primitive aspect, dentition similar to *Brachystephanus* except as follows. P^1 small and simple, protocone incipient. P^{2-4} with strong, basined anterior and posterior cingula. P^{3-4}, at least, with distinct anteromedian cuspule, on P^3 dependent on the cingulum and on P^4 with a separate, low crest running to the parastyle. P^{2-4} with posterior loph from protocone to ectoloph, but no anterior loph and no closed fossa. Buccal face of ectoloph somewhat less deeply excavated between paracone and metacone, and internal groove between protocone and hypocone less strong. Metacone fold vestigial on M^3. Talonid lophids on P_{2-4} running to apex of metaconid on lingual side of tooth rather than abutting against base of trigonid medially. On M_3 metaconid distinctly bifid at apex and entoconid not distinctly crested transversely.

1 Greek ξένος, strange, στέφανος, crown, in allusion to the upper premolar crowns, peculiar among notoungulates, and in euphony with *Brachystephanus.*

Bullae very large and occiput relatively broad, both about as in *Brachystephanus*. Porus acusticus externus much smaller. Meatus short but more distinct than in *Brachystephanus* and
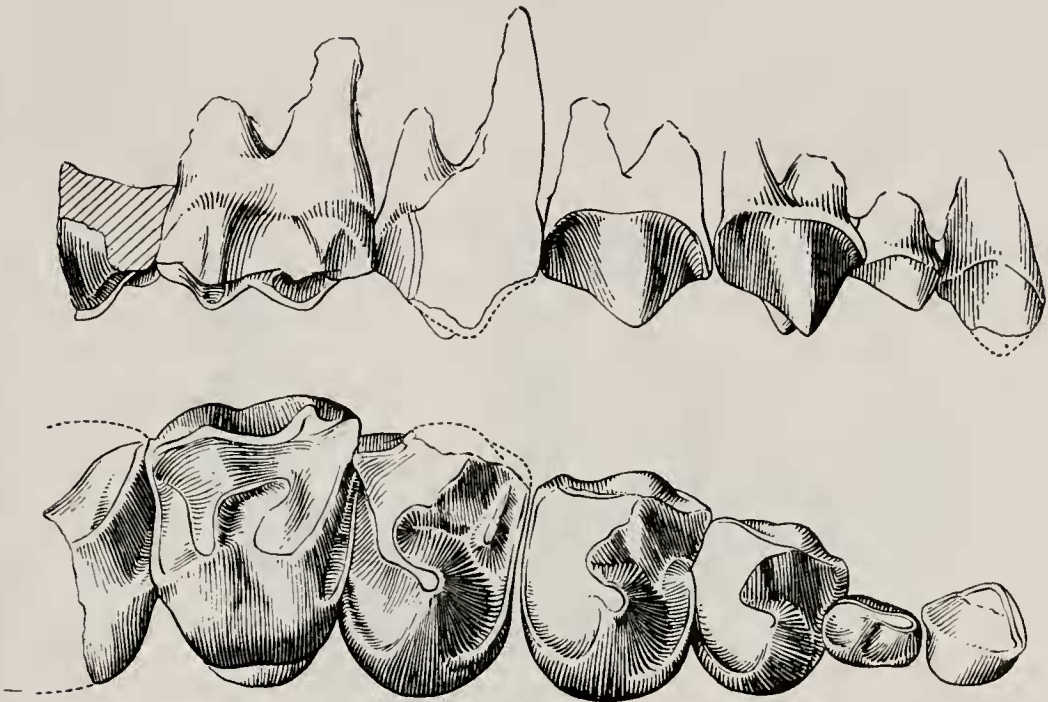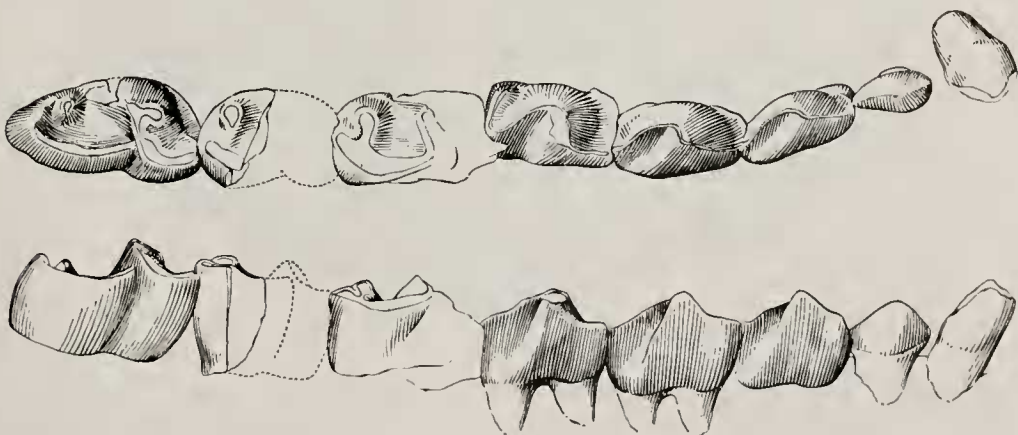

Fig. 8. *Xenostephanus chiottii*. Drawn from original of A.M.N.H. No. 45947, cast of type. Right C-M^2, labial and crown views. X about 3.

with a feeble crista meatus, which is, however, poorly differentiated from the postglenoid process. Paroccipital process probably considerably stronger than in *Brachystephanus*. Proportions of the occiput as in the latter genus.

Fig. 9. *Xenostephanus chiottii*. Drawn from original of A.M.N.H. No. 45947, cast of type. Right C-M$_3$, crown and labial views. X about 3.

Affinities: Xenostephanus has much the same resemblances to (presumably) earlier families as has *Brachystephanus*. The most distinctive teeth, the upper premolars, are, however, quite different from those of *Brachystephanus* and at least equally distant from those of any other genus known to us. They are, for instance, decidedly less like *Maxschlosseria* than are the corresponding teeth of *Brachystephanus*. Among such simple and primitive notoungulate dentitions, differences of this degree may
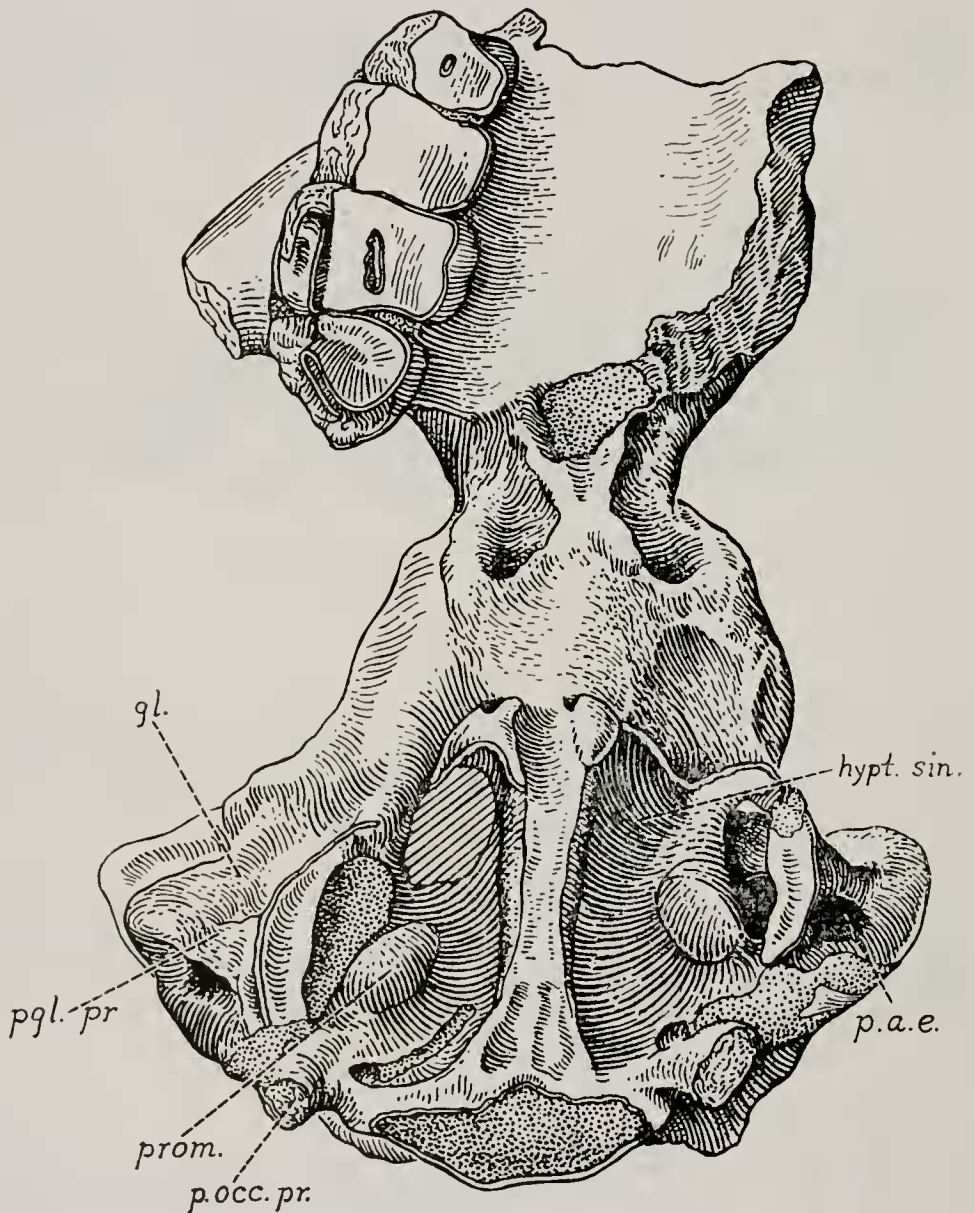

Fig. 10. *Xenostephanus chiottii*. M.H.N.M. No. 3008 P.V., incomplete skull. Ventral view. *gl.*, glenoid fossa; *hypt. sin.*, hypotympanic sinus; *p.a.e.*, porus acusticus externus; *pgl. pr.*, postglenoid process; *p. occ. pr.*, parocciptal process; *prom*, promontorium. X2.

reflect pertinence to wholly distinct families or even higher categories. The dental resemblance to *Brachystephanus* is, nevertheless, considerable, and no other definite affinities are suggested. The skulls are closely similar as far as known, except for the definite but small differences in the ear region noted in the diagnosis. *Xenostephanus* and *Brachystephanus* may be tentatively considered as divergent generic lines of the same general stock, perhaps survivors of a lineage near or in the Oldfieldthomasiidae, as already suggested for *Brachystephanus*.
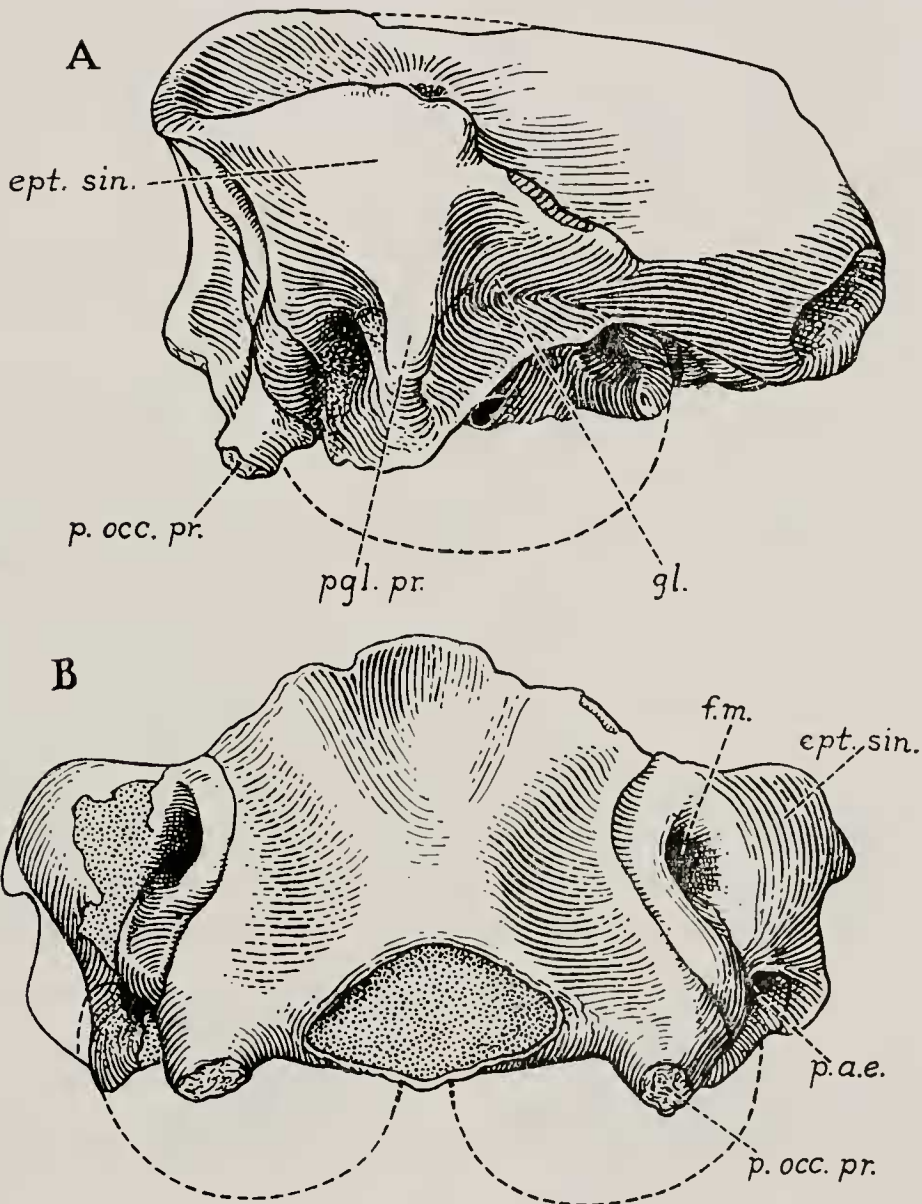

Fig. 11. *Xenostephanus chiottii*. M.H.N.M. No. 3008 P.V., incomplete skull. *A*, right lateral view of cranium. *B*, occipital view. *ept. sin.*, epitympanic sinus; *f.m.*, mastoid foramen; *gl.*, glenoid fossa. *p.a.e.*, porus acusticus externus; *pgl. pr.*, postglenoid process; *p. occ. pr.*, paroccipital process. X2.

XENOSTEPHANUS CHIOTTII,[1] new species

Figures 8-11

Type: A.M.N.H. No. 45947, partial skull and jaws with right upper C, P^{1-4}, M^{1-2}, left upper C, P^{1-4}, M^{2-3}, right lower C, P_{1-4}, M_{1-3}, left lower C, P_{1-4}, some of these teeth incomplete.

Hypodigm: Type and:

A.M.N.H. No. 45948, left lower jaw with C, P_{1-4}, M_{1-3}, some teeth broken.

M.L.P. No. 49-XI-21-20, fragment of left lower jaw with M_{2-3}.

M.C.Z. No. 7415, numerous small fragments of upper and lower jaws with identifiable parts of right P^4-M^1.

M.H.N.M. No. 3008 P.V., most of cranium and part of right maxilla with imperfect P^4-M^3.

Horizon and Locality: Divisadero Largo formation, 8 kilometers west of the city of Mendoza, Argentina.

Diagnosis: Sole known species of the genus as defined above.

Description: Little needs to be added to the points given in the generic definition or visible in the figures.

The skull is fairly well known between the type (specimen found by Minoprio of which A.M.N.H. 45947 is a cast) and M.H.N.M. No. 3008 P.V. (also collected by Minoprio). There is a definite postorbital constriction, more distinct than in *Brachystephanus.* The epitympanic sinus is well developed, but is probably relatively smaller than in *Brachystephanus.* The mastoid foramen and "posterior adventitious element," much as in *Oldfieldthomasia*, are more clearly visible in M.H.N.M. No. 3008 P.V. than in our materials of *Brachystephanus,* but the two genera probably do not differ significantly in this respect. The comparatively extremely small porus acusticus externus of *Xenostephanus* faces even more posteriorly than in *Brachystephanus* and suggests that the external ear was peculiar in some unknown way.

ALLALMEIA Rusconi, 1946

Allalmeia Rusconi, 1946a, (unnumbered page): 1946b, p. 18.

Type: Allalmeia atalaensis Rusconi, 1946.

Known Distribution: Divisadero Largo formation, Mendoza, Argentina.

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[1] For Dr. Olivo Chiotti, in recognition of his stratigraphic studies of the Divisadero Largo and adjacent formations.

Definition: (Redefinition by the present authors.) Small noto-
ungulates of primitive aspect. Dental formula $\overline{3 \cdot 1 \cdot 4 \cdot 3}$. Dentition
closely similar to that of *Brachystephanus* but differing in detail.
Canines poorly differentiated. P^1 very small. P^2 abruptly larger,
triangular. P^{3-4} with well developed protocone-parastyle loph
and forming deep, closed fossette in early wear stages. M^{1-3} with
strong, approximated parastyle and paracone ridges on buccal
faces; metacone ridge present but less distinct. Buccal face with
basal cingulum between paracone and metacone, deeply exca-
vated and forming small buccal fossette above flattened ectoloph
face. Protocone and hypocone well separated above base. Base
on lingual side broad, somewhat flattened and shelflike. Strong
anterior cingulum with tendency to extend around protocone
to lingual face. Approximately equal posterior cingulum, shorter,

Fig. 12. *Allalmeia atalaensis.* M.H.N.M. No. 507 P.V., type. Copy of
sketch by Patterson of crown view of right upper teeth. X about 1.5.

ending lingually posterior to hypocone. M^3 relatively larger than
in *Brachystephanus* or *Xenostephanus;* metacone and metaloph
reduced, metaloph not completely fused with small hypocone at
lingual end. Crista obliqua of lower premolars abutting against
base of metalophid, not running to metaconid.

Bullae relatively smaller than in *Brachystephanus* and *Xeno-
stephanus,* leaving fairly wide medial basioccipital-basisphenoid
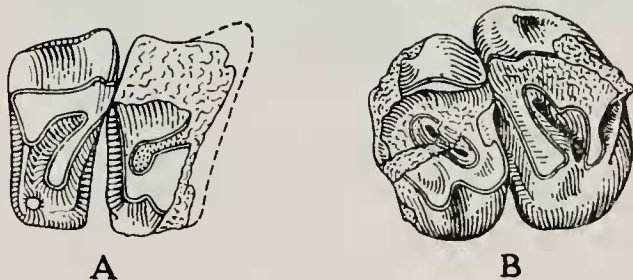exposure and not extending to posterior end of basicranium.

Fig. 13. *Allalmeia atalaensis.* *A,* M.L.P. No. 49-XI-21-21, right M^{2-3},
copy of sketch by Patterson. *B,* M.C.Z. No. 7412, left M^{2-3}. X2.
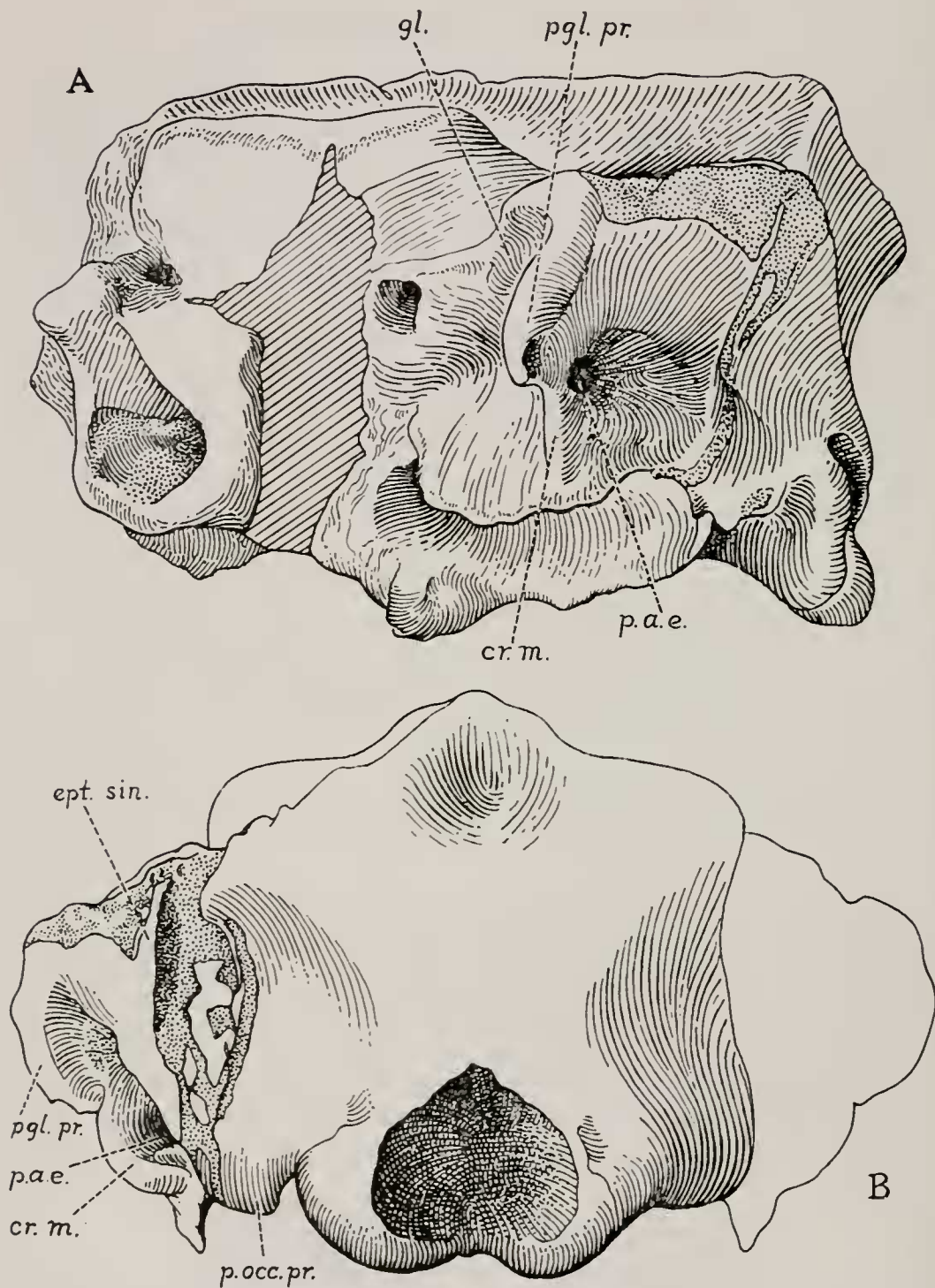
Fig. 14. *Allalmeia atalaensis.* M.H.N.M. No. 3009 P.V., cranium. *A*, left lateral view. *B*, occipital view. *cr. m.*, crista meatus; *ept. sin.*, epitympanic sinus; *gl.*, glenoid fossa; *p.a.e.*, porus acusticus externus; *pgl. pr.*, postglenoid process; *p. occ. pr.*, paroccipital process. X2.

Porus acusticus externus small, but relatively slightly larger than in *Xenostephanus*. Distinct but short meatus, relatively longer than in *Xenostephanus*, and simple crista meatus also somewhat better developed than in that genus, running to post-glenoid process but offset from it. Occiput relatively higher and narrower, distance between mastoid foramina less than total height of occiput.

Comments and Affinities: Our concept of *Allalmeia* is different from that of Rusconi (1946a, b) as a consequence of restudy with more specimens and more extensive comparative materials. As regards the dentition, the most important emendation is the observation that the apparent coronal outlines of the upper cheek teeth in Rusconi's figures are found to represent the root
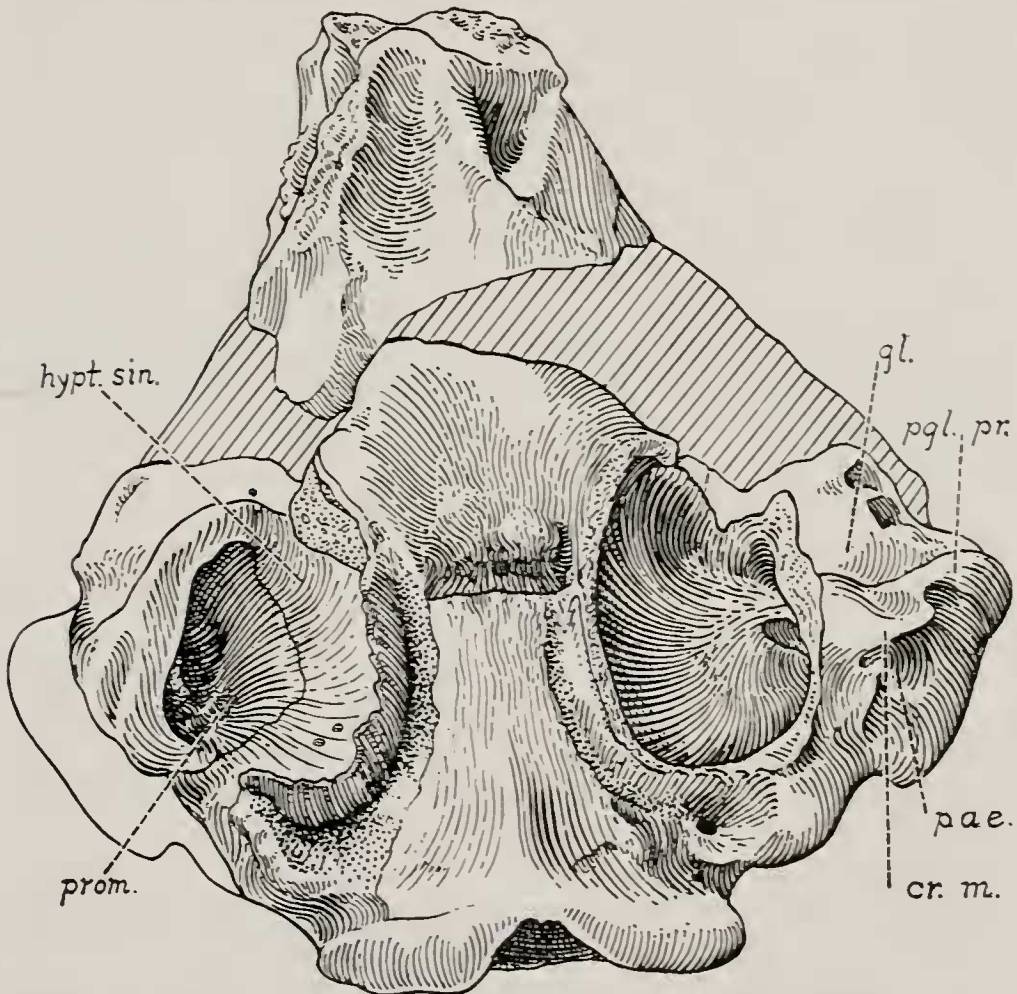

Fig. 15. *Allalmeia atalaensis.* M.H.N.M. No. 3009 P.V., cranium. Ventral view. *cr. m.,* crista meatus; *gl.,* glenoid fossa; *hypt. sin.,* hypotympanic sinus; *p.a.e.,* porus acusticus externus; *pgl. pr.,* postglenoid process; *prom.,* promontorium. X2.

bases, not the crowns proper, which are almost entirely broken away on all the teeth of Rusconi's specimen. The true coronal outlines are angulate as in all primitive notoungulates and not rounded buccally as shown in the original type figure. The dental formula was not correctly inferred from the type, alone. Like its allies in this fauna, *Allalmeia* has the full placental formula. Our additional specimens also reveal other dental and cranial characters not preserved in the type.

The original provisional reference of *Allalmeia* to the Notostylopidae is certainly incorrect. *Allalmeia* has none of the clear-cut characters diagnostic of that primitive but not generalized family. *Allalmeia* resembles its faunal associates *Brachysteph-anus* and *Xenostephanus* much more than it does any other known genera. The differences, while demanding generic separation, are not profound. Resemblance to *Brachystephanus* is especially close, and *Allalmeia* will probably find its correct taxonomic place next to that genus. For the present, then, and in a strongly provisional way it is likewise placed in the Oldfield-thomasiidae? with a decided question mark.

Rusconi's original specimen includes numerous associated elements of the postcranial skeleton. Like the teeth and skull, they have the characters of a very primitive, generalized notoungulate and lack diagnostic peculiarities of any of the contemporaneous or later families. Comparable parts are not known in the earlier Oldfieldthomasiidae and the skeleton does not, at present, cast any further light on affinities.

ALLALMEIA ATALAENSIS Rusconi, 1946

Figures 12-15

Allalmeia atalaensis Rusconi, 1946a (unnumbered page); 1946b, p. 18.

Type: M.H.N.M. No. 507 P.V., palate and lower jaw with most of the teeth (poorly preserved) and parts of associated skeleton.

Hypodigm: Type and:

M.L.P. No. 45-VII-10-9, symphysis and parts of mandibular rami with poorly preserved left $C-M_1$ and right P_3-M_3.

M.L.P. No. 45-VII-10-10, part of right maxilla with imperfect P^3-M^3.

M.L.P. No. 45-VII-10-16, part of left maxilla with imperfect
P^2-M^3.

(The three preceding M.L.P. specimens probably all belong to
the same individual, collected by Chiotti.)

M.L.P. No. 49-XI-21-21, fragment of right maxilla with M^3
and part of M^2.

M.C.Z. No. 7412, fragment of left maxilla with M^{1-2} and part
of M^3.

M.H.N.M. No. 3009 P.V., cranium and associated right maxilla
with very poorly preserved P^3-M^3 and much of lower jaw with
very poorly preserved left P_4-M_3 and roots of anterior teeth
on both sides.

Horizon and Locality: Divisadero Largo formation (type
locality and Papagallos). Mendoza, Argentina.

Diagnosis: Sole named species of the genus as defined above.

Description: The generic diagnosis and the general similarity
to *Brachystephanus* obviate the need for detailed description.
Preservation of the teeth is bad in almost all instances, but
comparison of all the specimens leaves little doubt of the essen-
tial characters. Most of our precise knowledge of dentition and
skull comes from specimens other than the type, and as there
is much variation among the specimens this leaves possible
slight doubts as to identification. The cranium is known only
from M.H.N.M. No. 3009 P.V., the poorly preserved dentition
of which has been directly compared with the type. There are,
of course, differences but they are so slight as not to warrant
specific separation. As noted in the generic diagnosis, known
differences in dentition from *Brachystephanus,* and in cranium
from *Xenostephanus,* are matters of relative proportions or of
structural details and are not fundamental or striking.

The known postcranial parts of the type, adequately described
by Rusconi (1946b), are slender, in keeping with the small size
of the animal, but show no evident specializations. The pes is
pentadactyl and more or less mesaxonic, but with digit IV longer
than II. Except in proportions generally correlated with weight,
the skeleton is almost as in Casamayoran Isotemnidae (see
Simpson, 1936b). One apparent difference, the great proximo-
distal elongation of the third trochanter, shown in the figure
of the femur (Rusconi, 1946b, fig. 18), perhaps is not real. The
specimen is imperfect in this region and is largely restored in
the figure.

Family MESOTHERIIDAE Alston, 1876

Subfamily TRACHYTHERINAE Simpson, 1945

TRACHYTHERUS? Ameghino, 1889

TRACHYTHERUS? MENDOCENSIS Simpson and Minoprio, 1949

Figures 16-17

Trachytherus mendocensis, Simpson and Minoprio, 1949, p. 18;
1950, p. 249.

Type: M.H.N.M. No. 2494 P.V., right P$^{2-3}$, M^1, and parts of
right M^2 and left P^2-M^1.

Hypodigm: Type and:

M.L.P. No. 45-VII-10-2, Chiotti Collection, right M^3.

Horizon and Locality: Type Divisadero Largo formation,
Mendoza, Argentina.

Diagnosis: Much smaller than other species referred to *Trachy-
therus;* type M^1 9.1 mm long and 8.3 mm wide on grinding
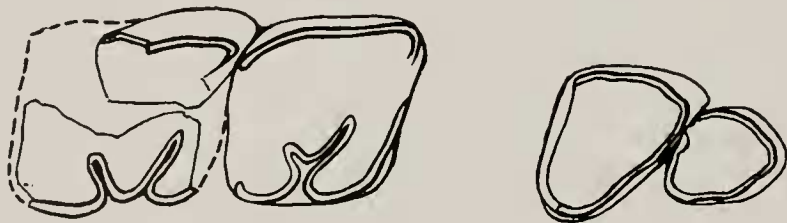surface. P$^{2-3}$ strongly transverse, obliquely triangular in section,

Fig. 16. *Trachytherus? mendocensis.* M.H.N.M. No. 2494 P.V., type,
right P$^{2-3}$, M$^{1-2}$, crown view. X2. (After Simpson and Minoprio.)

without grooves or ridges on rounded outer face. M^1 trapezoidal
in section, almost as wide as long in middle wear stage, outer face
smoothly curved. M$^{2-3}$ more angulate anteroexternally. M^3, at
least, with less basal widening and diminution of lingual fold
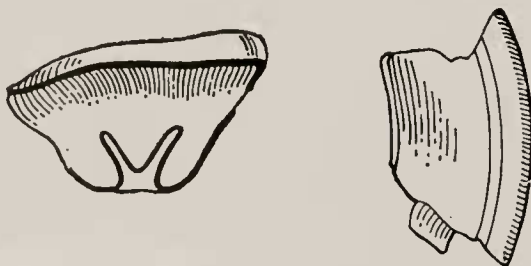and lobe than in *T. spegazzinianus.*

Fig. 17. *Trachytherus? mendocensis.* M.L.P. No. 45-VII-10-2, right M^3,
crown and anterior views. Copy of sketch by Patterson. X2.

Affinities: The previously undescribed M^3 in the Chiotti Collection almost certainly belongs to this species, and it adds somewhat to the characterization. The animal is clearly a trachytherine, and the available material does not permit clear-cut generic distinction from *Trachytherus*, which is not to say that it can be positively referred to that genus. We, therefore, modify the original designation by putting a question mark after the generic name. We suspect that further material will force generic separation, as suggested by wide specific separation from the type species of *Trachytherus.*

Family HEGETOTHERIIDAE Ameghino, 1894

Subfamily HEGETOTHERIINAE Ameghino, 1894

ETHEGOTHERIUM,[1] new genus

Type: Prohegetotherium carettei Minoprio, 1947.

Known Distribution: Divisadero Largo formation, Mendoza, Argentina.

Diagnosis: Hegetotheres resembling *Prohcgetotherium* but with anterior teeth slightly separated rather than appressed; canines in arc formed by cheek teeth, not buccal to it; P^1_1 smaller and less elongate than in *Prohegetotherium;* external grooves on upper molars median, not anterior, on ectoloph; P_2 relatively shorter; lobes of lower cheek teeth rounded rather than angular; anteroposterior axes of those teeth in sequence, not overlapping shingle-like as in *Prohegetotherium;* talonid of M_3 without external groove and with internal groove fainter than in *Prohegetotherium.*

Affinities: Comparisons made by Minoprio (1947) and Simpson and Minoprio (1949) were impeded by the inadequate and in part incorrect available data on the genotype of *Prohegetotherium, P. sculptum.* The type material of that species has now been restudied by Patterson, and a lower dentition almost certainly of the same species has been described and figured by Chaffee (1952). Adequate comparisons can, therefore, now be made for the first time. As indicated in the preceding diagnosis, the dentition of ''*Prohegetotherium*'' *carettei* proves to be markedly different from that of typical *P. sculptum.* It is, of course, uncertain whether these characters are quite constant

1 Anagram of *Hegetotherium.*

or will be found in all species that might eventually be referred to *Ethegotherium,* but there can be no doubt that in sum they warrant generic rank. *Ethegotherium* differs about as much from *Prohegetotherium* as the latter does from *Hegetotherium.* The reduction of posterior incisors, canines, and anterior premolars and the development of diastemata in that region seem to be a progressive, rodent-like specialization in *Hegetotherium* (and later hegetotheres). In that respect, *Ethegotherium* is distinctly more specialized than *Prohegetotherium* but less than *Hegetotherium.* Imbrication of the lower cheek teeth would also seem to be a specialization, apparently at least as advanced in *Prohegetotherium* as in *Hegetotherium* and absent in *Ethegotherium.* In some other characters such as the contours of the ectolophs and of the talonid of M_3, the three genera are distinct and divergent, without its being clear that one condition is more primitive or more specialized than another.
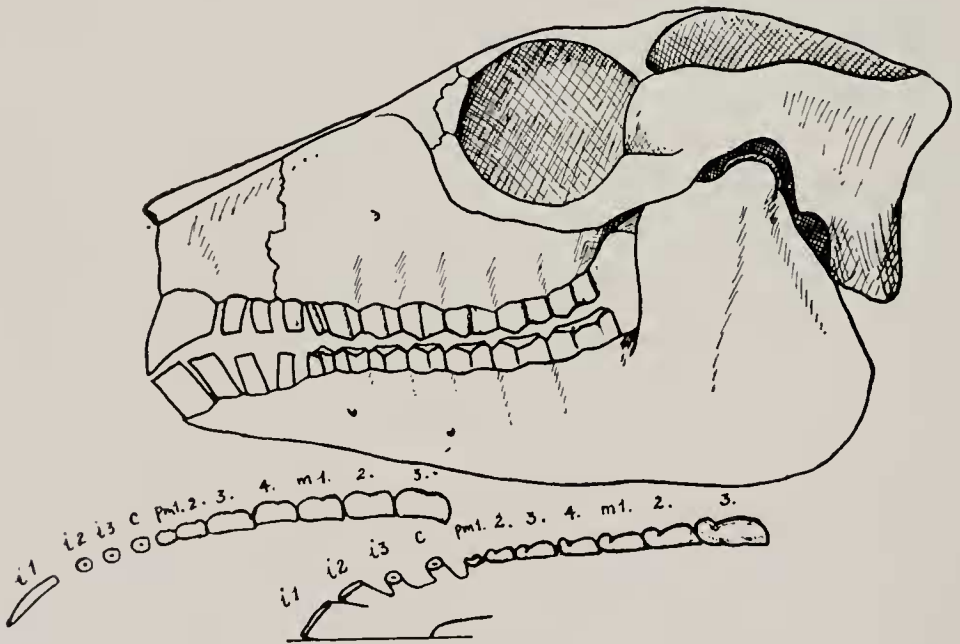

Fig. 18. *Ethegotherium carettei.* M.A.C.N. No. 16609, type, skull and jaws. Reconstructed left lateral view and crown outlines of upper and lower teeth. X1. (After Minoprio.)

Prohegetotherium may be somewhat nearer the ancestry of *Hegetotherium* than is *Ethegotherium,* but it is unlikely that known species of either of the earlier genera are directly ancestral to known species of *Hegetotherium.* The affinities of *Ethegotherium* are clearly in this group, the Hegetotheriinae, and not with

Pachyrukhos, Prosotherium, and other genera of different sub-families in the Hegetotheriidae. Unfortunately, useful comparison cannot be made with the Mustersan *Eohegetotherium,* the only supposed hegetotheriine so far named from pre-Deseadan beds. Ameghino's description is inadequate, and we have not been able to locate his types. Nevertheless, his statement that the molars are rooted, that the upper molars have no vertical grooves, and that the lower molars have a persistent fossette would preclude identity or close resemblance with *Ethegotherium,* and indeed that description suggests that *Eohegetotherium* is not a hegetotheriid.

ETHEGOTHERIUM CARETTEI (Minoprio, 1947), new combination

Figure 18 and Plate 5

Prohegetotherium carettei, Minoprio, 1947, p. 371; Simpson and Minoprio, 1949, p. 21.

Type: M.A.C.N. No. 16609. Skull and jaws.

Hypodigm: Type only.

Horizon and Locality: Type area of the Divisadero Largo formation, Mendoza, Argentina.

Diagnosis: Only known species of *Ethegotherium.*

Comments: We have no further material of this species, but Patterson has joined Minoprio in further study of the original on which the foregoing generic diagnosis has been based.

Notoungulata ?, indet.

M.A.C.N. No. 16610 is a fragment of a right lower jaw with poorly preserved P_3-M_2. It was at first identified as *Interatherium* sp. (Minoprio, 1947) and later as a probable interatheriid of indeterminate genus but not *Interatherium* (Simpson and Minoprio, 1949). Further study with better facilities now shows that this specimen definitely is not an interatheriid, but still does not permit identification. The teeth are brachydont and P_3-M_2 are all notably short and broad. P_{3-4} are submolariform but with talonids much smaller than trigonids. On M_2 the talonid is about as long as the trigonid and slightly narrower. These or other visible characters are insufficient for identification of the family or genus, but suggest that the animal is probably a rather peculiar notoungulate. The visible characters are distinct from those of any definitely identified mammal in the Divisadero Largo, and the presence of another genus (and, quite likely, family) is indicated.

Order and Family Uncertain

ACAMANA,[1] new genus

Type: Acamana ambiguus, below.

Known Distribution: Divisadero Largo formation, Mendoza, Argentina.

Definition: I^{1-2} transversely placed between anterior parts of opposite I^3s; section at alveoli elliptical with anteroposterior long axis. I^3 comparatively very large; circular in section at alveolus; with long, heavy, curving root ascending postero-dorsally in facial process of premaxilla. Diastema posterior to I^3, followed by C of moderate size, more or less the size of I^2. Long diastema posterior to canine. Palatine processes of premaxillae small and short, with small, nonconfluent anterior palatine foramina at premaxilla-maxillary suture. Palatine processes of maxillae in canine-premolar region broad, deeply and smoothly arched dorsally.
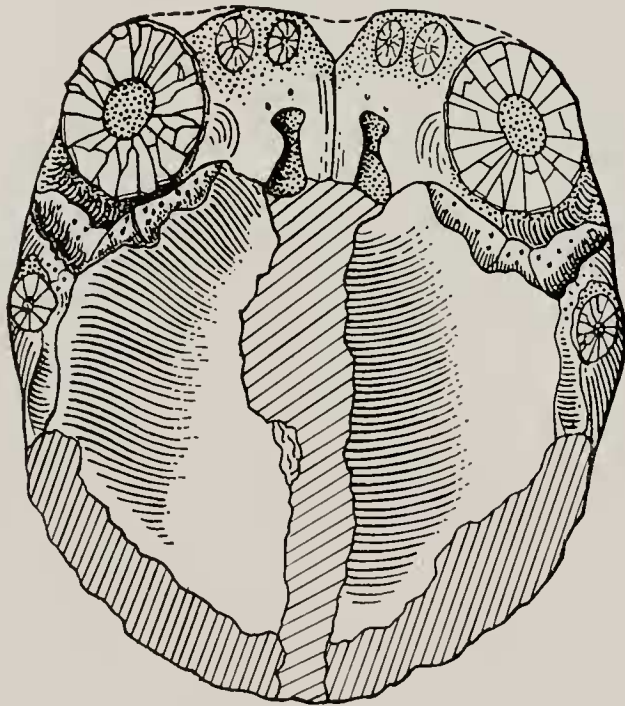

Fig. 19. *Acamana ambiguus.* M.H.N.M. No. 3010 P.V., type, part of rostrum. Palatal view, somewhat diagrammatic and with left side partly restored from right. X2/3.

1 Latinized from Aka-Manah, the name of a Persian demon. Again we follow the lead of Ameghino, who applied to a Patagonian fossil mammal the name *Asmodeus*, also a latinized version of the name of a Persian demon. It seems appropriate that so peculiar and, to a taxonomist, so annoying an animal should have a demoniac name. The name *Setebos* Roth, also applied to a Patagonian fossil mammal, is in the same spirit.

Affinities: As a precaution, the generic definition is based entirely on the most characteristic fragments and those certainly belonging to a single individual. Another possibly associated fragment is mentioned under the species, below, and adds somewhat to possible characters of the genus. The generic definition shows beyond any doubt that this is a very distinctive animal and one that should be readily recognizable if other specimens are found. So extraordinary an animal must be placed on record, and in spite of the inadequacy of the materials assignment of a name for purposes of discussion seems to us the lesser of two evils. This animal certainly does not belong to any genus in which the same parts are known. The possibility that the genus may have been known by, say, an isolated cheek tooth cannot be totally excluded but is remote.
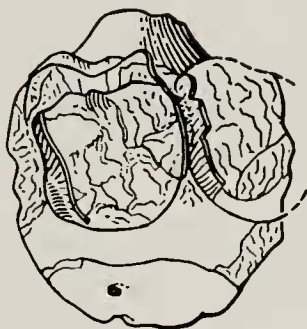

Fig. 20.   *Acamana ambiguus.* M.H.N.M. No. 3011 P.V., perhaps same individual as type (M.H.N.M. No. 3010 P.V.), fragment of left maxilla with incomplete M^{2-3}. Crown view. X2/3.

Anything even approximating this arrangement of the anterior upper dentition is unknown in any previously described South American genus, family, or order. The presence of tusks followed by diastemata is superficially astrapothere-like, but the resemblance is distant and relationship is at once excluded by the fact that in astrapotheres the tusks are canines and in *Acamana* certainly incisors. The presence of somewhat tusklike or caniniform incisors does characterize the Leontiniidae, but that resemblance also seems superficial. In leontiniids the caniniform incisors are much less enlarged than in *Acamana* and are I^1 or I^2 in all known cases, not I^3 as in *Acamana*. Diastemata are small or, usually, completely absent in leontiniids, and there are decidedly more differences than resemblances throughout this region. It is perhaps conceivable that *Acamana* is on an

extremely aberrant lineage of common origin with the Leontiniidae, but one must judge relationships by resemblances, here extremely tenuous, and not by the mere possibility that the observed large differences might somehow have diverged from a common ancestry.

No other comparisons seem to have any significance, and we think it nearly certain that *Acamana* belongs to an otherwise unknown family, although we prefer to await broader knowledge of the characters of the group before going beyond the minimum nomenclatural requirement of genus and species. It is by no means impossible that *Acamana* represents a new order, but definite espousal of that hypothesis is not now warranted. We feel that *Acamana* is probably a placental ungulate, but even that is uncertain, and we can go no further at present.

ACAMANA AMBIGUUS,[1] new species

Figures 19-20

Type: M.H.N.M. No. 3010 P.V., anterior part of palate and adjacent parts of face.

Hypodigm: Type only. Another fragment possibly of the same individual is mentioned below but is not now definitely included in the hypodigm.

Horizon and Locality: Divisadero Largo formation, bed G of section in stratigraphic part of this paper, Mendoza, Argentina.

Diagnosis: Only known species of *Acamana.*

Description: The principal fragments, constituting the type, are somewhat difficult to interpret but their characters must be close to those given in the definition and sketch reconstruction. I^{1-2} are evident on the right side only and even there I^1 is somewhat obscure but is probably about as shown. On the left side the alveolar margin posterior to I^3 was broken and the break has been polished to bring out what is preserved. Here the canine is represented only by a matrix-filled alveolus smaller at this section level than at the mouth as shown on the right side. Probably this indicates that the canine had a short and tapering root, rather than any great asymmetry on the two sides.

Perhaps belonging to the same individual or species is a fragment of the left maxilla with parts of M^{2-3}, M.H.N.M. No.

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1 Latin, "uncertain" (as to affinities). As Aka-Manah is male in Persian demonology, we construe *Acamana* as masculine. There are numerous exceptions to the rule that Latin nouns ending in -*a* are feminine, e.g. *nauta*, "sailor."

3011 P.V. The basal contour of M^2 is rounded subquadrate, slightly wider than long, with a rather sharp groove medial, on the buccal margin, between the two buccal roots. The heavier, single lingual root is only flattened or very slightly grooved on the lingual face. Of the crown, only enough remains to show that it was brachydont and had a sharp, narrow anterolingual basal cingulum. The anterior part of M^3 has about the same size and contour as that of M^2. The possibly reduced posterior part is not preserved. The rather short anterior root for the zygomatic arch is above the posterior half of M^2 and anterior half of M^3.

No standard dimensions can be measured accurately. As an approximate indication of size, the width of the snout outside I^3 is roughly 10 cm. and the transverse diameter of the root of I^3 is about 2½ cm. M^2 of the maxillary fragment measured roughly 22 by 28 mm. This is much the largest mammal so far identified in this formation, although some of the unidentified scraps next to be mentioned are from one or more animals of loosely comparable size.

Unidentified Fragments

Numerous other, still more fragmentary specimens of fossil mammals have been collected. As we are unable to make useful identifications of these, their only present interest is the suggestion that the fauna is richer than the list of identified materials indicates. Some of these fragments have, nevertheless, been mentioned in previous publication. Among them are the specimens briefly described (as indeterminate) by Simpson and Minoprio (1949, pp. 23-24, fig. 10 [1]), some of which formed the basis for the mention by Minoprio (1951, p. 66) of "un nuevo género contemporáneo a *Astraponotus*," i.e. a new genus of Mustersan age. We should make it explicit that no special taxonomic relationship to *Astraponotus* is established. It is indeed likely that a new genus is represented, but we cannot make a proper diagnosis or determine the relationships. There is some possibility that certain of the larger scraps belong to *Acamana*, but at present they are not useful in that connection. As discussed below, the age is now believed to be later than Mustersan.

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[1] In that figure the indicated orientation of the zygoma is incorrect. The view is lateroventral, the cavity shown in the upper middle part of the sketch is the glenoid fossa, and the anterior end is to the right.

STRATIGRAPHY

Our consideration of the stratigraphy of the Divisadero Largo formation depends mainly on an unpublished thesis by Olivo Chiotti and on extensive further observations by Minoprio (1951, 1958 and also hitherto unpublished data). Most of the other rather extensive published stratigraphic work on this general region refers primarily to earlier, especially Triassic, beds and has only background interest for the present subject. That literature has been reviewed by Romer (1960).

There have been much duplication and conflict of stratigraphic names in this region. The following summary sequence is now tentatively accepted.

> Mogotes formation. No vertebrate fossils, but certainly late Cenozoic.
>
> Higueral group. No vertebrate fossils in this region, but correlated with beds elsewhere containing late Tertiary mammals. Neogene.
>
> "Areniscas entrecruzadas" or "inestratificadas." Have not been given a geographic formation name, and could be included in the Higueral, as by Minoprio (1958). No vertebrate fossils. Neogene.
>
> Divisadero Largo formation. Mammalian fauna. Further discussed below.
>
> Papagallos formation. No described fossils. Further discussed below.
>
> Río Blanco or Victor formation. Some fossil plants. Triassic, possibly middle Triassic.
>
> Cacheuta formation. A considerable vertebrate fauna, certainly Triassic, probably middle Triassic.[1]
>
> (The thick pile of sediments below the Cacheuta, from Triassic down through the Paleozoic, does not concern us here.)

The Mogotes, Higueral and "Areniscas entrecruzadas" together form a great thickness of strata, over 3000 m. Disconformities within this part of the sequence appear to be local; no interruptions of regional significance have been noted by us or by others, and deposition appears to have been essentially

---

[1] The Río Blanco or Victor, the Cacheuta, and the underlying Potrerillos and Las Cabras formations constitute what was long called the Rhaetic of Mendoza. Frenguelli (1944), who made important studies of these beds, referred them simply to the Triassic. Minoprio (1958) established the age of the Cacheuta more exactly as middle Triassic, perhaps just reaching the late Triassic. Romer (1960) also places the Cacheuta probably in the middle Triassic but considers early Triassic a possibility.

continuous. No fossils have been found in these beds in this area. In the Cacheuta basin, some 30 km. to the southwest, an almost precisely similar sequence occurs. There, near the base of the Mariño (= Higueral), some 20 m. above the highest repetition of "areniscas entrecruzadas" lithology, Patterson found a cranial region of a nothrotheriine sloth similar to *Pronothrotherium* but of rather more primitive aspect. This fortunate find suggests that deposition of the sequence went on throughout much of Pliocene time and perhaps began toward the end of the Miocene. In the same region but at a higher level, in the "tobas grises inferiores" which immediately overlie the Mariño, the type of *Typotheriopsis silveyrai* was found (Cabrera, 1937). That specimen suggests somewhat later Pliocene age, and still other, as yet mostly unpublished, specimens also tend to confirm the extension of this cycle of deposition through much of the late Tertiary.

A disconformity marks the Divisadero Largo — "Areniscas entrecruzadas" contact. Near the base of the latter occur two or three conglomerate beds composed of well-rounded, lustrous pebbles; similar conglomerates also occur at the base of the "Areniscas entrecruzadas" in the Cacheuta Basin. Below the Divisadero Largo in the type area there is a heavy, ridge-forming red sandstone and conglomerate. This has the field name of "Conglomerado rojo" in (unpublished) studies of government petroleum geologists and has been termed the "Horizonte Papagayense" by Rusconi (1950, p. 6). If recognized as a separate formation, the name "Papagallos formation" would apply and we tentatively so list it. The basal unit of the Divisadero Largo, as distinct from the tentative Papagallos, is Minoprio's bed J. In places it rests with apparent conformity on the Papagallos. This is especially the case at Arroyo Divisadero Largo, where bed J is a dark brown sandstone with occasional small geodes that differs on inspection only in color from the underlying Papagallos. Southward, toward the Arroyo Papagallos drainage, however, bed J contains an increasing number of pebbles and cobbles until it becomes a massive conglomerate that clearly reflects a major change in sedimentation. Subsurface data (as yet unpublished) suggest that a long period of erosion preceded the deposition of the Divisadero Largo. The Papagallos formation is almost inseparable from the Divisadero Largo formation in some exposures, its full extent has not been clearly established, and its age is unknown. Its recognition as

a formation is therefore provisional.[1] (In the accompanying map, Figure 21, it is included in the Divisadero Largo.)

The Papagallos is disconformable upon the Río Blanco, the contact being marked by a basal conglomerate and by clastic dikes that extend into the underlying sediments. No fossils have been described from it. The late Dr. Eduardo Carette is reported to have found some reptilian remains but these appear to have been lost. Search by us has been unproductive.

The very thick Triassic sediments appear to form a continuous sequence (Minoprio, 1958; Romer, 1960), despite rather abrupt changes in lithology between formations.

The Divisadero Largo outcrops in a band running from somewhat east of north to somewhat west of south about eight kilometers west of the city of Mendoza. (See map, Figure 21.) Good, fossiliferous exposures occur mainly in two areas, one the type locality on the east side of the Cerro Divisadero Largo (Plate 6), and the other about two kilometers south-southwest, near Papagallos (Plate 7). The beds dip in a general way westward, at Divisadero Largo generally somewhat north of west at angles of about 40°-50° and at Papagallos somewhat south of west at angles of about 20°-35°. These exposures are on the east limb of a broad, rather complex syncline, the other limb of which, more steeply tilted, is some five or six kilometers to the west in the vicinity of the Puesto Chambón. The western exposures include beds tentatively correlated with the Divisadero Largo by Chiotti and by Minoprio. The sequence is, however, complicated by faulting and no fossils have been found. Possible occurrence of the Divisadero Largo formation in the Cacheuta Basin lacks confirmation at present.

Between the localities Divisadero Largo and Papagallos the formation is continuous and without important differences in gross lithology. Relative levels can be reasonably established and guide levels traced through satisfactorily, but some individual beds are more local in character. The following section by Minoprio (1951) at Papagallos, here somewhat abbreviated,

[1] The subsurface data at localities other than Divisadero Largo and Papagallos suggesting a significant disconformity between the Divisadero Largo formation and the Papagallos formation (that is, between the "estratos con anhidrita" and the "conglomerado rojo" of their nomenclature) have been obtained by geologists of the Yacimientos Petrolíferos Fiscales ("Y.P.F."). They have hitherto been working with the scheme here adopted, showing those two entities as distinct stratigraphic formations. At present, however, they are investigating the possibility that the Papagallos or "conglomerado rojo" is to be considered a basal facies in the Tertiary rather than a distinct formation, especially as regards its upper part. (Personal communication from Y.P.F. geologist Dr. Edgardo Rolleri to Minoprio, 24 March 1961.)
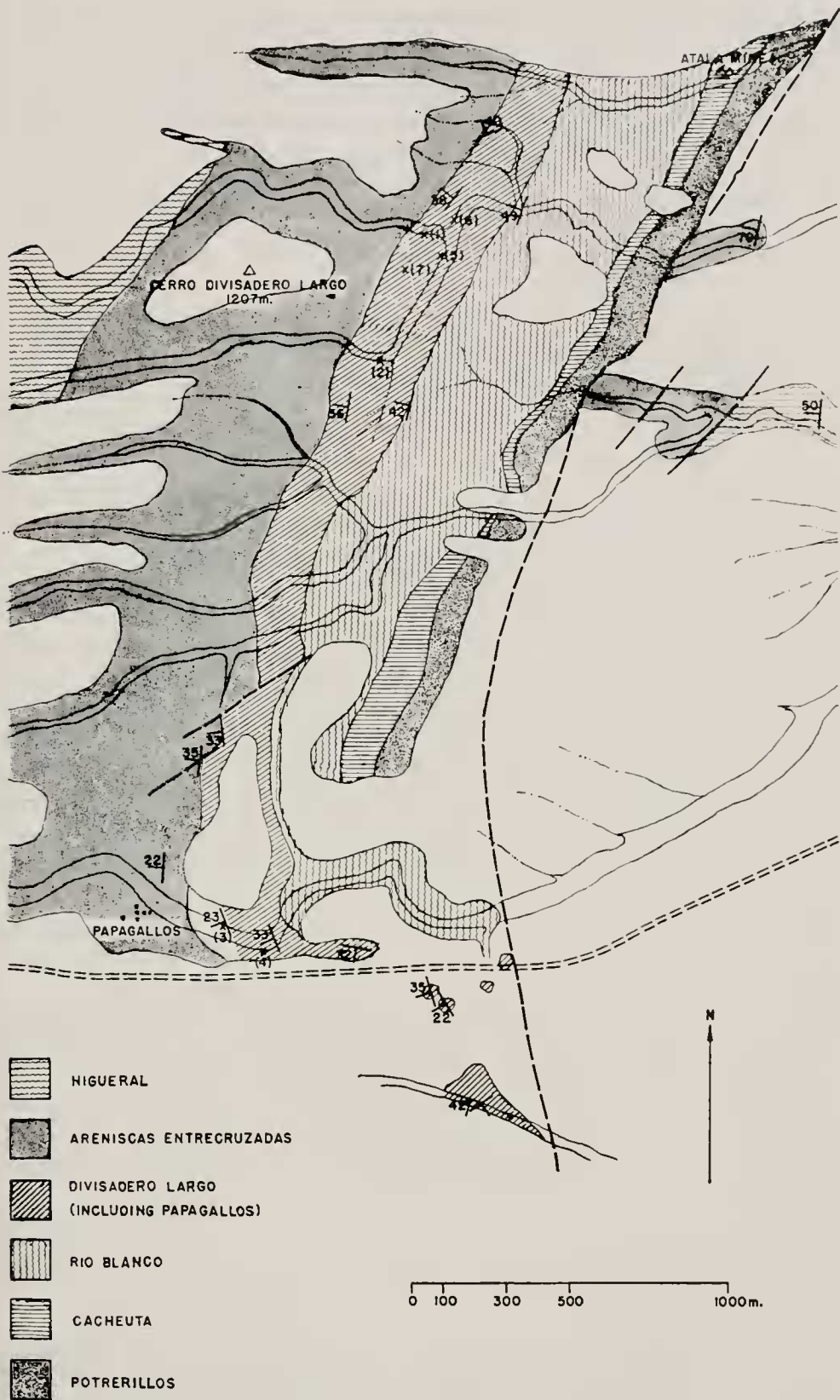
Fig. 21. Sketch map of the mammal-bearing exposures of the Divisadero Largo formation and of adjacent formations. Besides dip and strike symbols, some fossil localities are shown (X and number in parenthesis). (After Simpson and Minoprio, data from Chiotti with additions by Minoprio.)

is sufficiently characteristic of the whole fossiliferous area. The section has been checked and slightly modified by Patterson and, in a much more cursory way, by Simpson in the field.

    A. Conglomerate, pebbles 2-4 cm. in gray sandstone matrix. 2 m. Base of ''Areniscas entrecruzadas.''

∼∼∼∼∼∼∼∼Top of Divisadero Largo formation∼∼∼∼∼∼∼

    B-C. Thin-bedded clays, greenish above, reddish to violet below, with some sandstone. 100 m.

    D. Dark chocolate-colored sandstones, ''Upper chocolate cornice,'' a guide horizon. 3 m.

    E. Pale or light purplish, finebedded marl. 3 m.

    F. Chocolate, buff, or khaki fine sandstones, base harder and forming a lower ''chocolate cornice.'' 42 m.

    G. Lower pale chocolate, buff, or khaki fine sandstones. 65 m.

    H-I. Darker chocolate fine-grained sandstones. 60 m.

    J. Pale maroon conglomerate or puddingstone. 4 m.

∼∼∼∼∼∼∼∼Base of Divisadero Largo formation?∼∼∼∼∼∼∼

    K-L. Fine, bright-red sandstones with basal conglomerate. 57½ m. Papagallos formation (but see note on p. 282).

Petroleum geologists of the Yacimientos Petrolíferos Fiscales (''Y.P.F.,'' the government oil organization) in their field notes have been referring to Minoprio's B-C as ''areniscas abigarradas'' and D-J as ''estratos con anhidrita.'' Those two units, together, thus correspond with our (here slightly redefined) Divisadero Largo formation.

No determinate fossils have been found in A-E or J-L of Minoprio's Papagallos section or their lateral equivalents at Divisadero Largo or elsewhere. The known fauna is thus confined to F-I, hence to the lower and middle, not upper, parts of the Divisadero Largo formation and to the lower of the two Y.P.F. units.[1] Some surface finds had washed down from indeterminate levels and some fossils were collected without adequate stratigraphic information or with levels noted in ways we cannot reliably correlate with our subdivisions. We have, however, been able to make the following identification of fossils of known position in the sequence.

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[1] Patterson did find a fragment of an oldfieldthomasiid(?) mandible lying loose at the base of the ''upper chocolate cornice,'' bed D. If the record could be relied on this would be the highest fossil yet found in the sequence, but unfortunately it cannot be. The formation is now much visited and chance discarding at any level of essentially worthless specimens by casual collectors is a definite possibility.

F. Crocodile. Turtle. *Groeberia minoprioi. Adiantoides leali. Brachystephanus postremus. Xenostephanus chiottii. Trachytherus? mendocensis. Ethegotherium carettei.*

G.-H. Crocodile. *Phoradiadius divortiensis. Brachystephanus postremus. Allalmeia atalaensis. Acamana ambiguus.*

I. Snake. Crocodile. *Brachystephanus postremus. Allalmeia atalaensis.*

CORRELATION

The mammalian faunal list as far as now definitely established and the possible bearing of the various forms on correlation are as follows:

Marsupialia

Groeberiidae

Groeberia minoprioi. Radically unlike anything known from elsewhere, to the familial level at least. Throws no light on correlation. One specimen described.

Litopterna

Proterotheriidae ?

Phoradiadius divortiensis. Generically sharply distinct from anything else known and only doubtfully referred to a known Riochican to Chapalmalalan family. Perhaps somewhat more like known Colhuehuapian-Santacrucian proterotheres, but the resemblance is not close enough to be of high value in correlation and markedly earlier age is not excluded. Moderately common but all specimens very fragmentary.

Adianthidae

Adiantoides leali. Generically well distinct but apparently allied to and more primitive than Colhuehuapian-Santacrucian *Adianthus.* More sharply distinct from Deseadan *Proadiantus* but apparently at a more or less comparable level of specialization. Hitherto known range of family Deseadan-Santacrucian. One specimen, associated skull and jaws.

Notoungulata

Oldfieldthomasiidae ?

Brachystephanus postremus⎫
Allalmeia atalaensis⎬ Very distinct genera referred with strong doubt to a family
Xenostephanus chiottii⎭ otherwise known from Riochican to Mustersan. These forms are primitive in aspect or in evolutionary level and might suggest approximately

Casamayoran age, but they are not phyletically near any known Casamayoran genera. *Brachystephanus* the commonest known fossil in the formation. *Xenostephanus* and *Allalmeia* moderately abundant. Some associated materials of each. There may be some other, now undefinable forms in this general group.

Mesotheriidae

Trachytherus? mendocensis. *Trachytherus* is otherwise known only from the Deseadan. This distinctive species probably does not belong to that genus although certainly allied to it. It is quite unlike anything known from the Mustersan or earlier. The degree of specialization could correspond with Deseadan or could be somewhat earlier but still post-Mustersan. Two specimens identified, both fragmentary.

Hegetotheriidae

Ethegotherium carettei. Allied to but more primitive than Colhuehuapian-Santacrucian *Hegetotherium*. Phyletically distinct from Deseadan *Prohegetotherium* but apparently at a roughly comparable evolutionary level. One known specimen, associated skull and jaws.

Order and Family Uncertain

Acamana ambiguus. Radically unlike anything else known and at present with no bearing at all on correlation. One surely identified specimen, fragments of skull.

The known forms fall into three categories as regards their possible bearing on correlation:

1. Suggestive, in degree of evolutionary advance and in closest known relatives, of distinctly post-Mustersan, perhaps approximately Deseadan, age: *Phoradiadius, Adiantoides, Trachytherus?, Ethegotherium.*

2. Suggestive of earlier, perhaps approximately Casamayoran, age: *Brachystephanus, Allalmeia, Xenostephanus.*

3. Throwing no light at present on age determination within the Cenozoic: *Groeberia, Acamana.*

The third group may — indeed, must — be ignored as regards correlation. The first and second groups are in apparent conflict and at once raise the question as to whether in fact all these fossils are of appreciably the same age. Among earlier identified and described specimens (all those published before the present paper), it happened that so far as they were of known level all from the higher subdivision F belonged to the

apparently more advanced group 1 and those from the lower subdivisions H and I to the apparently less advanced group 2. It was, therefore, a virtually forced preliminary conclusion that those specimens might represent distinct faunas of (at least) two different ages. That hypothesis was accordingly expressed by one of us (Minoprio, 1951). The now greatly augmented data, however, do not support that view and suggest that a single fauna, that is, one without geologically appreciable differences in age, is represented.

It is now definitely established that a variety of forms of group 2, the apparently more primitive animals that suggested greater age for subdivisions H-I, occurs at all fossiliferous levels in the formation. *Brachystephanus postremus,* the only really common species in these collections, is positively identified throughout, from F down to I. That is very strong, if not absolutely conclusive, evidence against appreciable lapse of time. Certainly it precludes any such span as Casamayoran-Deseadan, as those two stages in their typical developments have no mammalian genera and few subfamilies or families in common. "Advanced" *Phoradiadius,* as far as levels are positively known, is from G-H, and is there definitely associated with "primitive" forms. It is true that the other "advanced" forms of known level are so far known only from F, but they are only three in number and are represented by four specimens. Obviously a species known from one or two specimens cannot be distributed throughout a sequence through which it nevertheless originally lived, and the particular level at which it is known is largely or entirely a matter of chance. Although the data do not demand an additional factor, it is also possible that sampling bias (unrelated to geological age) has been introduced somewhere along the line: differences of original ecology, of depositional conditions, or of recent recovery. Such possibilities are suggested by the facts that among the fossils so far known the species in the upper beds are more varied but individually less abundant than those of the lower beds, that only the smaller species are so far definitely recorded in the lowest beds, and that associated skeletal material (of any vertebrate group) of known level is all from the lowest beds. (There are, nevertheless, associated skulls and lower jaws from high levels.) However, those differences in the present rather small collections may, of course, prove to be due to chance rather than to sampling biases.

The physical stratigraphic evidence, although in itself inconclusive, is also consistent with unity of age and tends to

strengthen that conclusion. There are probable small intra-
formational hiatuses, as in virtually any deposit of this thick-
ness, but as the formation is now delimited — including all beds
with identified mammals — there is no intraformational con-
glomerate and nothing that looks like an important or regional
disconformity. The lithology is rather uniform, certainly not
so varied as in itself to suggest any marked change in condi-
tions or lapse of time. The thickness, even if maximum figures
are taken, is not greater than for many continental formations
known to be of appreciably the same geological age throughout.

We conclude that we are dealing with a fauna of a single
geological age and shall further discuss its correlation on that
basis.

Direct correlation of this extremely peculiar fauna is made
virtually impossible by the fact that it has no species and almost
certainly no genera in common with any other known fauna.
One of its families (Groeberiidae) is certainly, another (an un-
named family for *Acamana*) probably, unknown elsewhere. Two
family references (Proterotheriidae and Oldfieldthomasiidae)
are quite dubious. The respective positively known ranges of
those families are Riochican-Chapalmalalan (virtually the whole
Cenozoic) and Riochican-Mustersan. The three most definitely
identified families are Adianthidae (Deseadan-Santacrucian),
Mesotheriidae (Deseadan-Pampean), and Hegetotheriidae (du-
biously Mustersan, definitely Deseadan-Pampean). That is not
much help, beyond the suggestive fact that none of the definitely
identified families has hitherto been surely known before the
Deseadan.

Correlation of this fauna must be based, in the main, on evolu-
tionary level rather than on community of taxa, a notoriously
inconclusive procedure but one that in this case does lead to a
fairly exact conclusion. Although exceptions can occur, the
general rule in such cases is that the age of a fauna is more
closely indicated by its most advanced than by its more primitive
members. Late survival of primitive groups is much more
frequent, at least, than precocious appearance of advanced groups.
Pertinent instances are already known in South American faunas.
Protheosodon in the Deseadan of Patagonia is a condylarth, or
perhaps a very condylarth-like litoptern, decidedly pre-Deseadan
in evolutionary level (Loomis, 1914; Patterson, unpublished
study). The Deseadan genus *Trimerostephanos* is a member
of the predominantly Casamayoran family Isotemnidae, and

(regardless of family reference) is clearly a primitive form of pre-Deseadan aspect. Another isotemnid-like form and a condylarth, both Eocene in aspect, even survive in a certainly long post-Deseadan, approximately Friasian, fauna in Colombia (McKenna, 1956). In spite of the quite rapid evolutionary advance in most lineages and in general faunal characteristics from Casamayoran into Deseadan time, it is thus already known that some lineages did remain comparatively static. Discovery of additional examples should therefore not be unduly surprising, and that might be particularly likely in a fauna such as the Divisadero Largo that is outside the normal or usual paths of South American mammalian evolution as previously known.

Among the advanced forms in the Divisadero Largo, *Trachytherus? mendocensis* and *Ethegotherium carettei* have their closest known relatives in the Deseadan and seem to be on a comparable evolutionary level or possibly slightly more primitive. *Adiantoides leali* has its probably closest relative in the Santacrucian but is distinctly more primitive and more nearly on a level with its collateral relative *Proadiantus* of the Deseadan. *Phoradiadius* looks somewhat more like post-Deseadan than known Deseadan litopterns, but the apparent relationship is not close in either case and the comparable Deseadan litopterns are few and may not adequately represent the evolutionary levels of that time. As is evident from the degrees of confidence of family assignments, relationships of the advanced elements in the fauna with Deseadan forms seem to be distinctly closer than those of the primitive elements with pre-Deseadan groups. That agrees with and reinforces the conclusion that the latter are phylogenetic relicts.

It is thus highly probable that the fauna is approximately Deseadan in age. Later age seems quite improbable. Slightly earlier, but still decidedly post-Mustersan, age is by no means excluded. Survival of the primitive forms would be somewhat more probable at the earliest time assignment warranted by other evidence, which would be more or less immediately pre-Deseadan. Although negative evidence must be viewed with suspicion, especially in a fauna still so imperfectly known, it is just possible that the absence of rodents has a bearing here. Rodents were just beginning to appear in this part, at least, of South America in the Deseadan. A slightly pre-Deseadan fauna might also be expected to be pre-rodent. Absence of rodents may well be purely accidental, but small mammals are here well represented, and

all comparably varied Deseadan and post-Deseadan South American faunas with small mammals do include known rodents. Still more tenuous evidence that rodents were still absent is provided by *Groeberia,* most rodent-like known South American marsupial, which may have been occupying a niche later conquered by rodents. Even the survival of the rodent-sized ungulate herbivores might have been more likely in the absence of rodents.

The conclusion is that the age of the Divisadero Largo fauna is approximately early Deseadan or latest pre-Deseadan. As regards the latter possibility, it has long been realized from the evolutionary change in groups present in both Mustersan and Deseadan that a considerable time must have intervened. No mammalian faunas of intermediate age have been definitely identified, and at least one stage is here missing in the standard continental provincial sequence based on fossil mammals. The Divisadero Largo fauna may well belong in that gap, although if so, it probably belongs toward or at the end of the gap and does not fill the latter or divide it evenly. This cannot be made the basis for supplying a previously missing stage between Mustersan and Deseadan. In the first place, it is not certain that the Divisadero Largo does indeed belong there, and in the second place the known fauna is so scanty and what is known is so peculiar that it could not become a proper and useful standard for correlation.

GENERAL FAUNAL CHARACTERISTICS

The most striking peculiarity of this fauna is its taxonomic distinctness, already emphasized. Certainly all the species, probably all the genera, perhaps about a third of the families, and possibly even an order (for *Acamana*) are, on present knowledge, unique to this fauna. Moreover, most and perhaps all of these mammals do not seem to belong in or near lineages known from rich earlier and later faunas. The most likely exception is *Adiantoides,* which could conceivably be ancestral to *Adianthus,* but that is quite uncertain. With expectable sampling, ecological, and geographic differences, all other known South American mammalian faunas do fit reasonably well into a related continuum of faunal evolution. The Divisadero Largo fauna does not seem to be in or near that temporal mainstream but to be quite lateral to it. We do not know of any such markedly aberrant mammalian fauna from any other continent. Most suggestive, perhaps, is the Gashato fauna of Mongolia but there we

have no known Asiatic "mainstream" for comparison, and two of the genera (*Prodinoceras* and *Palaeostylops*) do tie in more or less closely with the North American sequence.

The evidence is that the Divisadero Largo fauna represents a sort of enclave, isolated in some way and probably peculiar in ecology. There is no evidence for geographic (or physiographic) isolation, and the isolating factors were probably themselves ecological. We are unable to propose any more definite hypothesis. The presence of turtles and crocodilians suggests only that there was surface water in the area and that the climate was at least warm temperate, but that is true of most "normal" South American Tertiary faunas, in many of which turtles and crocodilians are also fairly common elements, and in any case the Divisadero Largo sediments, like the majority of mammal-bearing beds everywhere, appear to be water-laid. The presence of a rather large snake is unusual but not unique, and the rarity of snakes in other South American Tertiary faunas is surely a matter of preservation rather than of the absence of those animals in the living faunas. The absence of carnivorous mammals in the known Divisadero Largo fauna is also certainly a matter of preservation and discovery and not an indicator of ecology. The fact that most of the known Divisadero Largo mammals (except *Acamana*) are small, both absolutely and in comparison with their nearest known relatives, may also be due to depositional conditions and chance or may possibly have some (quite unknown) ecological bearing.

Following Ameghino, *Pyrotherium* has long been considered the guide fossil for what is now called the Deseadan stage, and related genera are known from the earlier Casamayoran and Mustersan. The absence of pyrotheres from the Divisadero Largo fauna cannot, however, be considered particularly significant. Fairly well known local faunas certainly of Deseadan age but without *Pyrotherium* have already been reported (e.g. Chaffee, 1952). Leontiniids are in fact more constantly present in Deseadan faunas and more useful as guide fossils for that stage. Their absence in the Divisadero Largo, if not accidental, may again be ascribed to the manifest ecological peculiarity of this fauna. Deseadan pyrotheres are larger than any mammals yet known from the Divisadero Largo, and Deseadan leontiniids are also larger than any of the latter with the possible exception of *Acamana*.

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