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This volume is dedicated to Dr. Rainer Zangerl

A Primitive Pyrothere (Mammalia, Notoungulata) From the Early Tertiary of Northwestern Venezuela

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ABSTRACT

Proticia venezuelensis n. g. and sp., based on a partial mandible from rocks attributed to the Trujillo Formation, Paleocene to early Eocene, exposed on the southern flank of the Sierra de Baragua, State of Lara, is described. *Proticia* is the second colombitheriid pyrotherian to be recorded; it is possibly ancestral to the later *Colombitherium*. The early pyrotheres are briefly reviewed, and *Carolozittelia* and *Griphodon* retained in the Pyrotheriidae; *Archaeolophus* and *Carolozittelia* may have been based on different parts of the same animal. Some account of the skull of *Pyrotherium* is given, and evidence that the group constituted a suborder of the Notoungulata is presented.

INTRODUCTION

Señor B. Al Protic is a businessman of Caracas, whose avocation is prospecting for mineral deposits in the remoter areas of Venezuela. During 1964, while so engaged in the northwestern part of the State of Lara, he picked up part of a mandible of a fossil mammal and brought it back to his home. In late June of 1972 he invited me to examine the specimen. To my delighted surprise, it was evident at a glance that he had discovered the earliest fossil mammal so far encountered in Venezuela, a primitive pyrothere related to the recently described *Colombitherium* (Hoffstetter, 1970).

Our field party was then on the point of leaving for work in the State of Falcón, and nothing could at the moment be done toward

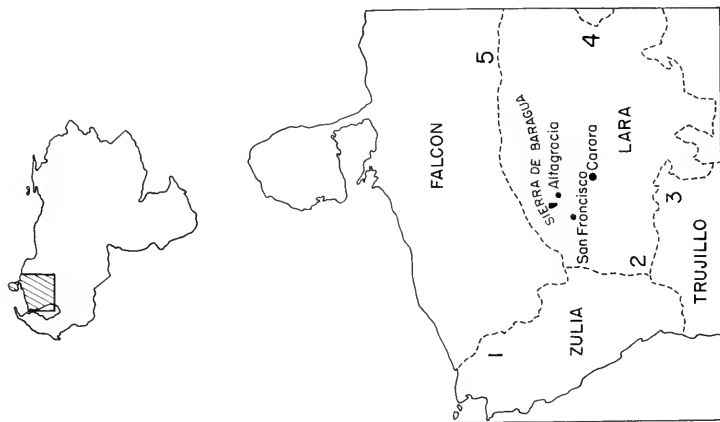
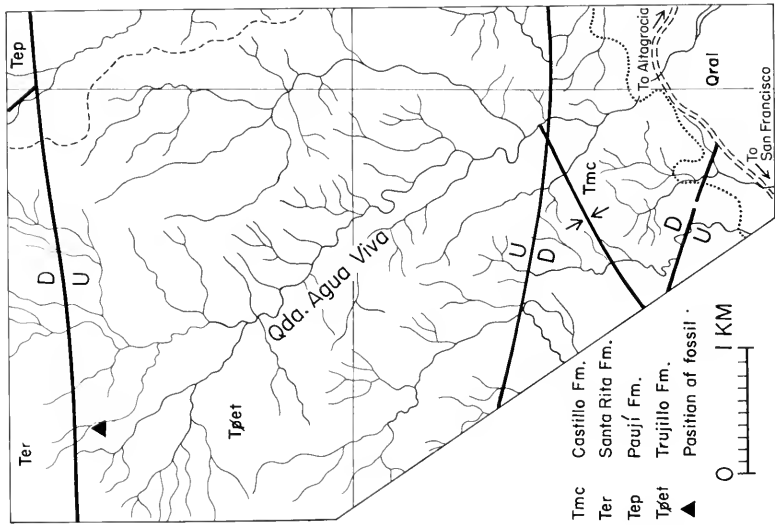


FIG. 1. The *Proticia* locality. The map on the right is modified from Wheeler (MS). The numbers at the lower left indicate the approximate positions of the stratigraphic columns of Figure 2.

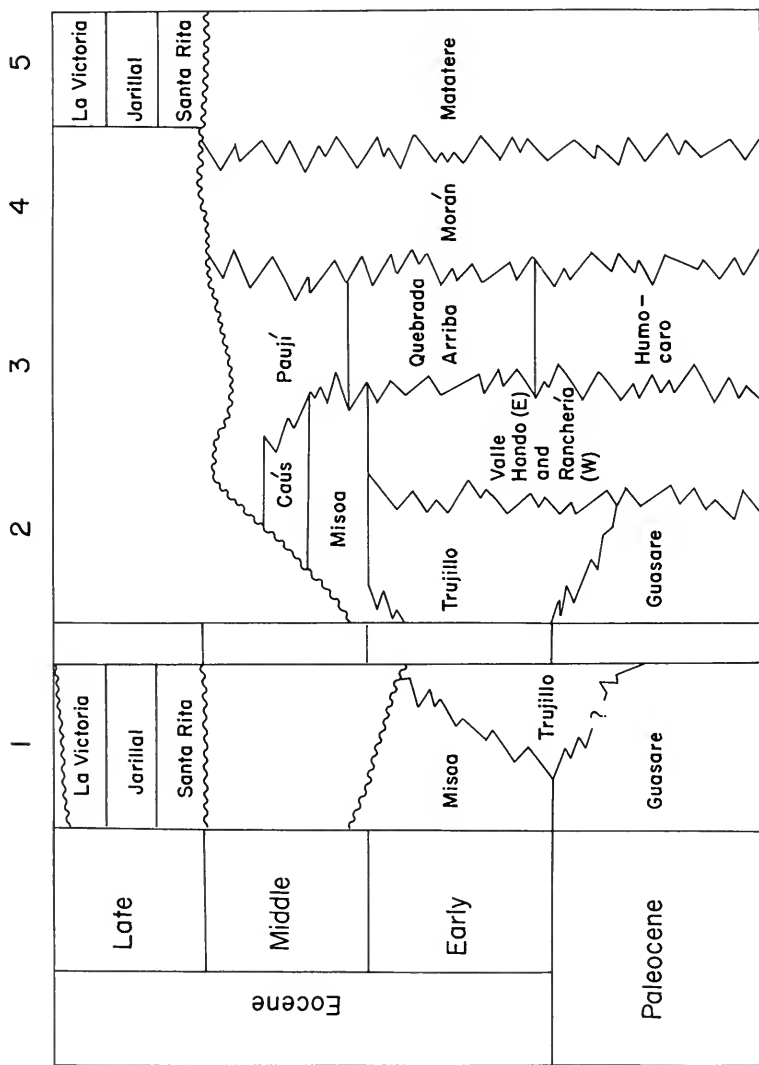


FIG. 2. Early Tertiary rock units east of Lake Maracaibo; data from Gonzalez de Juana et al. (1970). See Figure 1 for localities.

investigating this exciting find. While we were in the field, however, Sr. Protic retraced part of the route he had followed in 1964 and re-located the locality at which he had found the fossil. After our return to Caracas from Falcón, I was able, thanks to the Dirección de Geología of the Ministerio de Minas e Hidrocarburos, to visit the area in the company of a member of their staff, Ingeniero Servando Bastardo Garcia. Sr. Protic very kindly made the journey once again in order to point out the exact spot. This proved to be near the head of the Quebrada Agua Viva (or Marín, as it is known locally) in the western portion of the southern flank of the Sierra de Baragua, which forms part of the northern boundary of the Carora Plain (fig. 1).

The rocks exposed in the quebrada and its tributary system consist in the main of several thousand meters of dark gray to black lutites interbedded with thin, lighter colored sandstones, cut off at bottom and top by faults. This monotonous succession, in which one would hardly expect to find remains of terrestrial vertebrates, is relieved toward the top by the rather abrupt, yet conformable, appearance of thicker beds of yellow to light brown sandstones with some clay and silt partings. The fossil was found on the surface close to the base of a 10 m. thickness of these sandstones, from which it had presumably been derived. The specimen, weathered posteriorly, displays a freshly broken anterior surface. Prolonged search for the missing part met with no success, and a week of prospecting in the quebrada system failed to turn up any other vertebrate remains.

GEOLOGICAL RELATIONS AND AGE

The region now occupied by the Venezuelan Andes and the Seranias de Falcón-Lara-Yaracuy (of which the Sierra de Baragua is a part) would appear to have been unstable during early Tertiary time, the site of deposition of great thicknesses of predominantly clastic sediments. Subsidences and elevations, now in one part, now in another, resulted in changes in source areas, depths of local basins, and depositional environments. Parts of the area, and *Proticia* attests to this, were dry land at various times. In consequence, abrupt vertical changes in types of sediment and rapid lateral changes in facies may occur. Much of the work thus far reported has been local rather than regional, and numerous stratigraphic units have been named (see Gonzalez de Juana et al., 1970, for an admirable summary and for references). The Dirección de Geología is undertaking regional studies that will clarify matters, but for the

immediate present placement of the *Proticia* horizon within this complex (fig. 2) must be attempted. Fortunately, an unpublished report (Wheeler, MS, 1958) on the region containing the locality is in the files of the Creole Petroleum Corporation. A part of it was very kindly made available to me in Caracas. Without this aid I would indeed have been at sea, for this is a bewildering area for anyone coming freshly to it and limited to a brief visit.

Four rock units outcrop at the head of the Quebrada Agua Viva drainage system, each brought up or down into contact with one or more of the others along fault lines (fig. 1). The lowest, topographically, is the Castillo, of early Miocene age and containing numerous marine invertebrates; it has been traced into the area from the type locality in Buchivacoa, Falcón (Wheeler, 1960). Above the fault near the top of the drainage system two formations are present, one coarsely conglomeratic, the other lutitic. Wheeler (MS) identifies them as the Santa Rita, late Eocene, and the Paují, middle Eocene, respectively. A little distance to the west, in the Quebrada El Oro drainage, the two are in unconformable contact; this unconformity is regional (cf. fig. 2). The rock unit in which the fossil was found is identified by Wheeler as the Trujillo, Paleocene to early Eocene; it is widespread in the region and is seen to lie conformably beneath the Paují both to the east and to the west of the Quebrada Agua Viva. The lithology in the western part of the Sierra de Baragua closely matches that described for the type area. Some 25 km. to the east of Quebrada Agua Viva, in the Quebrada La Vera area, the unit becomes coarser in texture, and conglomerates make their appearance (Wheeler, MS). Lateral equivalence to part of the Matatere Formation, Paleocene to middle Eocene, farther to the northeast would seem possible (cf. fig. 2).

The Trujillo is a thick formation, whose base is nowhere visible in the area. At the Quebrada Palito, due north of Carora and some 17 km. east of the Quebrada Agua Viva, Wheeler estimated the exposed section—conformable with the Paují above—to total about 4,800 m., and the whole to considerably exceed 5,000 m. In the Quebrada Agua Viva he estimated a thickness of 2,930 m. (his section stopping short of the fossil locality and of the fault above it), and in the Quebrada Jobo, 11.5 km. to the southwest, of approximately 3,000 m. (the section also being incomplete above). It is difficult to match sections of the Trujillo. Exposures are essentially limited to the sides of the quebradas, the slopes between being covered by mantle and vegetation; the rocks are monotonously

similar; good marker beds are lacking; and fossils are extremely scarce. Wheeler's very tentative matching of his Agua Viva and Jobo sections places the top of the former about 1,600 m. below the top of the latter. On this assumption, the combined thickness of the two amounts to approximately 4,500 m. and the fossil locality is in the lower part of the upper 1,600 m., thus certainly within the upper half of the formation.

Granting all this, it is probable that the age of the specimen is early Eocene—probable but not quite certain. The base of the Trujillo is in places conformable upon the Colón Formation, Coniacian to Maestrichtian (Gonzalez de Juana et al., 1970, p. 173). This could be so in the Sierra de Baragua, in which case the lower part of the Trujillo would cover the whole of Paleocene time. The few microfossils that have been found in it in the area suffice to show that the lower part of the formation is Paleocene, but do not indicate how much of the succession was deposited during this epoch. If most of it was, then the possibility exists that the fossil could be of late Paleocene age. At the other extreme, there is no certainty that the top of the Trujillo in the area coincides with the end of early Eocene time. The Trujillo is conformable with the overlying Paují, now known to be of middle rather than late Eocene age (Walton, 1966), but farther to the west is another formation, the Misoa, also of middle Eocene age and older than the Paují. If the Misoa is laterally equivalent to part of the Trujillo as well as to part of the Paují in the area, then the fossil could conceivably be of early middle Eocene age. Amid these uncertainties I opt for early Eocene. As regards its morphology, the fossil itself is consistent with, although not of course proof of, such an age.¹ It is more primitive than *Colombitherium*, to which it may have been ancestral. The Colombian specimen came from the Gualanday Group, which is tentatively regarded as middle and late Eocene, although the possibility of a slightly younger age is not excluded (Hoffstetter, 1970, pp. 155-159).²

¹Samples of the matrix surrounding the specimen were submitted to the Escuela de Geología, Universidad Central de Venezuela for examination. There they were very kindly examined by Dr. Emanuel J. Nieves, who found "no pollen, spores or any organic material."

²In a more recent study, Anderson (1972) cites unpublished oil company data that indicate a range from middle Eocene to early Oligocene for the Gualanday. The type of *Colombitherium tolimense* was found on the surface near the contact between the lower conglomerate unit and the lower to middle transition unit, which is suggestive of late middle or early late Eocene age.

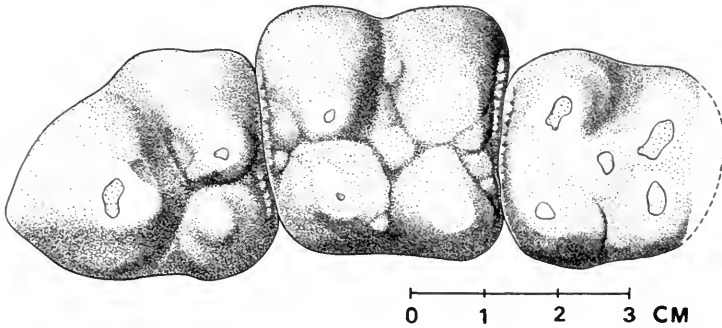


FIG. 3. *Proticia venezuelensis* n. g. and sp. $RP_3 - M_1$ of type in crown view. $\times 1/1$.

The history of the two known colombitheriid specimens is curiously similar. Each was picked up and preserved as an object of interest, and only later came to scientific attention. The describers of them were able to visit the localities and determine the stratigraphic positions, but found no additional materials. In both cases there is some doubt regarding the age of the beds from which the two were derived.

TAXONOMY AND MORPHOLOGY

Notoungulata
Pyrotheria
Colombitheriidae

Proticia new genus

Type species. — *P. venezuelensis* n. sp.

Distribution. — Early Eocene (probably), Venezuela (see above).

Diagnosis. — Cheek teeth more bunodont than those of *Colombitherium*, enamel of P_{3-4} higher on labial than on lingual faces, not evenly distributed around the crowns; P_4 and M_1 with low, blunt metalophids, hypoconids and entoconids distinct, not united to form hypolophids; M_1 small relative to premolars.

Etymology. — Named for Señor B. Al Protic.

Proticia venezuelensis new species

Type. — Museo de Historia Natural, Caracas, no. 237. Part of the right ramus and of the symphysis of a mandible with $P_3 - M_1$, the basal portion of the right tusk, and part of the alveolus of the left.

Hypodigm. — The type only.

Horizon and locality. — Upper part of the Trujillo Formation (Paleocene-early Eocene); near the head of the Quebrada Agua

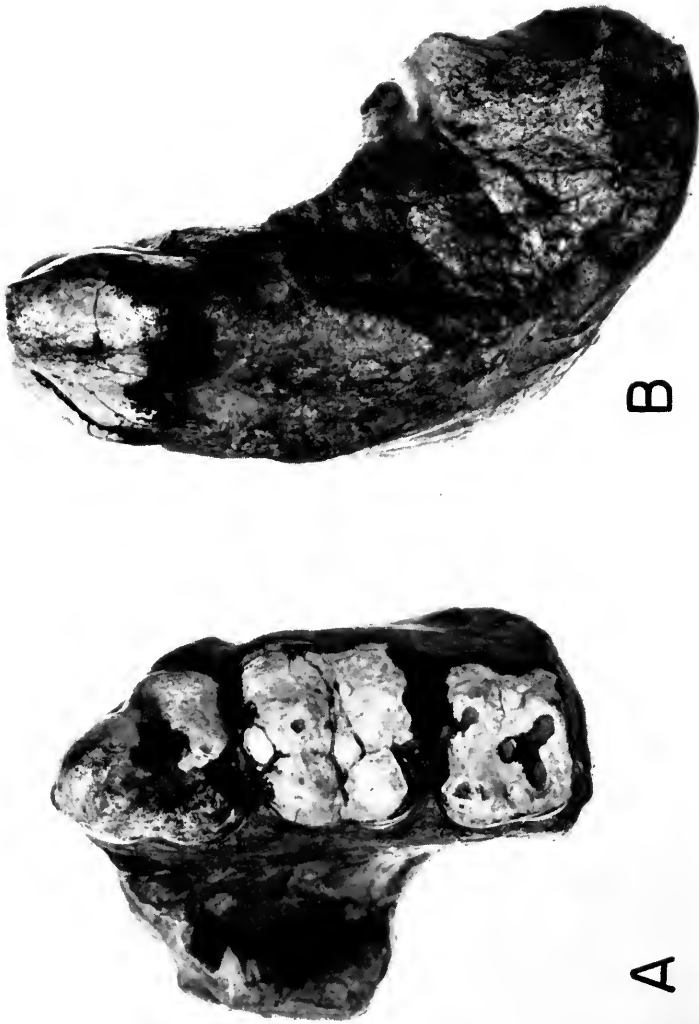


FIG. 4. *Proticia venezuelensis* n. g. and sp. Type in dorsal, A, and anterior, B, views; $\times 4/5$, approx. The particolored appearance of the enamel is due to partial erosion of a dark-stained superficial layer.

Viva, Sierra de Baragua, District of Torres, State of Lara, Venezuela (see above).

Diagnosis. — As for the genus.

Direct comparison with *Colombitherium tolimense*, known only from a partial maxilla with P³-M³, is not possible, but it is evident that *Proticia* is the more bunodont, and hence presumably the more primitive, of the two. In groups, such as the pyrotheres, evolving toward lophodonty, upper and lower dentitions as much out of evolutionary phase as are those of these two forms do not occur in association.

Description. — P₃ is irregularly triangular and somewhat longer than wide, consisting, in the unworn state, of a very large, rounded anterior cusp and two somewhat lower, much smaller rounded cusps arranged transversely; with wear all three would become confluent. The postero-external and -internal cusps are serially homologous with the hypoconid and entoconid, respectively, of the molars; a short, poorly defined crest runs antero-lingually from the apex of the former. A slight, crenulated posterior cingulum is present, situated about half way up the crown and confined to the middle of the posterior face. The anterior portion of the tooth is set off from the posterior by wide, shallow, vertical grooves, the anterior face is steeply inclined, and the posterior half shelves labially. The enamel extends farther down the crown anteriorly than posteriorly and labially than lingually, the greatest extension being antero-labial. The roots are long and stout, the anterior extending to within a short distance of the root of the tusk.

P₄ is the largest of the three teeth preserved; nearly quadrate in outline, it is slightly longer than wide and a little wider anteriorly than posteriorly. It bears four large, blunt, nearly subequal cusps, the apices of the anterior pair, protoconid and metaconid, being closer to each other than are those of the posterior pair, hypoconid and entoconid. Protoconid and metaconid are nearly, although not completely, united to form a low, heavy metalophid that is slightly higher than the posterior pair of cusps. In addition to these principal features are a smaller antero-central cusp, the paraconid, set off by very narrow, shallow grooves from the protoconid and metaconid, a central cusp demarcated from the principal ones by comparable grooves, and a postero-central cusp similarly separated from the hypoconid and entoconid. As on P₃, a poorly defined, blunt crest runs antero-lingually from the apex of the hypoconid; it forms, across the narrow groove between them, a wear surface with the central cusp, the two together constituting the crista obliqua.

Cuspules are present lingual to the paraconid and to the hypoconulid. Very slight cingula occur at the central portions of the anterior and posterior faces. Enamel extends farther down the crown labially than lingually and farthest antero-labially, although not to the extent seen in P_3 . The labial face is shelving.

The nearly quadrate M_1 is decidedly smaller than either P_3 or P_4 , a marked contrast to the size relations of the anterior cheek teeth in *Colombitherium tolimense* and, even more, to those of *Pyrotherium* and *Griphodon*. The tooth is somewhat wider anteriorly than posteriorly, and the protoconid and metaconid farther from each other than are the hypoconid and entoconid, the reverse of the relations between the cusps on P_4 . There is no paraconid, and no indication of a hypoconulid on the part preserved. The central cusp has been converted to a shallow pit by wear. A trace of an anterior cingulum is present, but nothing can be said as regards a posterior shelf, which presumably included the hypoconulid, as the back of the tooth is eroded away. By analogy with other early pyrotheres, there may have been a rather large one. The enamel is evenly distributed around the base of the crown, and the roots are shorter than those of the premolars. Wear is apical, as in *Colombitherium*, not oblique, as in pyrotheriids (cf. Hoffstetter, 1970, pp. 19-20, fig. 7).

The large, tusk-like incisor extended back beneath P_4 , at least. The exposed section, at the level of P_3 , reveals a tooth irregularly convex on the labial face and gently so on the lingual, slightly more than twice as deep as wide, and somewhat tapering ventrally.

The mandible is very deep and massive, deepest at the symphysis and shallowing a little posteriorly. The lateral face is gently convex, with a marked prominence over the posterior root of P_3 and an indication of outward flaring beneath M_1 , as in *Griphodon*. No foramen is clearly evident. A depressed, somewhat broken area beneath the anterior root of P_3 may mark its position, but this is uncertain. The

MEASUREMENTS IN MILLIMETERS

	P_3	P_4	M_1
Length	38.1	35.0	26.0+
Width, anterior	23.4	34.4	29.2
Width, posterior	31.6	32.9	26.8
Incisor, depth		36.0	
Incisor, width		16.4	
Ramus, depth at P_{3-4}		105.3	
Ramus, depth at P_4 - M_1		92.6	
Ramus, width at P_4		42.1	

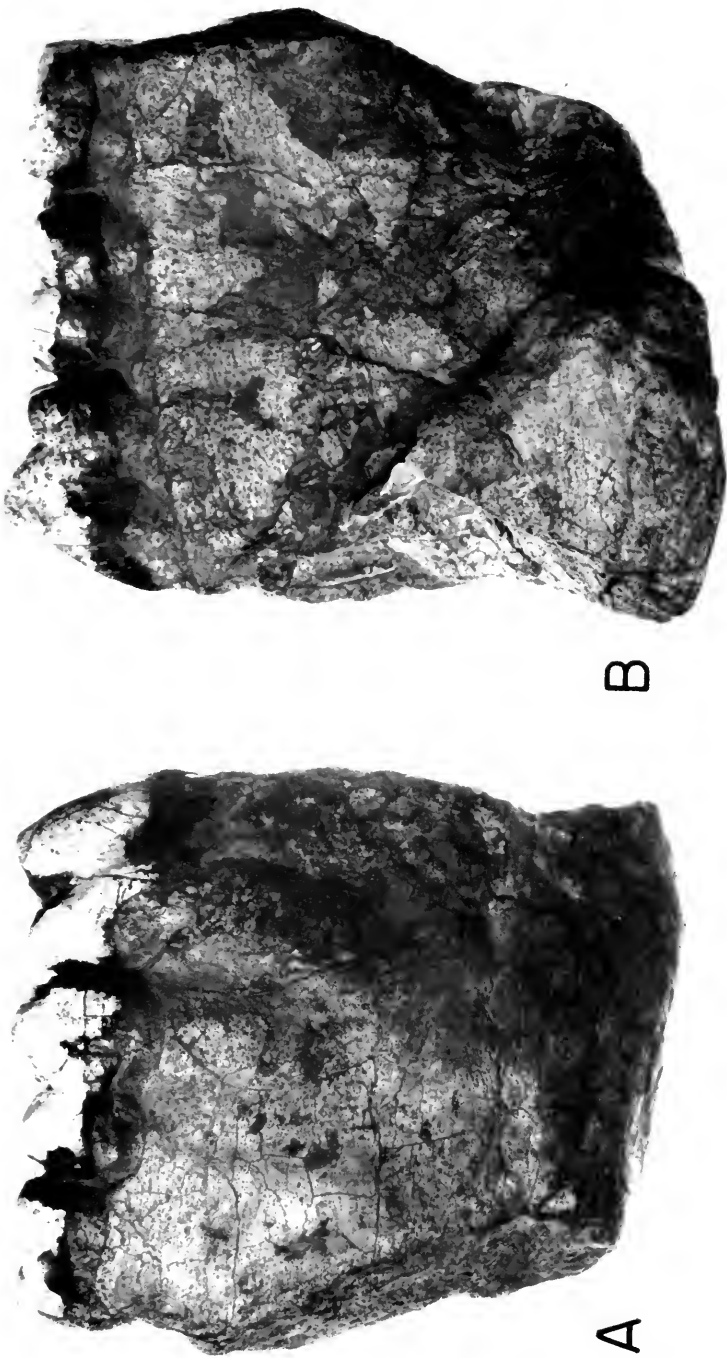


FIG. 5. *Proticia venezuelensis* n. g. and sp. Type in lateral, A, and medial, B, views; $\times 4/5$, approx.

medial face is concave ventrally beneath M_1 , but is otherwise flat and descends evenly to the symphysis, which extends to beneath P_4 and ascends rapidly, at an angle of about 45° , to the front of P_3 . From the close proximity of the two incisors and the narrowness of the symphysis it is evident that the tooth rows were nearly parallel and close together, as in *Colombitherium* and *Pyrotherium*.

Discussion.—The closest known relative of *Proticia* is certainly *Colombitherium*. In both, the quadrate cheek teeth are either on the way to or have achieved bilophodonty, and the lophs and lophids are relatively low; the posterior premolars, P_{3-4}^{3-4} , are nearly or quite molariform; and a central cusp is present in the middle of the median valleys of P_4 - M_3 .¹ Hoffstetter had little hesitation in referring *Colombitherium* to the Pyrotheria, and *Proticia* strongly supports this assignment. P_3 is in general similar to the corresponding tooth of *Pyrotherium*; in both there is a single, very large anterior cusp and a talonid that is incipiently molariform in the one and fully so in the other. The enlarged, tusk-like lower incisor and the narrow, parallel-sided palatal area of *Proticia* are definitely pyrotherian. Such characters forbid reference of these forms to the Xenungulata (Paula Couto, 1952), the only other group of native South American ungulates known to have evolved bilophodont molars. Within the Pyrotheria, Hoffstetter considered *Colombitherium* to be sufficiently distinct to warrant a separate family for its reception. The characters he (1970, pp. 166-167) cites justify this,² and *Proticia*, considerably less advanced toward lophodonty than the roughly contemporaneous *Carolozittelia*, confirms the view that two pyrotherian lineages existed. As Hoffstetter pointed out, *Colombitherium* is clearly distinct from any of the pre-Deseadan forms—*Carolozittelia*, *Griphodon*, *Propyrotherium*—that have been referred to the Pyrotheria, and this is even more evident in the case of *Proticia*.

¹Such may confidently be inferred for *Colombitherium* from the presence of correspondingly situated wear pits in the uppers; it is conceivable, further, that these pits are themselves remnants of small cusps present in the unworn state (cf. M_1 of *P. venezuelensis*, in which the cusp has been converted to a pit by wear; figs. 3, 4a).

²With one possible exception. Hoffstetter suspected the upper cheek tooth formula of *Colombitherium* to be P^3 - M^3 , not P^2 - M^3 as in *Pyrotherium*. The general similarity between *Pyrotherium* and *Proticia* in the anterior part of the lower cheek tooth row suggests that in the latter P^2 was present and in series, and the same may have been true of the Colombian species as well. P^3 of the type and only specimen of *C. tolimense* being incomplete anteriorly, the presence or absence of an interdental wear facet cannot be detected.

All pre-Deseadan pyrotheres are poorly known—the types of *Colombitherium* and *Proticia* are actually the best and the second-best specimens available. The affinities of two of them, *Carolozittelia* and *Griphodon*, have been questioned (Paula Couto, 1952, p. 387; Simpson, 1967, pp. 238, 240), due to certain resemblances to the xenungulate *Carodnia*, in which M_{1-2}^{1-2} are bilophodont. These teeth in *Carolozittelia*¹ indeed resemble those of *Carodnia*, but, as both Paula Couto and Simpson point out, M_3^3 are very different in the two. The small pyrotherian incisor described by Ameghino (1897, p. 447) as *Archaeolophus praecursor* probably represents the same animal as the molars described as *Carolozittelia tapiroides*.² The case for affinities with the Pyrotheria is, I think, the stronger of the two possibilities. The Peruvian *Griphodon*, of unknown but presumably Eocene age, is known from P_3 - M_1 , dm_4 , and the adjacent portion of the ramus (Anthony, 1924; Patterson, 1942). P_3 is unlike that of *Pyrotherium*, as Simpson noted, and of *Proticia*, but it is basically bilophodont, hence very different from the corresponding tooth of *Carodnia*. P_4 is almost fully bilophodont and definitely pyrotherian in aspect; the presence of a paraconid is a point of resemblance to *Proticia*. M_1 does resemble that of *Carodnia*, but the resemblance to *Propyrotherium* is just as striking; the posterior shelf is equally as large in both, and larger than the posterior cingulum of *Carodnia*. The lophids bear small denticles, as in *Propyrotherium* and *Pyrotherium*, and the heavy, thick ramus is more pyrotherian than xenungulate. I would retain *Griphodon* in the Pyrotheriidae.

The mutual affinities of these early pyrotheres are very far from clear. On the scanty evidence available, *Proticia* could have been ancestral to *Colombitherium* if the two were sufficiently separated in time; descent of the one from the other would have involved no major change, simply an increase in lophodonty and an enlargement of M_1 relative to the premolars. *Propyrotherium*, to judge from tusk and cheek teeth, may well have been the ancestor of *Pyrotherium*. M_1 of *Griphodon* differs from that of the Mustersan genus in being pinched at the waist—a resemblance to *Carodnia*—and slightly

¹ M^1 of *C. tapiroides* is represented by the type of *C. "eluta,"* stated to have come from the Deseadan but certainly Casamayoran in age; M_1 is unknown.

²*A. praecursor* was usually regarded by Ameghino as Deseadan in age, but he described it prior to recognition of the Casamayor fauna, and the other syntype of the species is an incomplete M_1 of a Casamayoran, not Deseadan, isotemnid. His one reference of it to the "fauna del *Notostylops*" (1899, p. 13) was correct.

longer relative to width. Ameghino's syntype lower cheek tooth of *Propyrotherium* (Simpson, 1967, pl. 45, fig. 8) has only a slight posterior cingulum, not a shelf, which indicates, contrary to my (1942) earlier opinion, that it is P_4 . As such, it differs from P_4 of *Griphodon* in the lack of any trace of a paraconid. On this slender basis the Peruvian form would appear to be the more primitive of the two. *Carolozittelia*, as Simpson has stressed, was probably not in the direct ancestry of *Pyrotherium*, but, for the present, I would retain it in the Pyrotheriidae rather than place it in a family of its own. Summing up, it appears that some radiation of the pyrotheres did occur, although available materials are quite insufficient for any real understanding of it. All that can be said at present is that colombitheriids and pyrotheriids diverged before Riochican time, and that, within the latter family, there was a trend or trends toward reduction of the posterior shelf of the lower molars, most notably of M_3 .

THE AFFINITIES OF THE PYROTHERIA

The cheek teeth of these early pyrotheres do not throw any certain light on the origin and affinities of the group. In the uppers, the lophs, composed of paracone-protococone and metacone-hypocone, are somewhat cusped at their extremities, and neither shows any clear indication of the former presence of a conule; *Colombitherium* may have had a cuspule in the median valley. *Proticia* reveals that the lophids are formed by the protoconid-metaconid and the hypoconid-entoconid, respectively. The hypoconulid did not participate in the posterior lophid of the molars, and was presumably incorporated in the large posterior shelf (a lophid in the case of M_3 of *Carolozittelia*) of the molars of the early pyrotheriids. No trace of a paraconid remains in the molars but a small one is present on P_4 of *Proticia* and *Griphodon*. So far as known, the lower premolars have only a slight posterior cingulum in contrast to the shelf of the molars. One can visualize, as did Ameghino (1902), teeth of this sort as derivable, structurally, from a condylarthran base. Possible difficulties, although by no means insuperable ones, would be the large size of the proto- and metaconules of known didolodontids and the tendency among them toward incorporation of the hypoconulid in a common lophid with the hypoconid and entoconid on M_{1-2} . Offsetting these are the rather bunodont structure of the known cheek teeth of *Proticia* and the presence of a cuspule in the crista obliqua (cf. *Didolodus*). However, the Notoungulata should also be taken

into consideration. In early and primitive members of this order there is little or no indication of conules in the loph, and the entoconid and hypoconid of the lower molars tend to form a lophid that excludes the hypoconulid. Should the colombitheriids prove to have a cuspule in the median valley of the upper molars, this would also be a point of resemblance to notoungulates. Enlargement of one or two pairs of incisors is not uncommon in members of this order.

Clues such as these, tenuous, ambiguous, can convey suggestions, but can carry us no further. The only adequately known pyrothere is *Pyrotherium* itself. Only one incomplete skull of this animal has so far been discovered, the prize of the late Professor F. B. Loomis' expedition to Patagonia in 1911-1912. Upon this skull, then, nearly all depends.

In 1914, Loomis described and figured the specimen, which he identified as *P. sorondoi*.¹ His rather summary description was in part incorrect and his figures were to a considerable degree inaccurate and idealized. He concluded, in essential agreement with Ameghino, that pyrotheres constituted a suborder of Proboscidea,² a view that has not received wide acceptance. The prevailing opinion is that of Gaudry (1909), who, after comparing *Pyrotherium* with other large hoofed mammals (but not, it may be noted, with any notoungulate), concluded that pyrotheres formed a distinct ungulate order.

Since Loomis' work there has been no firsthand study of the skull. Loan of the specimen by the Amherst College Museum, together with permission to carry out such further preparation as might be

¹This and several other Deseadan species placed in the genus by Ameghino—*trilophodon*, *pluteum*, *crassidens*—are indistinguishable from *P. romeri*, the type. Ameghino believed that *sorondoi* differed in the lack of P¹. The supposed P¹ of *romeri* (Museo Argentino no. A52-290, a referred specimen) is actually dm¹. Also attributable to the type species are *Parapyrotherium planum* and *Ricardowenia mysteriosa*. *Rodiotherium armatum*, referred to the family by Ameghino, is not a pyrothere but a leontiniid, a synonym of *Ancylocoelus frequens*. "*Pyrotherium giganteum*" based on a fragment of the alveolar portion of a tusk (now lost) may be, as Gaudry thought, an astrapothere; it is a *nomen vanum*.

²Earlier (1913, pp. 134-6), Loomis had proclaimed *Pyrotherium* a toxodont. Later (1921, p. 190), he withdrew his support of proboscidean relationships, advocating instead affinities with diprotodont marsupials (an idea that had previously been advanced around the turn of the century). On neither occasion did he present any evidence. Several early authors included pyrotheres among the notoungulates, but usually in company with the extraneous astrapotheres and litopterns. In recent times there has been some tendency to associate them with such unrelated groups as the pantodonts and uinatheres.

necessary, has now made such study possible. Upon examination, it was at once apparent that much of the surface had been obscured by a thick coating of orange shellac. Elimination of this revealed that a good deal of matrix had not been removed, and that this incomplete preparation had seriously misled Loomis in part of his interpretation. He had recognized that the skull had remained exposed on the surface before burial, but had not fully realized how very extensive the weathering had been. It is now quite evident that the specimen had lain palate down for a long time, long enough for complete loss of the cranial roof and of the dorsal half of the occiput, for erosion of the dorsal surface of the premaxillaries, and for extensive damage to the basicranium, which, due to the pronounced upward inclination of the basicranial axis relative to the palatal, had, like the roof, been wholly exposed to the action of the elements and of scavengers. When transported to its final burial place the skull came to rest on its side, and subsequently suffered further from lateral crushing. Cleaning has revealed a system of sinuses in the dorsal portion of the skull that was much more extensive than Loomis had supposed. The idealized nasals and adjacent parts of the frontals and the left postero-lateral corner of the cranial roof in Loomis' (1914) figure 111, for example, are not parts of the skull surface at all, but are floors of portions of this system.

Study of the specimen reveals that the pyrotheres were notoungulates, aberrant in some ways yet basically and unmistakably members of that order. This is not the place for detailed presentation of all the evidence, but a crucial part of it, the auditory region, may be presented, and one or two additional points touched upon.

Members of the Notoungulata are distinguished, as is well known (Roth, 1903; Patterson, 1932, 1936, 1937, 1952; Simpson, 1936, 1948, 1967), by the following combination of characters in this region: an inflated auditory bulla with a large hypotympanic sinus, an auditory meatus that is well ossified and frequently with a prominent ventral crest (crista meatus), a large epitympanic sinus in the squamosal, a large vagina processus hyoidei, the stylo-mastoid foramen opening between the crista meatus and the post-tympanic portion of the squamosal (or posterior adventitious bone), the canal of Huguier, for *N. chorda tympani*, opening externally at the posterior end of the fissura Glaseri, and an associated, complex venous sinus system. Other features of rather frequent occurrence are the presence of a styliform process at the anterior end of the bulla and a tendency for the dorsal part of the wall of the antero-

medial extremity of the bulla to overlap and to be appressed against the basicranium. There is clear evidence that in various notoungulates the bulla was a compound structure composed of ecto- and entotympanic elements, and that in some of them an adventitious bone or bones occur in this area of the skull. Both features may be characteristic for the order, the first of them almost surely so, but their presence is usually difficult to detect in adult specimens.

The postmortem weathering undergone by the skull at hand has affected the auditory region — the periotics have largely been destroyed, the dorsal and ventral portions of the bullae and the roof of the right epitympanic sinus lost, and other damage done — but the essential features can nevertheless be discerned (fig. 6). What remains of the auditory bulla suggests an egg-shaped structure of the sort met in such toxodontids as *Adinotherium* and *Nesodon*, and, as in those forms, consisting very largely of the hypotympanic sinus. Anteriorly, the medial wall slightly overlaps onto the base of the pterygoid. Whether or not a styliform process was present is uncertain. A large opening, the foramen pneumaticum, leads laterally from beneath the preserved remnants of the bulla to an extensive cavity in the squamosal; this, Loomis' (1914, p. 168, fig. 111) "ear chamber", is the epitympanic sinus. The left side of the specimen reveals that the sinus is beneath and separate from the sinus system that underlay the skull roof. Extending laterally from the bulla, between the postglenoid portion of the squamosal and the post-tympanic portion (or, possibly, the posterior adventitious bone), is a crest, incomplete laterally on both sides, that forms part of the ventral border of the porus acusticus externus. This is the crista meatus. Dorsally, the crista sends a short process posteriorly that fuses with the post-tympanic portion of the squamosal. Immediately below the point of fusion is a foramen, the stylomastoid. A foramen at the posterior end of the fissura Glaseri, just anterior to the crista meatus, is the canal of Huguier (this is Loomis' "foramen for the internal common carotid," and the fissura is his "Eustachian canal"; 1914, fig. 109A). Behind the bulla, between it and the paroccipital process of the exoccipital, is an oval structure, concave ventrally and rugose within the concavity. This is the tympanohyal fused with the enclosing vagina processus hyoidei. A tympanohyal within the vagina has been reported in *Toxodon* (Burmeister, 1864, p. 262) and *Pseudotypotherium* (Patterson, 1934). The porus acusticus externus is large, trumpet-shaped above (cf. *Pleurostylo-*
don, Riggs and Patterson, 1935, pl. 5), and somewhat open below,



A



B

FIG. 6.

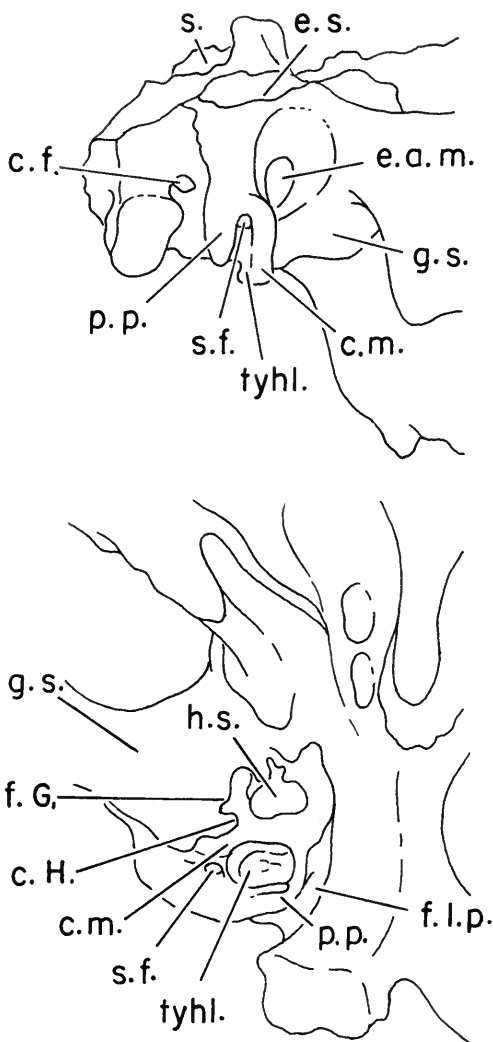


FIG. 6. *Pyrotherium romeri* Ameghino. Amherst Museum No. 3207. Auditory region of right side in lateral, A, and ventral, B, views; A, $\times 0.24$; B, $\times 0.31$.

c.f., condylar foramen; c. H., canal of Huguier; c.m., crista meatus (incomplete laterally); e.a.m., external auditory meatus (roof largely weathered away); e.s., epitympanic sinus (roof and much of floor weathered away); f. G., fissa Glaseri; f.l.p., foramen lacerum posterius; g.s., glenoid surface; h.s., hypotympanic sinus (sectioned by weathering); p.p., paroccipital process (weathered); s., sinus dorsal to epitympanic sinus (partly preserved on left side); s.f., stylomastoid foramen; tyhl., tympanohyal.

although by no means to the extent depicted by Loomis (1914, figs. 109A, 113); it is a little above the level of the glenoid surface. The roof of the auditory meatus, which floors part of the epitympanic sinus, is very thin, and erosion has destroyed most of it on both sides of the specimen.¹ As the base of the paroccipital process shows evidence of weathering, it is impossible to determine what its length may have been. A cast of what remains of the endocranial cavity² reveals traces of anterior periotic and transverse sinuses, but is too incomplete for certainty as to the presence of the lateral cerebral.

A combination of characters such as this is encountered in the Notoungulata—and in no other ungulate order. *Pyrotherium* differs from other members of the group in lacking any trace of a post-glenoid foramen, but this is a minor difference, and one very possibly linked to the antero-posterior compaction of the cranium associated with the strong upward inclination of the basicranial axis and the remarkable posterior shifting of the anterior narial opening. The angulation of this axis and the forward pitching of the occiput find a parallel within the Notoungulata among haplodontheriine toxodontids (e.g., *Toxodontherium*, Lydekker, 1893, pls. 6, 7; *Trigodon*, Ameghino, 1907, figs. 3, 4). The position of the narial opening, above and between the orbits, is unique in the order, but the gap between *Pyrotherium* and other notoungulates in this feature is partially bridged by *Homalodotherium*. The deep and heavy zygoma is continuous postero-dorsally with the occipital crest, as in other members of the order. Loomis believed the arch to be composed of the maxilla anteriorly and the jugal posteriorly, with the squamosal participating only to a very limited extent at the posterior root. There is no evidence for any of this. A suture between maxilla and jugal is clearly visible on the left side of the skull, and demonstrates that the latter bone contributed largely to the anterior root of the arch. The supposed suture between jugal and squamosal near the posterior root shown in Loomis' figure 112 is a crack, but traces of the suture he interpreted as the maxillo-jugal do exist, and these

¹The plate of bone considered by Loomis (1914, p. 168) to mark the division between the "cochlear" and "posterior ear chamber proper" portions of his "auditory chamber" (=epitympanic sinus) is actually a remaining portion of the roof of the meatus.

²Loomis stated that the brain was "diminutive." It was small in terms of the size of the skull, but in terms of actual dimensions — the endocast is over 80 mm. in width, not 50 as Loomis stated — it was comparable to the brains of such early Miocene forms as *Homalodotherium* and *Nesodon*.

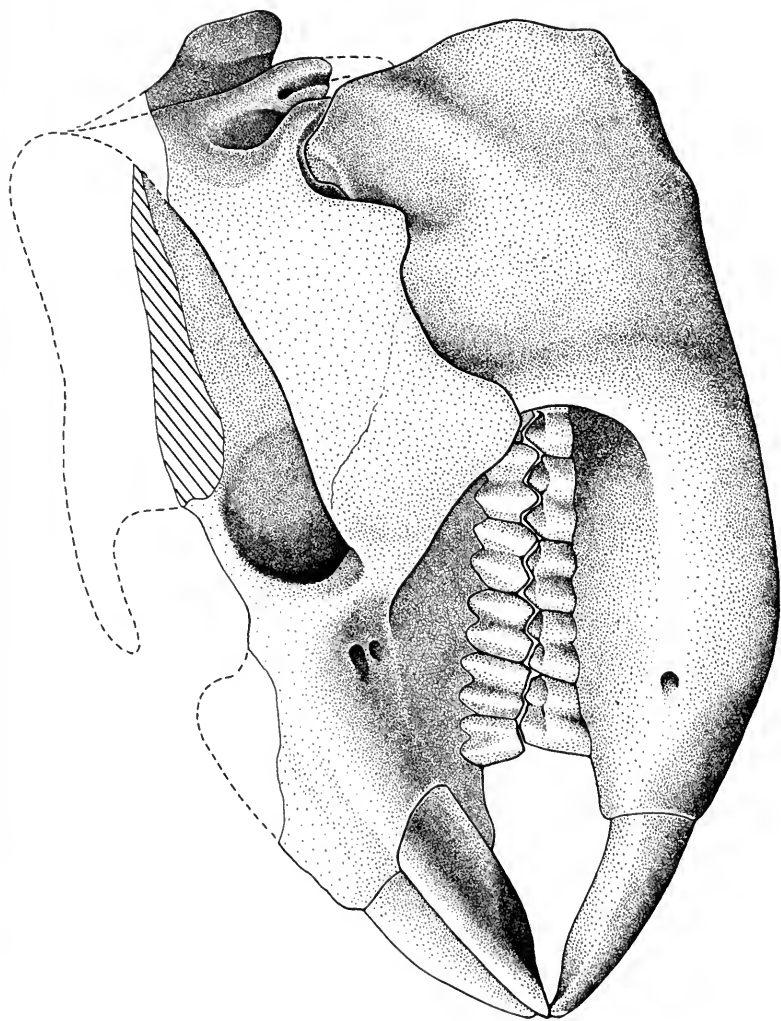


FIG. 7. *Pyrotherium romeri* Ameghino. Restoration of skull and mandible in left lateral view, $\times 1/6$.

indicate that the participation of jugal and squamosal in the formation of the zygoma was roughly equal, as in notoungulates generally (Interatheriidae excepted). Neither arch is complete, but nearly all of the structure can be seen on one side or the other. Most of the anterior portion is present on the right side, and this reveals that Loomis' reconstruction of a large notch above M_2 is without foundation. One additional feature may be mentioned. In nearly all notoungulates the antero-dorsal portions of the premaxillaries anterior to the narial opening extend upward into a median process, which varies in degree of prominence from small and pointed to heavy and blunt. Describers of notoungulate skulls have duly recorded and figured this structure for a century and more without, it would seem, realizing that, although of sporadic occurrence in other mammals, e.g., rodents, it is a rather good supplementary ordinal character. In *Pyrotherium* the process may have attained its apogee. Loomis did not realize how large it was in this animal, figuring and describing it as though limited to the anterior extremity of the fused premaxillae. The additional preparation has revealed an extensive eroded area, filled with cancellous bone (cf. *Toxodon*; Roth, 1898, pls. 5, 6), that extends back nearly to the anterior border of the narial opening. This eroded area indicates, I believe, the extent of the process, which is in some measure comparable to but much longer than that of other large members of the order. This and other possible features of the skull, as I interpret them, are shown in the reconstruction—hazarded against future discovery—offered in Figure 7.

That the Pyrotheria were notoungulates would seem evident. The group forms a fifth suborder to be added to the four—Notioprogonia, Hegetotheria, Typotheria, and Toxodonta—currently recognized. Pyrotheres probably arose early in the Paleocene and certainly attained large size rapidly. *Proticia*, if the tentative age assignment is approximately correct, is the largest early mammal so far encountered in South America, and *Pyrotherium* had, by the Deseadan, achieved roughly the bulk of the Pampean *Toxodon*. The ancestry of the suborder presumably lay in the Notioprogonia, and *Proticia* suggests that the ancestors may have been more bunodont than were the notioprogonians known from Riochican and Casamayoran deposits. But settling of these uncertainties lies in the future, when some knowledge of pre-Riochican mammals shall have been gained. Simpson, writing in 1945, noted: "As I write these lines, just one century of study of the Notoungulata has been com-

pleted. Another century may possibly suffice to understand the real phylogeny of this amazing group" (1945, p. 236n). Writing in 1975, I rather suspect that a century may still be required.

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ADDENDUM

THE TYPE LOCALITY AND STRATIGRAPHIC POSITION OF *Griphodon peruvianus*.

On the basis of Anthony's (1924) account and of correspondence with the collector, Mr. J. G. Richards, I (1942) concluded that the type of *G. peruvianus* had been found downstream from Yurimaguas "and therefore in the southwestern extremity of the Department of Loreto," and suggested that the horizon "should be somewhere within the upper half" of the Red Beds Series. I was wrong on both counts. In the course of field work on the Río Huallaga during 1974, I located the type locality: the farm house called Chicoca (not Chiococa as given in Anthony), answering in all essentials to Mr. Richard's account. It is upstream, not downstream, from Chipeza, situated approximately 1 km. west of the junction of the Quebrada Chipaote with the Río Huallaga, about midway on the stretch of the river between the Pongo de Vaquero to the west and the Pongo de Aguirre to the east (map in Rosenzweig, 1953). Chicoca is in the Departamento de San Martín, Provincia de San Martín.

Thanks to Rosenzweig's study of the geology of this area it is now possible to establish the position of *Griphodon* in the Red Beds Series with some precision. Exposures along the courses of the Quebrada Tununtunamba, to the north of the Huallaga, and of the Quebrada Chipaote, to the south, reveal a nearly continuous succes-

sion of the Red Beds. In the north these sediments lie conformably upon topographically higher Cretaceous rocks and dip southward at angles decreasing from 30° near the contact to 12° in the south; they total 5,085 m. in thickness, and in the vicinity of the Chipaote salt dome are overlain conformably by 1,325 m. of the Brown Beds Series. Mr. Richards found the type specimen in the Quebrada Chipaote "a few hundred feet" above its confluence with the Huallaga "in a 15' embankment of gravelly red clay" (not in "highly folded gypsum beds" as stated by Anthony). Rosenzweig's section reveals that this level in the series is about 1,870 m. (somewhat over one-third) above the base. Red Beds deposition evidently began in the early Paleocene (possibly even latest Cretaceous) and lasted until some time in the later Miocene, a span of perhaps 55 M.Y. If deposition was essentially continuous—and no major unconformities have so far been reported within the series—then an estimate of approximately middle Eocene age for the fossil is not unreasonable. *Griphodon* itself is not in contradiction, but the early pyrotheres are not as yet among the better index fossils. Confirmation or rejection of this age possibility will depend upon evidence provided by other, more diagnostic members of the "*Griphodon* fauna." Our party's search for such evidence was no more productive than was Rosenzweig's before us, being rewarded only by small, totally unidentifiable bone scraps.

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