PYROTHERIUM, A LARGE ENIGMATIC UNGULATE (MAMMALIA, *INCERTAE SEDIS*) FROM THE DESEADAN (OLIGOCENE) OF SALLA, BOLIVIA

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ABSTRACT. A well-preserved sample of *Pyrotherium* is described from at least two stratigraphic horizons in the Salla Beds of Bolivia. This sample is essentially indistinguishable from, and therefore conspecific with, the species *P. romeri* from Argentina. This represents the first description of this large herbivorous mammal outside of the classic '*Pyrotherium* Beds' of Argentina. The presence of this biochronologically diagnostic taxon further supports previous assignments of a Deseadan (Oligocene) age for the Salla Beds of Bolivia.

THE Age of Mammals in South America is characterized by a highly unique and endemic fauna. The pyrotheres, or 'fire-beasts' (in reference to their occurrence in volcanic ash deposits), which are known from the late Palaeocene to the Oligocene in South America, are among the most enigmatic of eutherian mammals. Although of uncertain affinities, the Oligocene terminal member of this group is so distinctive and commonly encountered that it gave rise to the term '*Pyrotherium* Beds' to characterize the Deseadan land mammal age as it was originally defined from Argentina (e.g. Ameghino 1895).

The original description of pyrotheres was based on the Deseadan genus *Pyrotherium* which has a diagnostic suite of characters including prominent upper and lower tusks, bilophodont cheek teeth, and large, graviportal limbs. Subsequently, more primitive forms have been described from earlier Tertiary localities in Argentina (see Simpson 1968), Colombia (Hoffstetter 1970), and Venezuela (Patterson 1977). The present paper describes new material from the Deseadan (Oligocene) Salla Beds of Bolivia. This paper is principally based on specimens collected during the 1960s by L. Branisa (then of LaPaz, Bolivia) for Princeton University. Other, more fragmentary, specimens were collected by the authors and associates during our 1981 and 1983 field seasons. The latter specimens do not contribute to an increased understanding of the morphology of Salla *Pyrotherium*. However, they are associated with precise stratigraphic data and they extend the palaeobiogeographic range of this distinctive taxon outside the classic Deseadan localities of Argentina.

The 'Estratos de Salla' have attracted much attention in the literature because of a very diverse and abundant Deseadan fauna (text-fig. 1). A general introduction to the geology of the Salla–Luribay basin has been presented by Hoffstetter (1968, 1976), Hoffstetter *et al.* (1971), and Villarroel and Marshall (1982). Various parts of the mammalian fauna have been presented including rodents (Hoffstetter 1976; Patterson and Wood 1982), marsupials (Villarroel and Marshall 1982), the earliest South American primate *Branisella* (Hoffstetter 1969; Wolff, in press, *b*), Argyrolagidae (Wolff, in press, *a*), and ungulates (Cifelli and Soria 1983*a*, *b*). The remainder of the rich Salla fauna presently is undescribed.

In early descriptions of *Pyrotherium* from the Deseado of Argentina, Ameghino (1895, 1902) believed these mammals to be similar and closely related to primitive proboscideans like *Palaeomastodon* from the late Oligocene Fayum of Egypt and *Deinotherium* from the early Miocene of the Old World. He believed that pyrotheres were the stem group from which the Old World proboscideans were ultimately descended. Loomis (1914) also considered *Pyrotherium* to be most

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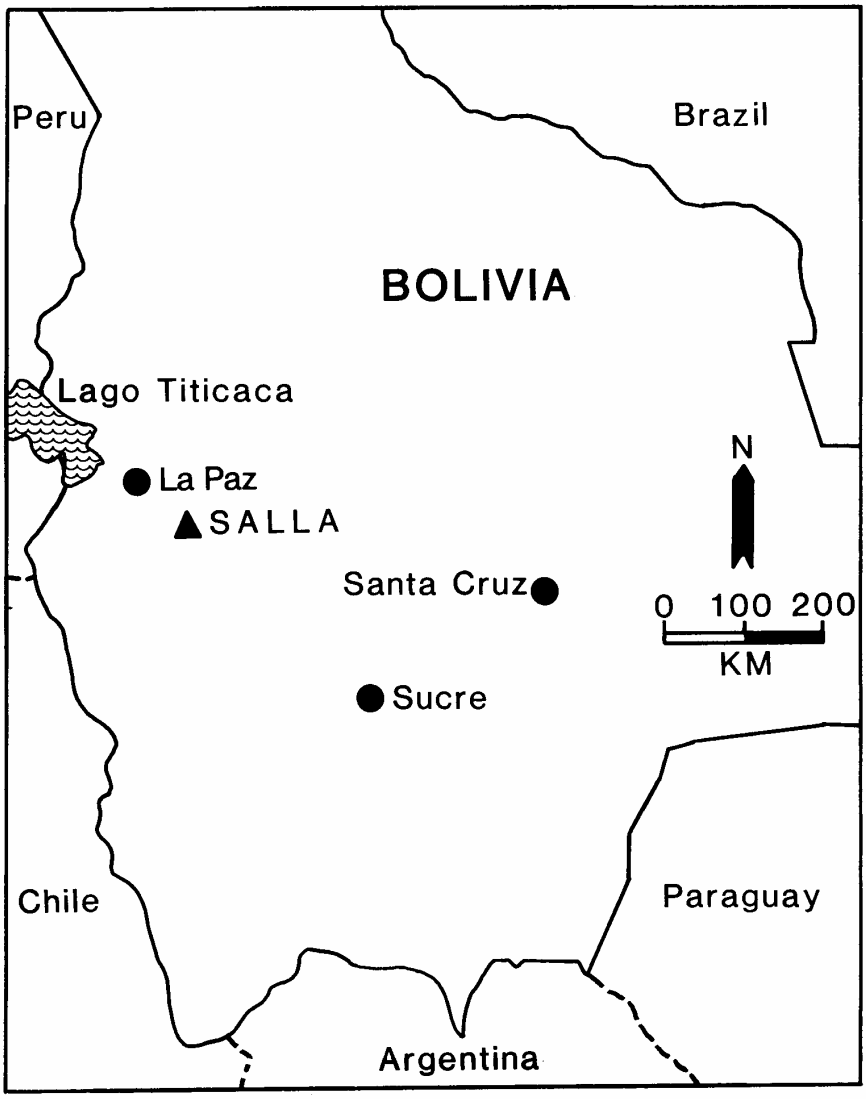


TEXT-FIG. 1. Location of the Salla Beds (triangle) of western Bolivia.

closely related to proboscideans. Gaudry (1909) concluded that *Pyrotherium* was unlike any known large mammal and did not fit into any then existing family. Patterson (1977), based on several basicranial characters, concluded that pyrotheres are notoungulates, although the characters used for this assessment have been criticized elsewhere (Simpson 1978, 1980; McKenna 1980). Other work (e.g. on tarsal bones) suggests similarities between pyrotheres and the Embrithopoda or Proboscidea (Cifelli 1983). All of the above mentioned hypotheses of relationships between pyrotheres and other eutherians require rather interesting palaeobiogeographical speculation. In the absence of any

unambiguous diagnostic characters, the pyrotheres are considered here as a separate order of eutherian mammals *incertae sedis*. Although the sample of *Pyrotherium* from Salla does not elucidate the phylogenetic affinities of this group, it is nevertheless important to place on record a description of this material from this relatively new and significant locality.

The following abbreviations are used in the text: LACM, Natural History Museum of Los Angeles County, Vertebrate Paleontology Collection; PU, Princeton University, Vertebrate Paleontology Collection; R, right side; L, left side; $\bar{x}$, mean; s, standard deviation; V, coefficient of variation; OR, observed range; mm, millimeters.

For relevant cheek teeth, the following measurements were taken: (1) greatest anteroposterior length including cingulum; (2) greatest transverse width across anterior loph and lophid; and (3) greatest transverse width across posterior loph and lophid. Because the dental homologies of advanced pyrotheres are uncertain, topographic names for dental characters are used in this paper (e.g. anterior loph rather than protoloph).

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order PYROTHERIA Ameghino, 1895
Family PYROTHERIIDAE Ameghino, 1895
Pyrotherium romeri Ameghino, 1889

Text-figs. 2–3

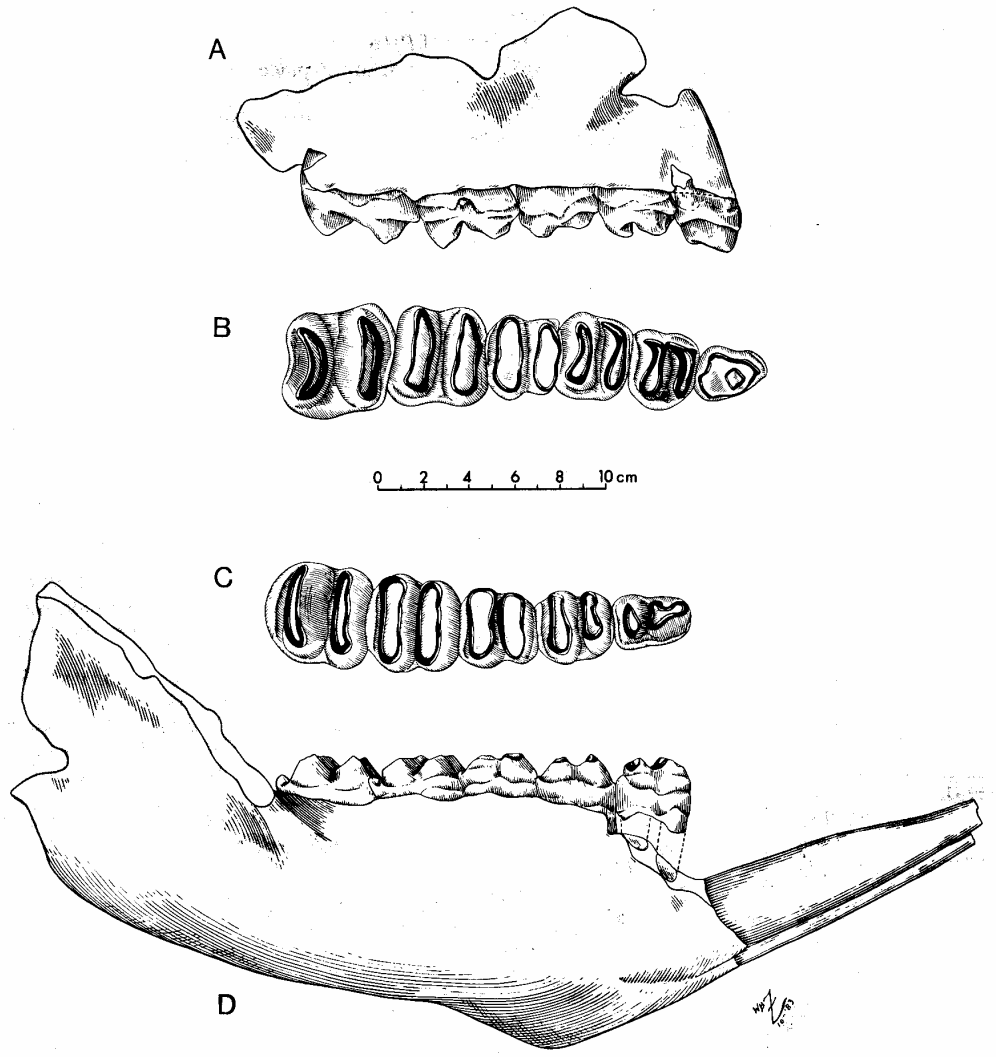
Referred material. Uppers: PU 20693, maxillary fragment with RP^2–M^3, LP^2, P^2–M^1; PU 21919, LP^3–M^1; PU 21917; RM^1–M^3; PU 22146, anterior part LM^3; PU 22143, LM^3 fragment; PU 22143, posterior loph of M^2 or M^3; PU 22144, posterior loph LM^3; PU 22145, LM^2; PU 22142, 21917, upper cheek teeth; PU 20683, premaxilla with parts of four incisors.

Lowers: PU 20679, mandible with fragment LI, R and LP_3–M_3; PU 20695, mandible with alveoli and RM_3; PU 21918, L ramus with M_2, M_3; PU 21989, R ramus with alveoli P_4, M_1, fragmentary M_2, M_3; PU 21921, fragmentary ramus with partial ?M_3; PU 22141, RP_3 fragment; PU 22147, LM_3 fragment; PU 20694, ramus with LP_3–M_3; PU 20684, mandible with R and LI, RP_3–M_3, LM_1–M_3 (also see uppers above); PU 20692, mandible with fragment R and LI, RP_3–M_3, LP_3, M_1–M_3; LACM 117571, LP_3–M_3; LACM 117572, RP_3, RM_3; LACM 117573, LP_3.

PU 22096, PU 22097, PU 22148; cheek tooth fragments. Also numerous uncatalogued specimens mostly consisting of tooth and postcranial fragments. There also are several uncatalogued fragments in the University of Florida—Servicio Geologia de Bolivia collection.

Stratigraphic distribution and age. Based on our field collecting and from specimens with relevant locality data in the PU Branisa collection, *Pyrotherium* occurs from at least two zones within the Salla Beds: (1) the lower part of the section above the Luribay Conglomerates (Branisa's Quebrada Chala Jahuira, Anchallani, V-12) and from the same general area, but *c.* 100 m below the base of the principal guide level, or 'Nivel Guia' (also see Villarroel and Marshall 1982); (2) the middle part of the section, which based on our field-work, includes the most fossiliferous concentrations (V-3, Tapial Pampa; also see Villarroel and Marshall 1982). Some of the better-preserved specimens in the Branisa collection come from Pasto Huarante. Unfortunately, the exact stratigraphic position of this locality is unknown (Branisa, pers. comm. 1983).

Description. As also noted for *Pyrotherium* from Argentina, the premaxillary region has four tusks; two on each half side and one behind the other. They emerge from the alveoli almost horizontally and curve downward to end almost vertically. The enamel is relatively thin, e.g. in contrast to proboscideans. The upper dentition consists of six cheek teeth, which are probably P^2–M^3. Relative to other Oligocene mammals from South America, *Pyrotherium* is very large as is reflected in its dental measurements (see Table 1). The P^2 is triangular in shape and consists of an anterior cone and two posterior cones connected by a loph (text-fig. 2). The P^3 and P^4 are molariform, i.e. they consist of well-developed anterior and posterior lophs as do M^1 to M^3. There is a well-developed 'heel' on M^3. On P^3–M^3 the lophs nearly comprise the total occlusal area of the tooth. In the premolars, these lophs sometimes merge at the external portion of the tooth almost forming an ectoloph. The enamel is breeched during early wear exposing the dentine (this character persists throughout later wear stages). In the upper cheek teeth, the plane of shear on the lophs is anteriad. The cingulum varies from well developed to



TEXT-FIG. 2. *Pyrotherium romeri* from the Salla Beds. A, PU 20693, lateral view of R maxillary fragment with P^3-M^3. B, PU 20693, occlusal view P^2-M^3. C, PU 20694, occlusal view of R P_3-M_3. D, PU 20694, lateral view of mandible with anterior tusks and R P_3-M_3.

absent; characteristically it is strong on the anterior and internal parts of the teeth and poorly developed, rudimentary, or absent on the external and posterior portions of the teeth. In both the upper and lower dentitions the enamel is frequently crenulated, particularly on the cingulum.

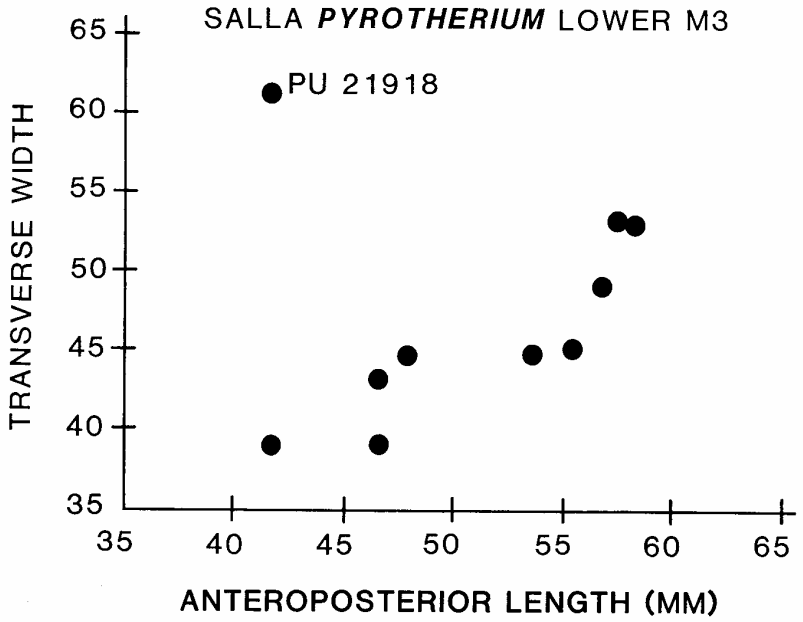
The mandible is relatively robust (text-fig. 2). The bony portion of the symphysis extends posteriorly to a position below P_4. The ascending portion of the ramus is dorsally abbreviated. Anteroventrally, the mandible is enlarged at the symphysis to accommodate the large pair of incisor tusks. The tusks are relatively robust and elongated with enamel only on the ventral side; dorsally dentine is exposed. The anteromost tip of the incisor

tusks is characteristically flattened by wear. The lower dentition consists of five teeth, presumably P_3–M_3. P_3 consists of an anteromost conid followed posteriorly by two lophids. P_4–M_3 are generally similar in the presence of well-developed anterior and posterior lophids. As is also seen in the upper dentition, the enamel is breeched during early wear exposing the dentine. The principal shear on the lophids is posteriad. The cingulum varies from well developed and continuous, particularly on the posterior portion of the teeth, to rudimentary or absent. In M_3 and, to a lesser extent in M_2, there is a well-developed heel which seems to consist of an inflated cingulum.

DISCUSSION

The genus *Pyrotherium* was originally proposed by Ameghino (1889) to include the species *P. romeri* based on material from Patagonia, southern Argentina. As was characteristic of his taxonomic philosophy, Ameghino (1895, et seq.) later named at least four other species of *Pyrotherium* of which *P. sorondoi* has been most commonly cited in the literature. Although all of these 'species' were of roughly similar size, Ameghino and some later workers (e.g. Loomis 1914) mistakenly believed that *P. romeri* could be distinguished from the other species by the presence of P^1. In a recent summary of pyrotheres, Patterson (1977) concluded that: (1) the 'P^1' of *P. romeri* is actually a deciduous tooth; and (2) all the Deseadan species of *Pyrotherium* are synonymous. Therefore, *P. romeri* stands as the senior species and it is used in the present report.

So far as can be determined, in all characters of the dentition, the Salla sample of *Pyrotherium* is indistinguishable from that of Argentina. Therefore, the Bolivian material is confidently referred to *P. romeri*. In the Salla sample of *P. romeri* there is considerable variation in size as evidenced by *V*s greater than 10 for certain characters (Table 1; text-fig. 3). With possible exception of one seemingly aberrant specimen (PU 21918, text-fig. 3), the Salla *P. romeri* corroborates Patterson's (1977) idea of a single morph. Comparisons of this sample with the measurements of three specimens of *P. romeri* from Argentina (Loomis 1914, p. 181) suggest that the Bolivian sample might be slightly smaller than



TEXT-FIG. 3. Bivariate plot of anteroposterior length versus transverse width of anterior loph for M_3 of Salla *Pyrotherium romeri* in the PU and LACM collections.

TABLE 1. Dental measurements (mm) for *Pyrotherium romeri* from Salla, Bolivia, based on specimens in the PU and LACM collections. Measurement abbreviations are as follows: AP, greatest anteroposterior length; TA, greatest transverse width across anterior loph(id), except for lower premolars; TP, greatest transverse width across posterior loph(id); TRL, greatest anteroposterior cheek tooth row length (P^2–M^3, P_3–M_3). Also see text.

	P2			P3			P4			M1			M2			M3			
	AP	TA	TP	AP	TA	TP	AP	TA	TP	AP	TA	TP	AP	TA	TP	AP	TA	TP	TRL
UPPER DENTITION																			
N	3	0	3	4	4	4	2	2	2	3	3	2	4	3	4	3	3	3	1
$\bar{x}$	31·47	—	25·70	31·40	32·83	35·53	33·10	36·20	37·75	35·27	38·20	37·95	42·25	46·0	45·4	51·17	50·47	48·13	224·0
s	2·91	—	1·51	2·94	1·06	3·32	1·70	3·68	1·06	1·27	0·70	0·64	0·89	1·42	1·47	3·64	0·95	1·56	—
V (%)	9·26	—	5·88	9·37	3·24	9·34	5·13	10·16	2·81	3·61	1·83	1·68	2·10	3·09	3·23	7·11	1·88	3·26	—
OR	28·4–	—	24·3–	27·7–	32·1–	30·7–	31·9–	33·6–	37·0–	35·9–	37·7–	37·5–	41·0–	44·4–	43·2–	47·0–	49·4–	46·9–	—
	34·2		27·3	34·1	34·4	38·2	34·3	38·8	38·5	36·1	37·9	38·4	43·0	46·9	46·2	53·7	51·2	49·9	
LOWER DENTITION																			
N	—	—	—	7	7	9	7	7	7	8	8	8	9	8	9	11	11	11	4
$\bar{x}$	—	—	—	35·36	18·17	25·66	35·30	28·75	32·13	35·76	31·98	35·51	43·04	42·14	47·17	49·94	47·48	46·34	191·93
s	—	—	—	2·31	1·76	3·18	2·52	3·32	3·13	2·43	3·74	2·54	2·80	8·10	6·87	6·51	6·89	6·06	13·29
V (%)	—	—	—	6·54	9·70	12·39	7·15	11·56	9·73	6·78	11·71	7·16	6·50	19·23	14·56	13·05	14·51	13·10	6·92
OR	—	—	—	32·7–	16·4–	21·5–	31·7–	25·4–	28·8–	32·2–	28·5–	33·0–	39·3–	37·6–	38·6–	41·7–	38·9–	38·1–	176·5–
				39·6	19·4	30·3	39·0	33·6	37·5	40·8	40·6	41·3	48·2	60·1	64·1	58·2	61·1	57·1	208·5

that of Argentina. However, more specimens and consistant measuring regimes would be necessary before any definite conclusion could be drawn from this possible difference.

In his preliminary faunal list Hoffstetter (1968) indicated a Deseadan age for the Salla Beds. One of the diagnostic taxa that he cited for this age assignment was *Pyrotherium* which Hoffstetter stated was common throughout the stratigraphic section. Our field-work confirms the presence of *P. romeri* from at least two horizons within the Salla Beds. However, it is neither as common nor as stratigraphically widespread as was observed by Hoffstetter. Perhaps the relative rarity during our recent field-work represents a collecting bias that has removed some of the more common, larger mammalian taxa during the two decades of prospecting in the Salla-Luribay basin. Of relevance to some of the allochthonous Salla taxa (i.e. rodents and *Branisella*), our field-work indicates that the principal fossil-bearing levels are concentrated in a relatively narrow stratigraphic interval some 75 m thick (between the Calabozo Pata I and Cebadal Churu/Huichinca levels of Villarroel and Marshall 1982) in the middle of our measured section (MacFadden, unpublished field-notes, 1981). These taxa co-occur with *P. romeri* within this zone thereby supporting a Deseadan age for the rodents, *Branisella*, and the other elements of the Salla fauna.

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