Reconstruction of the dentition of Propyrotherium saxeum Ameghino, 1901 (Mammalia, Pyrotheria): taxonomic and phylogenetic implications

Alejandro G. Kramarz [a] & Mariano Bond [b]

[a] CONICET; Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales Bernardino Rivadavia , Ángel Gallardo 470, C1405DJR, Ciudad Autónoma de Buenos Aires, Argentina

[b] CONICET; Departamento Científico Paleontología de Vertebrados , Museo de La Plata, Paseo del Bosque s/n , La Plata B1900FWA, Provincia de Buenos Aires, Argentina
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ARTICLE

RECONSTRUCTION OF THE DENTITION OF *PROPYROTHERIUM SAXEUM* AMEGHINO, 1901 (MAMMALIA, PYROTHERIA): TAXONOMIC AND PHYLOGENETIC IMPLICATIONS

ALEJANDRO G. KRAMARZ[*,1] and MARIANO BOND[2]
[1]CONICET; Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales Bernardino Rivadavia,
Ángel Gallardo 470, C1405DJR, Ciudad Autónoma de Buenos Aires, Argentina;
[2]CONICET; Departamento Científico Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n,
La Plata B1900FWA, Provincia de Buenos Aires, Argentina, constantino1453@yahoo.com.ar, agkramarz@macn.gov.ar

ABSTRACT—*Propyrotherium saxeum* is one the least known members of Pyrotheria, an enigmatic group of extinct, giant, endemic South American 'ungulates.' The species was originally described based upon two isolated cheek teeth and two tusk fragments. Later authors assigned additional isolated teeth to this taxon, but the position within the tooth row of all these teeth remained uncertain, preventing an accurate dental characterization and taxonomic distinction from other related species. Here we reexamine the type specimens of *P. saxeum* and additional materials previously reported as belonging to this species, and analyze several lots of still undescribed specimens, in order to reconstruct the cheek tooth series. Based on comparisons with better known pyrotheres, we conclude that the most probable cheek teeth formula is P2–M3/p2–m3. The cheek teeth gradually increase in size from front to back, and the upper cheek teeth have a gradual increase in loph curvature, as in *Pyrotherium*. All cheek teeth are bilophodont, but in premolars the anterior loph/id is transversely shorter than the posterior. All have lingual/labial cingulum/id; P3–M3 are subquadratic and three-rooted; p4–m3 are longer than wide, two-rooted, and bear a variably developed vestige of cristid obliqua. *Propyrotherium* is distinguishable from *Griphodon* and *Baguatherium*, but the distinction between these latter two taxa is uncertain with the current evidence. A revised cladistic analysis confirms that *Propyrotherium* is one of the earliest diverging pyrotheriids, but the resolution of its relationship with *Griphodon* and *Baguatherium* requires further evidence.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Pyrotheria are one of the strangest and least known groups among endemic South American 'ungulates.' These Paleogene mammals are characterized by having bilophodont cheek teeth, enlarged, tusk-like incisors and massive body, resembling proboscideans (Ameghino, 1895; but see Billet, 2010, for discussion of their supraordinal relationships). With the exception of the late Oligocene *Pyrotherium* Ameghino, 1888, pyrotheres are only known from few and very fragmentary remains, mostly partial dental series and isolated teeth (see Billet, 2010; Salas et al., 2006, and references therein). *Propyrotherium saxeum* is certainly the least understood among all pyrotheres. Ameghino (1901) described this species based upon two cheek teeth and two tusk fragments, surely belonging to different individuals. Simpson (1967) tentatively assigned to this species many isolated, mostly incomplete teeth and provided a formal diagnosis together with measurements and photos of some selected teeth. Nevertheless, Simpson admitted being unable to reconstruct the dentition because of the fragmentary condition of the available material, the fact that the upper and lower teeth were more similar than in most mammals, and the large disparity of size, proportions, and degree of wear of the available teeth complicated a comprehensive understanding of the material. Later authors (Patterson, 1942, 1977; Lucas, 1986; Salas et al., 2006) compared the types and the referred specimens with those of other pyrotheres and discussed their phylogenetic relationships, although with no ex-plicit justification (or at least incomplete) of the respective locus proposed for each isolated tooth.

In this contribution, we reexamine the type specimens of *P. saxeum* and those reported by Simpson (1967), and we analyze several lots of undescribed, isolated teeth stored at the Museo de La Plata and collected during the 1950s and 1960s in Paleogene localities in Chubut Province, Argentina (Fig. 1). Based on the integrated information and on comparisons with better known pyrotheres, we provide a provisional reconstruction of the dentition of *P. saxeum* (at least the premolar-molar series) and an improved differential diagnosis. Additionally, we herein discuss the taxonomic status of other little known pyrotheres and reanalyze their intraordinal phylogenetic relationships.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; **FMNH**, Field Museum of Natural History, Chicago; **MACN**, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires; **MPEF**, Museo Paleontológico Egidio Feruglio, Trelew; **MLP**, Museo de La Plata, La Plata.

SYSTEMATIC PALEONTOLOGY

Order? PYROTHERIA Ameghino, 1895
Family PYROTHERIIDAE Ameghino, 1895
Genus *PROPYROTHERIUM* Ameghino, 1901

Type Species—*Propyrotherium saxeum* Ameghino, 1901:387.
Distribution—Mustersan South American Land Mammal Age (SALMA) (late Eocene; Ré et al., 2010) and Tinguririrican
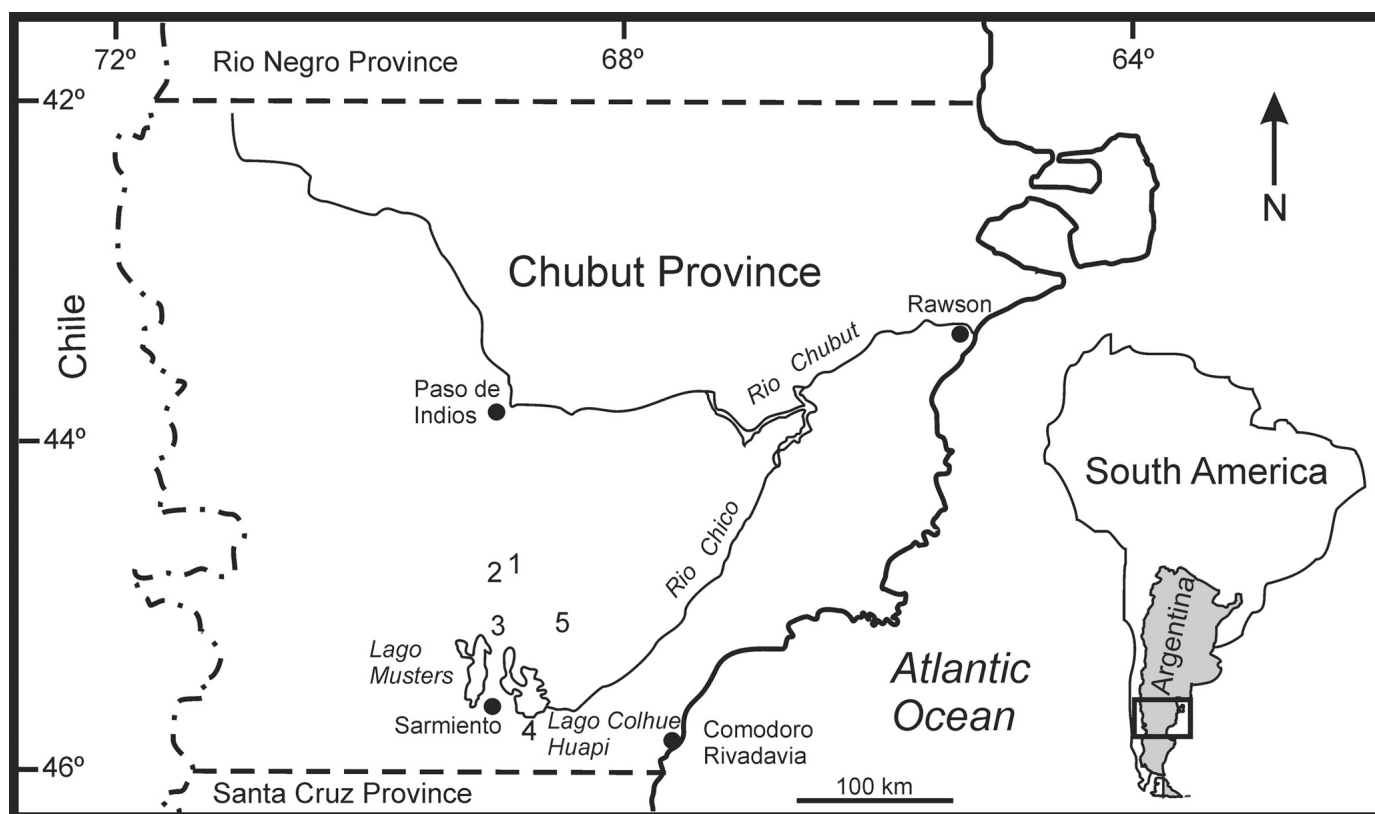
*Corresponding author.

FIGURE 1. Map of Central Patagonia showing the position of the localities bearing remains of *Propyrotherium saxeum* Ameghino, 1901, and other pyrotheres described in the text. **1**, Cerro Mentira; **2**, Cerro Talquino; **3**, Cerro del Humo; **4**; Gran Barranca south of Colhue Huapi Lake. The position of other localities mentioned in text (i.e., Mallín del Gato and Puesto Bota) is unknown.

SALMA (early Oligocene; Flynn et al., 2003; Ré et al., 2010). Patagonia.

PROPYROTHERIUM SAXEUM Ameghino, 1901
(Figs. 2, 3)

Syntype—MACN A 10929, an upper cheek tooth (probably a P4), a lower cheek tooth (probably a p4), and two tusk fragments.

Lectotype—The upper cheek tooth, designated by Simpson (1967:237).

Referred Specimens—AMNH 29391, right P3?; AMNH 29393, right m3?; AMNH 29394, right m1 or m2; AMNH unnumbered (labeled as 'O1'), partial left lower molar; AMNH unnumbered (labeled as 'O2'), partial left m1 or m2; AMNH unnumbered (labeled as 'O3'), right M3; AMNH unnumbered, left M1 or M2; AMNH unnumbered, partial right M1 or M2; AMNH unnumbered, right m1 or m2; AMNH unnumbered, left m1 or m2; MLP 55-III-10-1a, a right M1 or M2; MLP 55-III-10-1b, a right m1 or m2; MLP 55-III-10-1c-m, seven cheek tooth fragments and six tusk fragments; MLP 55-IX-28-1a, a M1 or M2; MLP 55-IX-28-1b, a right m1?; MLP 55-IX-28-1c, a left m1?; MLP 55-IX-28-1d, a right m2?; MLP 55-IX-28-1e, a partial right p3? (unerupted); MLP 55-IX-28-1f-z, 27 cheek tooth fragments, three tusk fragments, and an undetermined tooth; MLP 56-XII-18-309, left m1 or m2; MLP 61-IV-17-1-2, left m3.

Comments—The isolated lower molar AMNH 29392, figured by Simpson (1967) as belonging to *P. saxeum*, is here assigned to a separate taxon (see discussion below).

Provenance—The syntypes are supposed to come from Ameghino's 'couches à *Astraponotus*' at Colhue Huapi Norte (= Simpson's [1936] Cerro del Humo locality), which informally typify the Mustersan SALMA (late Eocene; Bond and Deschamps, 2010; Ré et al., 2010). The AMNH specimens are almost certainly from levels of equivalent age at Cerro Talquino (Simpson, 1967) (Fig. 1), Chubut Province. MLP 55-III-10-1 and MLP 55-IX-28-1 come from Sierra Chaira of Chubut (Fig. 1). MLP 56-XII-18-309 comes from Mallín del Gato in Chubut Province (geographic location unknown). MLP 61-IV-17-1-2 comes from the southern slope of Cerro Mentira (Fig. 1). The localities bearing the AMNH and MLP specimens are placed 20–50 km north the Lake Colhue Huapi, but their precise geographic and stratigraphic position are uncertain. According to the associated fauna, all could be regarded as being late Eocene in age, but the specimens MLP 55-III-10-1 were collected in association with notoungulate remains assignable to *Eomorphippus* (MLP 55-III-10-2-12), thus suggesting a Tinguirirican age (Flynn et al., 2003; López et al., 2010) (early Oligocene).

Emended Diagnosis—Size slightly larger than *Griphodon peruvianus* Anthony, nearly 35% larger than *Carolozittelia tapiroides* Ameghino, and 15% smaller than *Pyrotherium macfaddeni* Shockey and Anaya. Molars bilophodont, lophs/ids completely separated at the labial and lingual ends, with distinct terminal cusps. Lingual cingula and labial cingulids present, unlike *Griphodon peruvianus*. Upper molars nearly quadratic or wider than long, with the lophs curvature increasing from front to back, as in the species of *Pyrotherium*. Lower molars longer than wide, lophids nearly transverse (unlike *Carolozittelia tapiroides*), with distinct vestige of cristid obliqua (unlike the species of *Pyrotherium*); m3 with expanded posterior cingulid forming a heel or third lobe, larger than in the species of *Pyrotherium*, lower
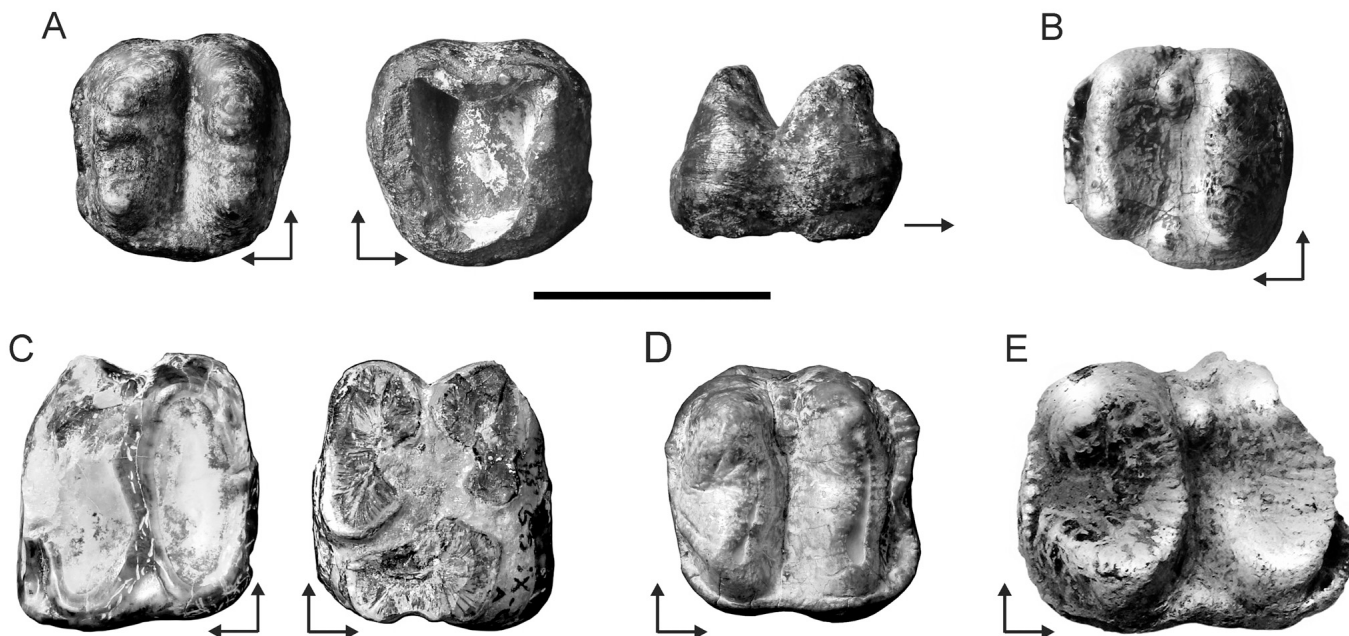
FIGURE 2. Upper cheek teeth of *Propyrotherium saxeum* Ameghino 1901. **A**, MACN A 10929 (lectotype), left P4? in occlusal, basal, and labial views; **B**, AMNH 29391, right P3? (shown as left); **C**, MLP 55-IX-28-1a, left M1 or M2 in occlusal and basal views; **D**, MLP 55-III-10-1a, right M1 or M2 in occlusal view; **E**, AMNH unnumbered (labeled as 'O3'), right M3. Arrows show anterior and labial sides. Scale bar equals 3 cm.

than in *Carolozittelia tapiroides*. P4/p4 (and probably also P3/p3) with anterior loph narrower (labiolingually) than the posterior one, unlike *Griphodon peruvianus* and *Baguatherium jaureguii*. P4 without labial crest connecting the transverse lophs, unlike *Baguatherium jaureguii*. Apomorphy of the taxon: posterior extension of the lingual end of the anterior loph on p4 closing the central valley.

Reconstructing the *Propyrotherium* Cheek Tooth Series

The upper cheek tooth of the syntype series (Fig. 2A) was interpreted by Ameghino (1901) as a molar. Simpson (1967) designated this tooth as lectotype and proposed that it was a P4, but gave no explicit justification. We agree with Simpson because (1) the posterior slope of the paracone has a slight posterior projection, which is also present in P3 of *Baguatherium jaureguii* Salas, Sánchez, and Chacaltana, 2006, and in P3–P4 of *Pyrotherium macfaddeni* Shockey and Anaya, 2004, but unlike in *Propyrotherium*, this element is longer and reaches the labial end of the posterior loph; and (2) the tooth is smaller than all the upper cheek teeth herein interpreted as upper molars (see Table 1).

The base of the crown bears a moderate, somewhat crenulated anterior cingulum, a very faint posterior cingulum, and a conspicuous lingual cingulum closing the lingual opening of the central valley. The latter is clearly equivalent to the longitudinal enamel crest connecting the bases of the protocone and the hypocone on P3–M1 of *B. jaureguii*, described by Salas et al. (2006) as an autapomorphy of this species. The preserved base of the crown is roughly triangular, suggesting the presence of one lingual and two labial roots.

The isolated, unworn cheek tooth AMNH 29391 (Fig. 2B; see also Simpson, 1967:pl. 45, fig. 7) is similar to the lectotype in size

(see Table 1; measurements of this specimen by Simpson, 1967:table 78, are wrong), and in having a moderate posterior projection of the paracone. However, it differs by being somewhat narrower and longer, and the anterior loph is comparatively shorter (transversally), as in P3 of *Pyrotherium romeroi*. Likewise, the base of the crown suggests the presence of two minor anterior roots and a main posterior root, as described by Salas et al. (2006) for P3 and P4 of *B. jaureguii*. Additionally, it has a conspicuous labial cuspule between the paracone and the metacone. We suggest that AMNH 29391 could represent a P3, but the possibility that it could belong to a deciduous premolar should not be discarded.

Several isolated upper molars are represented at the MLP and AMNH collections. The MLP 55-III-10-1a (Fig. 2D) is a moderately worn molar. Unlike the putative premolars, the crown is slightly wider anteriorly than posteriorly, the lophs are concave posteriorly, especially the posterior one, forming a marked inflection on the posterior slope of the lophs, and the paracone lacks posterior projection. The wear surfaces are oblique (nearly 35°) and hardly excavated. A minute enamel denticle is located on the labial portion of the central valley between the bases of the paracone and the metacone, and a set of even smaller denticles are on the labial opening of the valley. There is a continuous anterior-lingual-posterior cingulum, much broader and elevated on the anterior base and weaker on the posterior one. The lingual portion of the cingulum connects the bases of both lophs, but it is less prominent than the corresponding one in the lectotype (P4?). Three unnumbered upper molars at AMNH also bear a lingual cingulum, two of them bearing a broad and blunt cuspule between the protocone and the hypocone. The preserved base of MLP 55-III-10-1a indicates the presence of one lingual and two labial roots, as in the lectotype. A wear surface on the posterior

TABLE 1. Dental measurements (in mm) compared among *Propyrotherium saxeum* Ameghino, *Carolozittelia tapiroides* Ameghino, *Griphodon peruvianus* Anthony, *Baguatherium jaureguii* Salas, Sánchez, and Chacaltana, *Pyrotherium macfaddeni* Shockey and Anaya, and other taxa discussed in the text.

Taxon	Specimen	P3 APL	P3 TW	P4 APL	P4 TW	M1 APL	M1 TW	M2 APL	M2 TW	M1 or M2 APL	M1 or M2 TW	M3 APL	M3 TW
P. saxeum	MACN A 10929			30.0	30.1								
	AMNH 29391			29.5	28.0								
	MLP 55-III-10-1a									32.0	31.7		
	MLP 55-IX-28-1a									30.7	34.8		
	AMNH un-numbered (O3)											42.0	35.0
Pyrotheriidae sp. 1	MPEF PV 10605									35.1	—		
C. tapiroides	MACN A 10666							27.0*	24.3			28.5*	24.6
B. jaureguii	MUSM 436	32.7	33.1										
P. macfaddeni	PU 20693			33.0	36.7	35.2	38.4	42.3	46.0				

Taxon	Specimen	p3 APL	p3 TW	p4 APL	p4 TW	m1 APL	m1 TW	m2 APL	m2 TW	m1 or m2 APL	m1 or m2 TW	m3 APL	m3 TW
P. saxeum	MACN A 10929			28.0	25.1								
	MLP 56-XII-18-309									32.4	27.2		
	MLP 55-III-10-1b									33.9	27.2		
	MLP 55-IX-28-1c									34.6	28.5		
	MLP 55-IX -28-1d									36.9	32.4		
	MLP 55-IX-28-1b									34.5	28.2		
	AMNH 29394									35.0	29.0		
	MLP 61-IV-17-1-2											36.3	31.4
	AMNH 29393											35.5	30.0
Pyrotheriidae sp. 2	AMNH 29392											42.5	36.0
Pyrotheriidae sp. 3	MLP 55-IX-28-1e	20.7	13.4										
C. tapiroides	MACN A 10666									23.7	18.3	28.9	20.0*
G. peruvianus	AMNH 17724	—	16.0	29.5	21.5	32.2	25.8						
P. macfaddeni	PU 20684			32.5	31.4	34.0	33.0	40.6	42.0				
	PU 20692			32.0	28.2	35.8	32.8	41.3	38.6				
	PU 20694			31.4	29.3	33.2	36.1	36.1	38.7				
	MNHN Bol V 8518			40.5	25.3	31.8	36.1	33.5	47.1				

APL, maximum preserved anteroposterior length; **TW**, maximum preserved transverse width; *, estimated measurements. Measurements for *Griphodon peruvianus*, *Baguatherium jaureguii*, and *Pyrotherium macfaddeni* taken from Patterson (1942), Salas et al. (2006), and Shokey and Anaya (2005), respectively.

base indicates that it was not a M3. MLP 55-IX-28-1a (Fig. 2C) is an almost complete, much worn tooth, somewhat wider than the former. Two transverse wear facets occupy most of the occlusal surface, separated by a remnant of the central valley, which is almost obliterated on its lingual third. However, the lingual and labial ends of the lophs remain separated even at this stage of wear. At this stage there is no trace of the curvature of the lophs observed in MLP 55-III-10-1a. The wear surfaces are essentially horizontal (not oblique), somewhat elevated on the lingual side. The tooth preserves the bases of three massive roots. The lingual root is long in cross-section, wider anteriorly than posteriorly, with a small lingual notch and an opposed, stronger labial inflection. The posterolabial root is very wide (almost two-thirds of the crown width) and bears a marked anterior inflection. The antero-labial root is nearly a mirror image of the posterolabial root, but smaller.

An unworn (probably unerupted), incomplete molar at AMNH (unnumbered, labeled as '03') (Fig. 2E) is somewhat wider and much longer than the preceding teeth (see Table 1). The anterior loph is moderately curved, whereas the posterior one is somewhat narrower (transversally) and extremely curved. Based on that observed in *Carolozittelia* and *Pyrotherium*, where the lophs are more curved in M3 than in M2 and M1, this tooth is likely a M3. The enamel on the apex of the lophs and of the cingula is strongly crenulated, more than in other unworn upper teeth. A blunt cuspule is located at the labial portion of the central valley, between the paracone and the metacone, resembling the putative P3 AMNH 29391.

The lower cheek tooth of the syntype MACN A 10929 (Fig. 3A) was interpreted by Ameghino (1901) and Patterson (1942) as m1 or m2. Simpson (1967) believed that it was a p4 or m1 (later followed by Patterson, 1977). We here suggest that this tooth is more likely a posterior premolar because of the following reasons: (1) the anterior lophid is transversally shorter than the posterior, as in the p4 of *Pyrotherium*. This is consistent with our above interpretations for the upper premolars. Other lower cheek teeth here interpreted as molars also have a narrower anterior lophid, but not as much as in MACN A 10929. (2) It is significantly smaller than all the available cheek teeth here interpreted as lower molars (see Table 1). Patterson (1942) noted that this tooth bears a lingual crest departing from the posterior slope of the anterior lophid, isolating the central valley, a feature absent in the p4 of *G. peruvianus*. A similar but less marked feature occurs in some p4 of *P. romeroi* (e.g., MACN A 52-601). Moreover, based on Ameghino's drawing of this tooth, Patterson (1942) interpreted that it has a reduced posterior cingulid, at least compared with the m1 of *G. peruvianus*. However, the cingulid is strongly worn and the posterior edge is partially eroded; it was surely larger when complete, not as large as in the molars, but probably as large as in the p4 of *G. peruvianus*. The anterior wall of the posterior lophid bears a small bulge constraining the central valley, very likely representing a vestigial cristid obliqua, located more lingually than in the p4 of *Griphodon peruvianus* Anthony, 1924. The tooth bears an anterior root, which is markedly constricted at the central portion, and a posterior root, which is a mirror image of the anterior one.

The lower molars (Fig. 3B, C) are abundantly represented in the MLP and AMNH collections. The crowns are rectangular, longer than wide; the anterior margin is straight and the posterior is convex due to the extended posterior cingulid. The lophids are
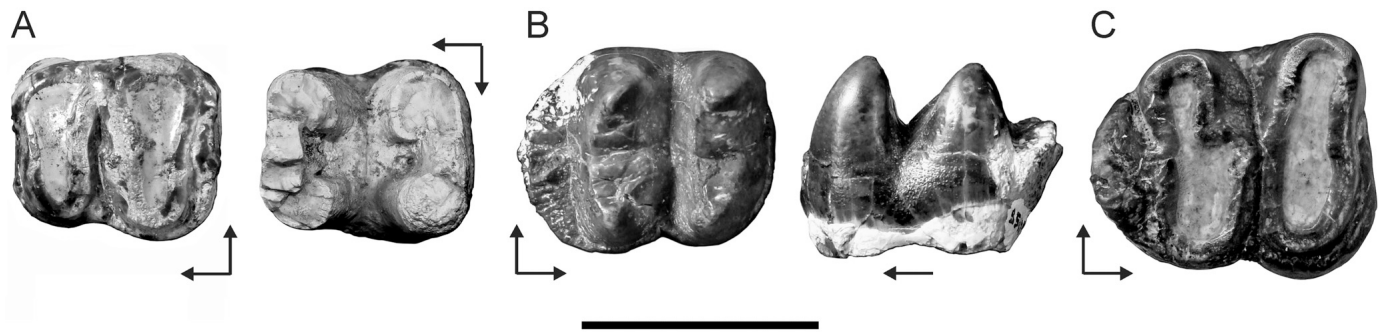
FIGURE 3. Lower cheek teeth of *Propyrotherium saxeum* Ameghino 1901. **A**, MACN A 10929 (syntype), left p4? in occlusal and basal views; **B**, MLP 55-III-10-1b, right m1 or m2 in oclusal and lingual views; **C**, AMNH 29393, right m3. Arrows show anterior and lingual sides. Scale bar equals 3 cm.

essentially transverse, but the anterior slopes are excavated, evidencing the terminal cusps. They have an anterior and a posterior root, very similar to those in the putative p4. These molars agree in general structure, height of lophids, and approximate size with the m1 of *Griphodon*. In general terms, they differ from the latter taxon in the following characters. (a) The lophids are more robust, especially at their bases; thus, the central valley is deeper and narrower. This feature makes the worn lophids look as comparatively lower than in *Griphodon*, but actually they are not. (b) A labial cingulid is present at the base of the hypoconid. In some specimens, the cingulid also reaches the base of the protoconid, and forms a variably developed elevation (as an enamel ridge or as a denticle) at the labial opening of the central valley. (c) The posterior cingulid is isolated from the entoconid and bears a more robust and bunoid central cuspule, less lophoid than in *Griphodon*.

Additionally, some specimens have further differences. The cristid obliqua is more elevated and anteriorly extended, resembling the condition in the p4 (e.g., AMNH 29393; Fig. 3C). In MLP 56-XII-18-309, this element is even more developed, reaching the base of the anterior lophid and clearly separating the labial portion of the central valley from the lingual one. The lingual margin of the crown shows a less marked inflection between the bases of the metaconid and the entoconid, thus the hourglass-shaped contour is not attained.

MLP 61-IX-17-1 and AMNH 29393 (Fig. 3C) are mostly the largest lower molars (Table 1). Both are much wider anteriorly than posteriorly, opposed to the premolar, and are likely m3. Among the remaining molars, the smallest and proportionally longer ones are probably m1 (e.g., MLP 55-III-10-1b; Fig. 3B), the largest and quadrangular ones being m2 (e.g., MLP 55-IX-28-1d). On m3, the posterior cingulid or heel is somewhat more expanded than on m1 and m2, but is proportionally smaller (especially lower) than on m3 of *Carolozittelia*.

Simpson (1967) found that cheek teeth with similar morphology, apparently posterior teeth, have very different sizes, and concluded that they might not be co-specific. We interpret that in *Propyrotherium saxeum*, the cheek tooth series has a gradual increase in size from front to back (as in *Pyrotherium* and *Carolozittelia*) and that the smallest cheek teeth listed by Simpson (i.e., the syntype and AMNH 29391) are not posterior teeth but premolars. Thus, all the teeth reported by Simpson may belong to a single species. The only exception seems to be AMNH 29392, which likely belongs to a distinct taxon (see discussion below).

Concerning the anterior premolars, we could not identify an unquestionably anterior wear facet for P2 in the putative P3

AMNH 29391. Simpson (1967:236) wrote that *Propyrotherium* probably lacked P2 because there was no possible P2 among the 30 molariform teeth stored at AMNH. However, in the same work (Simpson, 1967:237), he compared the type of *Promoeritherium australe* Ameghino, 1901, with the P2 of *Pyrotherium*, and concluded that, if it belongs to a pyrothere, it may be a P2 of *Propyrotherium*. Lucas (1986) proposed that the type of *Promoeritherium australe* probably is a p4 of *P. saxeum* because it nearly agrees in size and morphology with the p4 of *G. peruvianus*, considered by Schoch and Lucas (1985) as a junior synonym of *P. saxeum*. On the one hand, we consider that the type of *Promoeritherium australe* certainly resembles a generalized lower premolar by being longer than wide and by having an expanded, talonid-like posterolingual shelf. Nevertheless, this tooth is morphologically very distinct from the rectangular, bilophodont p4 of *G. peruvianus*, being more similar to the P2, and especially the DP2 (e.g., MACN A 52-290), of *Pyrotherium*. The type of *Promoeritherium australe* is structurally very different from all cheek teeth of *P. saxeum*, as well as the P2 of *Pyrotherium*, which is very different from its remaining cheek teeth. At present, all options seem to be equally probable. On the other hand, the absence of a putative P2 within the samples available does not necessarily imply the nonexistence of this dental locus; in fact, none of the available cheek teeth of *P. saxeum* can be interpreted as p2. Moreover, the tentative cheek teeth formula proposed by Simpson (P3–M3/p2–m3) is unlikely, because none of the known bilophodont mammals has a larger number of lower premolars than of upper premolars, and all pyrotheres for which upper premolars are known (i.e., *Colombitherium* Hoffstetter, 1970, *Baguatherium*, and *Pyrotherium*) positively have P2. Consequently, we conclude that *P. saxeum* very likely had at least three permanent upper premolars, independent of the identity of the type of *Promoeritherium australe*.

Additional Pyrothere Specimens

In the following sections, we describe and discuss the affinities of additional pyrothere specimens, reported by previous authors as tentatively belonging to *P. saxeum* and/or coming from the same localities as specimens here attributed to this species, but that likely belong to distinct taxa.

PYROTHERIIDAE sp. 1
(Fig. 4A)

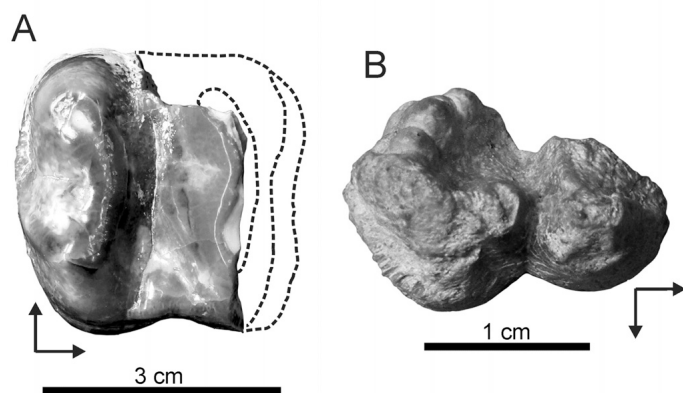**Referred Specimen**—MPEF PV 10605, an incomplete upper molar.

FIGURE 4. **A**, MPEF PV 10605, Pyrotheriidae sp. 1, partial right upper? molar (missing part reconstructed based on MLP 55-III-10-1a); **B**, MLP 55-IX-28-1e, Pyrotheriidae sp. 3, unworn right p3? Arrows show anterior and labial sides.

Provenance—Gran Barranca South of Colhue Huapi Lake (Fig. 1). Vera Member of the Sarmiento Formation at profile M (see Bellosi, 2010), Tinguiririran SALMA.

Comments—This fragmentary specimen was tentatively assigned to *Propyrotherium* by López et al. (2005), and represents the only record of Pyrotheria for levels positively assigned to the Tinguiririran SALMA.

Description and Comparisons—The general preserved features (i.e., two transverse, slightly curved lophs with distinct terminal cusps) agree with those of the molars here assigned to *P. saxeum*. It differs from *Carolozittelia tapiroides* in being much larger and massive, and in having transverse (not oblique) lophids, and from the species of *Pyrotherium* in being smaller and with much lower and less inclined crests. This tooth is tentatively interpreted as an upper molar because the only complete preserved loph matches well with the posterior loph of the upper molar MLP 55-III-10-1a (Fig. 2D) described above, and there is no trace of a structure equivalent to the cristid obliqua. The complete estimated size is slightly larger than the largest M1 and M2 attributed to *P. saxeum*, the lophs (at least the preserved one) are more robust, comparatively lower, and there is no trace of a lingual cingulum.

PYROTHERIIDAE sp. 2

Referred Specimen—AMNH 29392, an unworn m3?

Provenance—Cerro Talquino. Mustersan SALMA (Simpson, 1967).

Comments—This molar was listed and figured by Simpson (1967:pl. 45, figs. 4, 5) as a last cheek tooth. It is nearly as large as the m2 of *P. macfaddeni*, roughly larger than the incomplete M3 of *P. saxeum* described above, and significantly larger than all the m3 here assigned to *P. saxeum* (see Table 1), exceeding the probable intraspecific variation. The lophids are comparatively much lower (even unworn) and more massive, even more than in the MPEF PV 10605, being the posterior one with a slightly inverted curvature (i.e., concave to the back). If it is not an extreme variant of *P. saxeum*, it likely belongs to a closely related species, suggesting the occurrence of more than one pyrothere taxon in the same bearing levels.

PYROTHERIIDAE sp. 3
(Fig. 4B)

Referred Specimen—MLP 55-IX-28-1e, an unworn p3?

Provenance—Puesto Bota at Rio Chico of Chubut. Mustersan? SALMA.

Description and Comparisons—This tooth is an unworn, almost complete (the anterolingual part is missing) lower cheek tooth, proportionally much longer and narrower than the putative p4 of *P. saxeum*. The general morphology strongly resembles the unerupted p3 of *Griphodon*. However, there is no anterior lophid, and the posterior lophid is much more concave. The crest departing from the anterior slope of the protoconid is much more reduced. A longitudinal, somewhat crescentic crest, surely involving the hypoconid, ends anteriorly in a conspicuous cuspule, separated from the protoconid by a deep notch, deeper than in *Griphodon*, the protoconid being almost isolated. The posterior end of this crest dips down, forming a faint, almost vertical edge on the posterior wall of the crown, shorter and lower than in *Griphodon*. There is a conspicuous cingulid at the posterolingual base of the talonid, unlike in *Griphodon*; the cingulid ends abruptly on the posterior wall and does not form a distinct posterior shelf. The enamel on the posterior lophid bears larger and more distinct denticles than in *Griphodon*.

Comments—This tooth surely belongs to a pyrothere, but it is structurally distinct from all the teeth of *P. saxeum* here examined, except for the presence of a lingual cingulid. Furthermore, it is much smaller than the putative p4 of *P. saxeum*, and therefore too small to be the p3 (or even the dp3) of this species.

THE TAXONOMIC STATUS OF *GRIPHODON* AND *BAGUATHERIUM*

Propyrotherium, *Griphodon*, and *Baguatherium* have cheek teeth very similar in structure (bunolophodont, with two transverse, slightly inclined crests). The three taxa are based on fragmentary, mostly not homologous dental elements, preventing an accurate taxonomic segregation. The revision of the available teeth of *Propyrotherium* suggests that the lower cheek tooth included in the syntype (MACN A 10929) is very likely a p4, and thus it is comparable with the p4 of the holotype of *G. peruvianus*. The former is much worn and the latter is unerupted; even so, some features can be contrasted: the p4 of *Griphodon* is comparatively longer and narrower (as noted by Shockey and Anaya, 2005) and the lingual base of the crown is infolded between the lophids (as noted by Patterson, 1977); furthermore, the lophids have subequal transverse lengths, the central valley is entirely open on the lingual side, and the crown lacks a labial cingulid. Patterson (1977) also pointed out that the p4 of *Propyrotherium* lacks any trace of 'paraconid,' unlike in *Griphodon*, and Shockey and Anaya (2005) stated that it has less complex crown morphology. However, the crown is too worn to verify these features. The m1 of the holotype of *G. peruvianus* also differs from the lower molars here referred to *Propyrotherium* by having comparatively slender lophids, a more lophoid posterior cingulid, and by lacking a labial cingulid, besides other minor features. This tooth is barely smaller than the smallest available molars of *Propyrotherium*. Contrary to that proposed by Schoch and Lucas (1985), and in agreement with Shockey and Anaya (2005), *G. peruvianus* had enough differences to be kept as a separate taxon.

Concerning *Baguatherium jaureguii*, the only well-preserved cheek tooth of the holotype—and only known specimen—is the P3. Assuming that P3 and P4 are subequal (as in *Colombitherium* and *Pyrotherium*), it can be compared with the lectotype of *Propyrotherium* (here interpreted as P4). Both teeth bear an elevated lingual cingulum connecting the lophs. However, in *Baguatherium*, the posterior projection of the labial side of the anterior loph is more developed, extending toward the posterior loph and producing an occlusal pattern similar to the Greek symbol 'π' (pi-shaped sensu Shockey and Anaya, 2005), and the posterior cingulum is more pronounced. According to Salas et al. (2006), *Baguatherium* also differs in having less

TABLE 2. Taxon-character matrix modified from Salas et al. (2006) used for assessing phylogenetic relationships of *Propyrotherium saxeum* Ameghino and other pyratheres.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Notostylops	0	–	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Proticia	1	0	?	1	1	0	0	?	0	1	0	0	0	0	?	0	0
Colombitherium	1	0	?	?	?	0	0	?	0	?	0	0	0	0	0	0	?
Carolozittelia	2	1	0	?	0	1	1	1	0	?	0	0	0	1	0	0	?
Propyrotherium	2	0	?	1	0	1	1	?	0	?	1	1	0	2	1	0	?
Griphodon	2	0	?	?	0	?	1	?	0	?	1	1	0	2	?	0	0
Baguatherium	2	0	1	1	?	2	1	1	0	?	1	1	?	2	1	?	?
P. macfaddeni	2	0	1	1	1	2	2	1	1	1	1	1	1	2	0	1	1
P. romeroi	2	0	1	1	1	2	2	1	1	A	1	1	1	2	0	1	1

The hypothetical outgroup in the matrix by Salas et al. (2006) was replaced by *Notostylops*, and all characters for *Colombitherium* were rescored under the assumption that the holotype is a maxillary. Other changes are discussed in the text. Characters' state definitions are as listed in Salas et al. (2006), except for characters 1 and 17 (see text and Appendix 1). 'A' indicates polymorphism (states 1 and 2). '?' indicates missing or unknown character. '–' indicates non-applicable character.

excavated occlusal wear facets than in *Propyrotherium*, although we could not corroborate this feature. Compared with the putative P3 of *Propyrotherium* (AMNH 29391), *Baguatherium* differs in the same characters as from the P4; the lophs have subequal transverse length, and the crowns lack a cuspule on the labial opening of the central valley. The P3 of *Baguatherium* is slightly larger than the P4 and the putative P3 of *Propyrotherium*.

In sum, there are several dental characters supporting the taxonomic separation between *P. saxeum* and *G. peruvianus* as well as between *P. saxeum* and *B. jaureguii*. However, there are still no homologous anatomical elements for comparison between *G. peruvianus* and *B. jaureguii*, and therefore their taxonomic differentiation is problematic. Salas et al. (2006) did not compare both species explicitly, except that in *B. jaureguii* the occlusal wear facets are less oblique than in *G. peruvianus* (25° and 60°, respectively). However, this difference can be due to mere differences between the stages of wear (the P4 of the holotype of *B. jaureguii* is much more worn than the dp4–m1 of the holotype of *G. peruvianus*), as is consistently observed in *Pyrotherium*. Interestingly, in the cladistic analysis by Salas et al. (2006), both taxa have identical states for all the characters positively scored. The only difference that we were able to corroborate is the estimated size. The P3 of *B. jaureguii* is slightly larger than the P4 and the putative P3 of *Propyrotherium*. In turn, the m1 of *G. peruvianus* is hardly smaller than the smallest available lower molars of *Propyrotherium*. Thus, the estimated size of *B. jaureguii* should be somewhat larger than that of *G. peruvianus*. Apart from this subtle difference, at present there is no sufficient evidence supporting the separation of *B. jaureguii* in a distinct genus.

PHYLOGENETIC AFFINITIES OF *PROPYROTHERIUM*

Ameghino (1902) suggested that *Propyrotherium* was a basal pyrothere ancestral to *Pyrotherium*, and indirectly to proboscideans. Nevertheless, this hypothesis was rejected by Gaudry (1909) and almost all subsequent workers. Patterson (1942) interpreted *Propyrotherium* as closer to *Griphodon* than to any other pyrothere known at that time. Simpson (1967) concluded that *Propyrotherium* was a pyrothere closer to *Pyrotherium* than to *Carolozittelia*, and considered *Griphodon* as incertae sedis. Lucas (1986) performed a cladistic analysis and concluded that *Propyrotherium* (as senior synonym of *Griphodon*) was the sister group of *Pyrotherium*, essentially coinciding with Simpson's proposal, but with *Carolozittelia* in a more basal position than the *Colombitherium-Proticia* clade. In a further cladistic analysis, Salas et al. (2006) concluded that *Propyrotherium* is the second earliest diverging pyrotheriid (after *Carolozittelia*), being the sister group of an unresolved polytomy including *Griphodon*, *Baguatherium*, and the species of *Pyrotherium*. A recent cladistic analysis by Bil-

let (2010), in a wider systematic context, did not resolve the affinities among the post-Casamayoran pyratheres.

We herein performed a new cladistic analysis based on the data matrix by Salas et al. (2006), in which the character states were polarized with a hypothetical outgroup, coded 0 for every character. In our modified matrix (Table 2 and Supplementary Data), we polarized the character states using *Notostylops* Ameghino (Notoungulata) as the outgroup based on a recent phylogenetic proposal by Billet (2010). The inclusion of this outgroup merits the following comments:

Character 1. None of the states defined by Salas et al. (2006:appendix 1) is applicable to *Notostylops*. We replaced the state 'bunodont' by the state 'ectolophodont' (sensu Fortelius, 1985) to represent the condition in *Notostylops*, and the states are treated as unordered.

Character 2. None of the states defined by Salas et al. (2006) is applicable to *Notostylops*.

Character 4. *Notostylops* has moderately enlarged incisors, and only the lower ones are procumbent. Contrary to the statement of Billet (2010), we interpret that the incisors of *Notostylops* are not tusk-like.

Character 15. In *Baguatherium* and *Propyrotherium*, the lingual crest connecting the protoloph and the metaloph is derived from the lingual cingulum. The lingual crest connecting the protoloph and the metaloph in *Notostylops* is derived from the lingual cusps and a lingual cingulum is absent.

Besides the outgroup, we included the following modifications: Avila (2005) and Salas et al. (2006) reinterpreted the holotype of *Colombitherium tolimense* as a mandible (originally described as a maxilla by Hoffstetter, 1970). Following Billet et al. (2010; see also Bond and Kramarz, 2005), we accept Hoffstetter's original interpretation and have rescored all the applicable characters for this taxon (characters 5, 10, 15, and 17) accordingly.

Character 5. Salas et al. (2006) coded *Propyrotherium* as having nearly square lower cheek teeth (state 1). This is nearly correct for the lower cheek tooth of the syntype (here interpreted as a premolar), although the crown was surely longer when complete. All the remaining lower cheek teeth here assigned to *Propyrotherium* are consistently longer than wide, thus *Propyrotherium* is scored 0.

Character 6. Salas et al. (2006) coded *Carolozittelia* as having horizontal and excavated wear facets in lophs/lophids (state 0). Actually, we observed that this taxon has oblique and excavated wear facets (state 1).

Character 8. In the type specimen of *Carolozittelia*, the M1 was implanted closer to the sagittal plane than the M2; thus, the cheek tooth series converged anteriorly (state 1), as in all the taxa positively scored.

Character 10. Salas et al. (2006) coded *P. macfaddeni* and *P. romeroi* as having a long mandibular symphysis extending posteriorly to the level of m2 (state 2). We found that this feature is variable in *P. romeroi*: the symphysis extends to the level of m2 in FMNH 13929, to the level of m1–m2 in MACN A 52-601 and MACN Pv 9286, or only to the level of p4–m1 in FMNH 12987 (as described by Billet, 2010). In *P. macfaddeni*, the symphysis extends to the level of p4–m1 (in the holotype), or at most to the level of m1 (YPM PU 20679, 20692, 20684). This character is here scored as polymorphic (states 1+2) for *P. romeroi* and as state 1 for *P. macfaddeni*.

Character 11. Salas et al. (2006) coded *Propyrotherium* as having low lophs/ids (state 0). Actually, in *Propyrotherium* the lophs/ids are higher than long, as in *Griphodon* (see discussion above), thus *Propyrotherium* must be scored 1 for this character.

Character 15. The lingual longitudinal crest that connects both lophs, described as an autapomorphy of *Baguatherium* by Salas et al. (2006), is an elevated lingual cingulum, also present in the putative P4 (lectotype) of *P. saxeum* and in the upper molars referred here to this species (see discussion above). *Propyrotherium* must be scored 1 for this character.

Character 16. Salas et al. (2006) coded *Griphodon* as lacking a cristid obliqua (state 1). However, in the holotype and only known specimen, there is a distinct remnant of this structure in all preserved cheek teeth (Patterson, 1942:3), as developed as in the type of *Carolozittelia* and in some molars of *Propyrotherium*. *Griphodon* is here scored 0 for this character. Additionally, Salas et al. (2006) also coded *Baguatherium*, known only through maxillary teeth, as lacking this structure. Probably the authors interpreted that the absence of the corresponding wear facet on the upper teeth (i.e., on the posterior slope of the anterior loph) indicates the absence of cristid obliqua in the lowers. However, no upper molar of *Carolozittelia* and *Propyrotherium* has such a distinct facet, probably because the cristid is low and occludes only in very advanced stages of wear. Consequently, the absence of cristid obliqua in *Baguatherium* cannot be deduced from the wear pattern of the upper teeth. On the other hand, the available upper molars of *Carolozittelia* and *Propyrotherium* have a small notch on the posterior slope of the anterior loph, likely to receive the cristid obliqua, but still unworn. The upper molars of the species of *Pyrotherium* lack this notch, and concordantly the lower ones have no trace of the cristid. The only well preserved cheek tooth of *B. jaureguii* (P3) has a notch in this position, suggesting the presence of a cristid obliqua in the occluding lower tooth. We here prefer to score this character in *B. jaureguii* as unknown until more complete materials are available.

Character 17. It is not clear if the definition of this character by Salas et al. (2006:appendix 1) concerns only the lower premolars or the complete lower cheek tooth series. Actually, *Proticia* and *Griphodon* have a distinct 'paraconid' on p3 and p4 and dp4 and p4, respectively, but not on m1. Thus, these taxa should be coded as polymorphic if the character refers to the complete lower cheek tooth series. In order to avoid confusion, we herein redefined and rescored character 17 only for the lower premolars (the condition for the molars in all the taxa included in the ingroup is absent or unknown). On the other hand, Salas et al. (2006) interpreted that the anterior cingula of what they considered as p3–m1 of *Colombitherium* might be homologous to the 'paraconid' recognized in *Proticia*. Accepting that the holotype of *Colombitherium* is a right maxilla, the wear facet on the anterior cingulum is unlikely to be corresponding for the 'paraconid' (it should more properly located on the posterior slope of the posterior loph), thus the presence of a
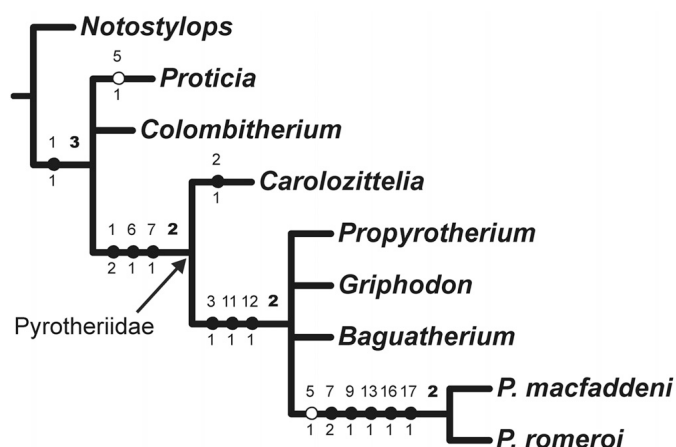

FIGURE 5. Strict consensus from four most parsimonious trees (length = 22, consistency index [CI] = 90, retention index [RI] = 91) generated by an exhaustive search based on the taxon-character matrix modified from Salas et al. (2006:appendix 2) shown in Table 2. Numbers in bold face are Bremer indices.

'paraconid' or an equivalent cusp in *Colombitherium* is uncertain.

The data matrix was analyzed using NONA 2.0 (Goloboff, 1999). We obtained four most parsimonious trees (length = 22, consistency index [CI] = 90, retention index [RI] = 91) by exhaustive searching, all differing in the position of *Baguatherium*, *Griphodon*, and *Propyrotherium*. The strict consensus tree is shown in Figure 5. In one of the trees, the position of these taxa is identical to that obtained by Salas et al. (i.e., *Baguatherium*, *Griphodon*, and the species of *Pyrotherium* form a polytomy excluding *Propyrotherium*). *Propyrotherium* does not appear as more related to the species of *Pyrotherium* than to *Baguatherium* and *Griphodon* in any of the trees. Our results agree with that of Salas et al. (2006) and differ from that of Lucas (1986) in the position of *Carolozittelia*, closer than *Colombitherium* and *Proticia* to the remaining pyrotheres. Lucas' (1986) proposal is based on the occurrence of three apomorphies supposedly shared by his 'colombitherines' and 'pyrotheriines': bilophodonty of P4/4, loss of hypoconulid lobe of m3, and presence of large, tusk-like incisors. Based on this phylogenetic scenario, Lucas (1986) interpreted that the bunodonty in 'colombitheriids' derived from an ancestral lophodont condition. However, the mentioned three characters are unlikely to be synapomorphies of this clade: the P4/4 of *Carolozittelia* is unknown, whereas the p4 of *Proticia* is not strictly bilophodont; the condition of the hypoconulid lobe of m3 is unknown in *Colombitherium* and *Proticia*, and only *Pyrotherium* positively lacks these feature; the presence of large, tusk-like incisors is unknown in *Carolozittelia* as well as in *Colombitherium*. Consequently, these characters do not support the relationships of the 'colombitheriids' alleged by Lucas (1986). Contrarily, our results suggest that *Carolozittelia* is the sister group of the clade including *Pyrotherium* and *Propyrotherium*, and the 'colombitherines' are excluded from Pyrotheriidae. This relationship is supported by three synapomorphies: fully bilophodont cheek teeth (character 1[2]), wear facets oblique and excavated (character 6[1]), and lophs/ids slightly anteriorly/posteriorly inclined (character 7[1]). The absence of a 'paraconid' (character 17), interpreted by Salas et al. (2006) as one of the synapomorphies of Pyrotheriidae, herein resulted as only uniting the species of *Pyrotherium*. A consistent increase of hypsodonty and lophodonty is deduced from these results, and

the bunodont condition in *Colombitherium* and *Proticia* would have not derived from a bilophodont one.

CONCLUSIONS

Propyrotherium, based on very scanty and fragmentary materials, was one of the least known pyrotheres. The revision of the type materials, the restudy of isolated cheek teeth at AMNH (Simpson, 1967), other specimens at MLP, and comparisons with other pyrotheres allowed a tentative reconstruction of the dental series and an improved diagnosis. We conclude that the cheek teeth included in the original syntype and other comparatively small teeth reported by Simpson (1967) are upper and lower posterior premolars, respectively, and that in *Propyrotherium saxeum*, cheek teeth increase in size gradually from front to back (as in *Pyrotherium*). The upper cheek teeth would also have a gradual increase in the curvature of the lophs. Although the taxonomic status of the type of *Promoeritherium australe* is uncertain, the most probable cheek teeth formula of *Propyrotherium saxeum* is P2–M3/p2–m3. All cheek teeth are bilophodont, but in the premolars (upper and lower) the anterior loph/id is labiolingually shorter than the posterior one. The P4–M3 have a lingual cingulum, two labial roots and a lingual one; the p4–m3 have a labial cingulid, an anterior and a posterior root and variably developed remnant of cristid obliqua. Our revision of all the available specimens of *Propyrotherium saxeum* makes it the best-known pre-Deseadan pyrothere. The reconstruction of the dental formula and attribution of isolated specimens is speculative and could be refuted by the discovery of more complete materials, but we think that it is the most reasonable one considering the available evidence.

Propyrotherium saxeum is structurally similar to the Peruvian pyrotheriids *Griphodon peruvianus* and *Baguatherium jaureguii*, but it shows some consistent differences with both taxa. It differs from the former by having distinct features in p4, lingual cingulids, and broader lophids in the molars, and from the latter by features of P4 and by being somewhat smaller. In contrast, *G. peruvianus* and *B. jaureguii*, based on non-comparable materials, seem to be indistinguishable so far, except for a moderate difference in size. New materials are needed to confirm that these species should be kept in separate genera.

The cladistic analysis based on the data matrix modified from Salas et al. (2006) confirms that *Propyrotherium* is one of the earliest and most basal known pyrotheriids (only *Carozittelia* occupying a more basal position); the analysis, however, does not allow a full elucidation of the sequence of speciation events and character evolution in early pyrotheres.

ACKNOWLEDGMENTS

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APPENDIX 1. List of characters and characters states used in the analysis of the relationships among pyrotheres (modified from Salas et al., 2006). Characters were polarized with respect to *Notostylops*. Characters treated as ordered are denoted by an asterisk (*).

(1) Occlusal structure of upper and lower cheek teeth: ectolophodont (0); buno-bilophodont (1); bilophodont (2).
(2) Orientation of lophs/lophids in occlusal view: straight (0); oblique (1).
(3) Relative width of palate: wide, average distance between molar tooth series wider than the width of P4 (0); narrow, equal, or less than width of P4 (1).
(4) Tusk-like incisors: absent (0); present (1).
(5) Shape of lower cheek teeth in occlusal view: elongate, longer than wide (0); square, length and width approximately equal (1).
(6) *Wear facets in lophs/lophids: horizontal and excavated (0); oblique and excavated (1); oblique and flat (2).
(7) *Orientation of lophs/lophids in lingual/labial view: vertical, 90° to 85° to horizontal plane (0); slightly anteriorly/posteriorly inclined (85° to 60° to horizontal plane) (1); greatly anteriorly/posteriorly inclined (60° or less to horizontal plane) (2).
(8) Orientation of cheek tooth series: almost parallel (0); tendency to converge anteriorly or almost converge anteriorly (1); stepwise (2). The character is constant (state 1) for the available sample.
(9) Loph/lophid enamel: consistent on all faces of lophs and lophids (0); relatively thicker on the anterior faces of lophs and posterior faces of lophids (1).
(10) *Length of mandibular symphysis: short (0); extends posteriorly to level p4–m1 (1); extends posteriorly to level of m2 (2).
(11) Loph/lophid height: low, less than or equal to length (0); high, height greater than length (1).
(12) Loph/lophid denticles or crenulations: absent (0); present (1).
(13) Cuspidate loph/lophid: present (0); absent (1).
(14) Anterior/posterior cingula in upper/lower cheek teeth: present but indistinct (0); well developed and either flat or with a conule (1); well developed, with a transverse crenulated crest (2).
(15) Lingual longitudinal crest that connects both lophs: absent (0); present (1).
(16) Cusp in the valley or 'cristid obliqua': present (0); absent (1).
(17) 'Paraconid' in lower premolars: present (0); absent (1).