



A NEW PRE-DESEADAN PYROTHERE (MAMMALIA) FROM NORTHERN PERU AND THE WEAR FACETS OF MOLARIFORM TEETH OF PYROTHERIA

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ABSTRACT—*Baguatherium jaureguii* gen. et sp. nov. from the early Oligocene of northern Peru is the best known pre-Deseadan pyrothere. It has a relatively wider palate and less oblique lophs on the molariform teeth than *Pyrotherium macfaddeni* and *Pyrotherium romeroi*. A conspicuous lingual crest connects the anterior and posterior lophs of molariform teeth. Nares are retracted. Phylogenetic analysis places *Baguatherium* with *Gryphodon* and *Pyrotherium* in an unresolved polytomy. In *Proticia* and *Colombitherium* the wear facets of the molariform teeth indicate a mainly grinding masticatory apparatus. In *Pyrotherium*, *Baguatherium*, *Gryphodon*, and to a lesser degree, *Propyrotherium*, the oblique wear facets generate a cutting surface caused by a greater antero-posterior component to dorsoventral mastication. The cingulae function like stops or buttresses. Considering its brachydont condition, this specialization and the increase in the molariform surface in *Baguatherium* and *Pyrotherium* may have improved masticatory efficiency in response to the expansion of open environments during the Oligocene.

INTRODUCTION

Pyrotheria are one of the most enigmatic and least studied orders of South American Cenozoic mammals due to the scarcity of known remains. Except for *Pyrotherium* Ameghino, 1889, from the Deseadan South American Land Mammal 'Age' (SALMA: late Oligocene) of Argentina (e.g., Ameghino, 1895, 1901, 1902; Gaudry, 1909; Loomis, 1914) and Bolivia (Hoffstetter, 1968; MacFadden and Frailey, 1984; Shockey and Anaya, 2004), pyrothere genera are only known from partial dental series. Because so little material has been recovered, basic aspects of pyrothere morphology and phylogenetic relationships have not been revealed (see Patterson, 1977; Cifelli, 1993; Lucas, 1993), and they have even been considered incertae sedis among the orders of eutherian mammals (MacFadden and Frailey, 1984).

The oldest genera of Pyrotheria, *Proticia* Patterson, 1977, and *Colombitherium* Hoffstetter, 1970, from the early? Eocene of Venezuela and Colombia, respectively, show such primitive features as bunolophodont molariform teeth and horizontal occlusal surfaces (Hoffstetter, 1970; Patterson, 1977). During the middle Eocene (Mustersan SALMA), *Propyrotherium* Ameghino, 1901, and *Gryphodon* Antony, 1924, demonstrate an evolutionary trend among pyrotheres of greater development of bilophodont teeth and oblique wear facets (Simpson, 1967; Patterson, 1942).

In Peru, Eocene and Oligocene continental mammals are uncommon, largely because the fossil-bearing beds of these epochs are located in areas of difficult access that have not been explored. During the 1990s, one of us (JS), explored the extensive sedimentary sequences in the northeastern region of the Peruvian Andes (Bagua, Amazonas), where exposures extend, with interruptions, from the Lower Cretaceous to the Pliocene (e.g., Mourier et al., 1988). In lower horizons of the El Milagro Formation (lower Oligocene), JS collected a partial maxilla of a pyrothere. This discovery was the first record of a fossil vertebrate in that geologic unit. In 2004, a new expedition led by RS and B. J. Shockey resulted in the discovery of additional pyrothere material, as well as remains of terrestrial crocodiles (*Sebecosuchia*) and tortoises.

The object of this study is to describe the pyrothere remains from Bagua and determine their affinities within Pyrotheria. In-

terpretations of masticatory functional anatomy of pyrotheres based upon dental macrowear are also provided.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, New York; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MCNC-VF, Museo de Ciencias Naturales de Caracas, Venezuela; MNHN DES, Deseadan collection from Patagonia of the Muséum national d'Histoire naturelle, Paris, France; MNHN GUA, Gualanday collection of the Muséum national d'Histoire naturelle, Paris, France; MNHN SAL, Salla collection of the Muséum national d'Histoire naturelle, Paris, France; MUSM, Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú; PU, Princeton Collection of the Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

Osteological Abbreviations—I, upper incisor; if, incisive foramen; L, left; M and m, upper and lower molar teeth, respectively; np, nasal passage; P and p, upper and lower premolar teeth, respectively; R, right.

Materials and Methods—All specimens of *Baguatherium jaureguii* (MUSM 436, MUSM 488, MUSM 514, MUSM 515) are housed in MUSM, Lima, and were collected from Bagua, Amazonas, Peru (early Oligocene). These specimens were compared with *Colombitherium tolimense* (MNHN GUA 2906, holotype), *Propyrotherium saxeuum* (AMNH 29392, AMNH 29393, AMNH 29394), *Gryphodon peruvianus* (AMNH 17724, holotype), *Pyrotherium macfaddeni* (PU 20693, holotype; PU 20684, MNHN SAL 21), and *Pyrotherium romeroi* (MNHN DES 1242, MNHN DES 1243, MNHN DES 1245). Characteristics of the molariform tooth wear facets were assessed through direct observation of the referred material, complemented by additional observations from the literature. The ratio of the molariform/palatal surface is an index that expresses the size of both upper molariform tooth series relative to the estimated area of the palate located between the molariform teeth. Measurements to a tenth of a millimeter were made using Mitutoyo digital calipers, whereas measurements to a millimeter were made using Mitutoyo nib style jaw calipers. The chronology of the South American Land Mammal 'Ages' used in this study is that proposed by Flynn and Swisher (1995).

GEOGRAPHIC SETTING, GEOLOGY, AND AGE

Pyrothere remains were discovered during two expeditions to the outcrops of the El Milagro Formation (= upper member of Sambimera Formation sensu Naeser et al., 1991), Bagua, Amazonas Department, northeastern Perú (Fig. 1). The El Milagro Formation, located in a geographic area known as Selva Alta ('High Jungle'), comprises a continuous, 700–1000 m thick sequence, of intercalated conglomerate, sandstone, and red mudstone layers. The base of the section grades conformably into the underlying unit (Cajaruro Formation—Eocene), while the top of the section is separated by an angular unconformity from the overlying Bellavista Formation (Pliocene). The horizon producing the pyrothere material, which was collected close to its base, is characterized by a high flow regime facies (predominantly sandstone and coarse to fine-grained conglomerate) with a few beds indicating less energetic flow regimes (mudstones and fine-grained sandstones). Localities ELM 3 and ELM 4 are 1.2 km southeast and 1.5 km northwest, respectively, of Esperanza village. These localities include at least 8 km² of well-exposed outcrops of this horizon.

In general, three sedimentary sequences can be recognized. The first is a high flow regime facies, indicated by a predominance of fine-to coarse-grained sandstone and conglomerate, with thin intervals of predominantly clayey siltstone. The second sequence is marked by sandstone and clayey siltstone. The uppermost sequence as a whole reflects increased hydrodynamic flow, with the sediments consisting of intercalations of sandstone and conglomerate with thin horizons of clayey siltstone. All three levels are dark red in color. The presence of gypsum laminae and diagenetic features in the lower levels indicates the local presence of evaporite deposits formed in a shallow and restricted subaqueous environment in a continental setting.

⁴⁰K/³⁹Ar dates from tuffs at Cerro Fila Larga (located close to the base of the El Milagro Formation) are imprecise, ranging

from 53.6 ± 3.1 Ma (early Eocene) to 68.1 ± 4.6 Ma (Late Cretaceous) (Mourier et al., 1988). The imprecision of these dates, combined with the evolutionary stage of the pyrothere from Bagua, cast considerable doubt on the Mourier et al. (1988) ages for the El Milagro Formation.

More recently collected ash samples from Cerro Fila Larga (below the level of the pyrothere sites ELM 3 and ELM 4) were dated using the fission track method, and yielded an age of 31.0 ± 3.1 Ma (Naeser et al., 1991). Flynn and Swisher (1995) consider the beginning of the Deseadan SALMA to be as old as 29 Ma based on data from Bolivia and Argentina while the span of the Tinguirirican SALMA has recently been proposed to be 31–?33 Ma (Flynn et al., 2003). The age estimate of Naeser et al. (1991) corresponds to the upper part of the lower Oligocene and lies closer to the Tinguirirican SALMA than to the beginning of the Deseadan SALMA. Tinguirirican faunas from Chile and Argentina include a diverse assemblage of taxa, but lack pyrotheres (Flynn et al., 2003), thus precluding comparisons with the material from Bagua. However, the age proposed by Naeser et al. (1991) for the El Milagro Formation, close to the Tinguirirican SALMA, is consistent with the evolutionary stage of the newly discovered taxon (see discussion).

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA

Order PYROTHERIA Ameghino, 1895

Family PYROTHERIIDAE Ameghino, 1889

Genus *PYROTHERIUM* Ameghino, 1889

BAGUATHERIUM, gen. nov.

Type Species—*Baguatherium jaureguii*, sp. nov.

Etymology—*Bagua*, in reference to Bagua, the area where the holotype and referred specimens were discovered, and *therium*, beast.

Diagnosis—As for the type and only species.

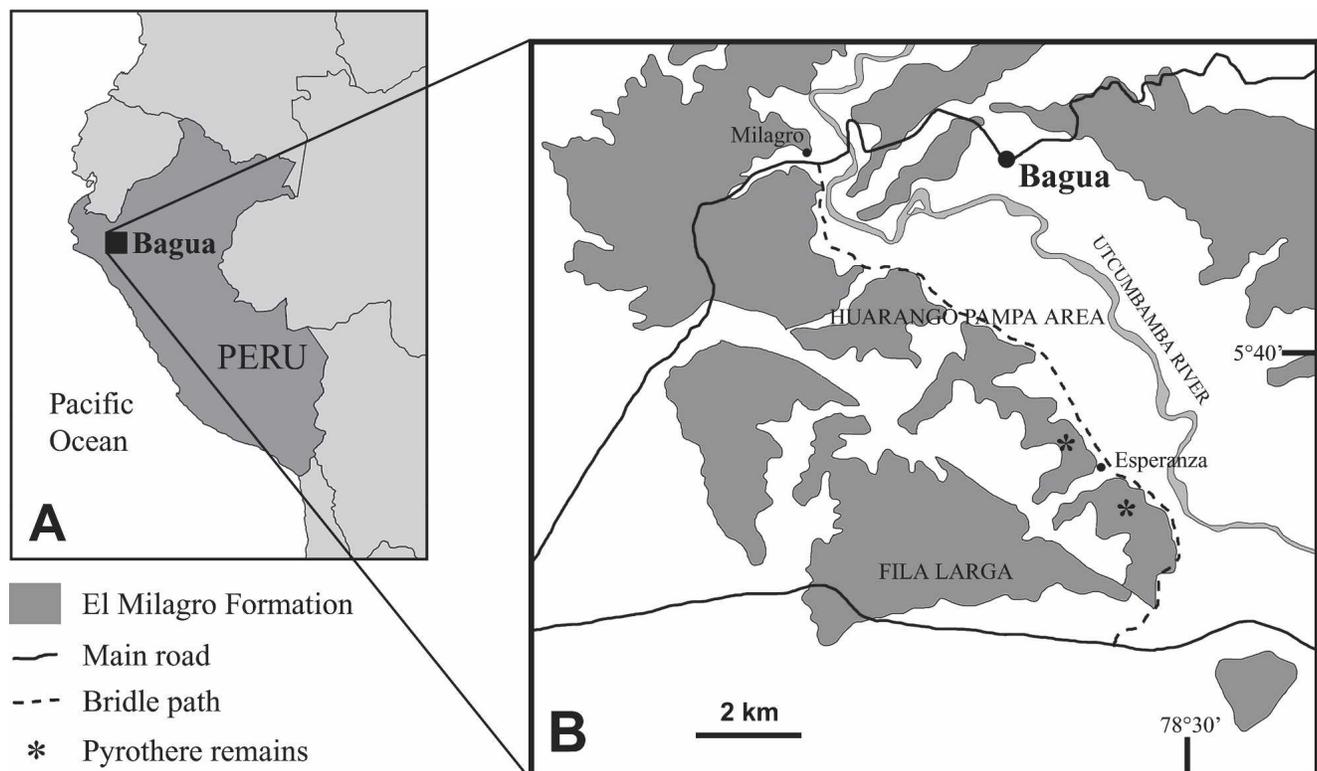


FIGURE 1. **A**, location of the study area in northeastern Peru; and **B**, geographic map of the Bagua area showing the outcrops of the El Milagro Formation and the fossil localities.

BAGUATHERIUM JAUREGUII, sp. nov.

(Figs. 2–5)

Holotype—MUSM 436, partial maxilla with right P2 and P3, natural molds of right P4 and M1, and partial left P4 (Fig. 2). A fragment of I2 is preserved.

Referred Specimens—MUSM 488, left femur (Fig. 3); MUSM 540, crown of ?p3; MUSM 541, anterior or posterior loph of molariform tooth. Collected from ELM 3 by R. Salas and B. Shockey in June 2004.

Type Locality—ELM 4; Esperanza, Huarangopampa Area, Bagua Grande, Amazonas Department, Peru.

Formation and Age—Basal levels of the El Milagro Formation, late early Oligocene, ca. 31.0 ± 3.1 Ma.

Etymology—*jaureguii*, to honor Ángel Jauregui, a prominent citizen and former Director of the Instituto Regional de Cultura, Bagua, for his important contribution to preserving local fossil sites.

Diagnosis—Similar in size to *Propyrotherium saxium* and *Pyrotherium macfaddeni*, and ~67% smaller than *P. romeroi* (based on P2-M1 length). Maxilla and palate proportionally wider than *P. macfaddeni* and *P. romeroi*; average distance between the dental series wider than the width of P4. P2 with an anterior conule and molariform teeth without cusps in the transverse valley. Sub-parallel dental series. Posterior margin of incisive foramen located on predentary portion of maxilla. Wear facets of lophs flat, less oblique than in *Gryphodon peruvianus* and *Pyrotherium*. Apomorphy of taxon: lingual crest connecting anterior and posterior lophs.

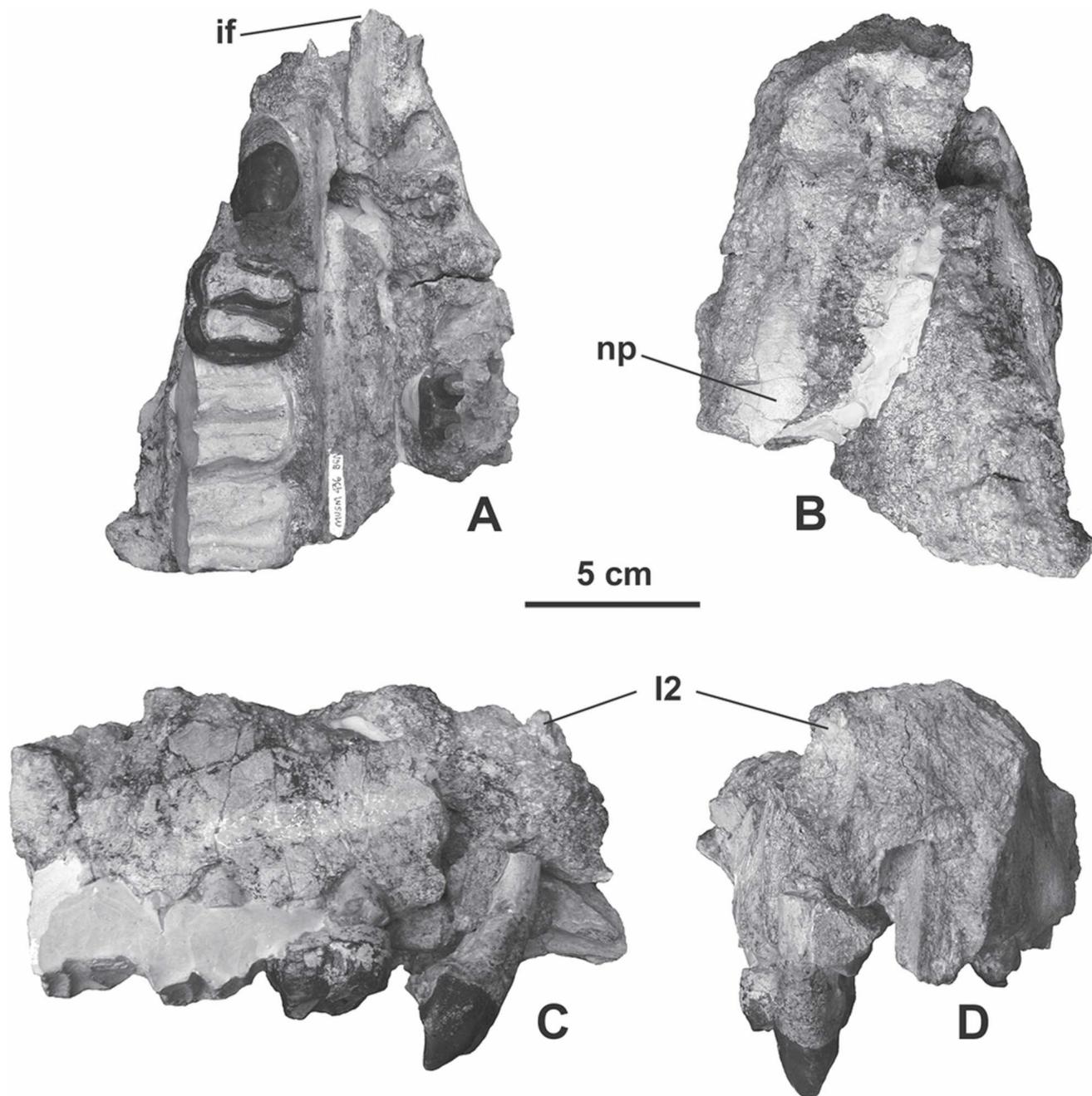


FIGURE 2. *Baguatherium jaureguii* gen. and sp. nov. Partial maxilla with P2–M1 (holotype, MUSM 436). **A**, occlusal view; **B**, dorsal view; **C**, right lateral view; and **D**, anterior view. **Abbreviations:** **if**, incisive foramen; **np**, nasal passage.



FIGURE 3. *Baguatherium jaureguii* gen. and sp. nov. Left femur (MUSM 488). **A**, anterior view; and **B**, medial view.

Description and Comparisons

The maxilla (holotype, MUSM 436) and the femur (MUSM 488) of *Baguatherium jaureguii* gen. et sp. nov. belong to adult individuals. MUSM 436 (Fig. 2) includes the anterior part of the maxilla extending to the level of M1. Dorsally, the maxilla is heavily weathered, although a segment of the nasal channel and a fragment of I2 are recognizable. The partial R P2, complete R P3, and partial L P4 are preserved. Additionally, casts of R P4 and R M1 were obtained from natural molds left by the molariform teeth in the matrix. MUSM 488 (Fig. 3) is a left femur that lacks its lateral margin.

Maxilla—MUSM 436 (Table 1) is comparable in size to *Pyrotherium macfaddeni* (PU 20693); thus, it is much smaller than *P. romeroi*. The dental formula of maxillary teeth of *B. jaureguii* appears to be the same as in *Pyrotherium* (P2–M3).

The preserved region indicates the skull is relatively wider than that of *Pyrotherium*. In *Baguatherium jaureguii* the ratio of the width of the maxilla at the level of P4–M1 to the length of P2–M1 is about 84, whereas in *P. macfaddeni* and *P. romeroi* it

TABLE 1. Dental and cranial measurements (mm) of *Baguatherium jaureguii* (holotype, MUSM 436), *Pyrotherium macfaddeni* (holotype, PU 20693), and *Pyrotherium romeroi* (MNYN DES 1243).

Dental and cranial measurement	<i>B. jaureguii</i>	<i>P. macfaddeni</i>	<i>P. romeroi</i>
P2 AP length	—	30.0	44.2
P2 ML width	20.5	24.6	30.2
P3 AP length	32.7	31.4	48.0
P3 ML width	33.1	37.4	51.0
P2–M1 length	131e	134.0	194.8
Minimum pre-molariform width maxilla	21 × 2 = 42e	—	56.4
Maxilla width: level of P4–M1	110e	100e	135.8
Palatal width: level of P4–M1	40.0	20.8	23.4

Minimum pre-molariform width of the maxilla was estimated by duplicating the minimum mediolateral measurement of the left maxilla. **Abbreviations:** AP, anteroposterior; e, estimate; M, upper molar; ML, mediolateral; P, upper premolar.

is 75 and 70, respectively. In *B. jaureguii* the pre-ventral area of the maxilla is narrow relative to the width of the maxilla at the level of P4–M1, as in *P. romeroi* (Fig. 4, Table 1). The posterior margin of the incisive foramen is located 26 mm mesial to the anterior edge of the P2, unlike in *P. romeroi*, where the incisive foramen extends posteriorly to the level of P2 (Fig. 4). In *B. jaureguii*, the palate is depressed at the level of the P2. The palate is not as narrow as in *P. macfaddeni* or *P. romeroi*, because the average distance between the left and right tooth series is similar to the width of P3 (~33mm). Unlike the two established species of *Pyrotherium*, in which the tooth series almost converge anteriorly, in *B. jaureguii* both are sub-parallel and only the P2 is oriented slightly toward the midline (Fig. 4).

A segment of the I2, and part of its alveolar wall located dorsal to the P2, can be observed in the anterodorsal portion of the maxilla (Fig. 2 C, D). As in *P. romeroi*, the I2 has a similar extension and a tusk-like shape. P2 is triangular in outline and is longer than wide, as in species of *Pyrotherium*; it has two roots, long and strong, directed posteriorly. It has a small anterior conule, whereas *P. macfaddeni* and *P. romeroi* possess a crenulated cingulum. The posterior portion of P2, including its second root, is missing. In the holotype of *B. jaureguii*, the anterior portion of P2 is worn much less than the posterior part: thus, the wear plane appears to be nearly perpendicular to the wear plane of the other cheek teeth. The P2 of *P. romeroi* and *P. macfaddeni* show that tooth wear is on the same plane as the posterior teeth, indicating that most of the anterior portion of the P2 occluded with the crown area of the p3. This implies that the P2 of *B. jaureguii* actually occluded with the anterior surface of p3, maybe due to a pathological condition. Indirectly, it confirms the lack of p2 in *B. jaureguii* as in *Pyrotherium*.

The P3 is molariform, bilophodont, and quadrangular, with its width and greatest length (labial) the same. The lophs have been worn to their bases and show an abrasion surface slightly inclined anteriorly. As in *P. macfaddeni*, the transverse valley between the two lophs is interrupted by the posterior projection of the labial side of the anterior loph that extends toward the posterior loph (the “pi-shaped appearance” of Shockey and Anaya, 2004: 484). A similar condition is also seen in some molariform teeth of *P. saxeum* (i.e., MACN 10929, lower cheek tooth). On the lingual side, a low longitudinal crest connects both lophs (also present in P4 and M1; Fig. 4A). This character has not been observed on any of the molariform teeth of *P. saxeum* (Simpson, 1967), and may be homologous to the enamel inflection observed in this position in *P. romeroi* and *P. macfaddeni*. The P3 bears small anterior and posterior cingulae; the anterior one is slightly broader. The labial enamel is higher than the lingual. The P3 and the P4 have two minor anterior roots and a major posterior one.

Only the lingual portion of the P4 is preserved. The wear facet is flat and more oblique than in the P3, but less than in *Gryphodon peruvianus* (m1), *P. macfaddeni*, and *P. romeroi* (Fig. 5). In *Proticia venezuelensis* and *Colombitherium tolimense*, the wear surfaces are nearly horizontal. Unlike *P. macfaddeni* and *P. romeroi*, the enamel of the mesial face of each loph is not thickened. There is a broad anterior cingulum. Lophs are slightly inclined anteriorly. The casts of P4 and M1 indicate that they were wider than long and the edges (anterior and posterior) of the lophs were slightly undulated.

The root of the zygomatic arch extends laterally just above the P4 and the M1 as in *P. romeroi* (Gaudry, 1909:pl. 1, fig. 1). Dorsally, a segment of the nasal passage extends up to the level of P4–M1 (Fig. 2). The surface of the nasal passage is concave and oriented posterodorsally, denoting a retracted position of the nares as in *P. romeroi*.

Femur—The femur (MUSM 488, Fig. 3) of *Baguatherium jaureguii* gen. et sp. nov. is only the second recorded of the order Pyrotheria. The other femur previously referred to the group is part of the well preserved hind limb (MNHN DES 1245) described and figured as *P. romeroi* by Gaudry (1909).

MUSM 488 is a left femur lacking its lateral margin. The morphology of the femur strongly resembles that of *P. romeroi* (MNHN DES 1245). The major difference between the femora of the two taxa is their size (Table 2). The maximum proximodistal length of *B. jaureguii* (MUSM 488) is 558 mm, while in *P. romeroi* (MNHN DES 1245) it is 630 mm. As in *P. romeroi*, the femur of *B. jaureguii* is long, flat, and compressed anteroposteriorly. The head projects proximally following the longitudinal axis of the femur. Despite the lack of a femoral neck, the head is higher than the greater trochanter. The medial femoral margin is highly concave. The lesser trochanter is well developed and is crest-like in appearance (not observed in *P. romeroi*). The proximal transverse width, between the head and greater trochanter, is clearly greater than the distal transverse width, between the epicondyles. The lateral and medial condylar articular surfaces contact the patellar trochlea. Both condyles are subequal in size, the lateral one being more convex than the medial one.

DISCUSSION

Pyrotherium, from the Deseadan SALMA, is the most derived and the best represented genus of Order Pyrotheria. *Pyrotherium romeroi* Ameghino, 1889, is known from cranial and appendicular material from several localities in Argentina (e.g., Ameghino, 1895; Gaudry, 1909; Loomis, 1914). *Pyrotherium macfaddeni*, from the Bolivian locality of Salla, was originally referred to *P. romeroi* by MacFadden and Frailey (1984) and has only recently been recognized as a distinct species by Shockey and Anaya (2004).

Baguatherium jaureguii is the first non-*Pyrotherium* pyrotheriid that permits direct observation of cranial characters. As expected for a pre-Deseadan pyrothere, it is more primitive than species of *Pyrotherium*. Compared with *P. romeroi* and *P. macfaddeni*, *B. jaureguii* presents: (1) a relatively wider maxilla and palate; (2) more parallel maxillary tooth series; (3) lophs that are less anteriorly inclined (i.e., more horizontal); and (4) possibly a less retracted incisive foramen (only compared with MNHN DES 1243, described in Gaudry, 1909). In contrast, *B. jaureguii* shares with these species a narrow premental region of the maxilla, the same maxillary dental formula (?-0-3-3), retracted nares, and the position of the zygomatic root at the level of P4–M1. *Pyrotherium macfaddeni* differs from *P. romeroi* in possessing a posterior projection of the labial side of the anterior loph of P3, which contacts the posterior loph (as in *B. jaureguii*), a wider palate, and in overall smaller size. The above-mentioned characters imply a close phylogenetic relationship among these three species, where *Baguatherium jaureguii* clearly shows the primitive states of characters observed in *P. macfaddeni* and *P. romeroi*. Possibly, the only apomorphy present in *B. jaureguii* is the longitudinal crest on the lingual side that connects both lophs (Fig. 4A).

The scarcity of material of other pyrotheres does not allow a rigorous or direct comparison between *Baguatherium jaureguii* and many other pyrothere taxa. *Propyrotherium* from the Eocene of Patagonia is one of the least understood pyrotheres. It is represented by numerous mandibular and maxillary teeth of

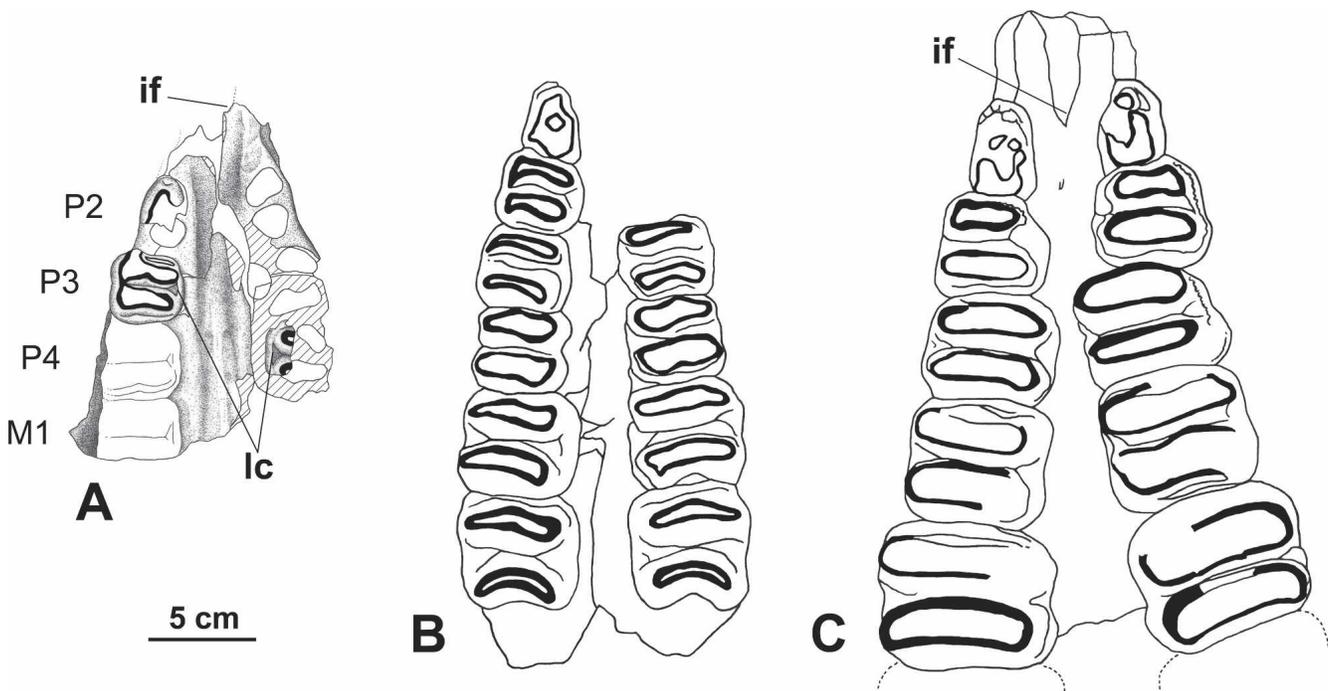


FIGURE 4. Comparative occlusal views of the maxilla in *Baguatherium jaureguii* and species of *Pyrotherium*. A, *Baguatherium jaureguii* (holotype, MUSM 436); B, *Pyrotherium macfaddeni* (holotype, PU 20693, from Shockey and Anaya, 2004); and C, *Pyrotherium romeroi* (MNHN DES 1243, from Gaudry, 1909). **Abbreviations:** if, incisive foramen; lc, longitudinal crest.

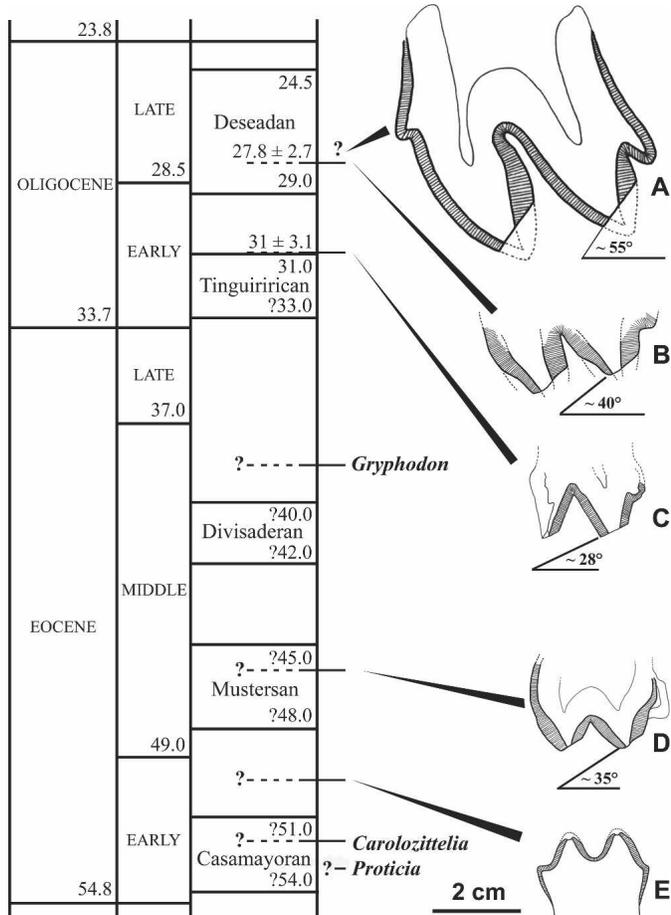


FIGURE 5. Longitudinal section of P4 in selected pyrotheres showing the wear facet angle and its chronologic distribution in South American Land Mammal 'Ages.' A, *Pyrotherium romeroi* (from Hoffstetter, 1970); B, *Pyrotherium macfaddenii*; C, *Baguatherium jaureguii*; D, *Propyrotherium saxum*; and E, *Colombitherium tolimense* (from Hoffstetter, 1970). Question marks indicate uncertain temporal placement. Chronology of the South American Land Mammal 'Ages' from Flynn and Swisher (1995). Flynn et al. (2003) is followed exclusively for the chronology of the Tinguirirican SALMA.

uncertain position, so comparisons are considerably restricted. Its estimated size and average inclination of loph wear facets are similar to those of *B. jaureguii*. Nevertheless, significant differences between these taxa are present. In *Propyrotherium* the upper molariform teeth bear small cusps in the transverse valley and on the cingulum, comparable to those of *Proticia* (Patterson, 1977) and *Colombitherium* (Hoffstetter, 1970). Additionally, the lophs are lower and the abrasion surface is less flat than in *B. jaureguii* (Fig. 5). Thus, compared to *Pyrotherium* and *B. jaureguii*, *Propyrotherium* exhibits primitive character states indicative of a less derived masticatory mechanism. According to Simpson (1967), *Propyrotherium* probably possessed only P3–M3, because there was no possible P2 among the 30 molariform teeth stored in the AMNH. Non-dental characters cannot be compared (i.e., palate and cranial width, nares position) due to lack of comparative material. *Propyrotherium* has been referred to the middle Eocene (Mustersan SALMA) according to the faunal association (e.g., Simpson, 1967; Marshall et al., 1983). However, the Mustersan SALMA has subsequently been suggested to be late Eocene based on new isotopic data (Kay et al., 1999). Considering that *B. jaureguii* comes from the upper part of the early Oligocene El Milagro Formation (Naeser et al.,

TABLE 2. Femur measurements (mm) of *Baguatherium jaureguii* (MUSM 488) and *Pyrotherium romeroi* (MNHN DES 1245).

Femur measurement	<i>B. jaureguii</i>	<i>P. romeroi</i>
Maximum length	558	630
Maximum proximal width	—	240
Minimum diaphysis width	104e	115
Maximum distal width	154	170
Patellar trochlea width	—	80

Abbreviation: e, estimate.

1991), the difference in age is consistent with the less derived morphology of *Propyrotherium*. The material referred to *Propyrotherium* housed in the AMNH includes, besides the tusks and cheek teeth, some incisor-like teeth (without collection numbers). These teeth have strong roots; the crowns are leaf shaped and have enamel only on their labial side. Shockey and Anaya (2004) mention the existence of a small incisor in *P. macfaddenii*, which may be homologous to the above mentioned teeth.

Gryphodon is known only from a mandibular fragment bearing dm4, m1, and un-erupted p3–4. These teeth differ from those of *B. jaureguii* by the inclination of the wear facets of the lophs. An initial oblique wear facet of 60° (relative to the horizontal plane) can be seen in dm4 and m1 of *Gryphodon*, while in *B. jaureguii* it is 25° in P4. In *Proticia* and *Colombitherium*, the earliest genera of the Pyrotheria, the molariform teeth are incipiently bilophodont and have horizontal wear facets (Hoffstetter, 1970; Patterson, 1977). *Carolozzitelia* Ameghino, 1901, from the Casamayoran SALMA of Chubut (Argentina), has remarkable differences with *B. jaureguii* and other pyrotheres. The partial maxilla of *Carolozzitelia* (holotype, MACN 10666) has M2–3 with curved and oblique lophs, and a palate with stepwise widening, at least in its posterior portion.

In *Pyrotherium* spp. and *B. jaureguii*, there is a noteworthy tendency toward an increase in size of the occlusal surfaces of the molariform teeth in proportion to the palatal surface of the maxilla, resulting in a large molariform area that circumscribes a narrow palate (Fig. 4A–C). In *B. jaureguii* the ratio of the combined occlusal surfaces of the molariform teeth to the palatal surface of the maxilla is about 70, whereas in *P. macfaddenii* and *P. romeroi* it is 80 and 85, respectively. In *P. romeroi*, the most derived species of *Pyrotherium*, the left and right maxillary series almost contact each other, particularly at the level of P4 (Fig. 4C). This unusual development may be related to the increase in body size and the necessity of better masticatory efficiency due to changing climatic conditions of the Eocene-Oligocene transition and earliest Oligocene 'climatic deterioration' (Wolfe, 1971; Prothero and Berggren, 1992; Prothero, 1994). Flynn and Swisher (1995) and Flynn et al. (2003) note that the Tinguiririca Fauna (early Oligocene) is the first Cenozoic mammal assemblage dominated by hypsodont mammals, suggesting that more open habitats (like savanna grasslands) occurred in South America earlier than in other continents. Considering the brachyodont condition in Pyrotheria, it is possible that the increase of the occlusal surface of the molariform teeth may have been in response to the appearance of more open environments in that epoch.

The morphology of the femur of *Baguatherium jaureguii* (MUSM 488) indicates that pyrotheres were clearly graviportal. The remarkably similar morphology of the proboscidean and pyrothere femur (i.e., long, flat, and compressed anteroposteriorly, a head that faces nearly upward and is clearly higher than the greater trochanter, both condyles subequal in size) and some other hind limb elements (e.g., Gaudry, 1909; Shockey and Anaya, 2004) imply that the general mechanics of support and movement in both groups are comparable.

Phylogenetic Affinities

A parsimony analysis was performed with PAUP 3.1.1. (Swofford, 1993) in order to determine the affinities of *Baguatherium jaureguii* within the Pyrotheria. The matrix included nine taxa (eight pyrothere species and a hypothetical outgroup, coded 0 for every character) and 17 dental, maxillary, and mandibular characters (Appendices 1 and 2). A hypothetical outgroup was used in this analysis because the ordinal relationships of Pyrotheria are unclear, and many of the characters used in this analysis would have been difficult or impossible to code in any non-pyrothere outgroup. Selected characters were ordered (indicated in Appendix 1) on the basis of developmental and metric criteria (following Croft et al., 2003). The analysis resulted in three most-parsimonious trees, each with a length of 26 steps. The strict consensus of these trees is presented in Figure 6.

The exhaustive search indicates that within Pyrotheria, the clade Pyrotheriidae (sensu Patterson, 1977) is well supported on the basis of three derived characters including character 1(2), fully bilophodont cheek teeth, character 7(1 and 2), lophs anteriorly and lophids posteriorly inclined, and character 17(1), 'paraconid' absent. This clade includes all taxa more closely related to *Pyrotherium* than to *Colombitherium* or *Proticia*. Although *Carolozittelia* presents conspicuous autapomorphies [2(1), stepwise palate; 8(2), oblique lophs/lophids] we retain it in the Pyrotheriidae following Patterson (1977). The analysis failed in supporting Colombitheriidae (*Proticia* + *Colombitherium*), suggesting that Colombitheriidae is paraphyletic.

Baguatherium forms a polytomy with *Gryphodon* and *Pyrotherium*. These taxa share 11(1), lophs and lophids with height greater than length, and 16(1), 'cristid obliqua' absent. The lack of resolution of this node likely results from our inability to code *Gryphodon* for many characters shared by *Baguatherium* and *Pyrotherium*. The clade *Pyrotherium* is well supported by advanced features of their dentition, 7(2), lophs and lophids greatly inclined, and 9(1), relatively thicker enamel on the anterior faces of lophs and on the posterior faces of lophids.

Molariform Tooth Wear Facets in Pyrotheria and the Identity of the Holotype of *Colombitherium*

Hoffstetter (1970), Patterson (1977) and others have divided Pyrotheria into two families based exclusively on the morphology of molariform teeth. "Colombitheriidae" (considered paraphyletic in this study) includes the earliest genera of the order (bunolophodont with horizontal wear facets): early? Eocene *Proticia* (represented by a partial mandible that preserves p3 and

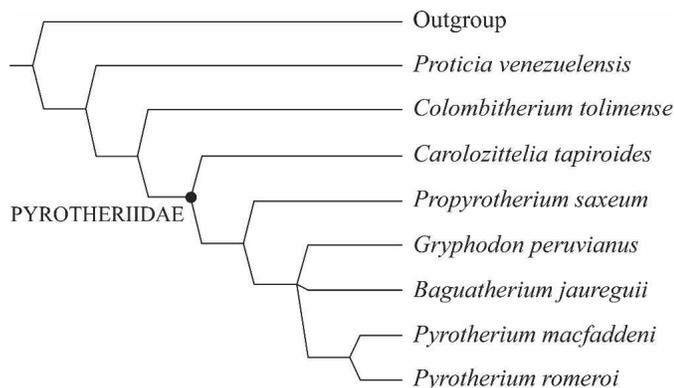


FIGURE 6. Strict consensus cladogram showing phylogenetic relationships of Pyrotheria, including *Baguatherium jaureguii* (26 steps; CI: 0.88; RI: 0.90). The outgroup is a hypothetical taxon coded 0 for every character. Selected characters were ordered as indicated in Appendix 1.

p4) and *Colombitherium* (founded on a partial maxilla, but see below). Pyrotheriidae (*Carolozittelia* + *Propyrotherium* + *Gryphodon* + *Baguatherium* + *Pyrotherium*), ranging from middle Eocene to late Oligocene, are characterized by a derived masticatory anatomy (lophodont with oblique wear facets). The characteristics of the molariform teeth and wear facets of Pyrotheria have been noted by several authors (i.e., Gaudry, 1909; Hoffstetter, 1970; Patterson, 1977). Among bunolophodont and lophodont pyrotheres, two well-defined wear patterns can be distinguished. In this study, these patterns have been revised and analyzed in order to interpret the possible masticatory mechanism of pyrotheres.

In *Colombitherium* and *Proticia*, wear facets are horizontal but do not generate flat surfaces because the dentine is depressed (i.e., excavated) compared to the enamel; the wear facets originate at the apex of the lophs and in the middle of some transverse valleys and cingulae (Fig. 5E). The lophs are vertical and moderately high. This suggests a predominantly grinding masticatory mechanism with dorsoventral, and possibly lateromedial, movements (Fig. 7A). On the other hand, species of *Pyrotherium*, *Baguatherium*, and *Gryphodon* developed oblique wear facets with variable degrees of inclination, which are virtually flat (dentine and enamel on the same plane). The lophs are inclined and high, resulting in a cutting edge (Hoffstetter, 1970) caused by a greater anteroposterior component to dorsoventral movement between the maxillary and mandibular tooth series (Fig. 7B). The wear facets of the lophids of *P. macfaddeni* (partial jaw, MNHN SAL 21) that present parasagittal abrasion marks corroborate this interpretation. *Propyrotherium* possesses combined characters (lophs/lophids inclined and moderately high) of both models (Fig. 5D).

In both masticatory models the cingulae would have served different functions. In *Proticia* there are no well-developed cingulae, but the 'paraconid' and the 'posterior central cusp' of p4 (Patterson, 1977) would have acted as cingulae (Fig. 8C). In *Colombitherium*, the anterior cingulae of P3-M1 are broad ('banquette shaped' of Hoffstetter, 1970) and present circular wear in the middle (only P4 and M1), where there should have been a conule. In *Pyrotherium* and *Baguatherium* the cingulae are crested and crenulated. Maxillary teeth have massive anterior cingulae, whereas mandibular teeth have massive posterior cingulae. Even though the teeth exhibit strong wear on the lophs, the cingulae show little abrasion. In *Proticia* and *Colombitherium* the 'cingulum' may have dorsoventrally contacted an opposing cusp producing the described pattern. In *Pyrotherium*, *Baguatherium*, and *Gryphodon* the cingulum of a maxillary tooth contacted the mesial surface of the corresponding anterior lophid. In mandibular teeth the cingulum contacted the distal surface of the posterior loph. In mandibular and maxillary teeth the wear plane of each cingulum forms a $\sim 90^\circ$ angle with the plane

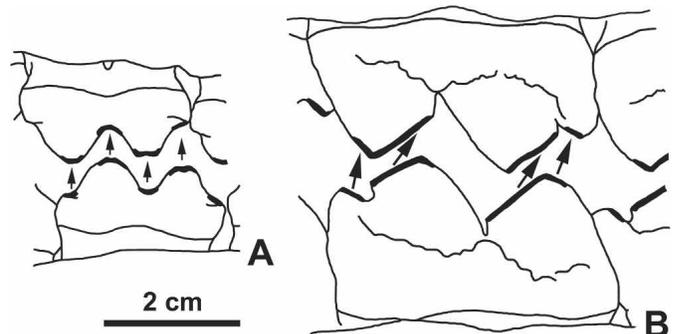


FIGURE 7. Diagram of upper and lower molariform tooth occlusion in **A**, non-pyrotheriid and **B**, pyrotheriid species. Wear surfaces are darkened and arrows show direction and correspondence of parts in occlusion.

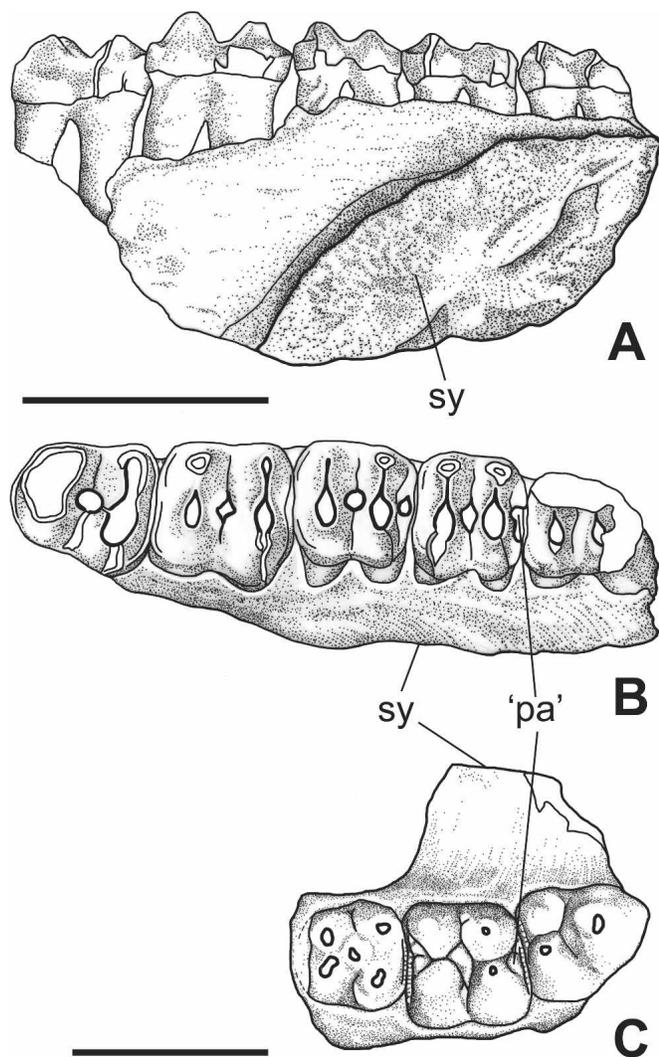


FIGURE 8. **A, B**, *Colombitherium tolimense*, partial left jaw with p3–m3 (new interpretation; holotype, MNHN GUA 2906). **A**, medial view; **B**, occlusal view. **C**, *Proticia venezuelensis*, partial right jaw with p3–m1 (holotype, MCNC-VF 237, from Patterson, 1977) in occlusal view. **Abbreviations:** pa, 'paraconid'; sy, symphysis. Scale bar equals 5 cm.

produced by the lophes. The greater anteroposterior component to dorsoventral mastication produced a cutting, inclined plane in the lophes and was controlled by the cingulae that served as stops and buttresses (Fig. 7B).

In modern mammals having bilophodont molars, vertical crests, and near horizontal occlusal surfaces (e.g., *Tapirus terrestris*), the anterior and posterior cingulae have nearly the same dimensions. The masticatory mechanism of *T. terrestris*, with lateromedial and typical dorsoventral movements (pers. obs.), corresponds to Turnbull's (1970) 'grinding' type. Functionally, the cingulae in *Proticia* and *Colombitherium* would have had a similar function to those of *T. terrestris*.

In the case of *Colombitherium*, this analysis and other characters support the interpretation that the holotype (MNHN GUA 2906), originally described as a maxilla, could instead be a mandible (Fig. 8A–B). Hoffstetter (1970) noted that, superficially, the holotype could be a left hemi-mandible. Nonetheless, he identified it as a right maxilla, because the anterior cingulum is more developed than the posterior one in P4 and M1, the external cusps are higher and develop occlusal wear later in life

than the internal ones, intermediate molariform teeth are square in outline, and the posterior cingulum of the last molariform tooth is extremely reduced.

We do not consider the anterior cingulae on the maxillary teeth to be inherent to the masticatory type proposed for *Colombitherium*. In *Proticia* the anterior and posterior structures (p4 and m1) that act as cingulae have similar dimensions, whereas in the mandible of *T. terrestris*, some anterior cingulae are broader than the posterior ones. The anterior cingulae of p3–m1 of *Colombitherium* (Fig. 8B–C) might be homologous to the 'paraconid' recognized in *Proticia* by Patterson (1977). Therefore, the existence of anterior cingulae in the jaw of *Colombitherium* can be considered a retained plesiomorphic condition. Concerning the height of the external and internal cusps, if we consider the plane of the symphysis to be in a vertical position, the heights are equivalent. Additionally, in the mandible of *Proticia* the molariform teeth are square in shape, as in *Colombitherium*.

Colombitherium has a p3–m3 with the posterior extension of the symphysis projecting to the level of m2 (Fig. 8A–B). This character state is present in the mandible of *Pyrotherium*. In *Colombitherium* and *Proticia* the roots of p3 project anteriorly, contrary to what is seen in the maxilla of *B. jaureguii*, and species of *Pyrotherium*, where roots of P2 and P3 project posteriorly. Likewise, p3 of *Colombitherium* has two minor posterior roots and a larger anterior one, whereas P3 of *B. jaureguii* has two minor anterior roots and a larger posterior one. As would be expected for a mandible, the *Colombitherium* specimen shows no lateral expansion that could be interpreted as part of the zygomatic arch.

CONCLUSIONS

Our comparative analysis indicates that *Baguatherium jaureguii* clearly has the incipient states of cranial characters observed in species of *Pyrotherium*. *Baguatherium jaureguii* is of smaller size and bears a wider maxilla and palate than *P. romeroi*. It also has a P2 with an anterior conule, and molariform teeth with a lingual crest that connects the anterior and posterior lophes. The present study reveals that Oligocene pyrotheres are characterized by: (1) maxillary tooth series that tend to converge anteriorly; (2) a wide molariform area enclosing a narrow palate; (3) high and inclined lophes/lophids; (4) oblique and almost flat wear facets; (5) a narrow pre dental region of the maxilla; (6) a maxillary dental formula of P2–M3; (7) retracted nares; and (8) the root of the zygomatic arch located at the level of P4 and M1.

The identity of the sister taxon to *Baguatherium jaureguii* is uncertain, due to the fragmentary fossil record within Pyrotheria. However, phylogenetic analysis shows that *Baguatherium* forms a polytomy with *Gryphodon* and *Pyrotherium*. The results support the monophyletic taxon Pyrotheriidae (*Carolozittelia* + *Propyrotherium* + *Gryphodon* + *Baguatherium* + *Pyrotherium*) based on the following characters and states: 1(2), fully bilophodont cheek teeth; 7(1 and 2), lophes anteriorly and lophids posteriorly inclined; and, 17(1), 'paraconid' absent. On the other hand, *Colombitheriidae* is revealed as a paraphyletic taxon.

In *Proticia* and *Colombitherium* the wear facets of the molariform teeth indicate a mainly grinding masticatory mechanism, with dorsoventral and possibly lateromedial movements. In the other members of the order, the wear facets generate a cutting surface that suggests a major anteroposterior component to dorsoventral masticatory movements. This specialization and the increase in the molariform surface might correlate with the development of new climatic conditions during the Eocene and Oligocene.

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APPENDIX 1. List of characters and characters states used in the analysis of the relationships among pyrotheres. Characters were polarized with respect to a hypothetical taxon. Selected characters were ordered and are denoted by an asterisk (*).

- (1) *Occlusal structure of upper and lower cheek teeth: bunodont (0); buno-bilophodont (1); bilophodont (2).
- (2) Orientation of loph/lophids: 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: elongate, longer than wide (0); square, length and width approximately equal (1).
- (6) *Wear facets in loph/lophids: horizontal and excavated (0); oblique and excavated (1); oblique and flat (2).
- (7) *Vertical orientation of loph/lophids: 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).
- (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 cingulae 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 'crisid obliqua': present (0); absent (1).
 (17) 'Paraconid': present (0); absent (1).

APPENDIX 2. Character matrix from eight pyrothere species (plus the hypothetical outgroup) and 17 characters (Appendix 1) used in the phylogenetic analysis (Fig. 6).

	1																1
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Proticia venezuelensis</i>	1	0	?	1	1	0	0	?	0	1	0	0	0	0	?	0	0
<i>Colombitherium tolimense</i>	1	0	?	?	1	0	0	?	0	2	0	0	0	0	?	0	0
<i>Carolozittelia tapiroides</i>	2	1	0	?	0	0	1	2	0	?	0	0	0	1	0	0	1
<i>Propyrotherium saxaeum</i>	2	0	?	1	1	1	1	?	0	?	0	1	0	2	0	0	1
<i>Gryphodon peruvianus</i>	2	0	?	?	0	?	1	?	0	?	1	1	0	2	?	1	0
<i>Baguatherium jaureguii</i>	2	0	1	1	?	2	1	1	0	?	1	1	?	2	1	1	?
<i>Pyrotherium macfaddenii</i>	2	0	1	1	1	2	2	1	1	2	1	1	1	2	0	1	1
<i>Pyrotherium romeroi</i>	2	0	1	1	1	2	2	1	1	2	1	1	1	2	0	1	1