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PYROTHERE SYSTEMATICS AND A CARIBBEAN ROUTE FOR LAND-MAMMAL DISPERSAL DURING THE PALEOCENE

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> "The pyrotheres are an unexplained mystery, so far as their origin and relationships are concerned".
>
> -W.B. Scott (1937: 544)

ABSTRACT

The pyrotheres are an extinct order of Paleocene-Oligocene South American mammals and encompass six valid genera: *Carodnia* Simpson, 1935; *Carolozittelia* Ameghino, 1901; *Proticia* Patterson, 1977; *Colombitherium* Hoffstetter, 1970; *Propyrotherium* Ameghino, 1901; and *Pyrotherium* Ameghino, 1889. Pyrotheria is a monophyletic order of mammals united with the Dinocerata in the monophyletic Mirorder Uintatheriamorpha. Thus, the pyrotheres are not members of the Ungulata, and their inclusion in the group as members of the Mirorder Meridiungulata should be discontinued. A phylogenetic relationship between pyrotheres and dinoceratans implies dispersal of the common ancestor of North American dinoceratans and South American pyrotheres during the Paleocene, prior to the Riochican. Paleocene volcanism in the Caribbean provided an archipelago for the dispersal of the common ancestor of dinoceratans and pyrotheres.

RESUMEN

Los pyroterios son un orden extinto de mamíferos Paleoceno-Oligoceno de América del Sur e incluye seis géneros válidos: *Carodnia* Simpson, 1935; *Carolozittelia* Ameghino, 1901; *Proticia* Patterson, 1977; *Colombitherium* Hoffstetter, 1970; *Propyrotherium* Ameghino, 1901; y *Pyrotherium* Ameghino, 1889. Pyrotheria es un orden de mamíferos monofilético unidos con el Dinocerata en el Mirorden monofilético Uintatheriamorpha. Por lo tanto, los pyroterios no son miembros de la Ungulata y su inclusión en el grupo de los miembros del Mirorden Meridiumgulata debería ser descontinuado. Existe un parentesco filogenético entre los pyroterios y los dinoceratos lo que implica la dispersión del ancestro común de los dinoceratos Norte Americanos y los pyroterios Sur Americanos durante el Paleoceno, anterior al Riochiquense. El volcanismo Paleoceno en el Caribe conformó un archipiélago para la dispersión del ancestro común de los dinoceratos y los pyroterios.

1. INTRODUCTION

The late George Gaylord Simpson referred to the evolutionary history of South America's land mammals as one of "splendid isolation" (Simpson, 1980). By this, Simpson meant that throughout most of the Cenozoic, South America's land mammals, and specially its diverse and unique "ungulates," evolved in almost total isolation from those of North America and the remaining continents. Simpson certainly recognized that primates and caviomorph rodents arrived in South America from elsewhere during the Oligocene and that notoungulates did exist in both North and South America near the end of the Paleocene. However, throughout his life, he remained steadfast in his conviction that South America's "ungulates" arose from Cretaceous "condylarths," an ancestry shared with North America, but by the beginning of the Paleocene were separated from their northern relatives and thereafter underwent an evolutionary diversification in isolation.

Perhaps the strangest and least understood of South America's unique fossil "ungulates" are the pyrotheres. First, and still best, known from the archetypal pyrothere, *Pyrotherium* Ameghino, 1889, the phylogenetic relationships of the pyrotheres have been debated for nearly a century. Referred to by Gaudry (1909: 3) as "parmi tant de curieuses créatures, tirées des couches tertiaires de la Patagonie," and epitomized by Scott (1937: 544) as the "strangest of known mammals," *Pyrotherium* has been considered everything from Eutheria *incertae sedis* to a close relative of any mammalian order whose representatives include taxa with bilophodont cheek-teeh and/or "amblypod" feet, including the Marsupialia, Dinocerata, Pantodonta, Embrithopoda, Proboscidea and Sirenia. Clearly, a close look at the phylogenetic relationships of the pyrotheres is long overdue. Since some have suggested that pyrotheres may be closely related to a mammalian order not present in South America during the Paleogene, the phylogenetic relationships of the Pyrotheria have important bearing on the question of the geographic and faunistic isolation of South America during the early Cenozoic.

This paper has three objectives: 1) to review the genus-level taxonomy of the pyrotheres; 2) to elaborate an already presented phylogenetic hypothesis of dinoceratan-pyrothere relationships (Lucas & Schoch, 1982; Tong & Lucas, 1982; Schoch & Lucas, 1985); and 3) to discuss the paleobiogeographical implications of this phylogenetic hypothesis. In this paper, AMNH refers to the American Museum of Natural History, New York; L refers to the maximum length of a tooth crown; and W refers to the maximum width of a tooh crown. The mammalian biochronology of the Cenozoic of South America follows Marshall et al. (1983).

2. TAXONOMY

2.1 Class MAMMALIA Linnaeus, 1758
Mirorder UINTATHERIAMORPHA Schoch & Lucas, 1985
1985 Uintatheriamorpha Schoch & Lucas, p. 33.

INCLUDED ORDERS: Dinocerata Marsh, 1873 (*sensu* Schoch & Lucas, 1985) and Pyrotheria Ameghino, 1895 (*sensu* this article).

DISTRIBUTION: Late Paleocene (Tiffanian) - middle Eocene (Uintan) of the western United States; late Paleocene - middle Eocene of Asia (People's Republic of China, Mongolian People's Republic and USSR); late Paleocene (Riochican) to late Oligocene (Deseadan) of South America (Argentina, Brazil, Bolivia, Peru, Colombia and Venezuela

DIAGNOSIS: See Schoch & Lucas (1985: 34).

DISCUSSION: Schoch & Lucas (1985) introduced the term Uintatheriamorpha to designate a monophyletic taxon of eutherian mammals that includes the orders Dinocerata and Xenungulata. This concept is modified here to embrace the Dinocerata and Pyrotheria. As indicated below, the Pyrotheria are a monophyletic taxon that includes the Xenungulata as a taxon of subordinal rank.

2.2 Order PYROTHERIA Ameghino, 1895

1895 Pyrotheria Ameghino, p. 608.

INCLUDED GENERA: *Carodnia* Simpson, 1935; *Carolozittelia* Ameghino, 1901; *Proticia* Patterson, 1977; *Colombitherium* Hoffstetter, 1970; *Propyrotherium* Ameghino, 1901; and *Pyrotherium* Ameghino, 1889 (for generic synonymies see below).

DISTRIBUTION: Late Paleocene (Riochican) to late Oligocene (Deseadan) of South America (Argentina, Brazil, Bolivia, Peru, Colombia and Venezuela)(Fig. 1).

REVISED DIAGNOSIS[1]: Uintatheriamorphs with bilophodont M^{1-2}_{1-2} and large postcingulids on M_{1-2}.

DISCUSSION: The concept of the Pyrotheria used here stems from a phylogenetic hypothesis (Fig. 5) that indicates monophyly of the xenungulate *Carodnia* and the "traditional" pyrotheres *Carolozittelia*, *Proticia*, *Colombitherium*, *Propyrotherium* and *Pyrotherium* (see later discussion). A phylogenetic classification of the Pyrotheria based on this phylogenetic hypothesis is presented in Table 1.

2.3 Suborder XENUNGULATA Paula Couto, 1952

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[1] The diagnoses of taxa presented in this article do not follow the traditional phenetic approach of listing a variety of morphological features which, in sum, describe the taxon. Instead, only features that are derived character-states of the taxon within the context of a phylogenetic hypothesis (Fig. 5) are listed here. More traditional diagnoses of most of the taxa diagnosed here are available in Simpson (1935, 1967) Scott (1937), Paula Couto (1952), Hoffstetter (1970) and Patterson (1977).

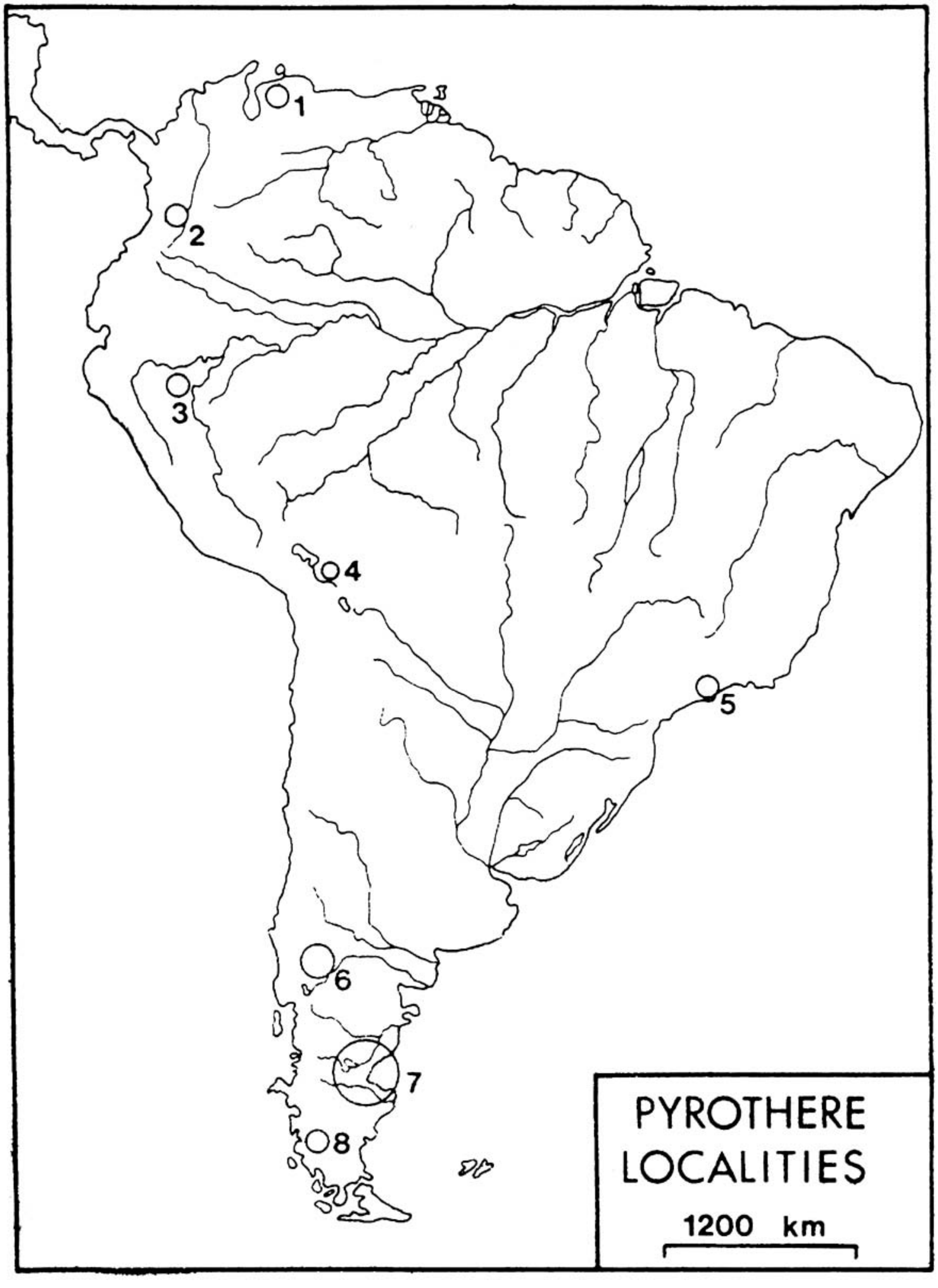

Figure 1: Map of South America showing pyrothere localities. 1. Lara, Venezuela (*Proticia*) 2. Gualanday, Colombia (*Colombitherium*) 3. Chiococa, Peru (*Propyrotherium*) 4. Salla, Bolivia (*Pyrotherium*) 5. Itaborai, Brazil (*Carodnia*) 6. Rio Neuquen, Argentina (*Pyrotherium*) 7. Lago Colhué-Huapi and other localities, Argentina (*Carodnia*, *Carolozittelia*, *Propyratherium*, *Pyrotherium*) 7. Lago Argentino (*Pyrotherium ?*).

TABLE 1. A classification of the Pyrotheria

Order PYROTHERIA Ameghino, 1895
- Suborder XENUNGULATA Paula Couto, 1952,
    - Genus *CARODNIA* Simpson, 1935
- Suborder EUPYROTHERIA, new
    - Family CAROLOZITTELIDAE Ameghino, 1901
        - Genus *CAROLOZITTELIA* Ameghino, 1901
    - Family PYROTHERIIDAE Ameghino, 1889
        - Subfamily COLOMBITHERIINAE Hoffstetter, 1970
            - Genus *COLOMBITHERIUM* Hoffstetter, 1970
            - Genus *PROTICIA* Patterson, 1977
        - Subfamily PYROTHERIINAE Ameghino, 1889
            - Genus *PROPYROTHERIUM* Ameghino, 1901
            - Genus *PYROTHERIUM* Ameghino, 1889

1952 Xenungulata Paula Couto, p. 370

INCLUDED GENUS: *Carodnia* Simpson, 1935.

DISTRIBUTION: Late Paleocene (Riochican) of Argentina and Brazil (Fig. 1).

REVISED DIAGNOSIS: Small pyrotheres (L M_1 = 22-25 mm) that lack the derived features of the Eupyrotheria (i.e., in *Carodnia* P^1_1 are present, P^2_2 are relatively large, P^{3-4}_{3-4} are relatively nonmolariform, M^3 is not bilophodont and M_3 lacks a hypoconid-entoconid cristid).

DISCUSSION: Paula Couto (1952: 386-387) presented an argument rooted in the concept of "morphological distance" as a key to phylogenetic relationships in order to justify naming a new order of mammals, the Xenungulata, for the single genus *Carodnia*. In particular, Paula Couto noted the differences between the premolars and third molars of *Carodnia* and *Pyrotherium*, as well as some dissimilarities in the postcrania of these two taxa, to justify exclusion of *Carodnia* from the Pyrotheria. Although most subsequent workers have maintained the Xenungulata (e.g., Simpson, 1945, 1967; Lavocat, 1958a, b; McKenna, 1980), at most hinting at pyrothere relatedness for *Carodnia* via *Carolozittelia*, the phylogenetic hypothesis presented here (also see Schoch & Lucas, 1985) indicates otherwise. This hypothesis (Fig. 5) identifies *Carodnia* as the sister taxon of a clade that includes *Carolozittelia*, *Proticia*, *Colombitherium*, *Propyrotherium* and *Pyrotherium*, the Pyrotheria of conventional usage In light of this, I question retaining the Xenungulata as an order of mammals coordinate with the Pyrotheria, and prefer instead to reduce the term Xenungulata to subordinal rank coordinate with a new suborder, the Eupyrotheria, that encompasses the other pyrotheres.

2.4 Genus *CARODNIA* Simpson, 1935

1935 *Carodnia* Simpson, p. 20, fig. 21.

1935 *Ctalecarodnia* Simpson, p. 22, fig. 22.

TYPE SPECIES: *Carodnia feruglioi* Simpson, 1935.

INCLUDE SPECIES: The type species, *C. cabrerai* (Simpson, 1935) and *C. vieirai* Paula Couto, 1952.

DISTRIBUTION: Same as for Xenungulata.

REVISED DIAGNOSIS: Same as for Xenungulata.

DISCUSSION: Simpson (1935) originally based *Carodnia* (=*Ctalecarodnia* Simpson, 1935; Paula Couto, 1952: 370; Simpson, 1967: 241) on isolated lower molars from the Rio Chico Formation in Chubut, Argentina. Paula Couto (1952) described and illustrated material of *C. vieirai* from Sao Jose de Itaborai, Brazil that represents most of the dentition and skeleton of this genus. Simpson (1967) described and illustrated additional isolated cheek teeth of *Carodnia* from Argentina. Tong & Lucas (1982) illustrated a left M^3, and Cifelli (1983a) described and illustrated an astragalus and calcaneum of *C. vieirai* from Brazil. The three nominal species of *Carodnia* are distinguished by minor meristic and metric differences in their cheek teeth that probably will be eliminated when a larger sample of fossils becomes available.

2.5 Suborder EUPYROTHERIA new

INCLUDED GENERA: *Carolozittelia* Ameghino, 1901; *Proticia* Patterson, 1977; *Colombitherium* Hoffstetter, 1970; *Propyrotherium* Ameghino, 1901; and *Pyrotherium* Ameghino, 1889.

DISTRIBUTION: Early Eocene (Casamayoran) to late Oligocene (Deseadan) of Argentina, Bolivia, Peru, Colombia and Venezuela (Fig. 1).

REVISED DIAGNOSIS: Pyrotheres with P_1^1 absent, P_2^2 relatively small, M^3 bilophodont and M_3 with hypoconid-entoconid cristid.

DISCUSSION: Unity of the Eupyrotheria (Pyrotheria of more traditional usage) as a monophyletic taxon is justified by the diagnostic shared-derived character states that distinguish the taxa enjoined here from *Carodnia*.

2.6 Family CAROLOZITTELIDAE Ameghino, 1901

1901 Carolozittelidae Ameghino, p. 387

INCLUDED GENUS: *Carolozittelia* Ameghino, 1901.

DISTRIBUTION: Early Eocene (Casamayoran) of Argentina.

REVISED DIAGNOSIS: Small eupyrotheres (length M_1 estimated to be about 22 mm) that lack the derived features of the Pyrotheriidae (i.e., in *Carolozittelia* a hypoconulid lobe is present on M_3, and the incisors are not enlarged, deeply rooted and tusk-like [P_4^4 of *Carolozittelia* are unknown, but I predict they are not bilophodont]).

DISCUSSION: Ameghino's (1901) therm Carolozittelidae is adopte here to identify a mono-generic family of eupyrotheres coordinate with the Pyrotheriidae.

2.7 *CAROLOZITTELIA* Ameghino, 1901

1901 *Carolozittelia* Ameghino, p. 388.

TYPE AND ONLY KNOWN SPECIES: *C. tapiroides* Ameghino, 1901. (Simpson [1967: 239] presented a cogent argument for considering Ameghino's

(1901: 388) *C. eluta* a *nomen vanum*.).

DISTRIBUTION: Same as for Carolozittelidae.

REVISED DIAGNOSIS: Same as for Carolozittelidae.

DISCUSSION: *Carolozittelia* is known only from its M^{2-3}_{2-3} and adhering dentary and maxillary bone. Ameghino (1902) and Simpson (1967) described and illustrated the available specimens. Cifelli (1983a: 24) suggested that an astragalus that is part of the holotype of *Albertogaudrya unica* but arguably does not belong to that taxon (Simpson, 1967: 231), may pertain to *Carolozittelia*. Cifelli (1983a: 24) stated that this astragalus "seems to have lacked the cuboid facet," even though, as he noted, the portion of the astragalar head critical to such a conclusion is missing.

2.8 Family **PYROTHERIIDAE** Ameghino, 1889

1889 Pyrotheriidae Ameghino, p. 894

INCLUDED GENERA: *Proticia* Patterson, 1977; *Colombitherium* Hoffstetter, 1970; *Propyrotherium* Ameghino, 1901; and *Pyrotherium* Ameghino, 1889.

DISTRIBUTION: Early Eocene? (Casamayoran) to late Oligocene (Deseadan) of Argentina, Bolivia, Peru, Colombia and Venezuela (Fig 1).

REVISED DIAGNOSIS: Eupyrotheres with bilophodont P^4_4, bilophodont M_3 (hypoconulid lobe absent) and large, deeply-rooted, tusk-like incisors.

DISCUSSION: Pyrotheriids are distinguished from *Carolozittelia* by the diagnostic, shared-derived characters listed above. The Pyrotheriidae is divided into two, divergent subfamilies, Colombitheriinae and Pyrotheriinae (Table 1).

2.9 Subfamily COLOMBITHERIINAE Hoffstetter, 1970

1970 Colombitheriidae Hoffstetter, p. 9.

INCLUDED GENERA: *Colombitherium* Hoffstetter, 1970 and *Proticia* **Patterson, 1977.**

DISTRIBUTION: Early-middle? Eocene of northern South America (Colombia and Venezuela) (Fig. 1).

REVISED DIAGNOSIS: Small pyrotheriids (L M_1 about 26 mm) with bulbous cheek-tooth cusps/cuspids and additional cusps/cuspids in the valleys between the cheek-tooth lophs/lophids.

DISCUSSION: The idea that the colombotheriines are not pyrotheres or are the most primitive pyrotheres (McKenna, 1980; Cifelli, 1985) is rejected here for reasons discussed below.

2.10 *COLOMBITHERIUM* Hoffstetter, 1970

1970 *Colombitherium* Hoffstetter, p. 9, figs. 4-7; pl. 1.

1985 *Columbitherium* [*lapsus calami*]: Schoch & Lucas, p. 35.

TYPE AND ONLY KNOWN SPECIES: *C. tolimense* Hoffstetter, 1970.

DISTRIBUTION: Gualanday Formation, Colombia, probably middle Eocene (Hoffstetter, 1970; Anderson, 1972; Patterson, 1977).

REVISED DIAGNOSIS: *Colombitherium* is distinguished from *Proticia* by its less bulbous cheek-tooth cusps and retention of cheek-tooth lophs/lophids.

DISCUSSION: *Colombitherium* is known only from the holotype of *C. tolimense*, a right maxillary fragment with P^3-M^3 (Fig. 2C). Hoffstetter (1970) argued that *Colombitherium* lacks a P^2, primarly because the P^3 is expanded anteriorly. However, since P^3 of *C. tolimense* is broken anteriorly (Hoffstetter, 1970: fig. 6C), it is impossible to determine if an intertitial wear facet is present (Patterson, 1977: 408).

2.11 *PROTICIA* Patterson, 1977

1977 *Proticia* Patterson, p. 403, figs. 3-5.

TYPE AND ONLY KNOWN SPECIES: *P. venezuelensis* Patterson, 1977.

DISTRIBUTION: Upper part of Trujillo Formation, Lara, Venezuela, probably early Eocene (Patterson, 1977).

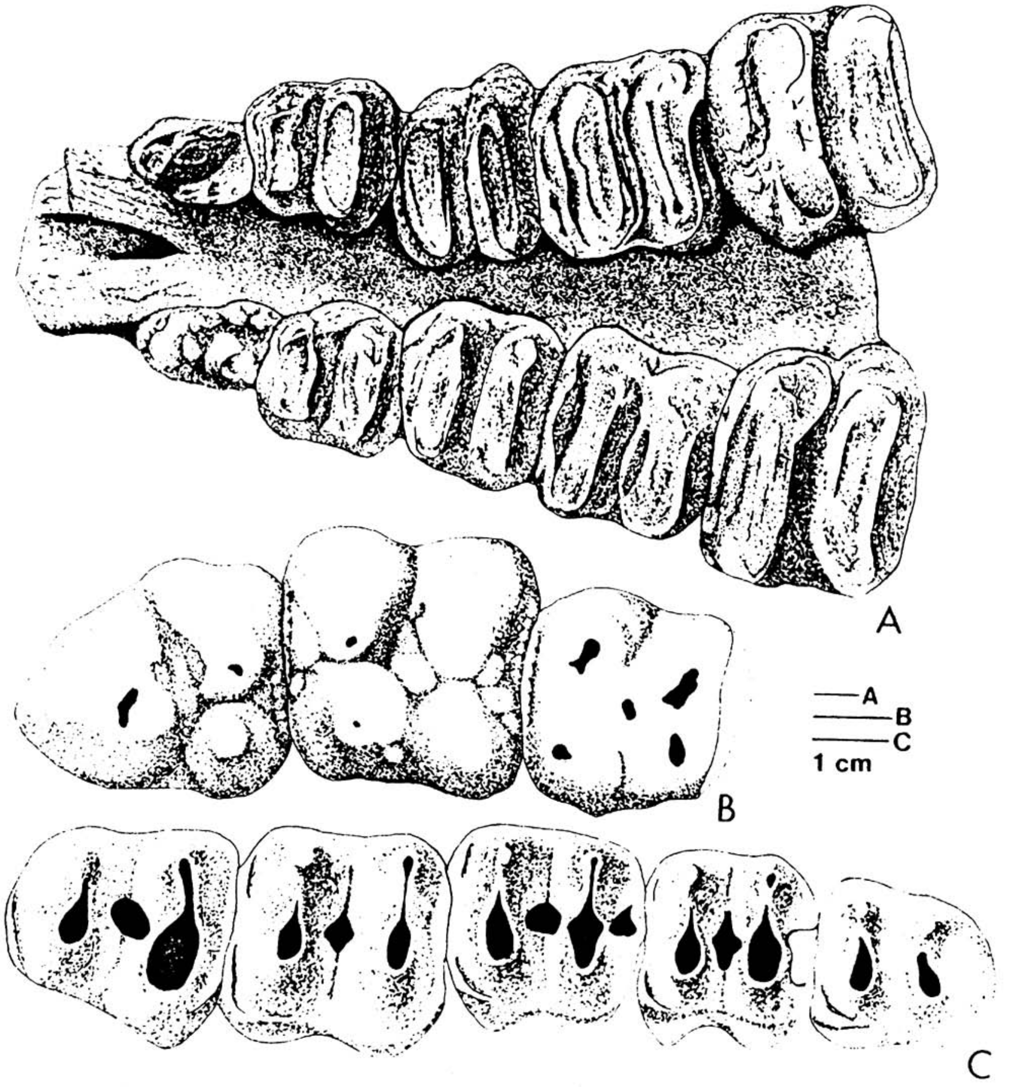

Figure 2. Cheek teeth of some pyrothères. A. *Pyrotherium romeri*, maxilla with left and right P^2-M^2, occlusal view (after Gaudry, 1909, pl. 2, fig. 1a). B. *Proticia venezuelensis*, right P_3-M_1, occlusal view (after Patterson, 1977, fig. 3). C: *Colombitherium tolimense*, restored right $P3$-M^3, occlusal view (after Hoffstetter, 1970, fig. 5).

REVISED DIAGNOSIS: *Proticia* is distinguished from *Colombitherium* by its more bulbous cheek-tooth cusps/cuspids and loss of cheek-tooth lophs/lophids.

DISCUSSION: *Proticia* is known only from a right dentary fragment bearing P_3-M_1 (Fig. 2B). It is about the same size as *Colombitherium*, but there is no question that *Proticia* does not represent the lower dentition of the same taxon whose upper dentition is represented by *Colombitherium* (see diagnoses of these taxa above and compare Fig. 2B with Fig. 2C).

2.12 PYROTHERIINAE Ameghino, 1889

1889 Pyrotheriidae Ameghino, p. 894.

INCLUDED GENERA: *Propyrotherium* Ameghino, 1901 and *Pyrotherium* Ameghino, 1889.

DISTRIBUTION: Middle Eocene (Mustersan) - late Oligocene (Deseadan) of Argentina, Bolivia and Peru (Fig. 1).

REVISED DIAGNOSIS: Pyrotheriids with: bilophodont premolars except P_2^2 and upper molar lophs canted forward and lower molar lophids canted bacwards so that loph-lophid wear is abapical.

DISCUSSION: *Propyrotherium* (includes *Griphodon*) and *Pyrotherium* are the most derived pyrotheres (see later discussion).

2.13 *PROPYROTHERIUM* Ameghino, 1901

1901 *Propyrotherium* Ameghino, p. 387.
1906 *Promoeritherium* Ameghino, p. 333.
1924 *Griphodon* Anthony, p. 1. fig. 1.

TYPE AND ONLY KNOWN SPECIES: *P. saxeum* Ameghino, 1901 (= *Promoeritherium australe* Ameghino, 1906; =*G. peruvianus* Anthony, 1924).

DISTRIBUTION: Middle Eocene (Mustersan) of Argentina and Peru (Fig.

REVISED DIAGNOSIS: Small pyrotheriines (LM_1 = 28-35 mm) that lack the cheek-tooth crown hypsodonty characteristic of *Pyrotherium*.

DISCUSSION: The few specimens of *Propyrotherium* are confined to cheek teeth, a tusk and part of a mandibular ramus (Ameghino, 1901, 1906; Anthony, 1924; Patterson, 1942; Simpson, 1967). Simpson (1967: 237) considered *Promoeritherium* (type species *P. australe* Ameghino, 1906) to be a *nomen dubium*. The single cheek tooth from Mustersan strata west of Lake Colhue-Huapi, Argentina that is the holotype of *P. australe* (Ameghino, 1906: fig. 160; Simpson 1967: pl. 45, fig. 9) probably is a left P_4. Its size (L = 26.5 mm, W = 19.5 mm: Simpson, 1967: 238) and morphology are close to that of the P_4 of "*Griphodon peruvianus*' (Patterson, 1942: 4, fig. 2), and even if it is not P_4, it arguably is an anterior cheek tooth that should be assigned to *Propyrotherium*.

Schoch & Lucas (1985: 35) suggested that *Griphodon* is a junior subjective synonym of *Propyrotherium*. The key to this synonymy is the conclusion that AMNH 29394 (Simpson, 1967: pl. 45, fig. 8) is a M_1 of *P. saxeum*. Simpson (1967) tentatively identified this tooth as a lower molar, but Patterson (1977: 410) identified it as a P_4. I find Patterson's identification difficult to accept in light of the absence of a paracristid and the presence of a large talonid and large posterior cingulid on AMNH 29394, features that invalidate its identification as a P_4, but instead are characteristic of a M_1 (compare the P_4 and the M_1 of "*G. peruvianus*" in Patterson, 1942: fig. 2). The size of this M_1 (L = 35 mm, W = 29 mm: Simpson, 1967: table 78) is close to that of the holotype of "*G. peruvianus*" (L = 32.2 mm, W = 25.8 mm: Patterson, 1942: 4). Therefore, I consider *Griphodon peruvianus* Anthony, 1924 to be a junior subjective synonym of *Propyrotherium saxeum* Ameghino, 1901.

2.14 *PYROTHERIUM* Ameghino, 1889

1889 *Pyrotherium* Ameghino, p. 618.
1901 *Ricardowenia* Ameghino, p. 390.
1902 *Parapyrotherium* Ameghino, p. 29.

TYPE AND ONLY KNOWN SPECIES: *P. romeri* Ameghino, 1889.

DISTRIBUTION: Oligocene (Deseadan) of Argentina and Bolivia.

REVISED DIAGNOSIS: Large pyrotheriines (LM_1 = 50-65 mm) with crown-hypsodont cheek teeth.

DISCUSSION: *Pyrotherium* is the best known pyrothere. Ameghino (1902), Gaudry (1909), Loomis (1914), Scott (1937) and Patterson (1977) have well described its skull (Fig. 3A), lower jaw (Figs. 3B-C), dentition (Figs. 2A, 3C) and postcrania.

Loomis (1914) recognized two valid species of *Pyrotherium*: *P. romeri* Ameghino, 1889, the type species, and *P. sorondoi* Ameghino, 1894, including, according to Loomis, the other species of *Pyrotherium* named by Ameghino as well as *Parapyrotherium planum* Ameghino, 1902. Patterson (1977), however, considered *P. romeri* to be the only valid species of *Pyrotherium*. This conclusion is followed here (also see MacFadden & Frailey, 1984), as is Patterson's assignment of *Ricardowenia mysteriosa* Ameghino, 1901 to *P. romeri*. However, two caveats need to be pointed out: 1. There is a striking amount of metric variation in the teeth assigned to *P. romeri* (MacFadden & Frailey, 1984: table 1). A thorough analysis of this variation may justify recognition of two, or more, species of *Pyrotherium*. 2. Most of the type specimens of the taxa subsumed here under *P. romeri* are so fragmentary that, strictly speaking, these taxa are best considered *nomina vana*. This is specially true of *Ricardowenia mysteriosa*, based only on a cheek-tooth fragment. As Loomis (1914: 163) aptly put it, "too little is known of this form to base a valid genus or even to associate it with *Pyrotherium*."

3. PHYLOGENETIC RELATIONSHIPS OF THE PYROTHERES

3.1 Previous hypotheses

The literature presents a wide range of ideas on pyrothere relationships that fall into three categories. First, that pyrotheres are not obviously related to any other order of mammals

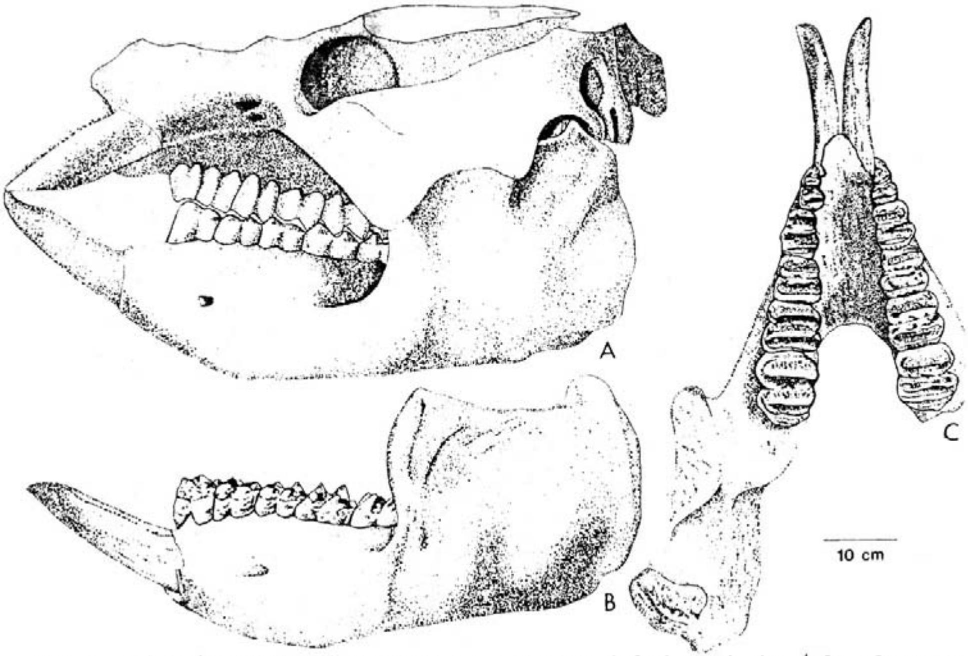

Figure 3: *Pyrotherium romeri*. A: Skull and lower jaw, left lateral view (after Patterson, 1977, fig. 7). B: Lower jaw, left lateral view (after Gaudry, 1909, pl. 3, fig. 1a). C: Occlusal view of lower jaw in B, with left and right I's and P_2-M_3 (after Gaudry, 1909, pl. 3, fig. 1).

(e.g., Gaudry, 1909; MacFadden & Frailey, 1984). Second, that pyrotheres are an endemic radiation of South American mammals whose relationships are to be sought with other South American "ungulates" (e.g., Loomis, 1913; Patterson, 1977). Third, that closest relationships are with North American or Old World orders, specially the Proboscidea (e.g., Ameghino, 1902; Loomis, 1914).

Rather than review these (and other) previous hypotheses of pyrothere relationships, I intead emphasize that with a few exceptions (alliance of the pyrotheres with the diprotodont marsupials is an example: Lydekker, 1893), pyrotheres have always been considered "ungulates." This opinion is well reflected by McKenna (1975) who placed the Xenungulata and Pyrotheria in his new Mirorder Meridiungulata, stating that "from an early, didolodont-like ancestor present in South America before the end of the Cretaceous, the six South American meridiungulate orders fragmented" (McKenna, 1975: 39). Szalay (1977) followed McKenna (1975) without further comment. In contrast to McKenna (1975), Szalay (1977) and most previous authors, I hypothesize that pyrotheres *are not ungulates*. Instead, they and the Dinocerata share an anagalid-like ancestry far removed from the ungulate radiation of the Eutheria.

3.2 Dental features and the current hypothesis

The phylogenetic hypothesis of pyrothere relationships presented here (Fig. 5) is based primarily on dental features (also see Lucas & Schoch, 1982; Tong & Lucas, 1982; Schoch and Lucas, 1985).

Monophyly of the "anagalid" *Pseudictops* (see Sulimski, 1968) and the Uintatheriamorpha is based on a number of evolutionary novelties of the dental apparatus (Fig. 4) not found in other ernotheres (*sensu* McKenna, 1975). These are (Fig. 5, node 1): broad incisors that are multicuspate or have papillate occlusal margins; P^{3-4}_{3-4} submolariform to molariform; M^{1-3}: stylar shelves extremely narrow or absent, parastyles, if present, small, low and isolated on the anterior cingula, paracones closer to the labial margins than metacones and paralophs and metalophs present, connecting the

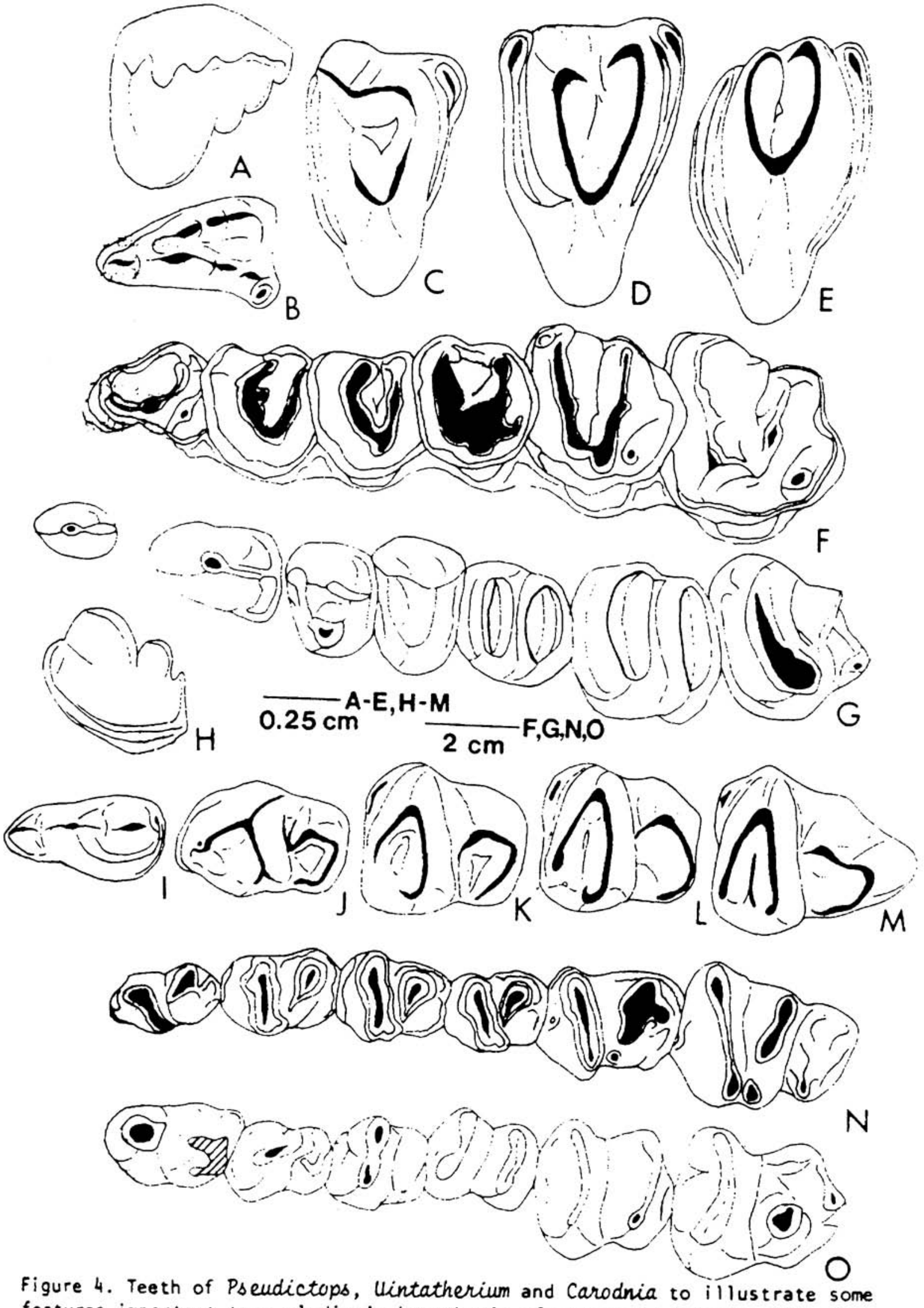

Figure 4. Teeth of *Pseudictops*, *Uintatherium* and *Carodnia* to illustrate some features important to a cladistic hypothesis of pyrothere relationships (Fig. 5). A-E, H-M: *Pseudictops lophiodon*, lateral view of left $I^{1,2 \text{ or } 3}$ (A), and occlusal views of left P1 or 2 (B), P^3 or 4 (C), M^1 or 2 (D) and M^3 (E); internal view of right $I_{1,2 \text{ or } 3}$ (H) and occlusal views of right P_1 or 2 (I), P_3 (J), P_4 (K), M_1 or 2 (L) and M_3 (M) (after Sulimski, 1968). F, N: *Uintatherium anceps*, occlusal views of left $P2$-M^3 (F) and right P_2-M_3 (N) (after Marsh, 1885). G, O: *Carodnia vieirai*, occlusal views of lefth $P1$-$M3$ (G) and left P_2-M_3 (O) (after Paula Couto, 1978).

paracones and metacones to the protocones; P^3-M^3 have larger posterior cingula; P_4-M_3 trigonids compressed anteroposteriorly; and horizontal ramus of the mandible deep and thick (robust). However, *Pseudictops* has autapomorphies that exclude it from the ancestry of the uintatheriamorphs. These are (Fig. 5, node 2): cheek teeth crown hypsodont; M_{1-3} have parastylids; and hind limb cursorial (tibia-fibula relatively long and slender, tarsus serial, astragalus and calcaneum lagomorph-like, metatarsals and phalanges relatively long).

Unity of the Uintatheriamorpha is justified by the possession of the following derived character-states (Fig. 5, node 3): M^{1-2} protoconules distinct and separate from protocones; M^{1-3} subcircular to square in outline; $M1 < M2 < M3$ and M1 < or equal to P4; M^3 with broad posterior shelf and variably expressed hypocome of hypoconal ridge; M_{1-3} paralophids very low or absent; and M_3 hypoconid and hypoconid crest (cristid obliqua) prominent and isolated (Fig. 4).

The monophyly of the Dinocerata (Fig. 5, node 4) was already justified by Schoch & Lucas (1985: 36). Monophyly of the Pyrotheria is based on their bilophodont M^{1-2}_{1-2} (the anterior lophs are metacone-protoconule crests) and large postcingulids on M_{1-2} (Fig. 5, node 5). *Carodnia* is the most primitive pyrothere, and stands as the plesiomorphic sister-taxon of more advanced pyrotheres, the Eupyrotheria.

The Eupyrotheria (Fig. 5, node 6) are distinguished from *Carodnia* by the following derived features: P^1_1 absent, P^2_2 small; M^3 bilophodont; and M_3 entoconid-hypoconid cristid present. *Carolozittelia*, the sole representative of the Carolozittelidae, is the plesiomorphic sister-taxon of the more advanced eupyrotheres, the Pyrotheriidae.

Pyrotheriid monophyly (Fig. 5, node 7) is predicated on the bilophodonty of P^4_4, loss of the hypoconulid lobe of M_3 so that tooth is bilophodont and presence of large, tusk-like incisors. Pyrotheriids are divided into two monophyletic subfamilies, the Colombitheriinae and the Pyrotheriinae.

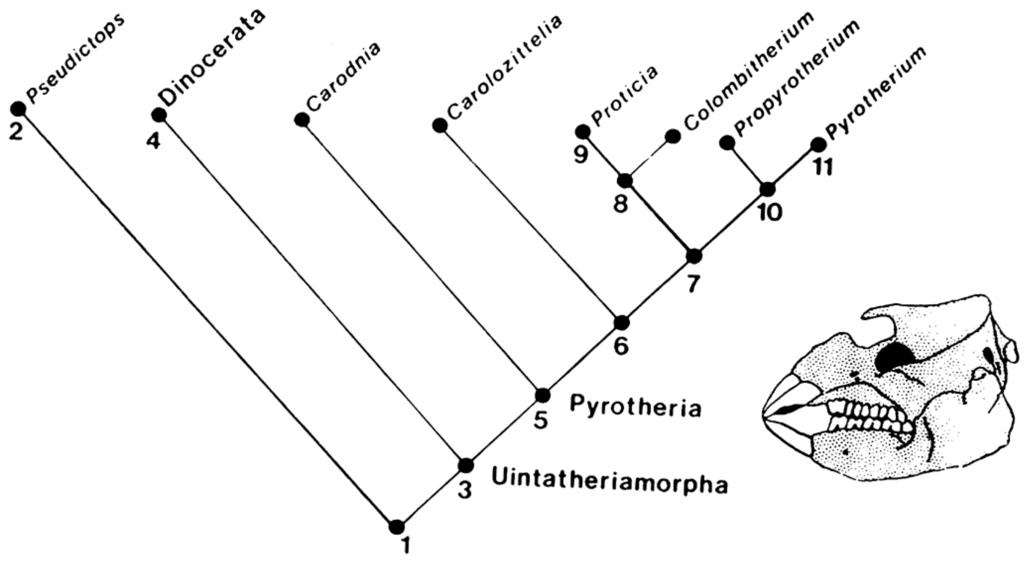

Figure 5: A cladistic hypothesis of pyrothere relationships. For character-states that correspond to the numbered node points see the text.

Colombitheriine monophyly is based on the presence of bulbous cheek-tooth cusps and additional cusps/cuspids in the valleys between the cheek-tooth lophs/lophids (Fig. 5, node 8). This conclusion rejects the suggestions of McKenna (1980) and Cifelli (1985) that colombitheriines are the most primitive pyrotheres or little advanced descendants of didolodontids, and probably not pyrotheres. Instead, I envision colombitheriine evolution as the evolution of bunodont pyrotheres from a bilophodont ancestry, an evolutionary pathway not different from the well-documented evolution of bunodont Hippopotamidae from lopho-selenodont Anthracotheriidae (Coryndon, 1978). The trend toward bunodonty in the Colombitheriinae reaches its extreme in *Proticia* in which the cheek-tooth lophids are essentially lost at the expense of producing extremely bulbous cuspids (Fig. 5, node 9).

In contrast, pyrotheriine monophyly is supported by the accentuation of trends that seem to characterize the main line of pyrothere evolution. Thus, the anteriorly canted upper molar lophs and posteriorly canted lower molar lophids, and bilophodonty of all the cheek teeth execpt P_2^2 (Fig. 5, node 10) are unique features of the pyrotheriines that involve little divergence from the trend already established in *Carodnia* and *Carolozittelia*. The cheek-tooth crown hypsodonty and very large size of *Pyrotherium* (Fig. 5, node 11) place it apart from *Propyrotherium* as the most derived pyrothere.

3.3 Features of the auditory region

Bony structures of the auditory region are often stressed in phylogenetic hypotheses of mammalian relationships despite the fact that little is understood of the precise functional significance of these structures. Without this understanding it is difficult to discriminate between similar auditory structures that are the product of convergence because they serve the same function, and those that are indicative of close relationship. Patterson's (1977) recent interpretation of the phylogenetic significance of the pyrothere auditory region well exemplifies these observations.

The only known auditory region of a pyrothere is that of *Pyrotherium romeri* described and illustrated by Patterson (1977: 413-416, fig. 6). Patterson (1977) argued that a number of auditory structures closely ally *Pyrotherium* (and, by inference, the Pyrotheria) with the Notoungulata: an inflated auditory bulla with a large hypotympanic sinus, a well ossified external auditory meatus with a prominent crista meatus, a large epitympanic sinus in the squamosal, a stylomastoid foramen that opens between the crista meatus and the post-tympanic portion of the squamosal and a canal of Huguier that opens externally at the posterior end of the fissura Glaeseri. According to Patterson (1977: 416), these auditory features of *Pyrotherium* are "encountered in the Notoungulata - and in no other ungulate order."

Simpson (1978: 325; 1980: 102-104) and McKenna (1980: 65) discounted Patterson's conclusion, arguing that the dental differences between pyrotheres and notoungulates are so great that close relationship seems unlikely. McKenna (1980) also suggested that the epitympanic sinus and foramen pneumaticum of pyrotheres and notoungulates are convergent.

I am in agreement with the basic arguments of Simpson and McKenna. The dental differences between pyrotheres and notoungulates are so great that it is difficult to accept a close relationship between the two orders. It is also significant that the auditory regions of the dinoceratans *Prodinoceras efremovi* (Flerov, 1957: figs. 1, 3; pl. 2) and *Uintatherium anceps* (Marsh, 1885: pls. 2, 5) display several of the features Patterson identified as indicative of a close relationship between the pyrotheres and notoungulates. These features are the large hypotympanic sinus, a prominent crista meatus, a stylomastoid foramen that opens between the crista meatus and the posttympanic portion of the squamosal and a canal of Huguier that opens externally at the posterior end of the fissura Glaeseri. An inflated, ossified auditory bulla, a well ossified external auditory meatus and a large epitympanic sinus are not present in uintatheres.

However, studies of living primates have well demonstrated that the bony external auditory meatus is designed to reduce physiological noise in species where the jaw joint borders directly on the external ear (Shaw, 1974; Packer & Sarmiento, 1984). An epitympanic sinus that is confluent with this meatus may be of additional help in reducing physiological noise and specially needed in herbivorous mammals in which large intake and lengthy processing of vegetable matter keeps the masticatory apparatus, specially the jaw joint, in prolonged use.

I find it significant that *Pyrotherium romeri* and the notoungulates (e.g., *Pleurostylodon modicus*: Simpson, 1967: fig. 33) to which Patterson allied it, lack a large postglenoid process so that the jaw joint abuts the external ear. The well ossified external auditory meatus and epitympanic sinus of these taxa thus appear to be adaptations to reducing physiological noise. This induces me to believe that these features have been converged upon. Uintatheres have large postglenoid processes that well separte their jaw joints (glenoid fossae) from their external ears. Thus, it is no surprise that they lack a well ossified external auditory meatus and a epitympanic sinus.

In addition, an inflated, osseous auditory bulla may not only protect the external ear from physiological noise, but also prevents deformation of the tympanic cavity by contraction of the masticatory muscles, specially the posterior belly of the digastric (Fleischer, 1978; MacPhee, 1981). The digastric originates on the mastoid-paroccipital (styloid) process which, in *Pyrotherium romeri* and notoungulates like *Pleurostylodon modicus*, is very close to (just postero-lateral of) the external ear. Furthermore, in *Pyrotherium romeri* the long lower tusks heavily "load" the anterior end of the mandible, suggesting that a large and powerful digastric was needed to abduct (depress) the lower jaw in a controlled fashion. These observations provide a functional explanation for the presence of an inflated auditory bulla in *Pyrotherium*. They also support the idea that this feature was converged on by *Pyrotherium* and notoungulates like *Pleurostylodon*. I find it significant that *Uintatherium* and the pantodont *Coryphodon* (Lucas, 1984) have large mastoid-paroccipital processes (and, hence, large digastrics). The origination points of their digastrics are well lateral of their external ears, and thus they probably had no need for ossified bullae. The case for pyrothere-notoungulate relationships argued by Patterson (1977) on the basis of features of the auditory region thus seems invalid.

3.4 Features of the pes

Among the Pyrotheria as here enjoined, only the astragalus and calcaneum of *Carodnia* and *Pyrotherium* are known with certainty (Gaudry, 1909; Cifelli, 1938a). Only Cifelli (1983a) has attempted to extract phylogenetic information on pyrothere relationships from these bones. In so doing, Cifelli (1983a: 23) concluded:

> The non-Neotropical amblypods, whether an artifical assemblage or a monophyletic group [1], fall into two categories characterized by different specializations of the tarsus: (1) Embrithopoda-Proboscidea; in which the calcaneofibular contact is modified and the astragalar head reduces and loses contact with the cuboid (serial tarsus) [2], and (2) Dinocerata; in which calcaneofibular contact is lost, the medial malleolar facet of the astragalus is well developed, and the astragalocuboid contact is expanded, so that the calcaneum virtually loses its weight-bearing function (alternating tarsus) [3]. Of the South American amblypods, *Carodnia* and the Pyrotheria are similar to the first group, whereas the Astrapotheria is similar to the second [4].

And, Cifelli (1983a: 24) later argued:

> If the paenungulates, in the sense enjoined here represent a monophyletic group [1], then two major clades are suggested: Astrapotheria-Dinocerata and Pyrotheria (including *Carodnia*)-Proboscidea-Embrithopoda [4]. This is, however, frankly speculative at this juncture, since it is only the vague "amblypod" tarsal features cited above, coupled with general trends (such as graviportal adaptation and gigantism) which unites this assemblage.

The numbers in brackets above index the following comments on Cifelli's conclusions:

1. Simpson (1945: 131) united the Pantodonta, Dinocerata, Pyrotheria, Proboscidea (including the deinotheres and barytheres), Embrithopoda, Hyracoidea and Sirenia (including the desmostylians) in a new superorder, the Paenungulata. Simpson (1945: 241) based this "frankly hypothetical" superordinal grouping on morphological features that are part of a graviportal "gestalt" possessed by most, specially the very large, members of the "paenungulate" orders.

McKenna & Manning (1977: 72) recognized a revised Paenungulata that included the Dinocerata, Proboscidea, Sirenia, Desmostylia, Hyracoidea, Perissodactyla and Embrithopoda. Their cladogram united these orders on the basis of two synapomorphies: "M3 becoming larger than M2; astragalar head develops somewhat flattened articulation with navicular bone" (McKenna & Manning, 1977: 72). M3 > M2, however, is present in a variety of herbivorous mammals, including some artiodactyls, pantodonts and marsupials. It signifies an increase in occlusal area at the back of the cheek-tooth row, a feature arguably converged on by many groups of mammalian herbivores. The vaguely expressed character-state "somewhat flattened articulation" between the astragalar head and navicular also is found in several "non-paenungulate" mammals, including the edentates (glyptodonts, *Myrmecophaga*). Also, the hyracoid pes differs so significantly from that of other "paenungulates" that it is difficult to see why McKenna & Manning (1977) included them in the group. Therefore, I see little basis for the Paenungulata as defined by McKenna & Manning (1977).

Cifelli's (1983a) Paenungulata included the Dinocerata, Pyrotheria, Proboscidea, Embrithopoda and Astrapotheria. However, its basis for unity was as weak as was Simpson's Paenungulata. In effect, Cifelli (1983a) united these orders on the basis of their "amblypod" tarsal pattern, a conclusion which he himself branded as "frankly speculative."

2. In an erratum attached to Cifelli (1983a), he noted that observations ostensibly made on an astragalus of *Arsinoitherium*

were actually made on an astragalus of *Palaeomastodon*. Thus Cifelli's (1983a) original conclusion that the embrithopod tarsus is serial is overturned. It is alternating, as Andrews (1906) clearly observed. Indeed, as Andrews (1906: 56) pointed out, the astragalus of *Arsinoitherium* "though superficially similar to that of *Elephas*, differs from it fundamentally." These fundamental differences include: an astragalocuboid articulation, a relatively large fibular surface on the calcaneum and a large and somewhat concave surface for the internal malleolus in *Arsinoitherium*, features not found in proboscideans. Furthermore, the embrithopod has calcaneofibular contact no more modified toward the proboscidean condition than in *Pyrotherium*. Clearly, the close relationship between the Embrithopoda and Proboscidea advocated by Cifelli (1983a) cannot be sustained.

3. Cifelli's claim that the calcaneum of the Dinocerata had lost its weight-bearing function simply is incorrect. The pes of the most primitive uintatheres (*Prodinoceras sensu* Schoch & Lucas, 1985) has calcaneofibular contact (Flerov, 1957: figs. 20, 22; Schoch & Lucas, 1985: pl. 3). This contact is variable (present but small or absent) within a single species of derived uintathere, *Uintatherium anceps* (Marsh, 1885: 152, pls. 55, 56). A reasonably large calcaneocuboid facet is present on the primitive uintatheres as well (Flerov, 1957: fig. 20; Schoch & Lucas, 1985: pl. 3). Indeed, the close similarity in pedal structure of *Arsinoitherium* and *Uintatherium* noted by Andrews (1906) makes it difficult to argue that the Dinocerata stand apart from other "non-Neotropical amblypods" on the basis of pedal structure.

4. The erratum to Cifelli (1983a) points out that there is a well-developed cuboid facet on the astragalus of *Pyrotherium*, contrary to the observations reported in the original paper. The erratum further states that this revised observation weakens the case for a close relationship of *Pyrotherium* and *Carodnia*, since Cifelli (1983a) argued that *Carodnia* lacks a cuboid facet on its astragalus. However, as Cifelli (1983: 10) noted, and as in clear

from a plaster cast of the astragalus of *Carodnia* provided to me by R. Cifelli, the area where the cuboid facet is located is broken and missing, rendering impossible an incontrovertible conclusion as to its presence or absence. Indeed, the overall configuration of the astragalus of *Carodnia* suggests to me that it had a small cuboid facet similar to that present in the primitive uintathere *Prodinoceras*. Thus, the alternating tarsus of pyrotheres makes it difficult to argue for pyrotherian affinity with the Proboscidea and Embrithopoda (which have a serial tarsus), contrary to Cifelli (1983a).

From the above observations, I conclude that no reasonable corroboration of the phylogenetic hypothesis "Paenungulata" exists in the work of Simpson (1945), McKenna & Manning (1977) and Cifelli (1983a). Furthermore, Cifelli's (1983a) pedal-based hypotheses of pyrothere and other "paenungulate" relationships do not stand up to close scrutiny. Clearly, a much better understanding of the pedal morphology of large mammals, one aimed at rooting out functionally induced convergence, must be in hand before the phylogenetic significance of this morphology can be assessed.

4. PALEOBIOGEOGRAPHICAL IMPLICATIONS

4.1 Pyrothere Paleobiogeography

The phylogenetic hypothesis of pyrothere relationships presented here suggests the following paleobiogeographical hypothesis (*sensu* Ball, 1975): The common ancestor of *Pseudictops* and the Uintatheriamorpha was an Asian mammal of pre-late Paleocene age. The descendants of this mammal were Asian *Pseudictops* and the progenitor(s) of the Uintatheriamorpha, a taxon that dispersed from Asia to North and South America prior to the late Paleocene. The Dinocerata and Pyrotheria diverged from this ancestor in late Paleocene time because of a vicariance event that separated North and South America near the end of the Paleocene. The austral endemism and divergent evolution of the pyrotheres bespeaks their geographic isolation from uintatheres throughout the remainder of the Paleogene.

4.2 Caribbean tectonics

Pyrotheres first appeared in South America during the Riochican (late Paleocene) at almost exactly the same time as the appearance of the Dinocerata in Asia and North America. The relatively small amount of morphological divergence between the earliest pyrotheres (*Carodnia*) and the earliest uintatheres (*Prodinoceras*) implies a common ancestor of these taxa during pre-Riochican, Paleocene time. The phylogenetic hypothesis presented here (Fig. 5) predicts that this ancestor must have achieved a trans-Caribbean distribution during the Paleocene via a land bridge, or so-called "sweepstakes" route (chain of islands). This dispersal route would have much antedated the long debated route that allowed entry of primates and caviomorph rodents into South America during the Oligocene. Also, it would have much postdated the recently discussed route between South and North America during the Late Cretaceous (Campanian) which apparently provided a pathway for the dispersal of various reptiles and, perhaps, primitive eutherians and metatherians (Bonaparte, 1984a 1984b; Seyfried and Sprechmann, 1985).

I find it significant that recent analyses of Caribbean plate tectonics based on geophysical and geological evidence suggest a probable land bridge/archipelago between North and South America during the Paleocene (e.g., Duncan & Hargraves, 1984; Mattson, 1984) These studies indicate that at about the beginning of the Paleocene (∿66 myBP), the Caribbean plate began to move eastward and "underthrust" South America. Island-arc volcanism, clastic and epiclastic sedimentation and deformation then commenced in the Greater Antilles and part of Central America (Costa Rica-Panama). The Central America arc thus formed apparently was isolated from North and South America by marine waters above the northern and southern transform-plate boundaries of the Caribbean plate. However the Greater Antilles arc (covering present-day Cuba, Hispanola, Puerto Rico, the Aves Ridge and the Lesser Antilles) was a rather dense volcanic archipelago that extended from the Yucatan platform to the subduction zone on the northern edge of South America

(Villa de Crura complex-Venezuelan basin). This island arc thus seems the most likely route for the trans-Caribbean dispersal of the common ancestor of pyrotheres and uintatheres during the Paleocene.

4.3 Uintatheriamorpha, Edentata, "Condylarthra" and Notoungulata: a generalized track?

The phylogenetic and paleobiogeographic hypotheses advanced here contradict the notion that South America was faunistically isolated from North America during the Paleocene. This contradiction, however, rests on the evidence provided by a relatively poorly known and unusual group of mammals, the Pyrotheria. As such, it might seem to be a weakly-supported challenge to a long held idea. Nevertheless, there are other groups of eutherian mammals that, together with the Uintatheriamorpha, may define a Paleocene generalized track (see Croizat et al., 1974) of eutherian distribution that encompassed Asia, North America and South America. These mammals are: 1) Edentata, with putative North American (e.g., Rose, 1978, 1979) and Asian (ting, 1979; Radinsky & Ting, 1984) representatives of Paleocene age; 2) Notoungulata, which includes the North American and Asian arctostylopids (e.g., Matthew, 1915; Matthew & Granger, 1925; Zheng, 1979); and 3) "Condylarthra," whose North American and Asian representatives are well known. Indeed, the probable close relationship of North American mioclaenine hyopsodontids and South American Didolodontidae/Litopterna led Cifelli (1983b) to argue that a common ancestor of these taxa achieved a trans-Caribbean distribution *during* the Paleocene.

Certainly there is a need for more rigorous phylogenetic hypotheses of the relationships of North American and Asian edentates, notoungulates and condylarths of Paleocene age and their South American counterparts. However, the generalized track their presently understood distribution suggests, and the phylogenetic hypothesis of pyrothere relationships advocated here, are a strong inducement to postulating a route for land-mammal dispersal between North and South America during the Paleocene.

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